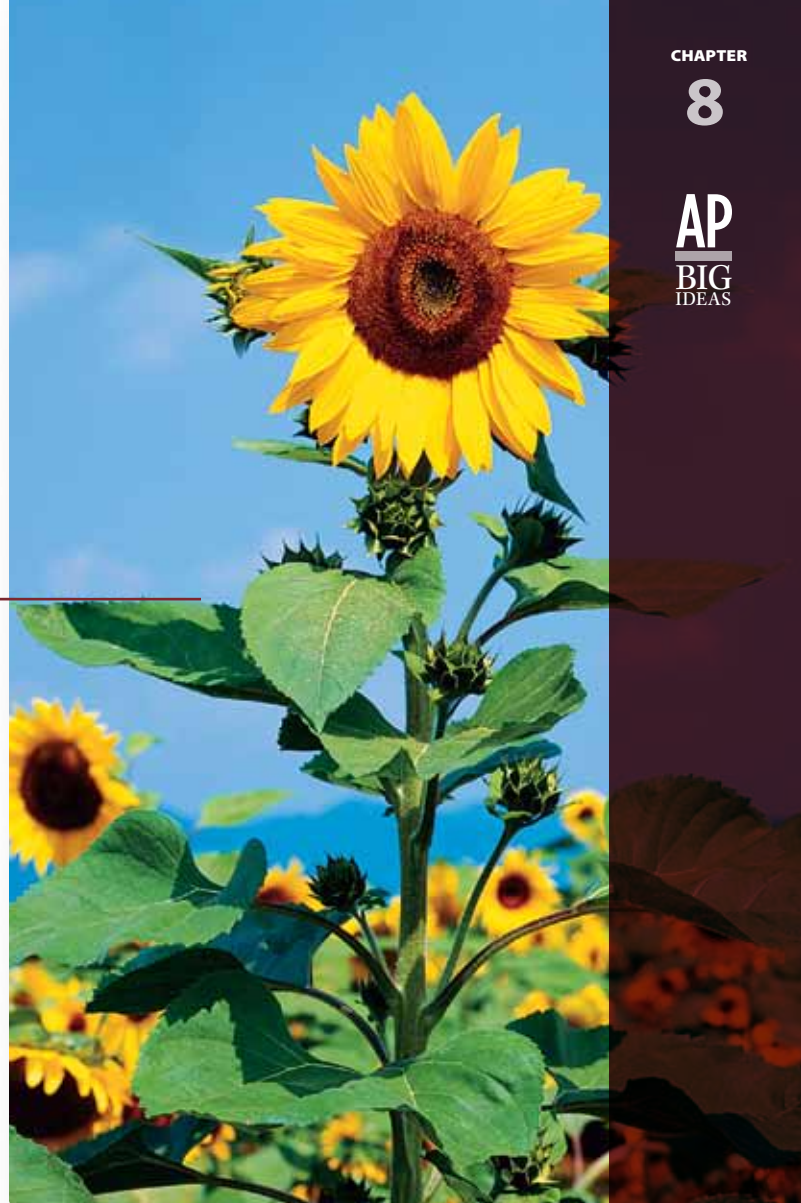


Chapter **8**

Photosynthesis

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Introduction

Chapter 7 explained how organisms capture and store energy from food for use in biological processes (EK.2.A.2). You can capture fireflies in a bottle, capture an image with a camera . . . but how do you capture energy? What puts energy into food in the first place? In this chapter, you will further explore these aspects of Big Idea 2. Of Earth's estimated 9 million species, only a small fraction, including these sunflowers, can capture energy and most of those species use the process called photosynthesis. Armed with specialized membranes, photosystems, and enzymes, they trap the Sun's radiant energy in the form of ATP, which is then used to make food. Ingenious. Silent. Nonpolluting. Recycling. Photosynthesis creates the ultimate "green" energy, the perfect solution to providing power for life on Earth. All living organisms use cellular respiration to obtain energy from food, and most of that energy comes from organisms that are able to capture it from the Sun.

8.1 Overview of Photosynthesis

Learning Outcomes

1. Explain the reaction for photosynthesis.
2. Describe the structure of the chloroplast.

Life is powered by sunshine. The energy used by most living cells comes ultimately from the Sun and is captured by plants, algae, and bacteria through the process of photosynthesis.

The diversity of life is only possible because our planet is awash in energy streaming Earthward from the Sun. Each day, the radiant energy that reaches Earth equals the power from about 1 million Hiroshima-sized atomic bombs. Photosynthesis captures about 1% of this huge supply of energy (an amount equal to 10,000 Hiroshima bombs) and uses it to provide the energy that drives all life.

Photosynthesis combines CO₂ and H₂O, producing glucose and O₂

Photosynthesis occurs in a wide variety of organisms, and it comes in different forms. These include a form of photosynthesis that does not produce oxygen (anoxygenic) and a form that does (oxygenic). Anoxygenic photosynthesis is found in four different bacterial groups: purple bacteria, green sulfur bacteria, green nonsulfur bacteria, and heliobacteria. Oxygenic photosynthesis is found in cyanobacteria, seven groups of algae, and essentially all land plants. These two types of photosynthesis share similarities in the types of pigments they use to trap light energy, but they differ in the arrangement and action of these pigments.

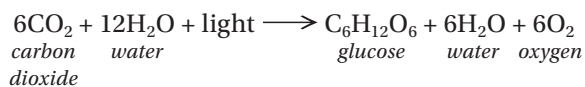
In the case of plants, photosynthesis takes place primarily in the leaves. Figure 8.1 illustrates the levels of organization in a plant leaf. As you learned in chapter 4, the cells of plant leaves contain organelles called chloroplasts, which carry out the photosynthetic process. No other structure in a plant cell is able to carry out photosynthesis (figure 8.2). Photosynthesis takes place in three stages:

1. capturing energy from sunlight;
2. using the energy to make ATP and to reduce the compound NADP⁺, an electron carrier, to NADPH; and
3. using the ATP and NADPH to power the synthesis of organic molecules from CO₂ in the air.

The first two stages require light and are commonly called the **light-dependent reactions**.

The third stage, the formation of organic molecules from CO₂, is called **carbon fixation**. This process takes place via a cyclic series of reactions. As long as ATP and NADPH are available, the carbon fixation reactions can occur either in the presence or in the absence of light, and so these reactions are also called the **light-independent reactions**.

The following simple equation summarizes the overall process of photosynthesis:



You may notice that this equation is the reverse of the reaction for respiration. In respiration, glucose is oxidized to CO₂ using O₂ as an electron acceptor. In photosynthesis, CO₂ is reduced to glucose using electrons gained from the oxidation of water. The oxidation of H₂O and the reduction of CO₂ requires energy that is provided by light. Although this statement is an oversimplification, it provides a useful “global perspective.”

In plants, photosynthesis takes place in chloroplasts

In the preceding chapter, you saw that a mitochondrion’s complex structure of internal and external membranes contribute to its function. The same is true for the structure of the chloroplast.

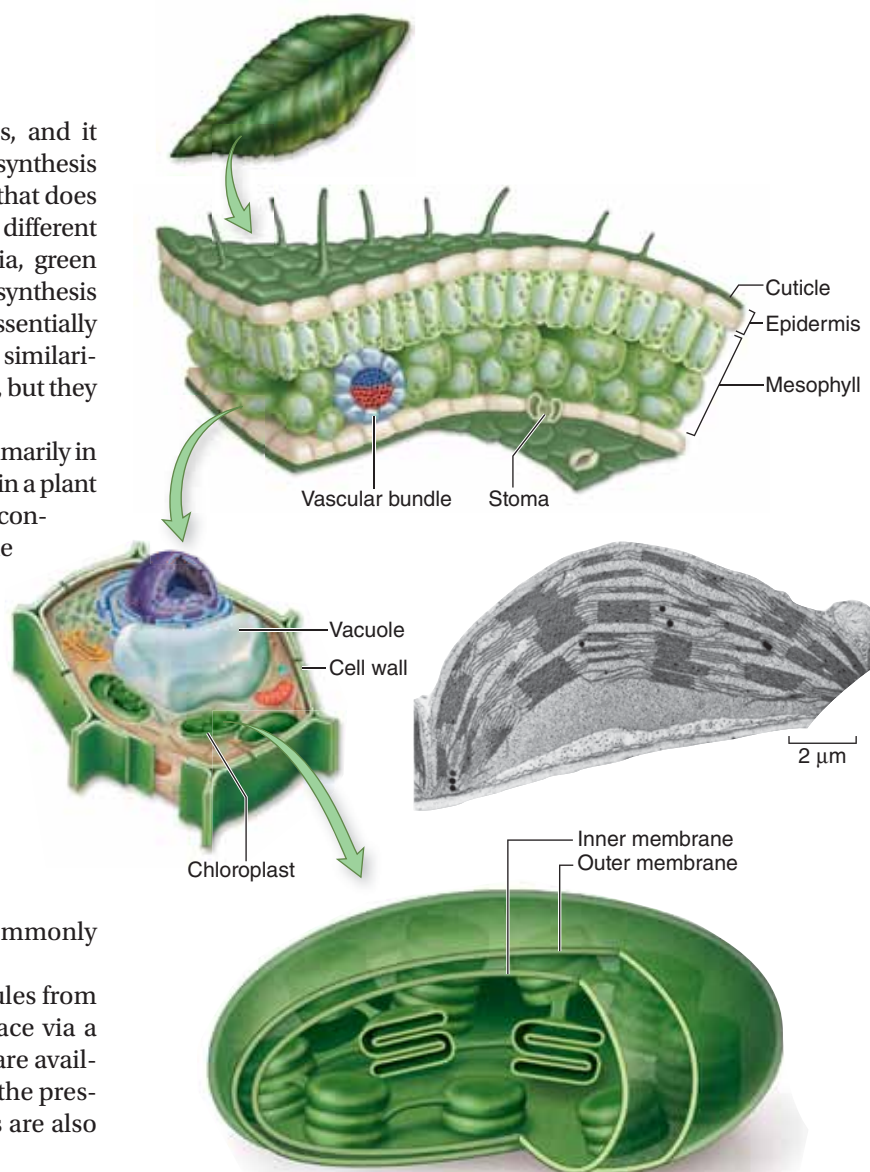


Figure 8.1 Journey into a leaf. A plant leaf possesses a thick layer of cells (the mesophyll) rich in chloroplasts. The inner membrane of the chloroplast is organized into flattened structures called thylakoid disks, which are stacked into columns called grana. The rest of the interior is filled with a semifluid substance called stroma.

The internal membrane of chloroplasts, called the *thylakoid membrane*, is a continuous phospholipid bilayer organized into flattened sacs that are found stacked on one another in columns called *grana* (singular, *granum*). The thylakoid membrane contains **chlorophyll** and other photosynthetic pigments for capturing light energy along with the machinery to make ATP. Connections between grana are termed *stroma lamella*.

Surrounding the thylakoid membrane system is a semi-liquid substance called **stroma**. The stroma houses the enzymes needed to assemble organic molecules from CO₂ using energy from ATP coupled with reduction via NADPH. In the thylakoid membrane, photosynthetic pigments are clustered together to form **photosystems**, which show distinct organization within the thylakoid.

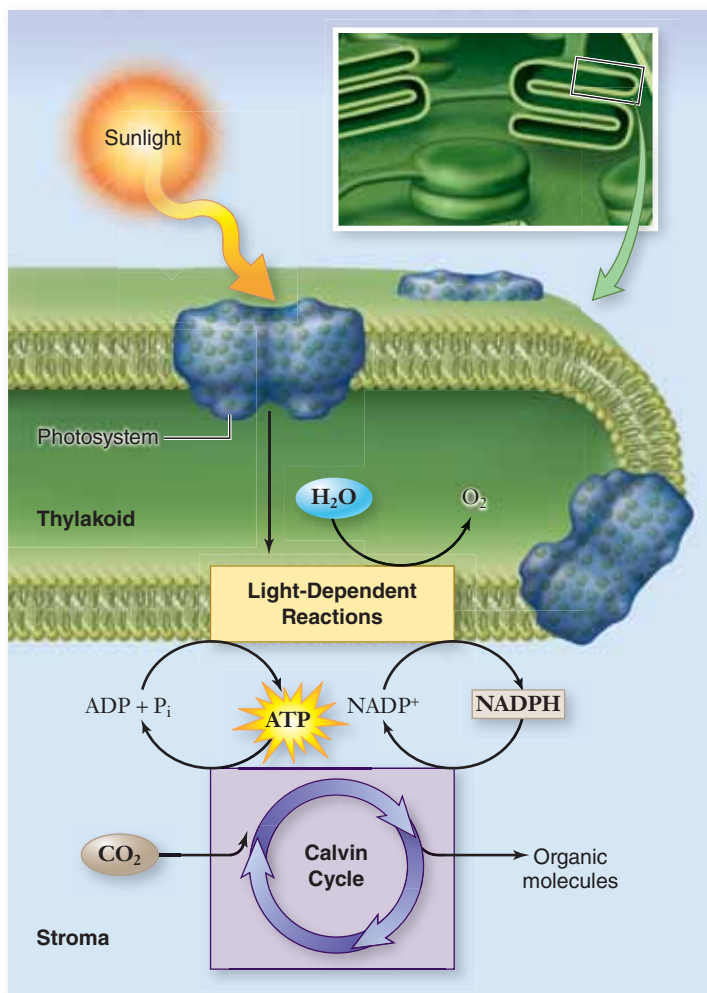


Figure 8.2 Overview of photosynthesis. In the light-dependent reactions, photosystems in the thylakoid absorb photons of light and use this energy to generate ATP and NADPH. Electrons lost from the photosystems are replaced by the oxidation of water, producing O₂ as a by-product. The ATP and NADPH produced by the light reactions is used during carbon fixation via the Calvin cycle in the stroma.

Each pigment molecule within the photosystem is capable of capturing photons, which are packets of energy. When light of a proper wavelength strikes a pigment molecule in the photosystem, the resulting excitation passes from one pigment molecule to another.

The excited electron is not transferred physically—rather, its *energy* passes from one molecule to another. The passage is similar to the transfer of kinetic energy along a row of upright dominoes. If you push the first one over, it falls against the next, and that one against the next, and so on, until all of the dominoes have fallen down.

Eventually, the energy arrives at a key chlorophyll molecule in contact with a membrane-bound protein that can accept an electron. The energy is transferred as an excited electron to that protein, which passes it on to a series of other membrane proteins that put the energy to work making ATP and NADPH.

These compounds are then used to build organic molecules. The photosystem thus acts as a large antenna, gathering the light energy harvested by many individual pigment molecules.

Learning Outcomes Review 8.1

Photosynthesis consists of light-dependent reactions that require sunlight, and others that convert CO₂ into organic molecules. The overall reaction is essentially the reverse of respiration and produces O₂ as a by-product. The chloroplast's inner membrane, the thylakoid, is the site in which photosynthetic pigments are clustered, allowing passage of energy from one molecule to the next. The thylakoid membrane is organized into flattened sacs stacked in columns called grana.

- How is the structure of the chloroplast similar to the mitochondria?

8.2 The Discovery of Photosynthetic Processes

Learning Outcomes

1. Describe experiments that support our understanding of photosynthesis.
2. Differentiate between the light-dependent and light-independent reactions.

The story of how we learned about photosynthesis begins over 300 years ago, and it continues to this day. It starts with curiosity about how plants manage to grow, often increasing their organic mass considerably.

Plants do not increase mass from soil and water alone

From the time of the Greeks, plants were thought to obtain their food from the soil, literally sucking it up with their roots. A Belgian doctor, Jan Baptista van Helmont (1580–1644) thought of a simple way to test this idea.

He planted a small willow tree in a pot of soil, after first weighing the tree and the soil. The tree grew in the pot for several years, during which time van Helmont added only water. At the end of five years, the tree was much larger, its weight having increased by 74.4 kg. However, the soil in the pot weighed only 57 g less than it had five years earlier. With this experiment, van Helmont demonstrated that the substance of the plant was not produced only from the soil. He incorrectly concluded, however, that the water he had been adding mainly accounted for the plant's increased biomass.

A hundred years passed before the story became clearer. The key clue was provided by the English scientist Joseph Priestly (1733–1804). On the 17th of August, 1771, Priestly put a living sprig of mint into air in which a wax candle had burnt out.

On the 27th of the same month, Priestly found that another candle could be burned in this same air. Somehow, the vegetation seemed to have restored the air. Priestly found that while a mouse could not breathe candle-exhausted air, air “restored” by vegetation was not “at all inconvenient to a mouse.” The key clue was that *living vegetation adds something to the air*.

How does vegetation “restore” air? Twenty-five years later, the Dutch physician Jan Ingenhousz (1730–1799) solved the puzzle. He demonstrated that air was restored only in the presence of sunlight and only by a plant’s green leaves, not by its roots. He proposed that the green parts of the plant carry out a process that uses sunlight to split carbon dioxide into carbon and oxygen. He suggested that the oxygen was released as O₂ gas into the air, while the carbon atom combined with water to form carbohydrates. Other research refined his conclusions, and by the end of the nineteenth century, the overall reaction for photosynthesis could be written as:



It turns out, however, that there’s more to it than that. When researchers began to examine the process in more detail in the twentieth century, the role of light proved to be unexpectedly complex.

Photosynthesis includes both light-dependent and light-independent reactions

At the beginning of the twentieth century, the English plant physiologist F. F. Blackman (1866–1947) came to the surprising conclusion that photosynthesis is in fact a multistage process, only one portion of which uses light directly.

Blackman measured the effects of different light intensities, CO₂ concentrations, and temperatures on photosynthesis. As long as light intensity was relatively low, he found photosynthesis could be accelerated by increasing the amount of light, but not by increasing the temperature or CO₂ concentration (figure 8.3). At high light intensities, however, an increase in temperature or CO₂ concentration greatly accelerated photosynthesis.

Blackman concluded that photosynthesis consists of an initial set of what he called “light” reactions, that are largely independent of temperature but depend on light, and a second set of “dark” reactions (more properly called light-independent reactions), that seemed to be independent of light but limited by CO₂.

Do not be confused by Blackman’s labels—the so-called “dark” reactions occur in the light (in fact, they require the products of the light-dependent reactions); his use of the word *dark* simply indicates that light is not *directly* involved in those reactions.

Blackman found that increased temperature increased the rate of the light-independent reactions, but only up to about 35°C. Higher temperatures caused the rate to fall off rapidly. Because many plant enzymes begin to be denatured at 35°C, Blackman concluded that enzymes must carry out the light-independent reactions.

O₂ comes from water, not from CO₂

In the 1930s, C. B. van Niel (1897–1985) working at the Hopkins Marine Station at Stanford, discovered that purple sulfur bacteria

do not release oxygen during photosynthesis; instead, they convert hydrogen sulfide (H₂S) into globules of pure elemental sulfur that accumulate inside them. The process van Niel observed was:



The striking parallel between this equation and Ingenhousz’s equation led van Niel to propose that the generalized process of photosynthesis can be shown as:



In this equation, the substance H₂A serves as an electron donor. In photosynthesis performed by green plants, H₂A is water, whereas in purple sulfur bacteria, H₂A is hydrogen sulfide. The product, A, comes from the splitting of H₂A. Therefore, the O₂ produced during green plant photosynthesis results from splitting water, not carbon dioxide.

When isotopes came into common use in the early 1950s, van Niel’s revolutionary proposal was tested. Investigators examined photosynthesis in green plants supplied with water containing heavy oxygen (¹⁸O); they found that the ¹⁸O label ended up in oxygen gas rather than in carbohydrate, just as van Niel had predicted:

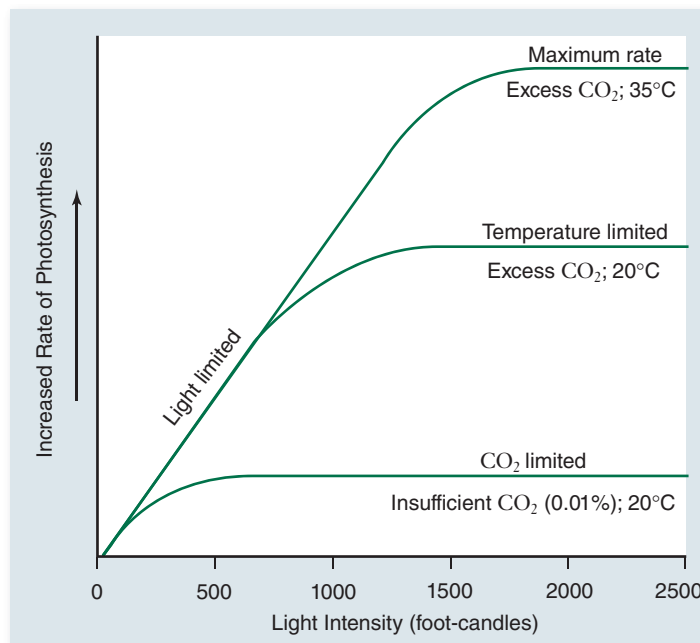


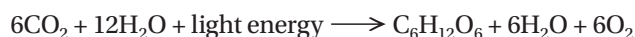
Figure 8.3 Discovery of the light-independent reactions. Blackman measured photosynthesis rates under differing light intensities, CO₂ concentrations, and temperatures. As this graph shows, light is the limiting factor at low light intensities, but temperature and CO₂ concentration are the limiting factors at higher light intensities. This implies the existence of reactions using CO₂ that involve enzymes.



Data analysis Blackman found that increasing light intensity above 2000 foot-candles did not lead to any further increase in the rate of photosynthesis. Can you suggest a hypothesis that would explain this?

8.3 Pigments

In algae and green plants, the carbohydrate typically produced by photosynthesis is glucose. The complete balanced equation for photosynthesis in these organisms thus becomes:



ATP and NADPH from light-dependent reactions reduce CO_2 to make sugars

In his pioneering work on the light-dependent reactions, van Niel proposed that the H^+ ions and electrons generated by the splitting of water were used to convert CO_2 into organic matter in a process he called *carbon fixation*. In the 1950s, Robin Hill (1899–1991) demonstrated that van Niel was right, light energy could be harvested and used in a reduction reaction. Chloroplasts isolated from leaf cells were able to reduce a dye and release oxygen in response to light. Later experiments showed that the electrons released from water were transferred to NADP^+ and that illuminated chloroplasts deprived of CO_2 accumulate ATP. If CO_2 is introduced, neither ATP nor NADPH accumulate, and the CO_2 is assimilated into organic molecules.

These experiments are important for three reasons: First, they firmly demonstrate that photosynthesis in plants occurs within chloroplasts. Second, they show that the light-dependent reactions use light energy to reduce NADP^+ and to manufacture ATP. Third, they confirm that the ATP and NADPH from this early stage of photosynthesis are then used in the subsequent reactions to reduce carbon dioxide, forming simple sugars.

Learning Outcomes Review 8.2

Early experiments indicated that plants “restore” air to usable form, that is, produce oxygen—but only in the presence of sunlight. Further experiments showed that there are both light-dependent and independent reactions. The light-dependent reactions produce O_2 from H_2O , and generate ATP and NADPH. The light-independent reactions synthesize organic compounds through carbon fixation.

- *Where does the carbon in your body come from?*

Learning Outcomes

1. Discuss how pigments are important to photosynthesis.
2. Relate the absorption spectrum of a pigment to its color.

For plants to make use of the energy of sunlight, some biochemical structure must be present in chloroplasts and the thylakoids that can absorb this energy. Molecules that absorb light energy in the visible range are termed **pigments**. We are most familiar with them as dyes that impart a certain color to clothing or other materials. The color that we see is the color that is not absorbed—that is, it is reflected. To understand how plants use pigments to capture light energy, we must first review current knowledge about the nature of light.

Light is a form of energy

The wave nature of light produces an electromagnetic spectrum that differentiates light based on its wavelength (figure 8.4). We are most familiar with the visible range of this spectrum because we can actually see it, but visible light is only a small part of the entire spectrum. Visible light can be divided into its separate colors by the use of a prism, which separates light based on wavelength.

A particle of light, termed a **photon**, acts like a discrete bundle of energy. We use the wave concept of light to understand different colors of light and the particle nature of light to understand the energy transfers that occur during photosynthesis. Thus, we will refer both to wavelengths of light and to photons of light throughout the chapter.

The energy in photons

The energy content of a photon is inversely proportional to the wavelength of the light: Short-wavelength light contains photons of higher energy than long-wavelength light (see figure 8.4). X-rays, which contain a great deal of energy, have very short wavelengths—much shorter than those of visible light.

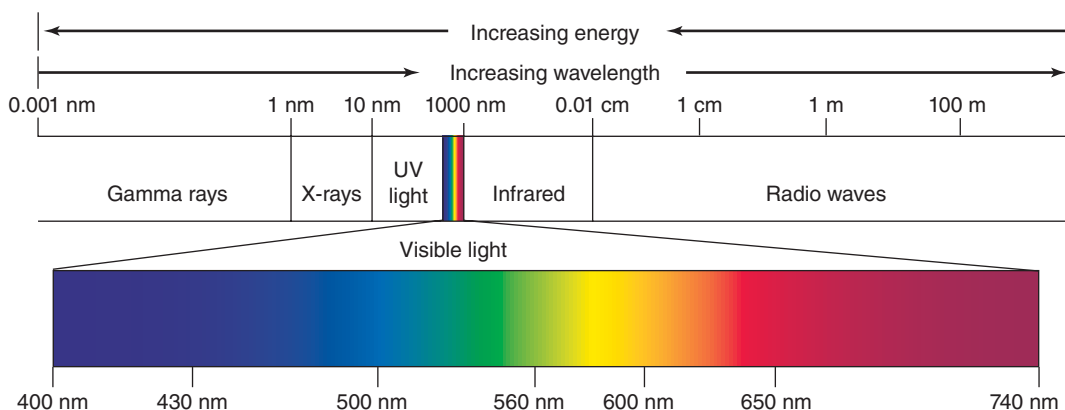


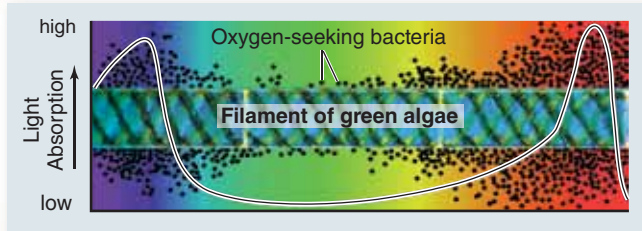
Figure 8.4 The electromagnetic spectrum. Light is a form of electromagnetic energy conveniently thought of as a wave. The shorter the wavelength of light, the greater its energy. Visible light represents only a small part of the electromagnetic spectrum between 400 and 740 nm.

SCIENTIFIC THINKING

Hypothesis: All wavelengths of light are equally effective in promoting photosynthesis.

Prediction: Illuminating plant cells with light broken into different wavelengths by a prism will produce the same amount of O₂ for all wavelengths.

Test: A filament of algae immobilized on a slide is illuminated by light that has passed through a prism. Motile bacteria that require O₂ for growth are added to the slide.



Result: The bacteria move to regions of high O₂, or regions of most active photosynthesis. This is in the purple/blue and red regions of the spectrum.

Conclusion: All wavelengths are not equally effective at promoting photosynthesis. The most effective constitute the action spectrum for photosynthesis.

Further Experiments: How does the action spectrum relate to the various absorption spectra in figure 8.5?

Figure 8.7 Determination of an action spectrum for photosynthesis.

Photons excite electrons in the porphyrin ring, which are then channeled away through the alternating carbon single- and double-bond system. Different small side groups attached to the outside of the ring alter the absorption properties of the molecule in the different kinds of chlorophyll (see figure 8.6). The precise absorption spectrum is also influenced by the local microenvironment created by the association of chlorophyll with different proteins.

The **action spectrum** of photosynthesis—that is, the relative effectiveness of different wavelengths of light in promoting photosynthesis—corresponds to the absorption spectrum for chlorophylls. This is demonstrated in the experiment in figure 8.7. All plants, algae, and cyanobacteria use chlorophyll *a* as their primary pigments.

It is reasonable to ask why these photosynthetic organisms do not use a pigment like retinal (the pigment in our eyes), which has a broad absorption spectrum that covers the range of 500 to 600 nm. The most likely hypothesis involves *photoefficiency*. Although retinal absorbs a broad range of wavelengths, it does so with relatively low efficiency. Chlorophyll, in contrast, absorbs in only two narrow bands, but does so with high efficiency. Therefore, plants and most other photosynthetic organisms achieve far higher overall energy capture rates with chlorophyll than with other pigments.

Carotenoids and other accessory pigments

Carotenoids consist of carbon rings linked to chains with alternating single and double bonds. They can absorb photons

with a wide range of energies, although they are not always highly efficient in transferring this energy. Carotenoids assist in photosynthesis by capturing energy from light composed of wavelengths that are not efficiently absorbed by chlorophylls (figure 8.5; see also figure 8.8).

Carotenoids also perform a valuable role in scavenging free radicals. The oxidation–reduction reactions that occur in the chloroplast can generate destructive free radicals. Carotenoids can act as general-purpose antioxidants to lessen damage. Thus carotenoids have a protective role in addition to their role as light-absorbing molecules. This protective role is not surprising, because unlike the chlorophylls, carotenoids are found in many different kinds of organisms, including members of all three domains of life.

You may have heard that eating carrots can enhance vision. If this effect is real, it is probably due to the high content of β -carotene in carrots. This carotenoid consists of two molecules of vitamin A joined together. The oxidation of vitamin A produces retinal, the pigment used in vertebrate vision.

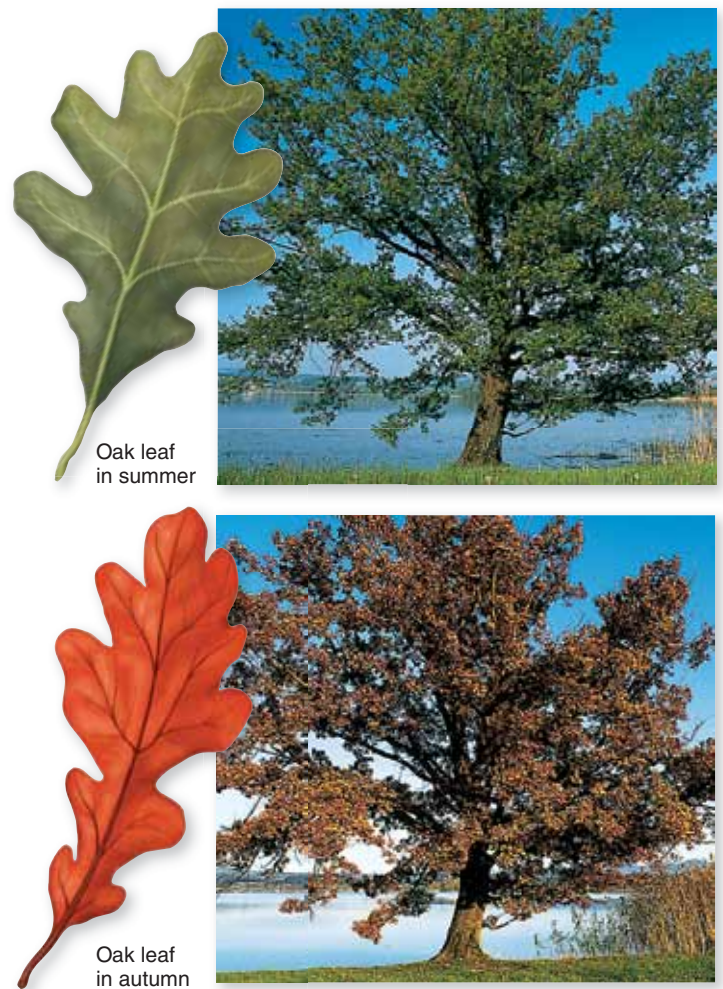


Figure 8.8 Fall colors are produced by carotenoids and other accessory pigments. During the spring and summer, chlorophyll in leaves masks the presence of carotenoids and other accessory pigments. When cool fall temperatures cause leaves to cease manufacturing chlorophyll, the chlorophyll is no longer present to reflect green light, and the leaves reflect the orange and yellow light that carotenoids and other pigments do not absorb.

Phycobiliproteins are accessory pigments found in cyanobacteria and some algae. These pigments contain a system of alternating double bonds similar to those found in other pigments and molecules that transfer electrons. Phycobiliproteins can be organized to form another light-harvesting complex that can absorb green light, which is reflected by chlorophyll. These complexes are probably ecologically important to cyanobacteria, helping them to exist in low-light situations in oceans. In this habitat, green light remains because red and blue light has been absorbed by green algae closer to the surface.

Learning Outcomes Review 8.3

A pigment is a molecule that can absorb light energy; its absorption spectrum shows the wavelengths at which it absorbs energy most efficiently. A pigment's color results from the wavelengths it does not absorb, which we then see. The main photosynthetic pigment is chlorophyll, which exists in several forms with slightly different absorption spectra. Many photosynthetic organisms have accessory pigments with absorption spectra different from chlorophyll; these increase light capture.

- What is the difference between an action spectrum and an absorption spectrum?

8.4 Photosystem Organization

Learning Outcomes

1. Describe the nature of photosystems.
2. Contrast the function of reaction center and antenna chlorophyll molecules.

One way to study the role that pigments play in photosynthesis is to measure the correlation between the output of photosynthesis and the intensity of illumination—that is, how much photosynthesis is produced by how much light. Experiments on plants show that the output of photosynthesis increases linearly at low light intensities, but finally becomes saturated (no further increase) at high-intensity light. Saturation occurs because all of the light-absorbing capacity of the plant is in use.

Production of one O₂ molecule requires many chlorophyll molecules

Given the saturation observed with increasing light intensity, the next question is how many chlorophyll molecules have actually absorbed a photon. The question can be phrased this way: “Does saturation occur when all chlorophyll molecules have absorbed photons?” Finding an answer required being able to measure both photosynthetic output (on the basis of O₂ production) and the number of chlorophyll molecules present.

Using the unicellular algae *Chlorella*, investigators could obtain these values. Illuminating a *Chlorella* culture with pulses of light with increasing intensity should increase the

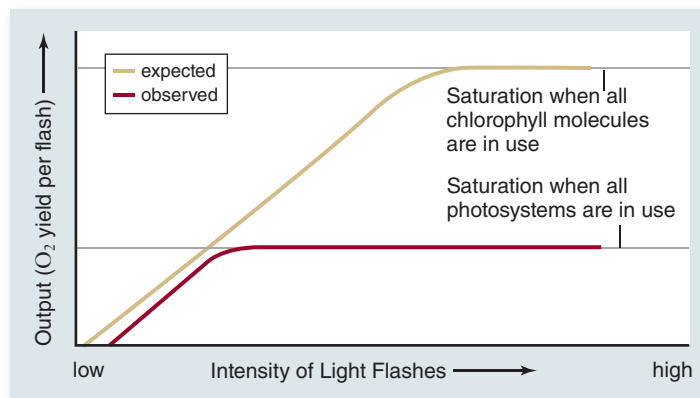


Figure 8.9 Saturation of photosynthesis. When photosynthetic saturation is achieved, further increases in intensity cause no increase in output. This saturation occurs far below the level expected for the number of individual chlorophyll molecules present. This led to the idea of organized photosystems, each containing many chlorophyll molecules. These photosystems saturate at a lower O₂ yield than that expected for the number of individual chlorophyll molecules.

Data analysis Draw the curves for photosystems that have a greater or lesser number of chlorophyll molecules than the curve shown.

yield of O₂ per pulse until the system becomes saturated. Then O₂ production can be compared with the number of chlorophyll molecules present in the culture.

The observed level of O₂ per chlorophyll molecule at saturation, however, turned out to be only one molecule of O₂ per 2500 chlorophyll molecules (figure 8.9). This result was very different from what was expected, and it led to the idea that light is absorbed not by independent pigment molecules, but rather by clusters of chlorophyll and accessory pigment molecules (photosystems). Light is absorbed by any one of hundreds of pigment molecules in a photosystem, and each pigment molecule transfers its excitation energy to a single molecule with a lower energy level than the others.

A generalized photosystem contains an antenna complex and a reaction center

In chloroplasts and all but one class of photosynthetic prokaryotes, light is captured by photosystems. Each photosystem is a network of chlorophyll *a* molecules, accessory pigments, and associated proteins held within a protein matrix on the surface of the photosynthetic membrane. Like a magnifying glass focusing light on a precise point, a photosystem channels the excitation energy gathered by any one of its pigment molecules to a specific molecule, the reaction center chlorophyll. This molecule then passes the energy out of the photosystem as excited electrons that are put to work driving the synthesis of ATP and organic molecules.

A photosystem thus consists of two closely linked components: (1) an *antenna complex* of hundreds of pigment

molecules that gather photons and feed the captured light energy to the reaction center; and (2) a *reaction center* consisting of one or more chlorophyll *a* molecules in a matrix of protein, that passes excited electrons out of the photosystem.

The antenna complex

The **antenna complex** is also called a light-harvesting complex, which accurately describes its role. This light-harvesting complex captures photons from sunlight (figure 8.10) and channels them to the reaction center chlorophylls.

In chloroplasts, light-harvesting complexes consist of a web of chlorophyll molecules linked together and held tightly in the thylakoid membrane by a matrix of proteins. Varying amounts of carotenoid accessory pigments may also be present. The protein matrix holds individual pigment molecules in orientations that are optimal for energy transfer.

The excitation energy resulting from the absorption of a photon passes from one pigment molecule to an adjacent molecule on its way to the reaction center. After the transfer, the excited electron in each molecule returns to the low-energy level it had before the photon was absorbed. Consequently, it is energy, not the excited electrons themselves, that passes from one pigment molecule to the next. The antenna complex funnels the energy from many electrons to the reaction center.

The reaction center

The **reaction center** is a transmembrane protein-pigment complex. The reaction center of purple photosynthetic bacteria is simpler than the one in chloroplasts but better understood. A pair of bacteriochlorophyll *a* molecules acts as a trap for photon energy, passing an excited electron to an acceptor precisely positioned as its neighbor. Note that here in the reaction center, the excited electron itself is transferred, and not just the energy, as was the case in the pigment-pigment transfers of the antenna complex. This difference allows the energy absorbed from

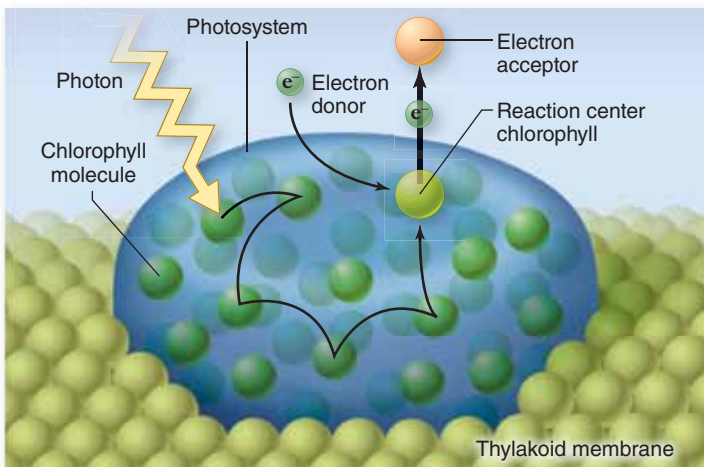


Figure 8.10 How the antenna complex works. When light of the proper wavelength strikes any pigment molecule within a photosystem, the light is absorbed by that pigment molecule. The excitation energy is then transferred from one molecule to another within the cluster of pigment molecules until it encounters the reaction center chlorophyll *a*. When excitation energy reaches the reaction center chlorophyll, electron transfer is initiated.

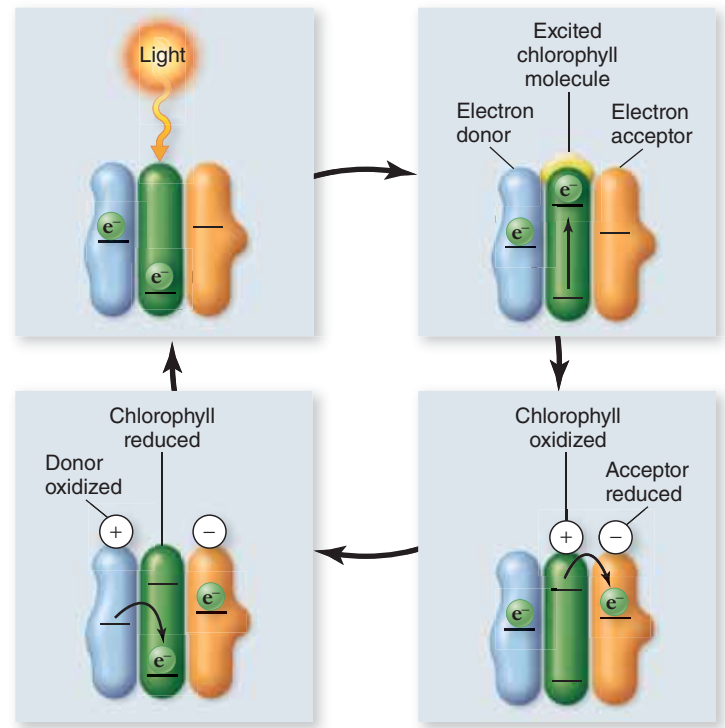


Figure 8.11 Converting light to chemical energy. When a chlorophyll in the reaction center absorbs a photon of light, an electron is excited to a higher energy level. This light-energized electron can be transferred to the primary electron acceptor, reducing it. The oxidized chlorophyll then fills its electron “hole” by oxidizing a donor molecule. The source of this donor varies with the photosystem as discussed in the text.

photons to move away from the chlorophylls, and it is the key conversion of light into chemical energy.

Figure 8.11 shows the transfer of excited electrons from the reaction center to the primary electron acceptor. By energizing an electron of the reaction center chlorophyll, light creates a strong electron donor where none existed before. The chlorophyll transfers the energized electron to the primary acceptor (a molecule of quinone), reducing the quinone and converting it to a strong electron donor. A nearby weak electron donor then passes a low-energy electron to the chlorophyll, restoring it to its original condition. The quinone transfers its electrons to another acceptor, and the process is repeated.

In plant chloroplasts, water serves as this weak electron donor. When water is oxidized in this way, oxygen is released along with two protons (H^+).

Learning Outcomes Review 8.4

Chlorophylls and accessory pigments are organized into photosystems found in the thylakoid membrane. The photosystem can be subdivided into an antenna complex, which is involved in light harvesting, and a reaction center, where the photochemical reactions occur. In the reaction center, an excited electron is passed to an acceptor; this transfers energy away from the chlorophylls and is key to the conversion of light into chemical energy.

- Why were photosystems an unexpected finding?

8.5 The Light-Dependent Reactions

Learning Outcomes

1. Compare the function of the two photosystems in green plants.
2. Explain how the light reactions generate ATP and NADPH.

As you have seen, the light-dependent reactions of photosynthesis occur in membranes. In photosynthetic bacteria, the plasma membrane itself is the photosynthetic membrane. In many bacteria, the plasma membrane folds in on itself repeatedly to produce an increased surface area. In plants and algae, photosynthesis is carried out by chloroplasts, which are thought to be the evolutionary descendants of photosynthetic bacteria.

The internal thylakoid membrane is highly organized and contains the structures involved in the light-dependent reactions. For this reason, the reactions are also referred to as the thylakoid reactions. The thylakoid reactions take place in four stages:

1. **Primary photoevent.** A photon of light is captured by a pigment. This primary photoevent excites an electron within the pigment.
2. **Charge separation.** This excitation energy is transferred to the reaction center, which transfers an energetic electron to an acceptor molecule, initiating electron transport.
3. **Electron transport.** The excited electrons are shuttled along a series of electron carrier molecules embedded within the photosynthetic membrane. Several of them react by transporting protons across the membrane, generating a proton gradient. Eventually the electrons are used to reduce a final acceptor, NADPH.
4. **Chemiosmosis.** The protons that accumulate on one side of the membrane now flow back across the membrane through ATP synthase where chemiosmotic synthesis of ATP takes place, just as it does in aerobic respiration (see chapter 7).

These four processes make up the two stages of the light-dependent reactions mentioned at the beginning of this chapter. Steps 1 through 3 represent the stage of capturing energy from light; step 4 is the stage of producing ATP (and, as you'll see, NADPH). In the rest of this section we discuss the evolution of photosystems and the details of photosystem function in the light-dependent reactions.

Some bacteria use a single photosystem

Photosynthetic pigment arrays are thought to have evolved more than 2 BYA in bacteria similar to the purple and green bacteria alive today. In these bacteria, a single photosystem is used that generates ATP via electron transport. This process returns the electrons back to the reaction center. For this

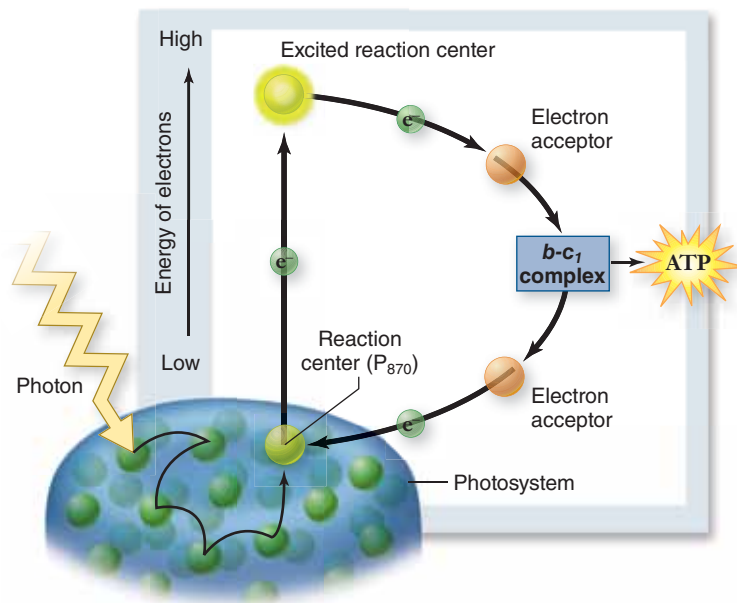


Figure 8.12 The path of an electron in purple nonsulfur bacteria. When a light-energized electron is ejected from the photosystem reaction center (P₈₇₀) it returns to the photosystem via a cyclic path that produces ATP but not NADPH.

reason, it is called cyclic photophosphorylation. These systems do not produce oxygen and so are also anoxygenic.

In the purple nonsulfur bacteria, peak absorption occurs at a wavelength of 870 nm (near infrared, not visible to the human eye), and thus the reaction center pigment is called P₈₇₀. Absorption of a photon by chlorophyll P₈₇₀ does not raise an electron to a high enough level to be passed to NADP, so they must generate reducing power in a different way.

When the P₈₇₀ reaction center absorbs a photon, the excited electron is passed to an electron transport chain that passes the electrons back to the reaction center, generating a proton gradient for ATP synthesis (figure 8.12). The proteins in the purple bacterial photosystem appear to be homologous to the proteins in the modern photosystem II.

In the green sulfur bacteria, peak absorption occurs at a wavelength of 840 nm. Excited electrons from this photosystem can either be passed to NADPH, or returned to the chlorophyll by an electron transport chain similar to the purple bacteria. They then use electrons from hydrogen sulfide to replace those passed to NADPH. The proteins in the green sulfur bacterial photosystem appear to be homologous to the proteins in the modern photosystem I.

Neither of these systems generates sufficient oxidizing power to oxidize H₂O. They are both anoxygenic and anaerobic. The linked photosystems of cyanobacteria and plant chloroplasts generate the oxidizing power necessary to oxidize H₂O, allowing it to serve as a source of both electrons and protons. This production of O₂ by oxygenic photosynthesis literally changed the atmosphere of the world.

Chloroplasts have two connected photosystems

In contrast to the sulfur bacteria, plants have two linked photosystems. This overcomes the limitations of cyclic photophosphorylation by providing an alternative source of electrons

from the oxidation of water. The oxidation of water also generates O_2 , thus oxygenic photosynthesis. The noncyclic transfer of electrons also produces NADPH, which can be used in the biosynthesis of carbohydrates.

One photosystem, called **photosystem I**, has an absorption peak of 700 nm, so its reaction center pigment is called P_{700} . This photosystem can pass electrons to NADPH similarly to the photosystem found in the sulfur bacteria discussed earlier. The other photosystem, called **photosystem II**, has an absorption peak of 680 nm, so its reaction center pigment is called P_{680} . This photosystem can generate an oxidation potential high enough to oxidize water. Working together, the two photosystems carry out a noncyclic transfer of electrons that generate both ATP and NADPH.

The photosystems were named I and II in the order of their discovery, and not in the order in which they operate in the light-dependent reactions. In plants and algae, the two photosystems are specialized for different roles in the overall process of oxygenic photosynthesis. Photosystem I transfers electrons ultimately to $NADP^+$, producing NADPH. The electrons lost from photosystem I are replaced by electrons from photosystem II. Photosystem II with its high oxidation potential can oxidize water to replace the electrons transferred to photosystem I. Thus there is an overall flow of electrons from water to NADPH.

These two photosystems are connected by a complex of electron carriers called the **cytochrome/ b_6-f complex** (explained shortly). This complex can use the energy from the passage of electrons to move protons across the thylakoid membrane to generate the proton gradient used by an ATP synthase enzyme.

The two photosystems work together in noncyclic photophosphorylation

Evidence for the action of two photosystems came from experiments that measured the rate of photosynthesis using two light beams of different wavelengths: one red and the other far-red. Using both beams produced a rate greater than the sum of the rates using individual beams of these wavelengths (figure 8.13). This surprising result, called the *enhancement effect*, can be explained by a mechanism involving two photosystems acting in series (that is, one after the other), one photosystem absorbs preferentially in the red, the other in the far-red.

Plants use photosystems II and I in series, first one and then the other, to produce both ATP and NADPH. This two-stage process is called **noncyclic photophosphorylation** because the path of the electrons is not a circle—the electrons ejected from the photosystems do not return to them, but rather end up in NADPH. The photosystems are replenished with electrons obtained by splitting water.

The scheme shown in figure 8.14, called a *Z diagram*, illustrates the two electron-energizing steps, one catalyzed by each photosystem. The horizontal axis shows the progress of the light reactions and the relative positions of the complexes, and the vertical axis shows relative energy levels of electrons. The electrons originate from water, which holds onto its electrons very tightly (redox potential = +820 mV), and end up in NADPH, which holds its electrons much more loosely (redox potential = -320 mV).

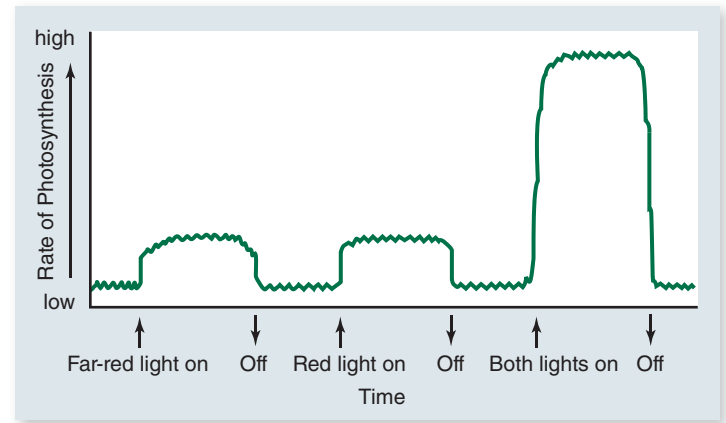


Figure 8.13 The enhancement effect. The rate of photosynthesis when red and far-red light are provided together is greater than the sum of the rates when each wavelength is provided individually. This result baffled researchers in the 1950s. Today, it provides key evidence that photosynthesis is carried out by two photochemical systems that act in series. One absorbs maximally in the far red, the other in the red portion of the spectrum.

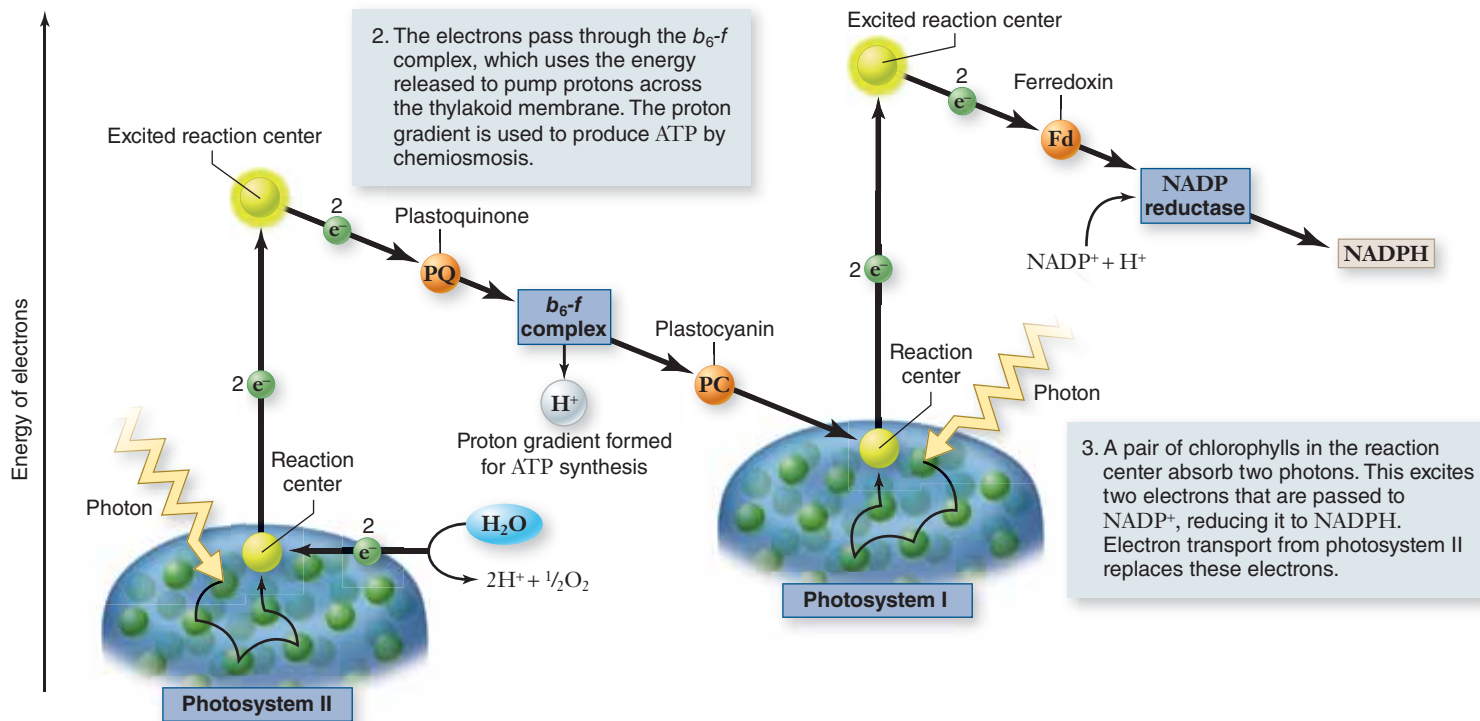
Data analysis If “both lights on” showed a rate equal to the sum of each light, what would you conclude?

Photosystem II acts first. High-energy electrons generated by photosystem II are used to synthesize ATP and are then passed to photosystem I to drive the production of NADPH. For every pair of electrons obtained from a molecule of water, one molecule of NADPH and slightly more than one molecule of ATP are produced.

Photosystem II

The reaction center of photosystem II closely resembles the reaction center of purple bacteria. It consists of a core of 10 transmembrane protein subunits with electron transfer components and two P_{680} chlorophyll molecules arranged around this core. The light-harvesting antenna complex consists of molecules of chlorophyll *a* and accessory pigments bound to several protein chains. The reaction center of photosystem II differs from the reaction center of the purple bacteria in that it also contains four manganese atoms. These manganese atoms are essential for the oxidation of water.

Although the chemical details of the oxidation of water are not entirely clear, the outline is emerging. Four manganese atoms are bound in a cluster to reaction center proteins. Two water molecules are also bound to this cluster of manganese atoms. When the reaction center of photosystem II absorbs a photon, an electron in a P_{680} chlorophyll molecule is excited, which transfers this electron to an acceptor. The oxidized P_{680} then removes an electron from a manganese atom. The oxidized manganese atoms, with the aid of reaction center proteins, remove electrons from oxygen atoms in the two water molecules. This process requires the reaction center to absorb four photons to complete the oxidation of two water molecules, producing one O_2 in the process.



1. A pair of chlorophylls in the reaction center absorb two photons of light. This excites two electrons that are transferred to plastoquinone (PQ). Loss of electrons from the reaction center produces an oxidation potential capable of oxidizing water.

Figure 8.14 Z diagram of photosystems I and II. Two photosystems work sequentially and have different roles. Photosystem II passes energetic electrons to photosystem I via an electron transport chain. The electrons lost are replaced by oxidizing water. Photosystem I uses energetic electrons to reduce NADP⁺ to NADPH.

The role of the b₆-f complex

The primary electron acceptor for the light-energized electrons leaving photosystem II is a quinone molecule. The reduced quinone that results from accepting a pair of electrons (*plastoquinone*) is a strong electron donor; it passes the excited electron pair to a proton pump called the **b₆-f complex** embedded within the thylakoid membrane (figure 8.15). This complex closely resembles the bc₁ complex in the respiratory electron transport chain of mitochondria, discussed in chapter 7.

Arrival of the energetic electron pair causes the b₆-f complex to pump a proton into the thylakoid space. A small, copper-containing protein called *plastocyanin* then carries the electron pair to photosystem I.

Photosystem I

The reaction center of photosystem I consists of a core transmembrane complex consisting of 12 to 14 protein subunits with two bound P₇₀₀ chlorophyll molecules. Energy is fed to it by an antenna complex consisting of chlorophyll *a* and accessory pigment molecules.

Photosystem I accepts an electron from plastocyanin into the “hole” created by the exit of a light-energized electron. The absorption of a photon by photosystem I boosts the electron leaving the reaction center to a very high energy level. The electrons are passed to an iron-sulfur protein called *ferredoxin*. Unlike photosystem II and the bacterial photosystem, the plant photosystem I does not rely on quinones as electron acceptors.

Making NADPH

Photosystem I passes electrons to ferredoxin on the stromal side of the membrane (outside the thylakoid). The reduced ferredoxin carries an electron with very high potential. Two of them, from two molecules of reduced ferredoxin, are then donated to a molecule of NADP⁺ to form NADPH. The reaction is catalyzed by the membrane-bound enzyme *NADP reductase*.

Because the reaction occurs on the stromal side of the membrane and involves the uptake of a proton in forming NADPH, it contributes further to the proton gradient established during photosynthetic electron transport. The function of the two photosystems is summarized in figure 8.15.

ATP is generated by chemiosmosis

Protons are pumped from the stroma into the thylakoid compartment by the b₆-f complex. The splitting of water also produces added protons that contribute to the gradient. The thylakoid membrane is impermeable to protons, so this creates an electrochemical gradient that can be used to synthesize ATP.

ATP synthase

The chloroplast has ATP synthase enzymes in the thylakoid membrane that form a channel, allowing protons to cross back out into the stroma. These channels protrude like knobs on the external surface of the thylakoid membrane. As protons pass out of the thylakoid through the ATP synthase channel, ADP is phosphorylated to ATP and released into the stroma (see figure 8.15). The stroma contains the enzymes that catalyze the reactions of carbon fixation—the Calvin cycle reactions.

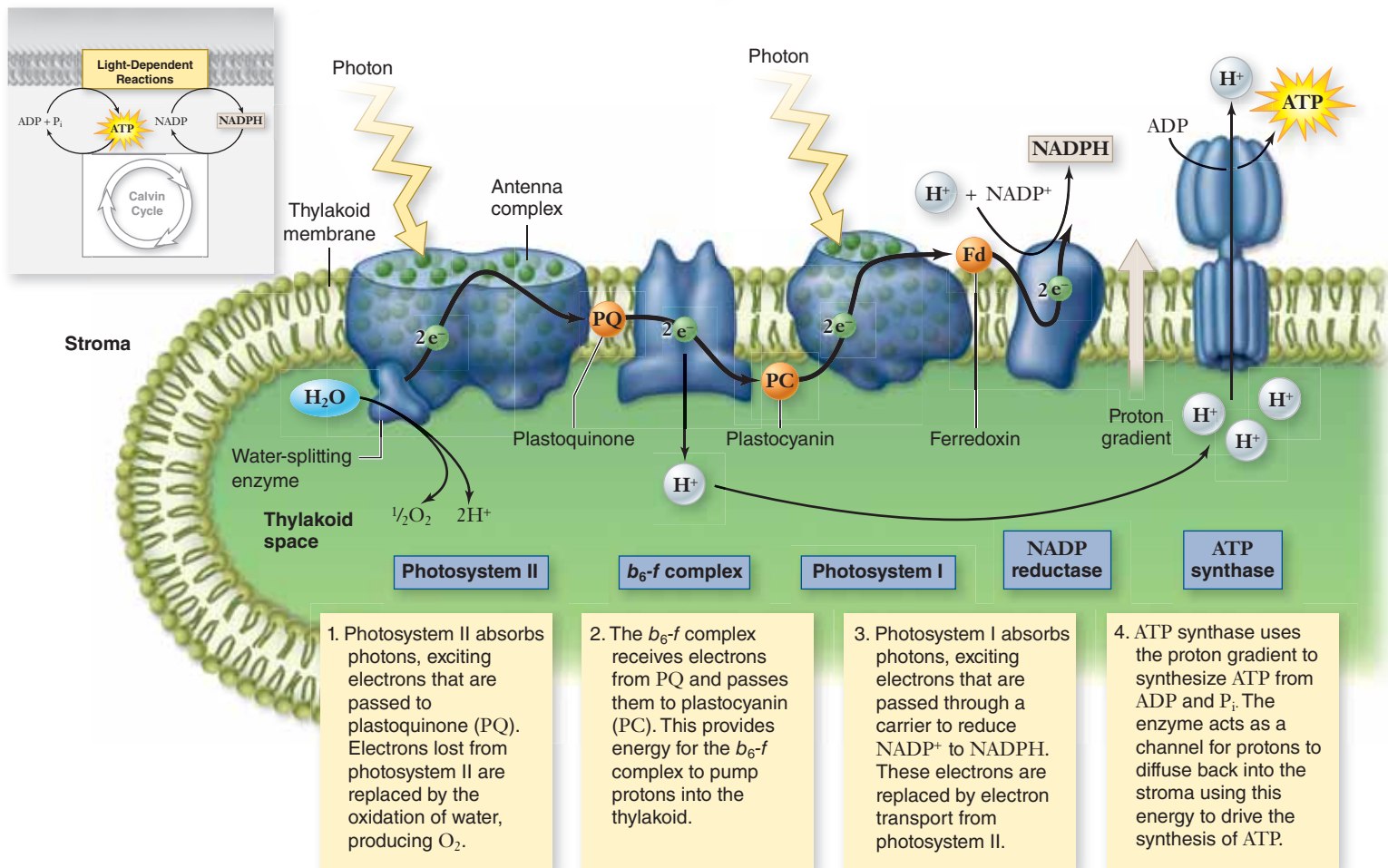


Figure 8.15 The photosynthetic electron transport system and ATP synthase. The two photosystems are arranged in the thylakoid membrane joined by an electron transport system that includes the b₆-f complex. These function together to create a proton gradient that is used by ATP synthase to synthesize ATP.

This mechanism is the same as that seen in the mitochondrial ATP synthase, and, in fact, the two enzymes are evolutionarily related. This similarity in generating a proton gradient by electron transport and ATP by chemiosmosis illustrates the similarities in

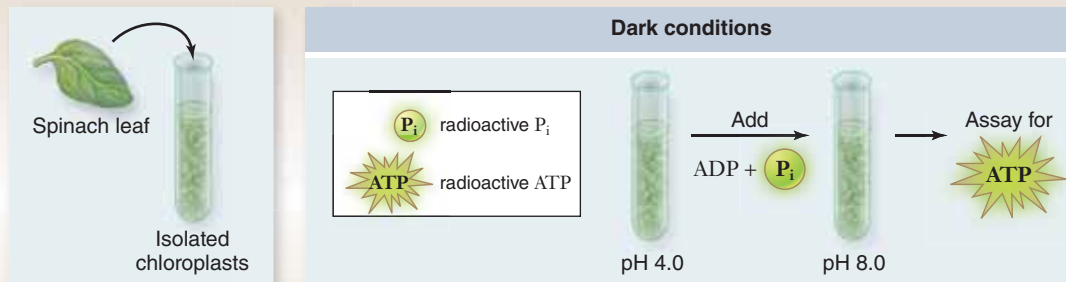
structure and function in mitochondria and chloroplasts. Evidence for this chemiosmotic mechanism for photophosphorylation was actually discovered earlier (figure 8.16) and formed the background for experiments using the mitochondrial ATP synthase.

SCIENTIFIC THINKING

Hypothesis: Photophosphorylation is coupled to electron transport by a proton gradient.

Prediction: If a proton gradient can be formed artificially, then isolated chloroplasts will phosphorylate ADP in the dark.

Test: Isolated chloroplasts are incubated in acid medium, then transferred in the dark to a basic medium to create an artificial proton gradient.



Result: Isolated chloroplasts can phosphorylate ADP in the dark as assayed by the incorporation of radioactive PO₄ into ATP.

Conclusion: The energy from electron transport in the chloroplast is coupled to the phosphorylation of ADP by a proton gradient.

Further Experiments: How would the use of agents that inhibit electron transport affect this outcome? How could such agents be used as a further test of the hypothesis?

Figure 8.16 The Jagendorf acid bath experiment.

The production of additional ATP

The passage of an electron pair from water to NADPH in noncyclic photophosphorylation generates one molecule of NADPH and slightly more than one molecule of ATP. But as you will learn later in this chapter, building organic molecules takes more energy than that—it takes 1.5 ATP molecules per NADPH molecule to fix carbon.

To produce the extra ATP, many plant species are capable of short-circuiting photosystem I, switching photosynthesis into a *cyclic photophosphorylation* mode, so that the light-excited electron leaving photosystem I is used to make ATP instead of NADPH. The energetic electrons are simply passed back to the b_6-f complex, rather than passing on to NADP⁺. The b_6-f complex pumps protons into the thylakoid space, adding to the proton gradient that drives the chemiosmotic synthesis of ATP. The relative proportions of cyclic and noncyclic photophosphorylation in these plants determine the relative amounts of ATP and NADPH available for building organic molecules.

Thylakoid structure reveals components' locations

The four complexes responsible for the light-dependent reactions—namely photosystems I and II, cytochrome b_6-f , and ATP synthase—are not randomly arranged in the thylakoid. Researchers are beginning to image these complexes with the atomic force microscope, which can resolve nanometer scale structures, and a picture is emerging in which photosystem II is found primarily in the grana, whereas photosystem I and ATP synthase are found primarily in the stroma lamella. Photosystem I and ATP synthase may also be found in the edges of the grana that are not stacked. The cytochrome b_6-f complex is found in the borders between grana and stroma lamella. One possible model for the arrangement of the complexes is shown in figure 8.17.

The thylakoid itself is no longer thought of only as stacked disks. Some models of the thylakoid, based on electron microscopy and other imaging, depict the grana as folds of the interconnecting stroma lamella. This kind of arrangement is more similar to the folds seen in bacterial photosynthesis, and it would therefore allow for more flexibility in how the various complexes are arranged relative to one another.

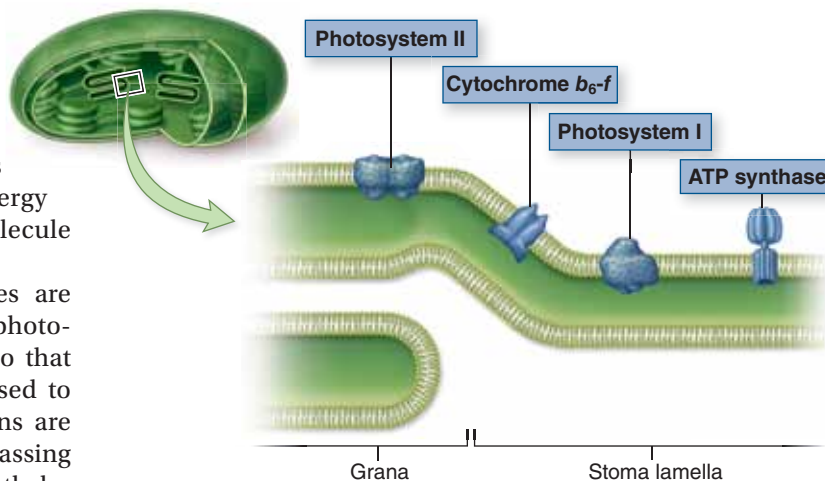


Figure 8.17 Model for the arrangement of complexes within the thylakoid. The arrangement of the two kinds of photosystems and the other complexes involved in photosynthesis is not random. Photosystem II is concentrated within grana, especially in stacked areas. Photosystem I and ATP synthase are concentrated in stroma lamella and the edges of grana. The cytochrome b_6-f complex is in the margins between grana and stroma lamella. This is one possible model for this arrangement.

8.6 Carbon Fixation: The Calvin Cycle

Learning Outcomes

1. Describe carbon fixation.
2. Demonstrate how six CO₂ molecules can be used to make one glucose.

Carbohydrates contain many C—H bonds and are highly reduced compared with CO₂. To build carbohydrates, cells use energy and a source of electrons produced by the light-dependent reactions of the thylakoids:

1. **Energy.** ATP (provided by cyclic and noncyclic photophosphorylation) drives the endergonic reactions.
2. **Reduction potential.** NADPH (provided by photosystem I) provides a source of protons and the energetic electrons needed to bind them to carbon atoms. Much of the light energy captured in photosynthesis ends up invested in the energy-rich C—H bonds of sugars.

Calvin cycle reactions convert inorganic carbon into organic molecules

Because early research showed temperature dependence, photosynthesis was predicted to involve enzyme-catalyzed reactions. These reactions form a cycle of enzyme-catalyzed steps much like the Krebs cycle of respiration. Unlike the Krebs cycle, however, carbon fixation is geared toward producing new compounds, so the nature of the cycles is quite different.

Learning Outcomes Review 8.5

The chloroplast has two photosystems located in the thylakoid membrane that are connected by an electron transport chain. Photosystem I passes an electron to NADPH. This electron is replaced by one from photosystem II. Photosystem II can oxidize water to replace the electron it has lost. A proton gradient is built up in the thylakoid space, and this gradient is used to generate ATP as protons pass through the ATP synthase enzyme.

- If the thylakoid membrane were leaky to protons, would ATP still be produced? Would NADPH?

The cycle of reactions that allow carbon fixation is called the **Calvin cycle**, after its discoverer, Melvin Calvin (1911–1997). Because the first intermediate of the cycle, phosphoglycerate, contains three carbon atoms, this process is also called **C₃ photosynthesis**.

The key step in this process—the event that makes the reduction of CO₂ possible—is the attachment of CO₂ to a highly specialized organic molecule. Photosynthetic cells produce this molecule by reassembling the bonds of two intermediates in glycolysis—fructose 6-phosphate and glyceraldehyde 3-phosphate (G3P)—to form the energy-rich 5-carbon sugar **ribulose 1,5-bisphosphate (RuBP)**.

CO₂ reacts with RuBP to form a transient 6-carbon intermediate that immediately splits into two molecules of the

three-carbon *3-phosphoglycerate (PGA)*. This overall reaction is called the *carbon fixation reaction* because inorganic carbon (CO₂) has been incorporated into an organic form: the acid PGA. The enzyme that carries out this reaction, **ribulose bisphosphate carboxylase/oxygenase** (usually abbreviated **rubisco**) is a large, 16-subunit enzyme found in the chloroplast stroma.

Carbon is transferred through cycle intermediates, eventually producing glucose

We will consider how the Calvin cycle can produce one molecule of glucose, although this glucose is not produced directly by the cycle (figure 8.18). In a series of reactions, six molecules of CO₂ are bound to six RuBP by rubisco to produce 12 molecules

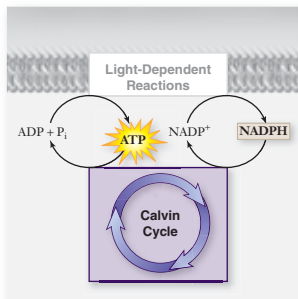
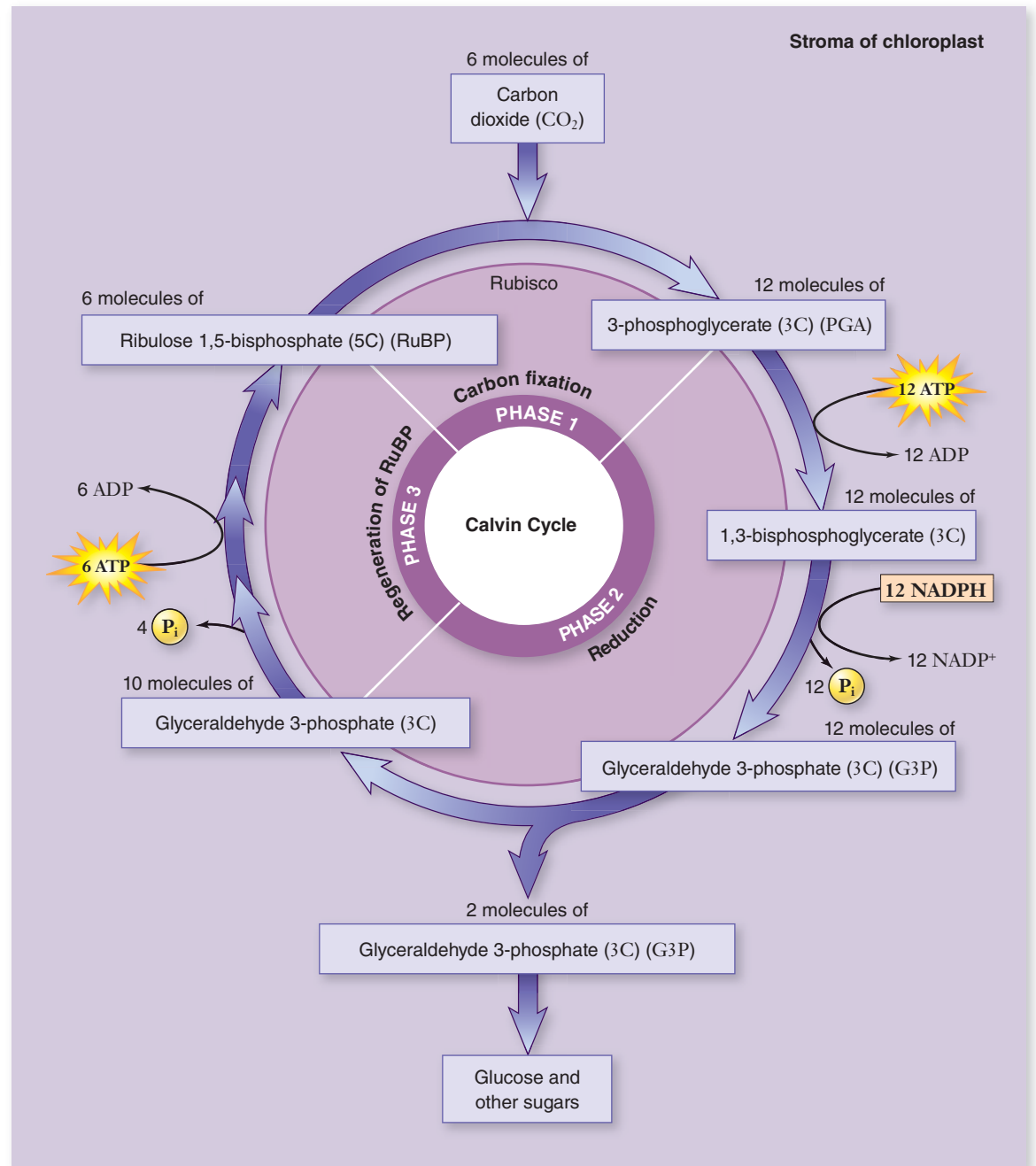
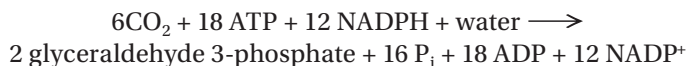


Figure 8.18 The Calvin cycle. The Calvin cycle accomplishes carbon fixation: converting inorganic carbon in the form of CO₂ into organic carbon in the form of carbohydrates. The cycle can be broken down into three phases: (1) carbon fixation, (2) reduction, and (3) regeneration of RuBP. For every six CO₂ molecules fixed by the cycle, a molecule of glucose can be synthesized from the products of the reduction reactions, G3P. The cycle uses the ATP and NADPH produced by the light reactions.



of PGA (containing $12 \times 3 = 36$ carbon atoms in all, 6 from CO_2 and 30 from RuBP). The 36 carbon atoms then undergo a cycle of reactions that regenerates the six molecules of RuBP used in the initial step (containing $6 \times 5 = 30$ carbon atoms). This leaves two molecules of *glyceraldehyde 3-phosphate (G3P)* (each with three carbon atoms) as the net gain. (You may recall G3P as also being the product of the first half of glycolysis, described in chapter 7.) These two molecules of G3P can then be used to make one molecule of glucose.

The net equation of the Calvin cycle is:



With six full turns of the cycle, six molecules of carbon dioxide enter, two molecules of G3P are produced, and six molecules of RuBP are regenerated. Thus six turns of the cycle produce two G3P that can be used to make a single glucose molecule. The six turns of the cycle also incorporated six CO_2 molecules, providing enough carbon to synthesize glucose, although the six carbon atoms do not all end up in this molecule of glucose.

Phases of the cycle

The Calvin cycle can be thought of as divided into three phases: (1) carbon fixation, (2) reduction, and (3) regeneration of RuBP. The carbon fixation reaction generates two molecules of the 3-carbon acid PGA; PGA is then reduced to G3P by reactions that are essentially a reverse of part of glycolysis; finally, the PGA is used to regenerate RuBP. Three turns around the cycle incorporate enough carbon to produce a

new molecule of G3P, and six turns incorporate enough carbon to synthesize one glucose molecule.

We now know that light is required *indirectly* for different segments of the CO_2 reduction reactions. Five of the Calvin cycle enzymes—including rubisco—are light-activated; that is, they become functional or operate more efficiently in the presence of light. Light also promotes transport of required 3-carbon intermediates across chloroplast membranes. And finally, light promotes the influx of Mg^{2+} into the chloroplast stroma, which further activates the enzyme rubisco.

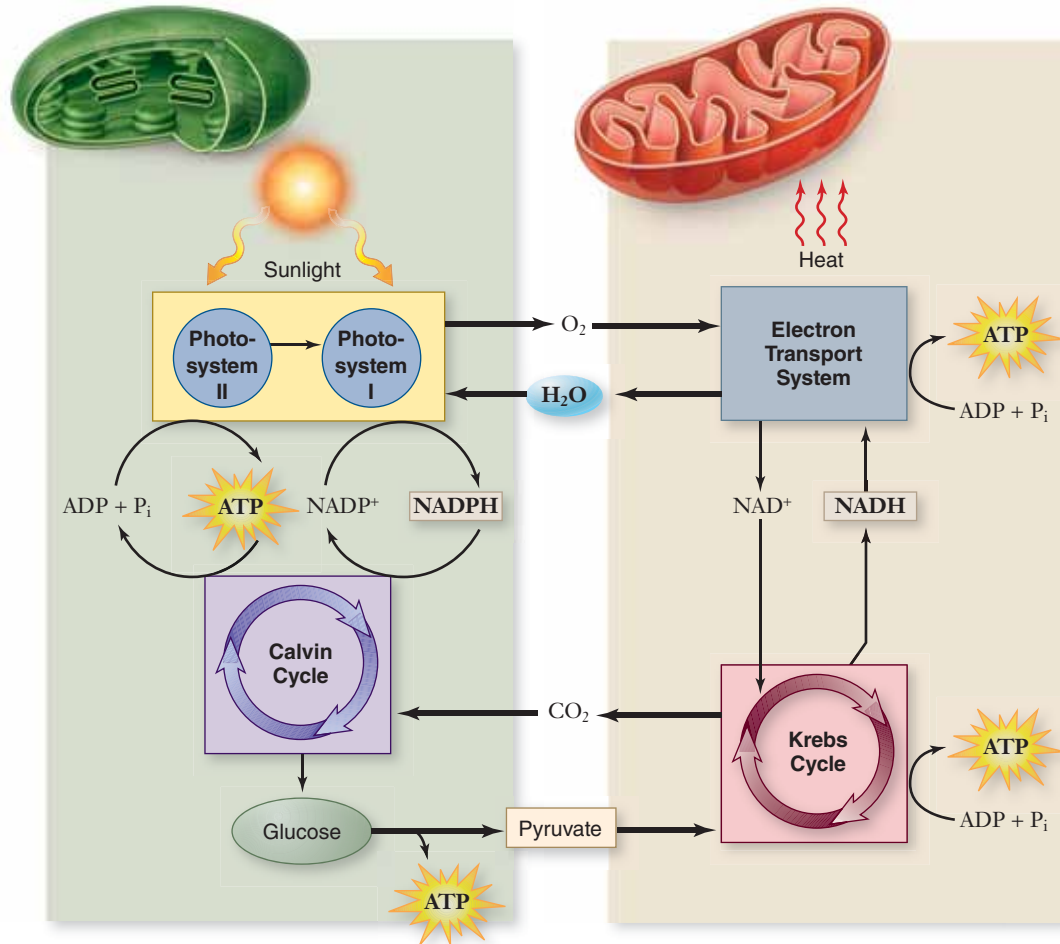
Output of the Calvin cycle

Glyceraldehyde 3-phosphate is a 3-carbon sugar, a key intermediate in glycolysis. Much of it is transported out of the chloroplast to the cytoplasm of the cell, where the reversal of several reactions in glycolysis allows it to be converted to fructose 6-phosphate and glucose 1-phosphate. These products can then be used to form sucrose, a major transport sugar in plants. (Sucrose, table sugar, is a disaccharide made of fructose and glucose.)

In times of intensive photosynthesis, G3P levels rise in the stroma of the chloroplast. As a consequence, some G3P in the chloroplast is converted to glucose 1-phosphate. This takes place in a set of reactions analogous to those occurring in the cytoplasm, by reversing several reactions similar to those of glycolysis. The glucose 1-phosphate is then combined into an insoluble polymer, forming long chains of starch stored as bulky starch grains in the cytoplasm. These starch grains represent stored glucose for later use.

Figure 8.19 Chloroplasts and mitochondria: completing an energy cycle.

Water and O_2 cycle between chloroplasts and mitochondria within a plant cell, as do glucose and CO_2 . Cells with chloroplasts take in CO_2 and H_2O and produce glucose and O_2 . Cells without chloroplasts, such as animal cells, take in glucose and O_2 and produce CO_2 and H_2O . This leads to global cycling of carbon through photosynthesis and respiration (see figure 57.1).



The energy cycle

The energy-capturing metabolisms of the chloroplasts studied in this chapter and the mitochondria studied in chapter 7 are intimately related (figure 8.19). Photosynthesis uses the products of respiration as starting substrates, and respiration uses the products of photosynthesis as starting substrates. The production of glucose from G3P even uses part of the ancient glycolytic pathway, run in reverse. Also, the principal proteins involved in electron transport and ATP production in plants are evolutionarily related to those in mitochondria.

Photosynthesis is but one aspect of plant biology, although it is an important one. In chapters 36 through 41, we examine plants in more detail. We have discussed photosynthesis as a part of cell biology because photosynthesis arose long before plants did, and because most organisms depend directly or indirectly on photosynthesis for the energy that powers their lives.

Learning Outcomes Review 8.6

Carbon fixation takes place in the stroma of the chloroplast, where inorganic CO_2 is incorporated into an organic molecule. The key intermediate is the 5-carbon sugar RuBP that combines with CO_2 in a reaction catalyzed by the enzyme rubisco. The cycle can be broken down into three stages: carbon fixation, reduction, and regeneration of RuBP. ATP and NADPH from the light reactions provide energy and electrons for the reduction reactions, which produce G3P. Glucose is synthesized when two molecules of G3P are combined.

- How does the Calvin cycle compare with glycolysis?

8.7 Photorespiration

Learning Outcomes

1. Distinguish between how rubisco acts to make RuBP and how it oxidizes RuBP.
2. Compare the function of carbon fixation in the C_3 , C_4 , and CAM pathways.

Evolution does not necessarily result in optimum solutions. Rather, it favors workable solutions that can be derived from

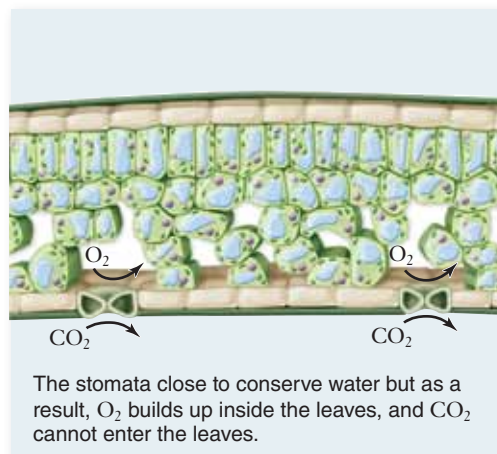
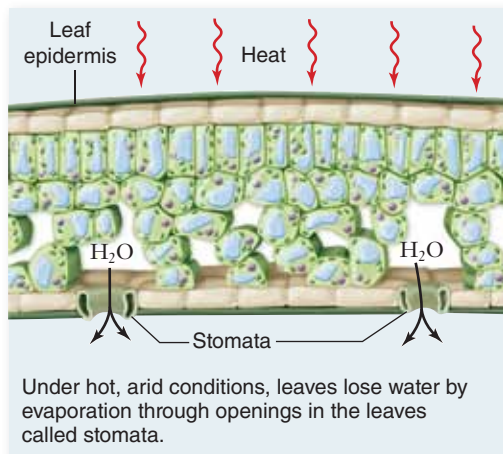


Figure 8.20 Stoma. A closed stoma in the leaf of a tobacco plant. Each stoma is formed from two guard cells whose shape changes with turgor pressure to open and close. Under dry conditions plants close their stomata to conserve water.

features that already exist. Photosynthesis is no exception. Rubisco, the enzyme that catalyzes the key carbon-fixing reaction of photosynthesis, provides a decidedly suboptimal solution. This enzyme has a second enzymatic activity that interferes with carbon fixation, namely that of *oxidizing* RuBP. In this process, called **photorespiration**, O_2 is incorporated into RuBP, which undergoes additional reactions that actually release CO_2 . Hence, photorespiration releases CO_2 , essentially undoing carbon fixation.

Photorespiration reduces the yield of photosynthesis

The carboxylation and oxidation of RuBP are catalyzed at the same active site on rubisco, and CO_2 and O_2 compete with each other at this site. Under normal conditions at 25°C , the rate of the carboxylation reaction is four times that of the oxidation reaction, meaning that 20% of photosynthetically fixed carbon is lost to photorespiration.

This loss rises substantially as temperature increases, because under hot, arid conditions, specialized openings in the leaf called *stomata* (singular, *stoma*) (figure 8.20) close to conserve water. This closing also cuts off the supply of CO_2 entering the leaf and does not allow O_2 to exit (figure 8.21). As a result, the low- CO_2 and high- O_2 conditions within the leaf favor photorespiration.

Figure 8.21 Conditions favoring photorespiration. In hot, arid environments, stomata close to conserve water, which also prevents CO_2 from entering and O_2 from exiting the leaf. The high- O_2 /low- CO_2 conditions favor photorespiration.

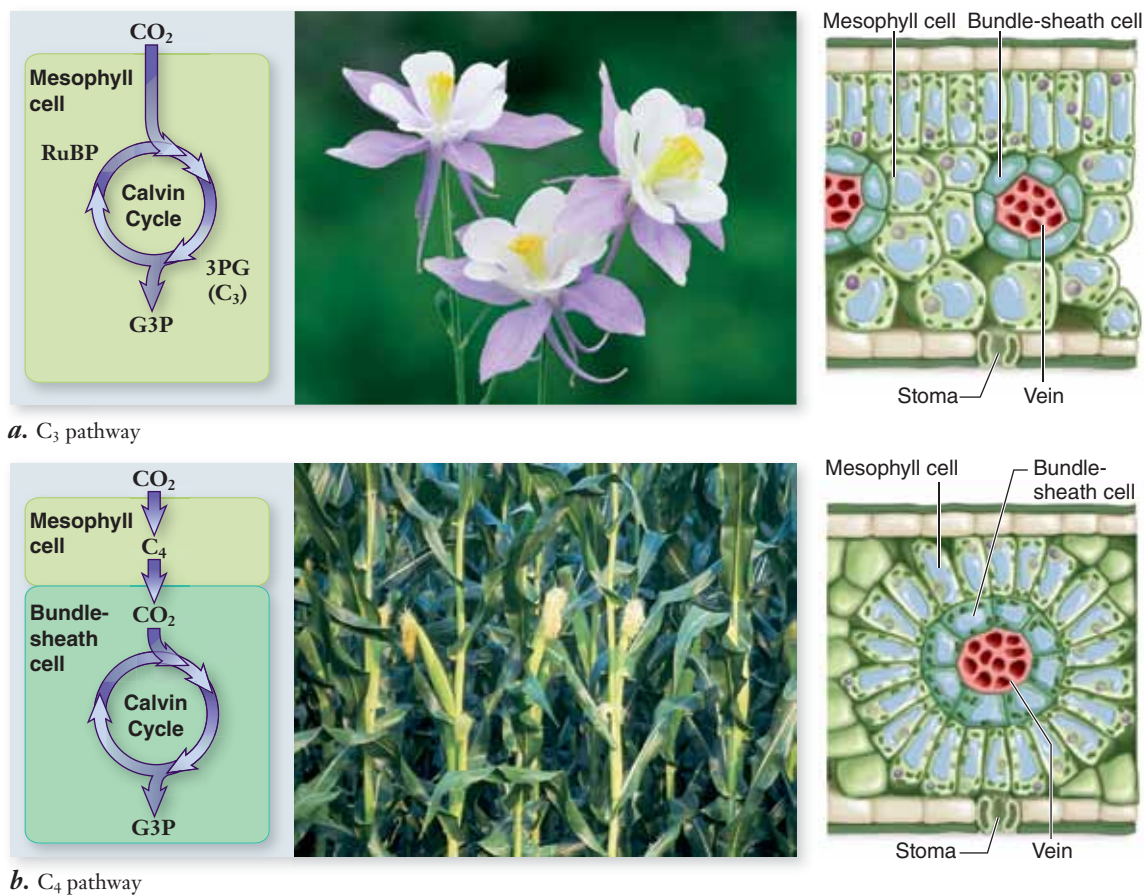


Figure 8.22 Comparison of C₃ and C₄ pathways of carbon fixation. *a.* The C₃ pathway uses the Calvin cycle to fix carbon. All reactions occur in mesophyll cells using CO₂ that diffuses in through stomata. *b.* The C₄ pathway incorporates CO₂ into a 4-carbon molecule of malate in mesophyll cells. This is transported to the bundle sheath cells where it is converted back into CO₂ and pyruvate, creating a high level of CO₂. This allows efficient carbon fixation by the Calvin cycle.

Plants that fix carbon using only C₃ photosynthesis (the Calvin cycle) are called **C₃ plants** (figure 8.22*a*). Other plants add CO₂ to phosphoenolpyruvate (PEP) to form a 4-carbon molecule. This reaction is catalyzed by the enzyme *PEP carboxylase*. This enzyme has two advantages over rubisco: it has a much greater affinity for CO₂ than rubisco, and it does not have oxidase activity.

The 4-carbon compound produced by PEP carboxylase undergoes further modification, only to be eventually decarboxylated. The CO₂ released by this decarboxylation is then used by rubisco in the Calvin cycle. This allows CO₂ to be pumped directly to the site of rubisco, which increases the local concentration of CO₂ relative to O₂, minimizing photorespiration. The 4-carbon compound produced by PEP carboxylase allows CO₂ to be stored in an organic form, to then be released in a different cell, or at a different time to keep the level of CO₂ high relative to O₂.

The reduction in the yield of carbohydrate as a result of photorespiration is not trivial. C₃ plants lose between 25% and 50% of their photosynthetically fixed carbon in this way. The rate depends largely on temperature. In tropical climates, especially those in which the temperature is often above 28°C, the problem is severe, and it has a major effect on tropical agriculture.

The two main groups of plants that initially capture CO₂ using PEP carboxylase differ in how they maintain high levels of CO₂ relative to O₂. In **C₄ plants** (figure 8.22*b*), the capture of CO₂ occurs in one cell and the decarboxylation occurs in an adjacent cell. This represents a spatial solution to the problem of photorespiration. The second group, **CAM plants**, perform both reactions in the same cell, but capture CO₂ using PEP carboxylase at night, then decarboxylate during the day. CAM stands for **crassulacean acid metabolism**, after the plant family Crassulaceae (the stonecrops, or hens-and-chicks), in which it was first discovered. This mechanism represents a temporal solution to the photorespiration problem.

C₄ plants have evolved to minimize photorespiration

The C₄ plants include corn, sugarcane, sorghum, and a number of other grasses. These plants initially fix carbon using PEP carboxylase in mesophyll cells. This reaction produces the organic acid oxaloacetate, which is converted to malate and transported to bundle-sheath cells that surround the leaf veins. Within the bundle-sheath cells, malate is decarboxylated to produce pyruvate and CO₂ (figure 8.23). Because the

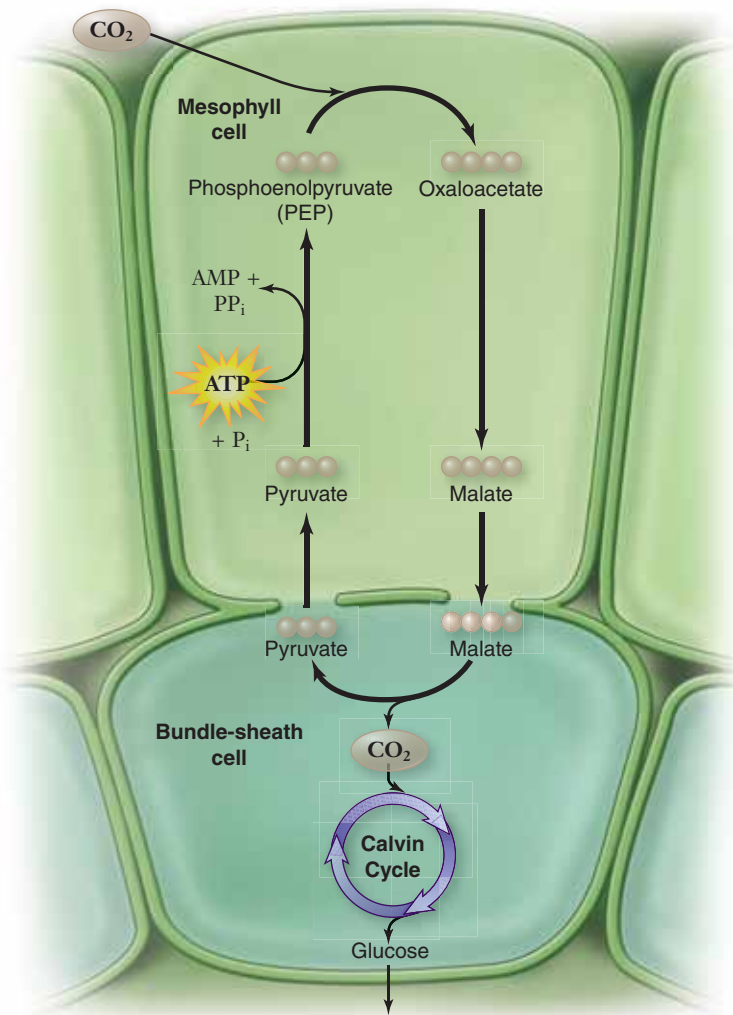


Figure 8.23 Carbon fixation in C_4 plants. This process is called the C_4 pathway because the first molecule formed, oxaloacetate, contains four carbons. The oxaloacetate is converted to malate, which moves into bundle-sheath cells where it is decarboxylated back to CO_2 and pyruvate. This produces a high level of CO_2 in the bundle-sheath cells that can be fixed by the usual C_3 Calvin cycle with little photorespiration. The pyruvate diffuses back into the mesophyll cells, where it is converted back to PEP to be used in another C_4 fixation reaction.

bundle-sheath cells are impermeable to CO_2 , the local level of CO_2 is high and carbon fixation by rubisco and the Calvin cycle is efficient. The pyruvate produced by decarboxylation is transported back to the mesophyll cells, where it is converted back to PEP, thereby completing the cycle.

The C_4 pathway, although it overcomes the problems of photorespiration, does have a cost. The conversion of pyruvate back to PEP requires breaking two high-energy bonds in ATP. Thus each CO_2 transported into the bundle-sheath cells cost the equivalent of two ATP. To produce a single glucose, this requires 12 additional ATP compared with the Calvin cycle alone. Despite this additional cost, C_4 photosynthesis is advantageous in hot dry climates where photorespiration would remove more than half of the carbon fixed by the usual C_3 pathway alone.

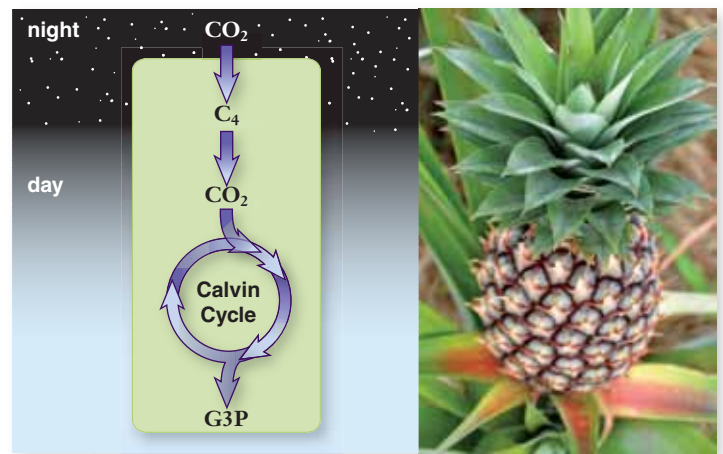


Figure 8.24 Carbon fixation in CAM plants. CAM plants also use both C_4 and C_3 pathways to fix carbon and minimize photorespiration. In CAM plants, the two pathways occur in the same cell but are separated in time: The C_4 pathway is utilized to fix carbon at night, then CO_2 is released from these accumulated stores during the day to drive the C_3 pathway. This achieves the same effect of minimizing photorespiration while also minimizing loss of water by opening stomata at night when temperatures are lower.

The Crassulacean acid pathway splits photosynthesis into night and day

A second strategy to decrease photorespiration in hot regions has been adopted by the CAM plants. These include many succulent (water-storing) plants, such as cacti, pineapples, and some members of about two dozen other plant groups.

In these plants, the stomata open during the night and close during the day (figure 8.24). This pattern of stomatal opening and closing is the reverse of that in most plants. CAM plants initially fix CO_2 using PEP carboxylase to produce oxaloacetate. The oxaloacetate is often converted into other organic acids, depending on the particular CAM plant. These organic compounds accumulate during the night and are stored in the vacuole. Then during the day, when the stomata are closed, the organic acids are decarboxylated to yield high levels of CO_2 . These high levels of CO_2 drive the Calvin cycle and minimize photorespiration.

Like C_4 plants, CAM plants use both C_3 and C_4 pathways. They differ in that they use both of these pathways in the same cell: the C_4 pathway at night and the C_3 pathway during the day. In C_4 plants the two pathways occur in different cells.

Learning Outcomes Review 8.7

Rubisco can also oxidize RuBP under conditions of high O_2 and low CO_2 . In plants that use only C_3 metabolism (Calvin cycle), up to 20% of fixed carbon is lost to this photorespiration. Plants adapted to hot, dry environments are capable of storing CO_2 as a 4-carbon molecule and avoiding some of this loss; they are called C_4 plants. In CAM plants, CO_2 is fixed at night into a C_4 organic compound; in the daytime, this compound is used as a source of CO_2 C_3 metabolism when stomata are closed to prevent water loss.

- How do C_4 plants and CAM plants differ?



Chapter Review

8.1 Overview of Photosynthesis

Photosynthesis is the conversion of light energy into chemical energy (figure 8.2).

Photosynthesis combines CO_2 and H_2O , producing glucose and O_2 .

Photosynthesis has three stages: absorbing light energy, using this energy to synthesize ATP and NADPH, and using the ATP and NADPH to convert CO_2 to organic molecules. The first two stages consist of light-dependent reactions, and the third stage of light-independent reactions.

In plants, photosynthesis takes place in chloroplasts.

Chloroplasts contain internal thylakoid membranes and a fluid matrix called stroma. The photosystems involved in energy capture are found in the thylakoid membranes, and enzymes for assembling organic molecules are in the stroma.

8.2 The Discovery of Photosynthetic Processes

Plants do not increase mass from soil and water alone.

Early investigations revealed that plants produce O_2 from carbon dioxide and water in the presence of light.

Photosynthesis includes both light-dependent and light-independent reactions.

The light-dependent reactions require light; the light-independent reactions occur in both daylight and darkness. The rate of photosynthesis depends on the amount of light, the CO_2 concentration, and temperature.

O_2 comes from water, not from CO_2 .

The use of isotopes revealed the individual origins and fates of different molecules in photosynthetic reactions.

ATP and NADPH from light-dependent reactions reduce CO_2 to make sugars.

Carbon fixation requires ATP and NADPH, which are products of the light-dependent reactions. As long as these are available, CO_2 is reduced by enzymes in the stroma to form simple sugars.

8.3 Pigments

Light is a form of energy.

Light exists both as a wave and as a particle (photon). Light can remove electrons from some metals by the photoelectric effect, and in photosynthesis, chloroplasts act as photoelectric devices.

Each pigment has a characteristic absorption spectrum (figure 8.5).

Chlorophyll *a* is the only pigment that can convert light energy into chemical energy. Chlorophyll *b* is an accessory pigment that increases the harvest of photons for photosynthesis.

Carotenoids and other accessory pigments further increase a plant's ability to harvest photons.

8.4 Photosystem Organization (figure 8.10)

Production of one O_2 molecule requires many chlorophyll molecules.

Measurement of O_2 output led to the idea of photosystems—clusters of pigment molecules that channel energy to a reaction center.

A generalized photosystem contains an antenna complex and a reaction center.

A photosystem is a network of chlorophyll *a*, accessory pigments, and proteins embedded in the thylakoid membrane. Pigment molecules of the antenna complex harvest photons and feed light energy to the reaction center. The reaction center is composed of

two chlorophyll *a* molecules in a protein matrix that pass an excited electron to an electron acceptor.

8.5 The Light-Dependent Reactions

The light reactions can be broken down into four processes: primary photoevent, charge separation, electron transport, and chemiosmosis.

Some bacteria use a single photosystem (figure 8.12).

An excited electron moves along a transport chain and eventually returns to the photosystem. This cyclic process is used to generate a proton gradient. In some bacteria, this can also produce NADPH.

Chloroplasts have two connected photosystems (figure 8.14).

Photosystem I transfers electrons to NADP^+ , reducing it to NADPH. Photosystem II replaces electrons lost by photosystem I. Electrons lost from photosystem II are replaced by electrons from oxidation of water, which also produces O_2 .

The two photosystems work together in noncyclic photophosphorylation (figure 8.14).

Photosystem II and photosystem I are linked by an electron transport chain; the b_6-f complex in this chain pumps protons into the thylakoid space.

ATP is generated by chemiosmosis.

ATP synthase is a channel enzyme; as protons flow through the channel down their gradient, ADP is phosphorylated producing ATP, similar to the mechanism in mitochondria. Plants can make additional ATP by cyclic photophosphorylation.

Thylakoid structure reveals components' locations.

Imaging studies suggest that photosystem II is primarily found in the grana, while photosystem I and ATP synthase are found in the stroma lamella.

8.6 Carbon Fixation: The Calvin Cycle (figure 8.18)

Calvin cycle reactions convert inorganic carbon into organic molecules.

The Calvin cycle, also known as C_3 photosynthesis, uses CO_2 , ATP, and NADPH to build simple sugars.

Carbon is transferred through cycle intermediates, eventually producing glucose.

The Calvin cycle occurs in three stages: carbon fixation via the enzyme rubisco's action on RuBP and CO_2 ; reduction of the resulting 3-carbon PGA to G3P, generating ATP and NADPH; and regeneration of RuBP. Six turns of the cycle fix enough carbon to produce two excess G3Ps used to make one molecule of glucose.

8.7 Photorespiration

Photorespiration reduces the yield of photosynthesis.

Rubisco can catalyze the oxidation of RuBP, reversing carbon fixation. Dry, hot conditions tend to increase this reaction.

C_4 plants have evolved to minimize photorespiration.

C_4 plants fix carbon by adding CO_2 to a 3-carbon molecule, forming oxaloacetate. Carbon is fixed in one cell by the C_4 pathway, then CO_2 is released in another cell for the Calvin cycle (figure 8.23).

The Crassulacean acid pathway splits photosynthesis into night and day.

CAM plants use the C_4 pathway during the day when stomata are closed, and the Calvin cycle at night in the same cell (figure 8.24).



Review Questions

UNDERSTAND

- The *light-dependent* reactions of photosynthesis are responsible for the production of
 - glucose.
 - CO₂.
 - ATP and NADPH.
 - H₂O.
- Which region of a chloroplast is associated with the capture of light energy?
 - Thylakoid membrane
 - Outer membrane
 - Stroma
 - Both a and c are correct.
- The colors of light that are most effective for photosynthesis are
 - red, blue, and violet.
 - green, yellow, and orange.
 - infrared and ultraviolet.
 - All colors of light are equally effective.
- During noncyclic photosynthesis, photosystem I functions to _____, and photosystem II functions to _____.
 - synthesize ATP; produce O₂
 - reduce NADP⁺; oxidize H₂O
 - reduce CO₂; oxidize NADPH
 - restore an electron to its reaction center; gain an electron from water
- How is a reaction center pigment in a photosystem different from a pigment in the antenna complex?
 - The reaction center pigment is a chlorophyll molecule.
 - The antenna complex pigment can only reflect light.
 - The reaction center pigment loses an electron when it absorbs light energy.
 - The antenna complex pigments are not attached to proteins.
- The ATP and NADPH from the light reactions are used
 - in glycolysis in roots.
 - directly in most biochemical reactions in the cell.
 - during the reactions of the Calvin cycle to produce glucose.
 - to synthesize chlorophyll.
- The carbon fixation reaction converts
 - inorganic carbon into an organic acid.
 - CO₂ into glucose.
 - inactive rubisco into active rubisco.
 - an organic acid into CO₂.
- C₄ plants initially fix carbon by
 - the same pathway as C₃ plants, but they modify this product.
 - incorporating CO₂ into oxaloacetate, which is converted to malate.
 - incorporating CO₂ into citrate via the Krebs cycle.
 - incorporating CO₂ into glucose via reverse glycolysis.
- In the cytoplasm immediately outside the chloroplast
- In the antenna complex
- The excited electron from photosystem I
 - can be returned to the reaction center to generate ATP by cyclic photophosphorylation.
 - is replaced by oxidizing H₂O.
 - is replaced by an electron from photosystem II.
 - Both a and c are correct.
- If the Calvin cycle runs through six turns
 - all of the fixed carbon will end up in the same glucose molecule.
 - 12 carbons will be fixed by the process.
 - enough carbon will be fixed to make one glucose, but they will not all be in the same molecule.
 - one glucose will be converted into six CO₂.
- Which of the following are similarities between the structure and function of mitochondria and chloroplasts?
 - They both create internal proton gradients by electron transport.
 - They both generate CO₂ by oxidation reactions.
 - They both have a double membrane system.
 - Both a and c are correct.
- Given that the C₄ pathway gets around the problems of photorespiration, why don't all plants use it?
 - It is a more recent process, and many plants have not had time to evolve this pathway.
 - It requires extra enzymes that many plants lack.
 - It requires special transport tissues that many plants lack.
 - It also has an energetic cost.
- If the thylakoid membrane became leaky to ions, what would you predict to be the result on the light reactions?
 - It would stop ATP production.
 - It would stop NADPH production.
 - It would stop the oxidation of H₂O.
 - All of the choices are correct.
- The overall process of photosynthesis
 - results in the reduction of CO₂ and the oxidation of H₂O.
 - results in the reduction of H₂O and the oxidation of CO₂.
 - consumes O₂ and produces CO₂.
 - produces O₂ from CO₂.

APPLY

- The overall flow of electrons in the light reactions is from
 - antenna pigments to the reaction center.
 - H₂O to CO₂.
 - photosystem I to photosystem II.
 - H₂O to NADPH.
- If you could measure pH within a chloroplast, where would it be lowest?
 - In the stroma
 - In the lumen of the thylakoid

SYNTHESIZE

- Compare and contrast the fixation of carbon in C₃, C₄, and CAM plants.
- Diagram the relationship between the reactants and products of photosynthesis and respiration.
- Do plant cells need mitochondria? Explain your answer.

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