Flowering Plants as Photosynthesizers

Photosynthesis takes place in the green portions of plants. The leaves of a flowering plant contain mesophyll tissue in which cells are specialized for photosynthesis (Fig. 7.2). The raw materials for photosynthesis are water and carbon dioxide. The roots of a plant absorb water, which then moves in vascular tissue up the stem to a leaf by way of the leaf veins. Carbon dioxide in the air enters a leaf through small openings called **stomata** (sing., stoma). After entering a leaf, carbon dioxide and water diffuse into **chloroplasts** [Gk. *chloros*, green, and *plastos*, formed, molded], the organelles that carry on photosynthesis.

A double membrane surrounds a chloroplast, and its semifluid interior called the **stroma** [Gk. *stroma*, bed, mattress]. A different membrane system within the stroma forms flattened sacs called **thylakoids** [Gk. *thylakos*, sack, and *eides*, like, resembling], which in some places are stacked to form **grana** (sing., granum), so called because they looked like piles of seeds to early microscopists. The space of each thylakoid is thought to be connected to the space of every other thylakoid within a chloroplast, thereby forming an inner compartment within chloroplasts called the thylakoid space.

The thylakoid membrane contains **chlorophyll** and other pigments that are capable of absorbing solar energy, the type of energy that drives photosynthesis. The stroma contains an enzyme-rich solution where carbon dioxide is first attached to an organic compound and is then reduced to a carbohydrate.

Therefore, it is proper to associate the absorption of solar energy with the thylakoid membranes making up the grana and to associate the reduction of carbon dioxide to a carbohydrate with the stroma of a chloroplast.

Human beings, and indeed nearly all organisms, release carbon dioxide into the air. This is some of the same carbon dioxide that enters a leaf through the stoma and is converted to carbohydrate. Carbohydrate, in the form of glucose, is the chief source of chemical energy for most organisms.

Check Your Progress 7.1

1. List three major groups of photosynthetic organisms.
2. Which part of a chloroplast absorbs solar energy, and which part forms a carbohydrate?

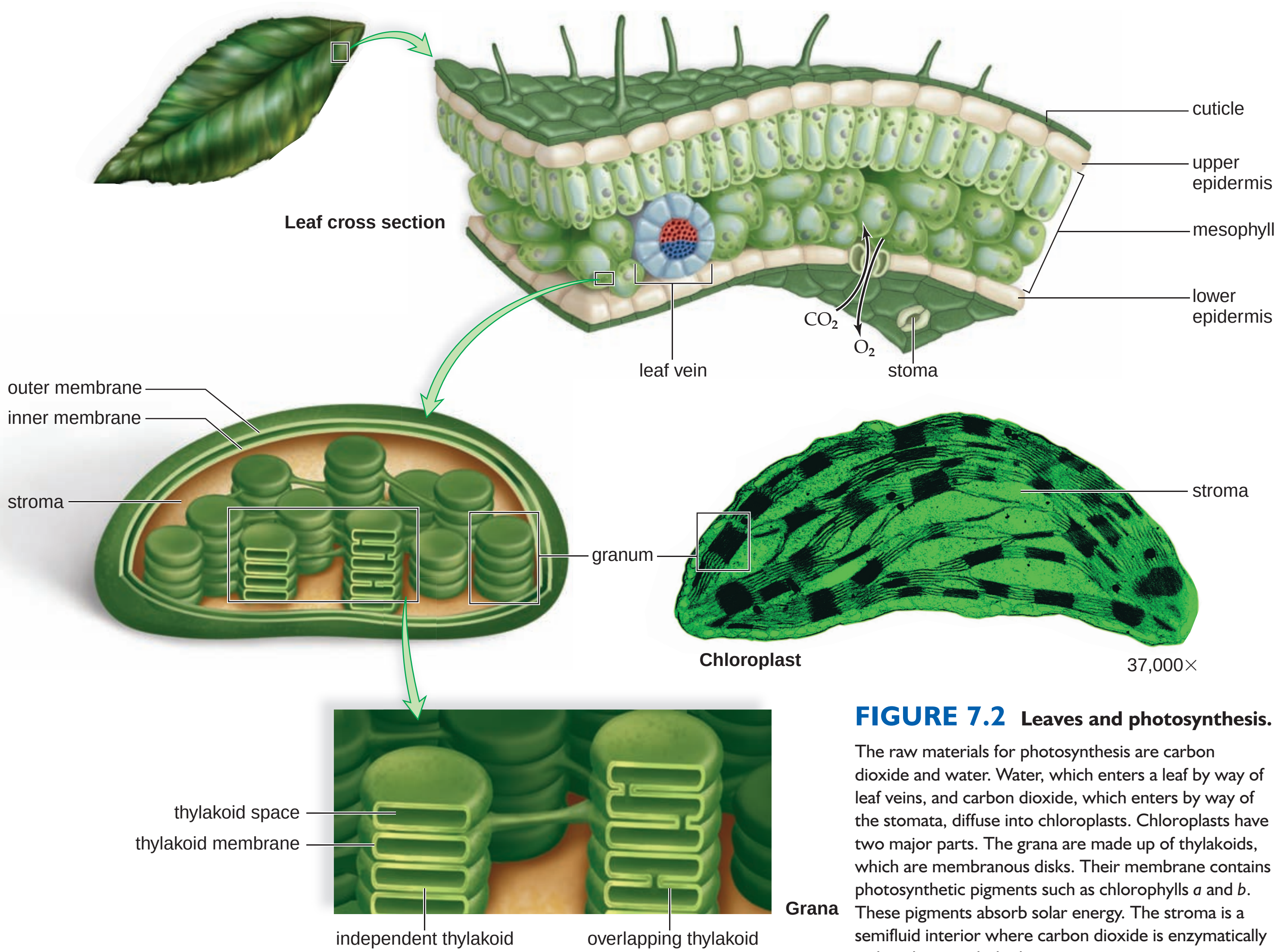


FIGURE 7.2 Leaves and photosynthesis. The raw materials for photosynthesis are carbon dioxide and water. Water, which enters a leaf by way of leaf veins, and carbon dioxide, which enters by way of the stomata, diffuse into chloroplasts. Chloroplasts have two major parts. The grana are made up of thylakoids, which are membranous disks. Their membrane contains photosynthetic pigments such as chlorophylls *a* and *b*. These pigments absorb solar energy. The stroma is a semifluid interior where carbon dioxide is enzymatically reduced to a carbohydrate.

7.2 The Process of Photosynthesis

This overall equation can be used to represent the process of photosynthesis:

$$CO_2 + 2H_2O \xrightarrow{\text{solar energy}} (CH_2O) + H_2O + O_2$$

In this equation, (CH_2O) represents carbohydrate. If the equation were multiplied by six, the carbohydrate would be $C_6H_{12}O_6$, or glucose.

The overall equation shows that photosynthesis involves oxidation-reduction (redox) and the movement of electrons from one molecule to another. Recall that oxidation is the loss of electrons, and reduction is the gain of electrons. In living things, as discussed on page 112, the electrons are very often accompanied by hydrogen ions so that oxidation is the loss of hydrogen atoms $(H^+ + e^-)$, and reduction is the gain of hydrogen atoms. This simplified rewrite of the above equation makes it clear that carbon dioxide has been reduced, and water has been oxidized:

$$CO_2 + H_2O \xrightarrow{\text{solar energy}} (CH_2O) + O_2$$

Reduction: $CO_2 \rightarrow (CH_2O)$; Oxidation: $H_2O \rightarrow O_2$

It takes hydrogen atoms and also energy to reduce carbon dioxide. From our study of energy and enzymes in Chapter 6, you expect that solar energy will not be used directly during photosynthesis, and instead it will be converted to ATP molecules. ATP is the energy currency of cells and, when cells need something, they spend ATP. In this case, solar energy will be used to generate the ATP needed to reduce carbon dioxide to a carbohydrate. Of course, we always want to keep in mind that this carbohydrate represents the food produced by land plants, algae, and cyanobacteria that feeds the biosphere.

A review of page 112 will also lead you to suspect that the electrons needed to reduce carbon dioxide will be carried by a coenzyme. $NADP^+$ is the coenzyme of oxidation-reduction (redox coenzyme) active during photosynthesis. When $NADP^+$ is reduced, it has accepted two electrons and one hydrogen atom, and when it is oxidized, it gives up its electrons:

$$NADP^+ + 2\,e^- + H^+ \longrightarrow NADPH$$

What molecule supplies the electrons that reduce NADPH during photosynthesis? Put a sprig of *Elodea* in a beaker, and supply it with light, and you will observe a bubbling (Fig. 7.3). The bubbling occurs because the plant is releasing oxygen as it photosynthesizes. A very famous experiment performed by C. B. van Niel of Stanford University found that the oxygen given off by photosynthesizers comes from water. This was the first step toward discovering that water splits during photosynthesis. When water splits, oxygen is released and the hydrogen atoms $(H^+ + e^-)$ are taken up by NADPH. Later, NADH reduces carbon dioxide to a carbohydrate.

FIGURE 7.3
Photosynthesis releases oxygen.
Bubbling indicates that the aquatic plant *Elodea* releases O_2 gas when it photosynthesizes.

Van Niel performed two separate experiments. When an isotope of oxygen, ^{18}O, was a part of water, the O_2 given off by the plant contain ^{18}O. When ^{18}O was a part of carbon dioxide supplied to a plant, the O_2 given off by a plant did not contain the ^{18}O. Why not?

Two Sets of Reactions

Many investigators have contributed to our understanding of the overall equation of photosynthesis and to our current realization that photosynthesis consists of two separate sets of reactions. F. F. Blackman was the first to suggest, in 1905, that enzymes must be involved in the reduction of carbon dioxide to a carbohydrate and that, therefore, the process must consist of two separate sets of reactions. We will call the two sets of reactions the light reactions and the Calvin cycle reactions.

Light Reactions

The **light reactions** are so named because they only occur when solar energy is available (during daylight hours). The overall equation for photosynthesis gives no hint that the green pigment chlorophyll, present in thylakoid membranes, is largely responsible for absorbing the solar energy that drives photosynthesis. During the light reactions, solar energy energizes electrons that move down an electron transport chain (see Figure 6.12). As the electrons move down the chain, energy is released and captured for the production of ATP molecules. Energized electrons are also taken up by $NADP^+$, which becomes NADPH. This equation can be used to summarize the light reactions because, during the light reactions, solar energy is converted to chemical energy:

$$\text{solar energy} \longrightarrow \text{chemical energy (ATP, NADPH)}$$

Calvin Cycle Reactions

The **Calvin cycle reactions** are named for Melvin Calvin, who received a Nobel Prize for discovering the enzymatic reactions that reduce carbon dioxide to a carbohydrate in the stroma of chloroplast (Fig. 7.5). The enzymes that are able to speed the reduction of carbon dioxide during both day and night are located in the semifluid substance of the stroma.

During the Calvin cycle reactions, CO_2 is taken up and then reduced to a carbohydrate that can later be converted to glucose. This equation can be used to summarize the Calvin cycle reactions because, during these reactions, the ATP and NADPH formed during the light reactions are used to reduce carbon dioxide:

$$\underset{\text{(ATP, NADPH)}}{\text{chemical energy}} \longrightarrow \underset{\text{(carbohydrate)}}{\text{chemical energy}}$$

Summary

Figure 7.4 can be used to summarize our discussion so far. This figure shows that during the light reactions, (1) solar energy is absorbed, (2) water is split so that oxygen is released, and (3) ATP and NADPH are produced.

During the Calvin cycle reactions, (1) CO_2 is absorbed and (2) reduced to a carbohydrate (CH_2O) by utilizing ATP and NADPH from the light reactions (see bottom set of red arrows). The top set of red arrows takes ADP + Ⓟ and $NADP^+$ back to light reactions, where they become ATP and NADPH once more so that carbohydrate production can continue.

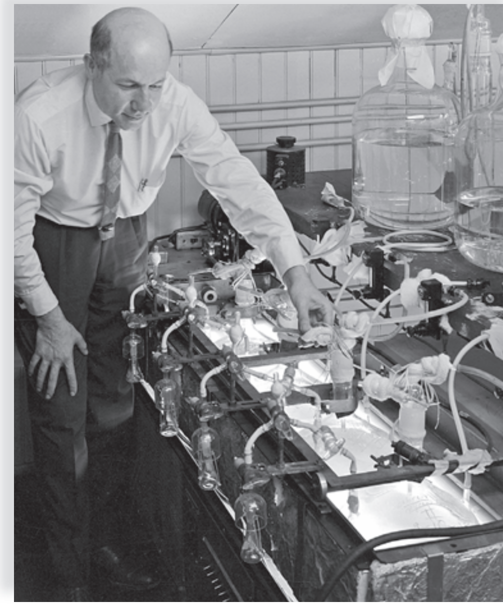


FIGURE 7.5 Melvin Calvin in the laboratory.

Melvin Calvin used tracers to discover the cycle of reactions that reduce CO_2 to a carbohydrate.

Check Your Progress 7.2

1. Show that the overall equation for photosynthesis is a redox reaction.
2. In general terms, describe the light reactions and the Calvin cycle reactions.

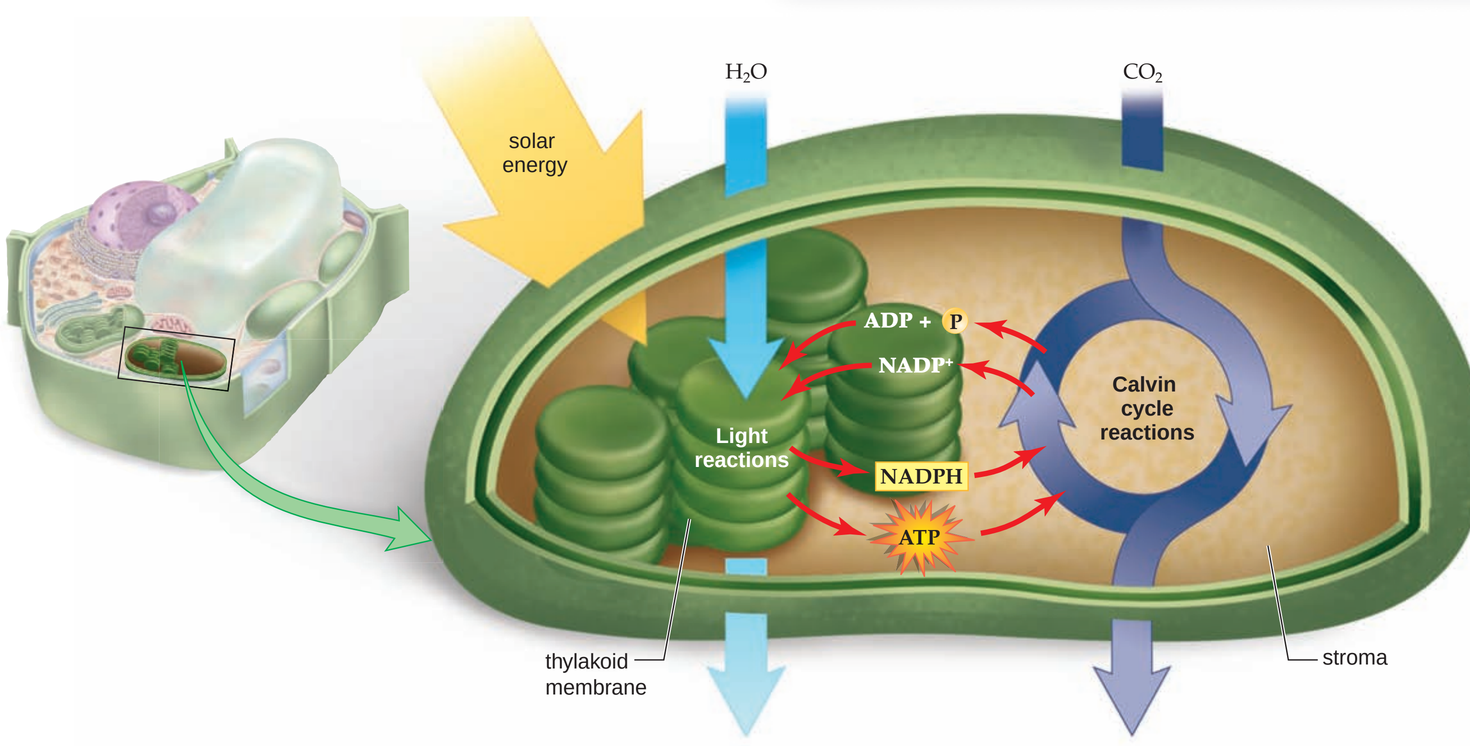


FIGURE 7.4 Overview of photosynthesis.

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

7.3 Plants as Solar Energy Converters

Solar energy can be described in terms of its wavelength and its energy content. Figure 7.6*a* lists the different types of radiant energy from the shortest wavelength, gamma rays, to the longest, radio waves. Most of the radiation reaching the Earth is within the visible-light range. Higher-energy wavelengths are screened out by the ozone layer in the atmosphere, and lower-energy wavelengths are screened out by water vapor and carbon dioxide before they reach the Earth's surface. The conclusion is, then, that organic molecules and processes within organisms, such as vision and photosynthesis, are chemically adapted to the radiation that is most prevalent in the environment—**visible light** (Fig. 7.6*a*).

Pigment molecules absorb wavelengths of light. Most pigments absorb only some wavelengths; they reflect or transmit the other wavelengths. The pigments found in chloroplasts are capable of absorbing various portions of visible light. This is called their **absorption spectrum.** Photosynthetic organisms differ by the type of chlorophyll they contain. In plants, chlorophyll *a* and chlorophyll *b* play prominent roles in photosynthesis. **Carotenoids** play an accessory role. Both chlorophylls *a* and *b* absorb violet, blue, and red light better than the light of other colors. Because green light is transmitted and reflected by chlorophyll, plant leaves appear green to us. The carotenoids, which are shades of yellow and orange, are able to absorb light in the violet-blue-green range. These pigments become noticeable in the fall when chlorophyll breaks down.

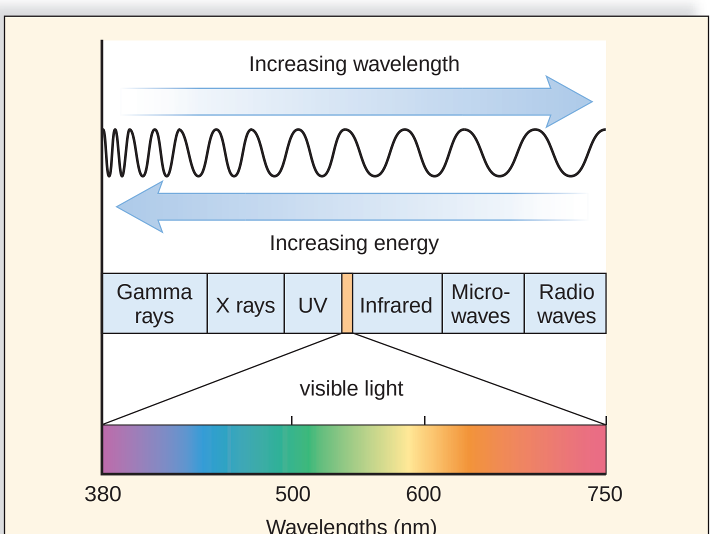
How do you determine the absorption spectrum of pigments? To identify the absorption spectrum of a particular pigment, a purified sample is exposed to different wavelengths of light inside an instrument called a spectrophotometer. A spectrophotometer measures the amount of light that passes through the sample, and from this it is possible to calculate how much was absorbed. The amount of light absorbed at each wavelength is plotted on a graph, and the result is a record of the pigment's absorption spectrum (Fig. 7.6*b*).

Light Reactions

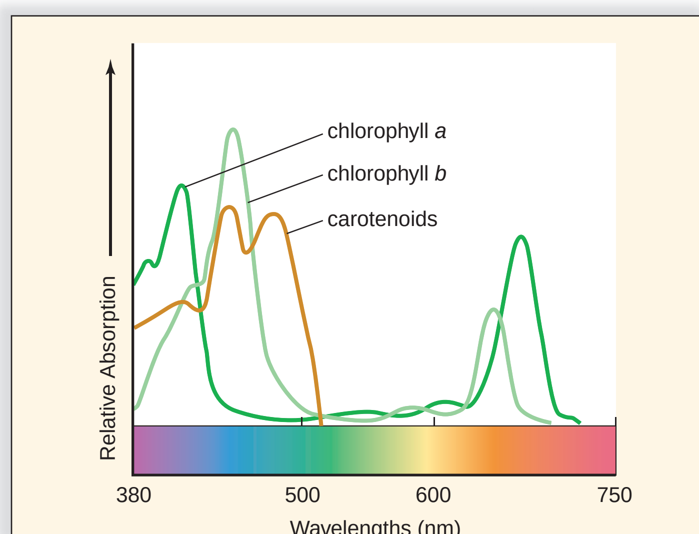
The light reactions utilize two photosystems, called photosystem I (PS I) and photosystem II (PS II). The photosystems are named for the order in which they were discovered, not for the order in which they occur in the thylakoid membrane or participate in the photosynthetic process. A **photosystem** consists of a pigment complex (molecules of chlorophyll *a*, chlorophyll *b*, and the carotenoids) and electron acceptor molecules within the thylakoid membrane. The pigment complex serves as an "antenna" for gathering solar energy.

Noncyclic Pathway

During the light reactions, electrons usually follow a **noncyclic pathway** that begins with photosystem II (Fig. 7.7). The pigment complex absorbs solar energy, which is then passed from one pigment to the other until it is concentrated in a particular pair of chlorophyll *a* molecules, called the *reaction center.* Electrons (e^-) in the reaction center become so energized that they escape from the reaction center and move to nearby electron acceptor molecules.



a. The electromagnetic spectrum includes visible light.



b. Absorption spectrum of photosynthetic pigments.

FIGURE 7.6 **Photosynthetic pigments and photosynthesis.**

a. The wavelengths in visible light differ according to energy content and color. **b.** The photosynthetic pigments in chlorophylls *a* and *b* and the carotenoids absorb certain wavelengths within visible light. This is their absorption spectrum.

PS II would disintegrate without replacement electrons, and these are removed from water, which splits, releasing oxygen to the atmosphere. Notice that with the loss of electrons, water has been oxidized, and that indeed, the oxygen released during photosynthesis does come from water. Many organisms, including plants and even ourselves, use this oxygen within their mitochondria. The hydrogen ions (H^+) stay in the thylakoid space and contribute to the formation of a hydrogen ion gradient.

An electron acceptor sends energized electrons, received from the reaction center, down an electron transport chain (ETC), a series of carriers that pass electrons from one to the other (see Fig. 6.13). As the electrons pass from one carrier to the next, energy is captured and stored in the form of a hydrogen ion (H^+) gradient. When these hydrogen ions flow down their electrochemical gradient through ATP synthase complexes, ATP production occurs (see page 124). Notice that this ATP will be used by the Calvin cycle reactions in the stroma to reduce carbon dioxide to a carbohydrate.

When the PS I pigment complex absorbs solar energy, energized electrons leave its reaction center and are captured by electron acceptors. (Low-energy electrons from the *electron transport chain* adjacent to PS II replace those lost by PS I.) The electron acceptors in PS I pass their electrons to $NADP^+$ molecules. Each one accepts two electrons and an H^+ to become a reduced form of the molecule, that is, NADPH. This NADPH will be used by the Calvin cycle reactions in the stroma to reduce carbon dioxide to a carbohydrate.

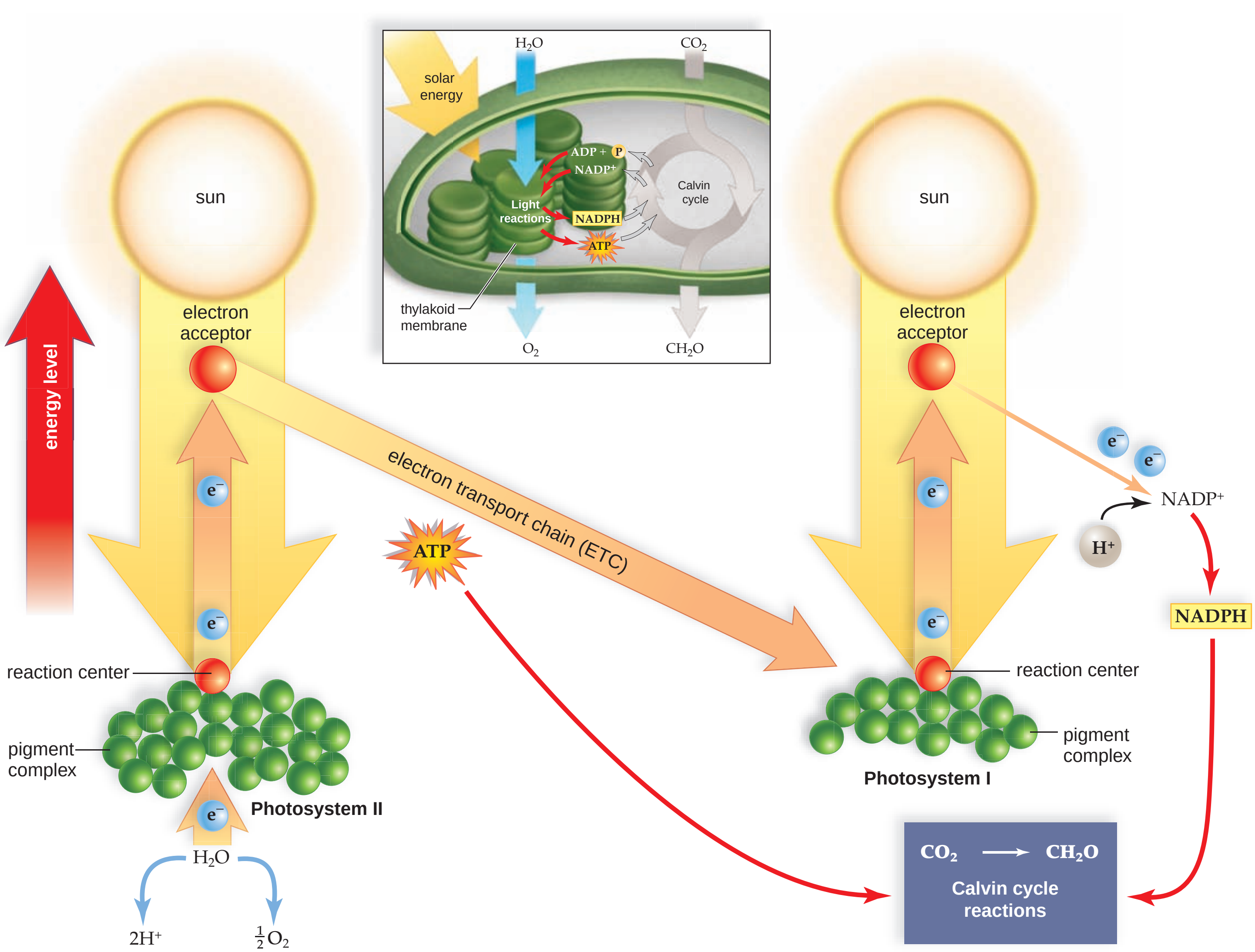


FIGURE 7.7 **Noncyclic pathway: Electrons move from water to $NADP^+$.**

Energized electrons (replaced from water, which splits, releasing oxygen) leave photosystem II and pass down an electron transport chain, leading to the formation of ATP. Energized electrons (replaced by photosystem II by way of the ETC) leave photosystem I and pass to $NADP^+$, which then combines with H^+, becoming NADPH.

The Organization of the Thylakoid Membrane

As we have discussed, the following molecular complexes are in the thylakoid membrane (Fig. 7.8):

PS II, which consists of a pigment complex and electron-acceptor molecules, receives electrons from water as water splits, releasing oxygen.

The electron transport chain (ETC), consisting of Pq (plastoquinone) and cytochrome complexes, carries electrons from PS II to PS I. Pq also pumps H^+ from the stroma into the thylakoid space.

PS I, which also consists of a pigment complex and electron-acceptor molecules, is adjacent to NADP reductase, which reduces $NADP^+$ to NADPH.

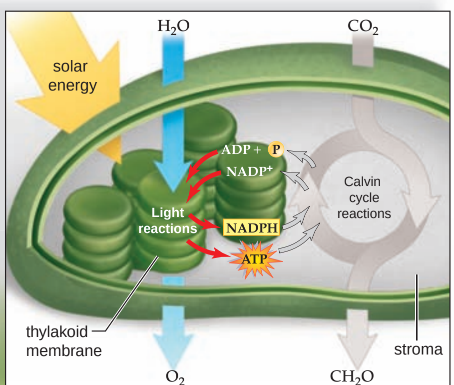
The ATP synthase complex has a channel and a protruding ATP synthase, an enzyme that joins ADP + Ⓟ.

ATP Production

The thylakoid space acts as a reservoir for hydrogen ions (H^+). First, each time water is oxidized, two H^+ remain in the thylakoid space. Second, as the electrons move from carrier to carrier along the electron transport chain, the electrons give up energy, which is used to pump H^+ from the stroma into the thylakoid space. Therefore, there are more H^+ in the thylakoid space than in the stroma. The flow of H^+ (often referred to as protons in this context) from high to low concentration provides kinetic energy that allows an **ATP synthase complex** enzyme to enzymatically produce ATP from ADP + Ⓟ. This method of producing ATP is called **chemiosmosis** because ATP production is tied to the establishment of an H^+ gradient (see Fig. 6.13).

Check Your Progress 7.3

1. What part of the electromagnetic spectrum is utilized for photosynthesis?
2. What two molecules are produced as a result of the noncyclic electron pathway of the light reactions?



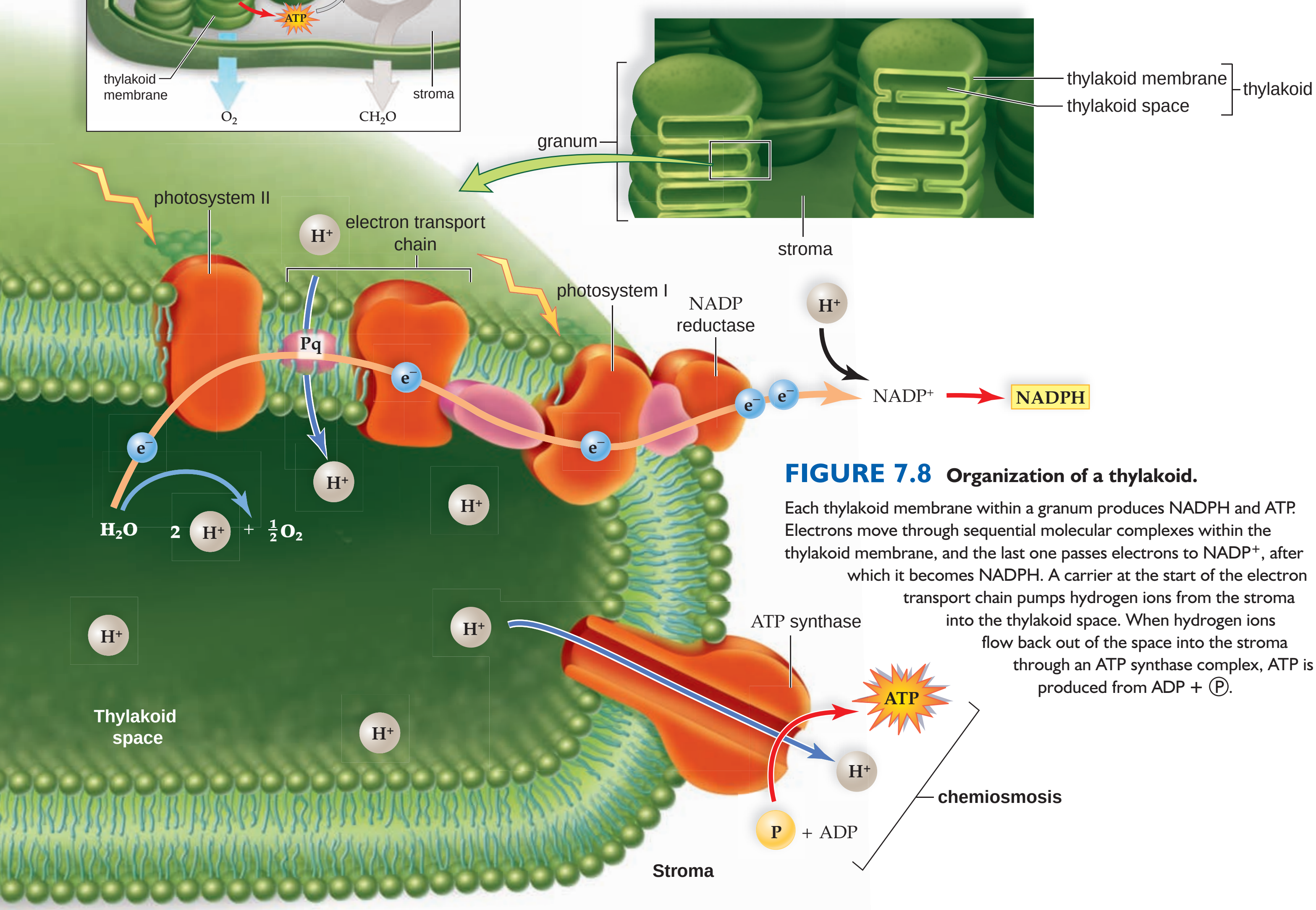


FIGURE 7.8 Organization of a thylakoid.

Each thylakoid membrane within a granum produces NADPH and ATP. Electrons move through sequential molecular complexes within the thylakoid membrane, and the last one passes electrons to $NADP^+$, after which it becomes NADPH. A carrier at the start of the electron transport chain pumps hydrogen ions from the stroma into the thylakoid space. When hydrogen ions flow back out of the space into the stroma through an ATP synthase complex, ATP is produced from ADP + Ⓟ.

ecology focus

Tropical Rain Forest Destruction and Global Warming

Al Gore, former presidential candidate, won the 2007 Nobel Peace Prize for raising public awareness concerning global warming. The Nobel Committee said that "global warming could induce large-scale migrations and lead to greater competition for the Earth's resources. As such, it may increase the danger of violent conflicts and wars, within and between countries." **Global warming** refers to an expected rise in the average global temperature during the twenty-first century due to the introduction of certain gases into the atmosphere. For at least a thousand years prior to 1850, atmospheric carbon dioxide (CO_2) levels remained fairly constant at 0.028%. Since the 1850s, when industrialization began, the amount of CO_2 in the atmosphere has increased to 0.038% (Fig. 7A*a*).

Role of Carbon Dioxide

In much the same way as the panes of a greenhouse, CO_2 and other gases in our atmosphere trap radiant heat from the sun. Therefore, these gases are called greenhouse gases. Without any greenhouse gases, the Earth's temperature would be about 33°C cooler than it is now. Likewise, increasing the concentration of greenhouse gases is predicted to cause global warming.

Certainly, the burning of fossil fuels adds CO_2 to the atmosphere. But another factor that contributes to an increase in atmospheric CO_2 is tropical rain forest destruction.

Role of Tropical Rain Forests

Between 10 and 30 million hectares of rain forests are lost every year to ranching, logging, mining, and otherwise developing areas of the forest for human needs. The clearing of forests often involves burning them (Fig. 7A*b*). Each year, deforestation in tropical rain forests accounts for 20–30% of all CO_2 in the atmosphere. The consequence of burning forests is greater trouble for global warming because burning a forest adds CO_2 to the atmosphere and, at the same time, removes trees that would ordinarily absorb CO_2.

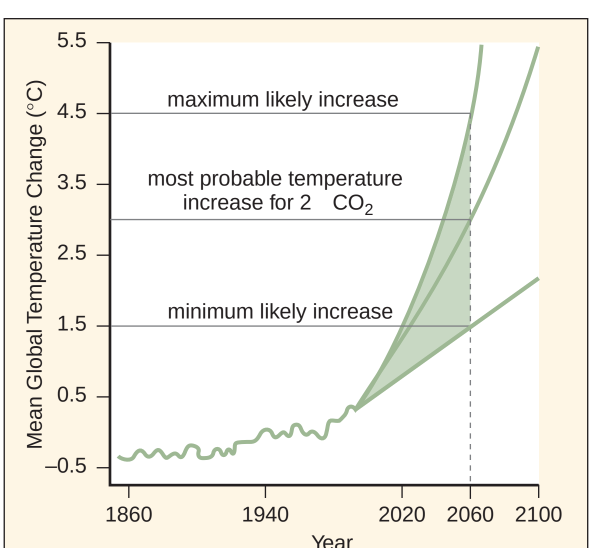
The Argument for Preserving Forests

The process of photosynthesis and also the oceans act as a sink for CO_2. Despite their reduction in size from an original 14% to 6% of land surface today, tropical rain forests make a substantial contribution to global CO_2 removal. Taking into account all ecosystems, marine and terrestrial, photosynthesis produces organic matter that is 300 to 600 times the mass of people currently on Earth this year. Tropical rain forests contribute greatly to the uptake of CO_2 and the productivity of photosynthesis because they are the most efficient of all terrestrial ecosystems.

Tropical rain forests occur near the equator. They can exist wherever temperatures are above 26°C and rainfall is heavy (from 100–200 cm) and regular. Huge trees with buttressed trunks and broad, undivided, dark-green leaves predominate. Nearly all land plants in a tropical rain forest are woody, and woody vines are also abundant.

It might be hypothesized that an increased amount of CO_2 in the atmosphere will cause photosynthesis to increase in the remaining portion of the forest. To study this possibility, investigators measured atmospheric CO_2 levels, daily temperature levels, and tree girth in La Selva, Costa Rica, for 16 years. The data collected demonstrated relatively lower forest productivity at higher temperatures. These findings suggest that, as temperatures rise, tropical rain forests may add to ongoing atmospheric CO_2 accumulation and accelerated global warming rather than the reverse. All the more reason to slow global warming and preserve forests.

Some countries have programs to combat the problem of deforestation. In the mid-1970s, Costa Rica established a system of national parks and reserves to protect 12% of the country's land area from degradation. The current Costa Rican government wants to expand the goal by increasing protected areas to 25% in the near future. Similar efforts in other countries may help slow the ever-increasing threat of global warming.



a.

b.

FIGURE 7A Global warming.
a. *Mean global temperature change is expected to rise due to the introduction of greenhouse gases into the atmosphere.* ***b.*** *The burning of tropical rain forests adds* CO_2 *to the atmosphere and at the same time removes a sink for* CO_2*.*

7.4 Calvin Cycle Reactions

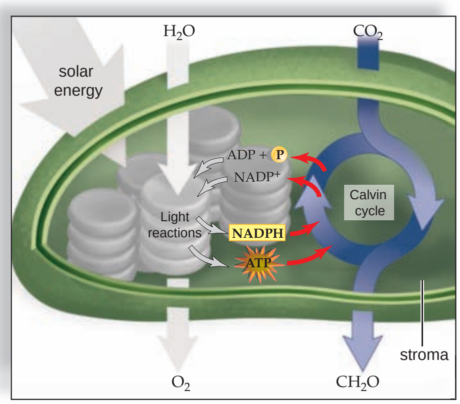
The Calvin cycle reactions occur after the light reactions. The Calvin cycle is a series of reactions that produce carbohydrate before returning to the starting point once more (Fig. 7.9). The cycle is named for Melvin Calvin, who, with colleagues, used the radioactive isotope ^{14}C as a tracer to discover the reactions making up the cycle.

This series of reactions uses carbon dioxide from the atmosphere to produce carbohydrate. How does carbon dioxide get into the atmosphere? We and most other organisms take in oxygen from the atmosphere and release carbon dioxide to the atmosphere. The Calvin cycle includes (1) carbon dioxide fixation, (2) carbon dioxide reduction, and (3) regeneration of RuBP (ribulose-1,5-bisphosphate).

Fixation of Carbon Dioxide

Carbon dioxide (CO_2) fixation is the first step of the Calvin cycle. During this reaction, carbon dioxide from the atmosphere is attached to RuBP, a 5-carbon molecule. The result is one 6-carbon molecule, which splits into two 3-carbon molecules.

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



Metabolites of the Calvin Cycle

RuBP	ribulose-1,5-bisphosphate
3PG	3-phosphoglycerate
BPG	1,3-bisphosphoglycerate
G3P	glyceraldehyde-3-phosphate

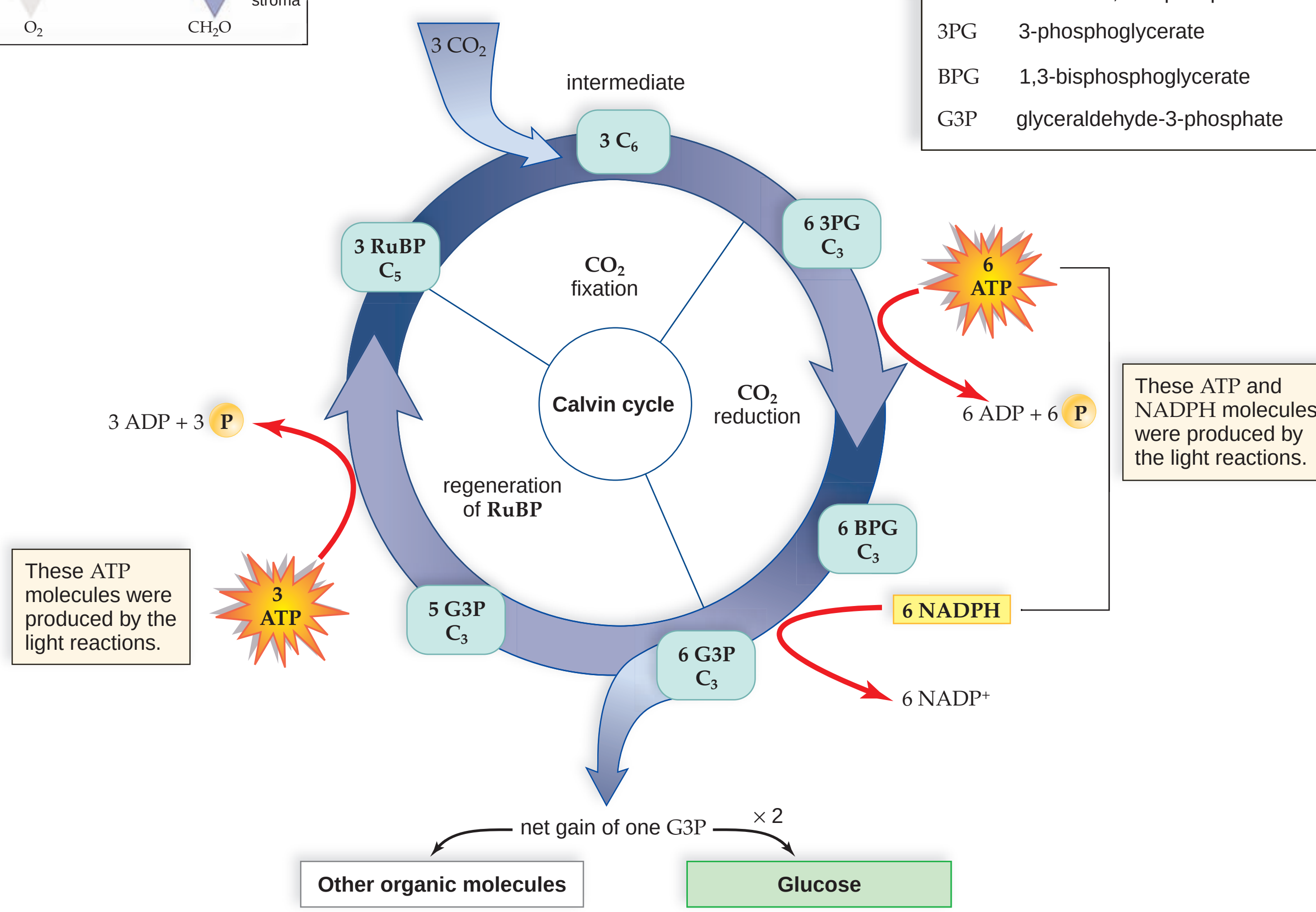
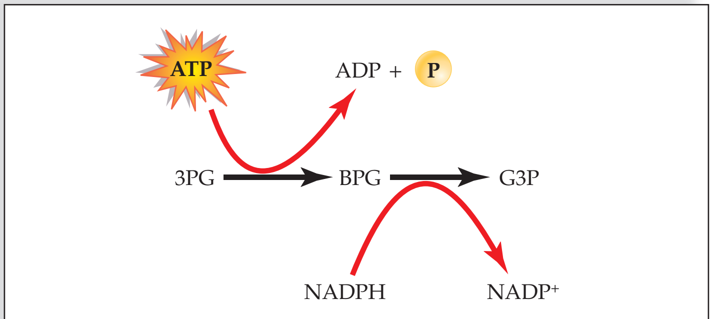


FIGURE 7.9 The Calvin cycle reactions.

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

Reduction of Carbon Dioxide

The first 3-carbon molecule in the Calvin cycle is called 3PG (3-phosphoglycerate). Each of two 3PG molecules undergoes reduction to G3P in two steps:

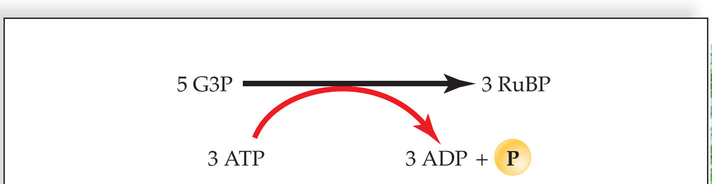


As 3PG becomes G3P, ATP becomes ADP + P, and NADPH becomes $NADP^+$.

This is the sequence of reactions that uses some ATP and NADPH from the light reactions. This sequence signifies the reduction of carbon dioxide to a carbohydrate because R—CO_2 has become R—CH_2O. Energy and electrons are needed for this reduction reaction, and these are supplied by ATP and NADPH.

Regeneration of RuBP

Notice that the Calvin cycle reactions in Figure 7.9 are multiplied by three because it takes three turns of the Calvin cycle to allow one G3P to exit. Why? Because, for every three turns of the Calvin cycle, five molecules of G3P are used to re-form three molecules of RuBP and the cycle continues. Notice that 5×3 (carbons in G3P) = 3×5 (carbons in RuBP):



As five molecules of G3P become three molecules of RuBP, three molecules of ATP become three molecules of ADP + P.

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

The Importance of the Calvin Cycle

G3P (glyceraldehyde-3-phosphate) is the product of the Calvin cycle that can be converted to other molecules a plant needs. Notice that glucose phosphate is among the organic molecules that result from G3P metabolism (Fig. 7.10). This is of interest to us because glucose is the molecule that plants and animals most often metabolize to produce the ATP molecules they require for their energy needs.

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

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

A plant can use the hydrocarbon skeleton of G3P to form fatty acids and glycerol, which are combined in plant oils. We are all familiar with corn oil, sunflower oil, or olive oil used in cooking. Also, when nitrogen is added to the hydrocarbon skeleton derived from G3P, amino acids are formed.

Check Your Progress 7.4

1. What are three major steps of the Calvin cycle?
2. List the substances that a plant cell can make from G3P, the product of the Calvin cycle.

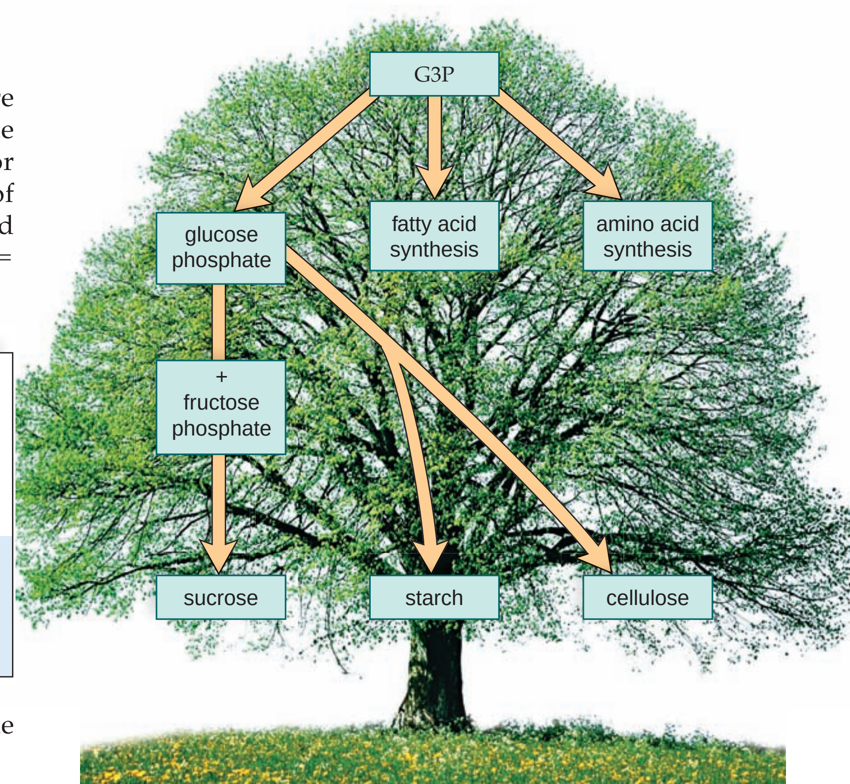


FIGURE 7.10 Fate of G3P.

G3P is the first reactant in a number of plant cell metabolic pathways. Two G3Ps are needed to form glucose phosphate; glucose is often considered the end product of photosynthesis. Sucrose is the transport sugar in plants; starch is the storage form of glucose; and cellulose is a major constituent of plant cell walls.

7.5 Other Types of Photosynthesis

The majority of land plants such as azaleas, maples, and tulips carry on photosynthesis as described and are called **C_3 plants** (Fig. 7.11*a*). C_3 plants use the enzyme RuBP carboxylase to fix CO_2 to RuBP in mesophyll cells. The first detected molecule following fixation is the 3-carbon molecule 3PG:

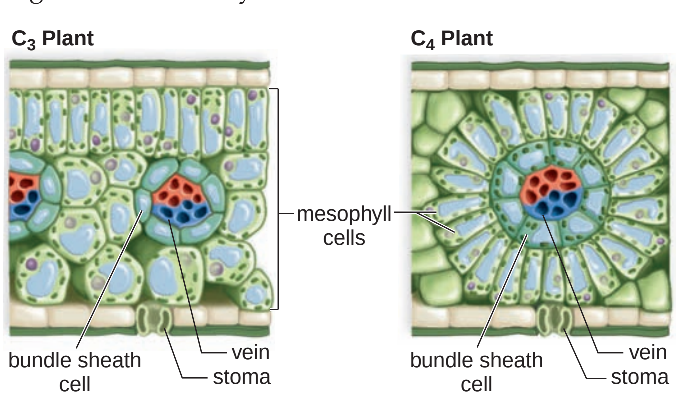
$$\text{RuBP} + CO_2 \xrightarrow{\text{RuBP carboxylase}} 2\ \text{3PG}$$

As shown in Figure 7.2, leaves have small openings called stomata through which water can leave and carbon dioxide (CO_2) can enter. If the weather is hot and dry, the stomata close, conserving water. (Water loss might cause the plant to wilt and die.) Now the concentration of CO_2 decreases in leaves, while O_2, a by-product of photosynthesis, increases. When O_2 rises in C_3 plants, RuBP carboxylase combines it with RuBP instead of CO_2. The result is one molecule of 3PG and the eventual release of CO_2. This is called **photorespiration** because in the presence of light *(photo)*, oxygen is taken up and CO_2 is released *(respiration)*.

An adaptation called C_4 photosynthesis enables some plants to avoid photorespiration.

C_4 Photosynthesis

In a C_3 plant, the mesophyll cells contain well-formed chloroplasts and are arranged in parallel layers. In a C_4 leaf, the bundle sheath cells, as well as the mesophyll cells, contain chloroplasts. Further, the mesophyll cells are arranged concentrically around the bundle sheath cells:

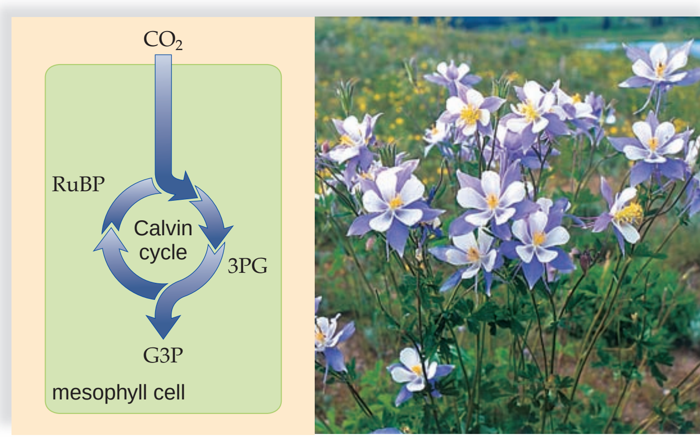


C_4 plants use the enzyme PEP carboxylase (PEPCase) to fix CO_2 to PEP (phosphoenolpyruvate, a C_3 molecule). The result is oxaloacetate, a C_4 molecule:

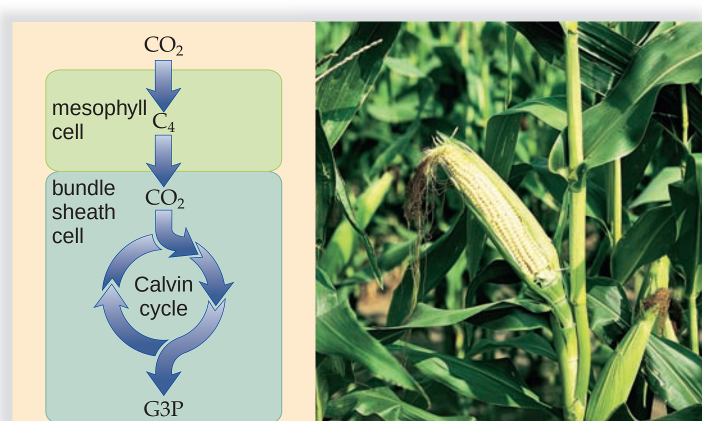
$$\text{PEP} + CO_2 \xrightarrow{\text{PEPCase}} \text{oxaloacetate}$$

In a C_4 plant, CO_2 is taken up in mesophyll cells, and then malate, a reduced form of oxaloacetate, is pumped into the bundle sheath cells (Fig. 7.11*b*). Here, and only here, does CO_2 enter the Calvin cycle. It takes energy to pump molecules, and you would think that the C_4 pathway would be disadvantageous. Yet in hot, dry climates, the net photosynthetic rate of C_4 plants such as sugarcane, corn, and Bermuda grass is about two to three times that of C_3 plants such as wheat, rice, and oats. Why do C_4 plants enjoy such an advantage? The answer is that they can avoid photorespiration, discussed previously. Photorespiration is wasteful because it is not part of the Calvin cycle. Photorespiration does not occur in C_4 leaves because PEPCase, unlike RuBP carboxylase, does not combine with O_2. Even when stomata are closed, CO_2 is delivered to the Calvin cycle in the bundle sheath cells.

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



a. CO_2 fixation in a C_3 plant, blue columbine, *Aquilegia caerulea*



b. CO_2 fixation in a C_4 plant, corn, *Zea mays*

FIGURE 7.11 Carbon dioxide fixation in C_3 and C_4 plants.

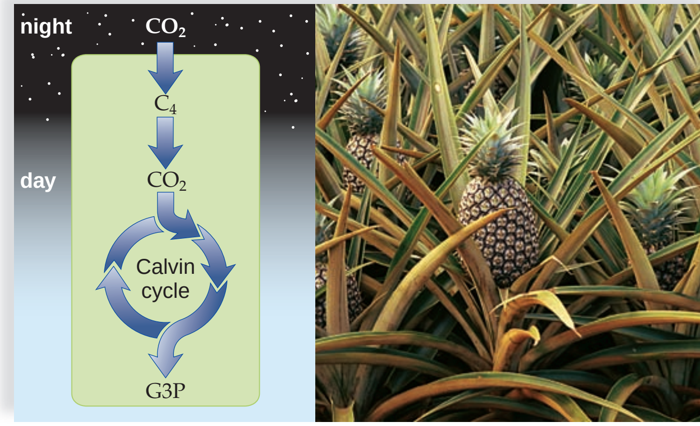
a. In C_3 plants, CO_2 is taken up by the Calvin cycle directly in mesophyll cells. **b.** C_4 plants form a C_4 molecule in mesophyll cells prior to releasing CO_2 to the Calvin cycle in bundle sheath cells.

CAM Photosynthesis

CAM stands for crassulacean-acid metabolism; the Crassulaceae is a family of flowering succulent (water-containing) plants that live in warm, dry regions of the world. CAM was first discovered in these plants, but now it is known to be prevalent among other groups of plants.

Whereas a C_4 plant represents partitioning in space—carbon dioxide fixation occurs in mesophyll cells and the Calvin cycle occurs in bundle sheath cells—CAM is partitioning by the use of time. During the night, CAM plants use PEPCase to fix some CO_2, forming C_4 molecules, which are stored in large vacuoles in mesophyll cells. During the day, C_4 molecules (malate) release CO_2 to the Calvin cycle when NADPH and ATP are available from the light reactions (Fig. 7.12). The primary advantage for this partitioning again has to do with the conservation of water. CAM plants open their stomata only at night, and therefore only at that time does atmospheric CO_2 enter the plant. During the day, the stomata close; this conserves water, but CO_2 cannot enter the plant.

Photosynthesis in a CAM plant is minimal because a limited amount of CO_2 is fixed at night, but it does allow CAM plants to live under stressful conditions.



CO_2 fixation in a CAM plant, pineapple, *Ananas comosus*

FIGURE 7.12 Carbon dioxide fixation in a CAM plant. CAM plants, such as pineapple, fix CO_2 at night, forming a C_4 molecule that is released to the Calvin cycle during the day.

Photosynthesis and Adaptation to the Environment

The different types of photosynthesis give us an opportunity to consider that organisms are metabolically adapted to their environment. Each method of photosynthesis has its advantages and disadvantages, depending on the climate.

C_4 plants most likely evolved in, and are adapted to, areas of high light intensities, high temperatures, and limited rainfall. C_4 plants, however, are more sensitive to cold, and C_3 plants do better than C_4 plants below 25°C. CAM plants, on the other hand, compete well with either type of plant when the environment is extremely arid. Surprisingly, CAM is quite widespread and has evolved in 23 families of flowering plants, including some lilies and orchids! And it is found among nonflowering plants, including some ferns and cone-bearing trees.

Check Your Progress 7.5

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

Connecting the Concepts

"Have You Thanked a Green Plant Today?" is a bumper sticker that you may have puzzled over until now. Plants, you now know, capture solar energy and store it in carbon-based organic nutrients that are passed to other organisms when they feed on plants and/or on other organisms. In this context, plants are called autotrophs because they make their own organic food. Heterotrophs are organisms that take in preformed organic food.

The next chapter considers cellular respiration, the process that produces ATP molecules. We have to keep in mind that cells cannot create energy, and therefore when we say that the cell produces ATP, we mean that it converts the energy within glucose molecules to that found in ATP molecules, with a loss of heat, of course. Why do cells carry out this wasteful process? Because ATP is the energy currency of cells and is able to contribute energy to many different cellular processes and reactions.

In the carbon cycle, living and dead organisms contain organic carbon and serve as a reservoir of carbon. Some 300 million years ago, a host of plants died and did not decompose. These plants were compressed to form the coal that we mine and burn today. (Oil has a similar origin, but it most likely formed in marine sedimentary rocks that included animal remains.)

The amount of carbon dioxide in the atmosphere is increasing steadily, in part because we humans burn fossil fuels to run our modern industrial society. This buildup of carbon dioxide will contribute to global warming. Autotrophs such as plants take in carbon dioxide when they photosynthesize. Carbon dioxide is returned to the atmosphere when autotrophs and heterotrophs carry on cellular respiration. In this way, the very same carbon atoms cycle from the atmosphere to autotrophs, then to heterotrophs, and then back to autotrophs again. Energy does not cycle, and therefore all life is dependent on the ability of plants to capture solar energy and produce carbohydrate molecules.

summary

7.1 Photosynthetic Organisms

Photosynthesis produces carbohydrates and releases oxygen, both of which are used by the majority of living things. Cyanobacteria, algae, and land plants carry on photosynthesis. In plants, photosynthesis takes place in chloroplasts. A chloroplast is bounded by a double membrane and contains two main components: the semifluid stroma and the membranous grana made up of thylakoids.

7.2 The Process of Photosynthesis

The overall equation for photosynthesis shows that it is a redox reaction. Carbon dioxide is reduced, and water is oxidized. During photosynthesis, the light reactions take place in the thylakoid membranes, and the Calvin cycle reactions take place in the stroma.

7.3 Plants as Solar Energy Converters

Photosynthesis uses solar energy in the visible-light range. Specifically, chlorophylls *a* and *b* absorb violet, blue, and red wavelengths best. This causes chlorophyll to appear green to us. The carotenoids absorb light in the violet-blue-green range and are yellow to orange pigments.

The noncyclic electron pathway of the light reactions begins when solar energy enters PS II. In PS II, energized electrons are picked up by electron acceptors. The oxidation (splitting) of water replaces these electrons in the reaction-center chlorophyll *a* molecules. Oxygen is released to the atmosphere, and hydrogen ions (H^+) remain in the thylakoid space. An electron acceptor molecule passes electrons to PS I by way of an electron transport chain. When solar energy is absorbed by PS I, energized electrons leave and are ultimately received by $NADP^+$, which also combines with H^+ from the stroma to become NADPH.

Chemiosmosis requires an organized membrane. The thylakoid membrane is highly organized: PS II is associated with an enzyme that oxidizes (splits) water, the cytochrome complexes transport electrons and pump H^+; PS I is associated with an enzyme that reduces $NADP^+$, and ATP synthase produces ATP.

The energy made available by the passage of electrons down the electron transport chain allows carriers to pump H^+ into the thylakoid space. The buildup of H^+ establishes an electrochemical gradient. When H^+ flows down this gradient through the channel present in ATP synthase complexes, ATP is synthesized from ADP and Ⓟ by ATP synthase. This method of producing ATP is called chemiosmosis.

7.4 Calvin Cycle Reactions

The energy yield of the light reactions is stored in ATP and NADPH. These molecules are used by the Calvin cycle reactions to reduce CO_2 to carbohydrate, namely G3P, which is then converted to all the organic molecules a plant needs.

During the first stage of the Calvin cycle, the enzyme RuBP carboxylase fixes CO_2 to RuBP, producing a 6-carbon molecule that immediately breaks down to two C_3 molecules. During the second stage, CO_2 (incorporated into an organic molecule) is reduced to carbohydrate (CH_2O). This step requires the NADPH and some of the ATP from the light reactions. For every three turns of the Calvin cycle, the net gain is one G3P molecule; the other five G3P molecules are used to re-form three molecules of RuBP. This step also requires ATP for energy. It takes two G3P molecules to make one glucose molecule.

7.5 Other Types of Photosynthesis

In C_4 plants, as opposed to the C_3 plants just described, the enzyme PEPCase fixes carbon dioxide to PEP to form a 4-carbon molecule, oxaloacetate, within mesophyll cells. A reduced form of this molecule is pumped into bundle sheath cells, where CO_2 is released to the Calvin cycle. PEPCase has an advantage over RuBP carboxylase because RuBP carboxylase, but not PEPCase, combines O_2 with RuBP instead of CO_2 when the stomata close and the concentration of O_2 rises. C_4 plants avoid this complication by a partitioning of pathways in space. Carbon dioxide fixation occurs utilizing PEPCase in mesophyll cells, and the Calvin cycle occurs in bundle sheath cells.

In CAM plants, the stomata are open only at night, conserving water. PEPCase fixes CO_2 to PEP only at night, and the next day, CO_2 is released and enters the Calvin cycle within the same cells. This represents a partitioning of pathways in time: Carbon dioxide fixation occurs at night, and the Calvin cycle occurs during the day. CAM was discovered in desert plants, but since then it has been discovered in many different types of plants.

understanding the terms

absorption spectrum 122
ATP synthase complex 124
autotroph 118
C_3 plant 128
C_4 plant 128
Calvin cycle reactions 121
CAM 129
carbon dioxide (CO_2) fixation 126
carotenoid 122
chemiosmosis 124
chlorophyll 119
chloroplast 119
global warming 125
grana (sing., granum) 119
heterotroph 118
light reactions 120
noncyclic pathway 122
photorespiration 128
photosynthesis 118
photosystem 122
RuBP carboxylase 126
stomata 119
stroma 119
thylakoid 119
visible light 122

Match the terms to these definitions:

a. ______________ Energy-capturing portion of photosynthesis that takes place in thylakoid membranes of chloroplasts and cannot proceed without solar energy; it produces ATP and NADPH.

b. ______________ Photosynthetic unit where solar energy is absorbed and high-energy electrons are generated; contains an antenna complex and an electron acceptor.

c. ______________ Process usually occurring within chloroplasts, whereby chlorophyll traps solar energy and carbon dioxide is reduced to a carbohydrate.

d. ______________ Series of photosynthetic reactions in which carbon dioxide is fixed and reduced to G3P.

reviewing this chapter

1. Why is it proper to say that almost all living things are dependent on solar energy? 118
2. Name the two major components of chloroplasts, and associate each with one of two sets of reactions that occur during photosynthesis. How are the two sets of reactions related? 119–21
3. Write the overall equation of photosynthesis and associate each participant with either the light reactions or the Calvin cycle reactions. 120–21
4. Discuss the electromagnetic spectrum and the combined absorption spectrum of chlorophylls *a* and *b* and the carotenoids. Why is chlorophyll a green pigment, and the carotenoids a yellow-orange pigment? 122
5. Trace the noncyclic electron pathway, naming and explaining all the events that occur as the electrons move from water to $NADP^+$. 122–23

6. How is the thylakoid membrane organized? Name the main complexes in the membrane. Give a function for each. 124
7. Explain what is meant by chemiosmosis, and relate this process to the electron transport chain present in the thylakoid membrane. 124
8. Describe the three stages of the Calvin cycle. Which stage uses the ATP and NADPH from the light reactions? 126–27
9. Compare C_3 and C_4 photosynthesis, contrasting the actions of RuBP carboxylase and PEPCase. 128–29
10. Explain CAM photosynthesis, contrasting it to C_4 photosynthesis in terms of partitioning a pathway. 129

testing yourself

Choose the best answer for each question.

1. The absorption spectrum of chlorophyll
   a. is not the same as that of carotenoids.
   b. approximates the action spectrum of photosynthesis.
   c. explains why chlorophyll is a green pigment.
   d. shows that some colors of light are absorbed more than others.
   e. All of these are correct.
2. The final acceptor of electrons during the noncyclic electron pathway is
   a. PS I.
   b. PS II.
   c. ATP.
   d. $NADP^+$.
   e. water.
3. A photosystem contains
   a. pigments, a reaction center, and electron acceptors.
   b. ADP, Ⓟ, and hydrogen ions (H^+).
   c. protons, photons, and pigments.
   d. cytochromes only.
   e. Both b and c are correct.

For questions 4–8, match each item to those in the key. Use an answer more than once, if possible.

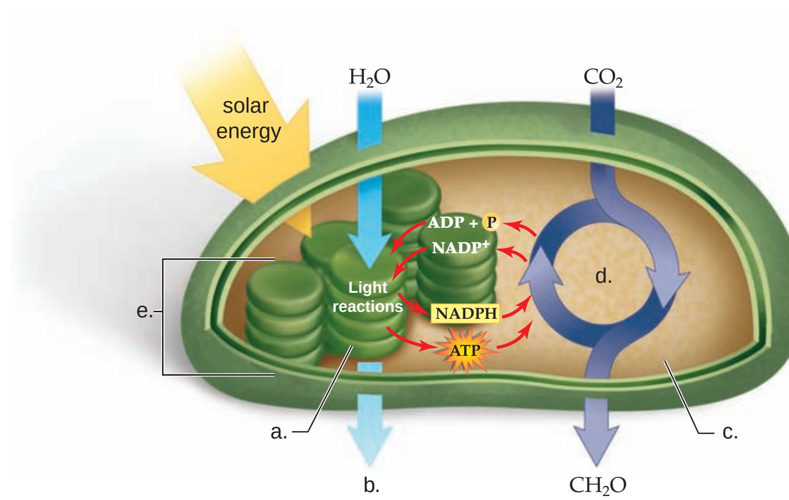
KEY:

a. solar energy
b. chlorophyll
c. chemiosmosis
d. Calvin cycle

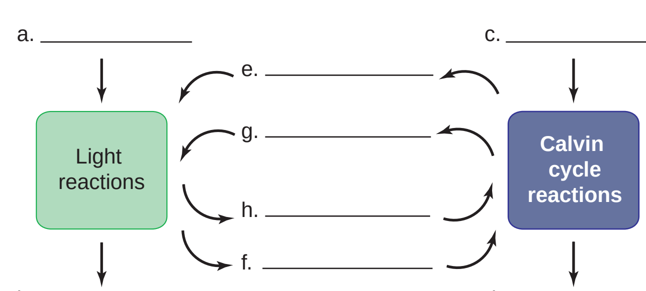
4. light energy
5. ATP synthase
6. thylakoid membrane
7. green pigment
8. RuBP

For questions 9–11, indicate whether the statement is true (T) or false (F).

9. RuBP carboxylase is the enzyme that fixes carbon dioxide to RuBP in the Calvin cycle. ________
10. When 3PG becomes G3P during the light reactions, carbon dioxide is reduced to carbohydrate. ________
11. NADPH and ATP cycle between the Calvin cycle and the light reactions constantly. ________
12. The NADPH and ATP from the light reactions are used to
    a. split water.
    b. cause RuBP carboxylase to fix CO_2.
    c. re-form the photosystems.
    d. cause electrons to move along their pathways.
    e. convert 3PG to G3P.
13. Chemiosmosis
    a. depends on complexes in the thylakoid membrane.
    b. depends on an electrochemical gradient.
    c. depends on a difference in H^+ concentration between the thylakoid space and the stroma.
    d. results in ATP formation.
    e. All of these are correct.
14. The function of the light reactions is to
    a. obtain CO_2.
    b. make carbohydrate.
    c. convert light energy into a usable form of chemical energy.
    d. regenerate RuBP.
15. Label the following diagram of a chloroplast:



    f. The light reactions occur in which part of a chloroplast?
    g. The Calvin cycle reactions occur in which part of a chloroplast?
16. The oxygen given off by photosynthesis comes from
    a. H_2O.
    b. CO_2.
    c. glucose.
    d. RuBP.
17. Label the following diagram using these labels: water, carbohydrate, carbon dioxide, oxygen, ATP, ADP + Ⓟ, NADPH, and $NADP^+$.

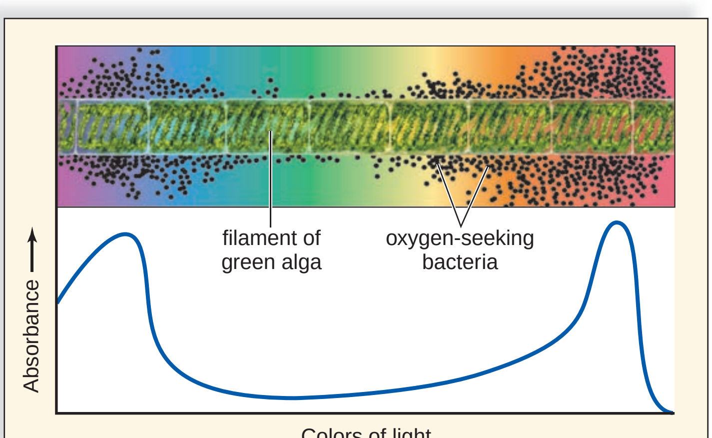


18. The glucose formed by photosynthesis can be used by plants to make
    a. starch.
    b. cellulose.
    c. lipids and oils.
    d. proteins.
    e. All of these are correct.

19. The Calvin cycle reactions
    a. produce carbohydrate.
    b. convert one form of chemical energy into a different form of chemical energy.
    c. regenerate more RuBP.
    d. use the products of the light reactions.
    e. All of these are correct.
20. CAM photosynthesis
    a. is the same as C_4 photosynthesis.
    b. is an adaptation to cold environments in the Southern Hemisphere.
    c. is prevalent in desert plants that close their stomata during the day.
    d. occurs in plants that live in marshy areas.
    e. stands for chloroplasts and mitochondria.
21. Compared to RuBP carboxylase, PEPCase has the advantage that
    a. PEPCase is present in both mesophyll and bundle sheath cells, but RuBP carboxylase is not.
    b. RuBP carboxylase fixes carbon dioxide (CO_2) only in C_4 plants, but PEPCase does it in both C_3 and C_4 plants.
    c. RuBP carboxylase combines with O_2, but PEPCase does not.
    d. PEPCase conserves energy, but RuBP carboxylase does not.
    e. Both b and c are correct.
22. C_4 photosynthesis
    a. is the same as C_3 photosynthesis because it takes place in chloroplasts.
    b. occurs in plants whose bundle sheath cells contain chloroplasts.
    c. takes place in plants such as wheat, rice, and oats.
    d. is an advantage when the weather is hot and dry.
    e. Both b and d are correct.

thinking scientifically

1. In 1882, T. W. Engelmann carried out an ingenious experiment to demostrate that chlorophyll absorbs light in the blue and red portions of the spectrum. He placed a single filament of a green alga in a drop of water on a microscope slide. Then he passed light through a prism and onto the string of algal cells. The slide also contained aerobic bacterial cells. After some time, he peered into the microscope and saw the bacteria clustered around the regions of the algal filament that were receiving blue light and red light, as shown in the illustration. Why do you suppose the bacterial cells were clustered in this manner?



2. In the fall of the year, the leaves of many trees change from green to red or yellow. Two hypotheses can explain this color change: (**a**) In the fall, chlorophyll degenerates, and red or yellow pigments that were earlier masked by chlorophyll become apparent. (**b**) In the fall, red or yellow pigments are synthesized, and they mask the color of chlorophyll. How could you test these two hypotheses?

bioethical issue

The World's Food Supply

The Food and Agriculture Organization of the United Nations warns that the world's food supply is dwindling rapidly and food prices are soaring to historic levels. Their records show that the reserves of cereals are severely depleted, and presently only 12 weeks of the world's total consumption is stored, which is much less than the average of 18 weeks' consumption in storage during the years 2000–2005. Only 8 weeks of corn are in storage compared to 11 weeks during this same time period.

Various reasons are offered for a possible calamitous shortfall in the world's grain supplies in the near future. Possible causes are an ever larger world population, water shortages, climate change, and the growing costs of fertilizer. Also of concern is the converting of corn into ethanol because of possible huge profits.

There are apparently no quick fixes to boost supplies. In years past, newly-developed hybrid crops led to enormous increases in yield per acre, but they also caused pollution problems that degrade the environment. Even if the promised biotech advances in drought-, cold-, and disease-resistant crops are made, they will not immediately boost food supplies. Possible solutions have been offered. Rather than exporting food to needy countries, it may be better to improve their ability to grow their own food, especially when you consider that transportation costs are soaring. Also, it would be beneficial to achieve zero population growth as quickly as possible and use renewable energy supplies other than converting corn to ethanol. The use of ethanol only contributes to global warming, which is expected to be a contributing factor to producing less grain. What do you think should be done to solve the expected shortage in the world's food supply, and how should your solution be brought about?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

8

Cellular Respiration

a bacterium with undulating flagella, an ocelot climbing a tree, a snail moving slowly to hide under a rock, or humans marching past giant cacti—are all making and using ATP—and so are the cacti. ATP is ancient, a molecular fossil, really. Its molecular structure, plus its presence in the first cell or cells that arose on planet Earth, accounts for it being the universal energy currency of cells.

ATP is unique among the cell's storehouse of chemicals; amino acids join to make a protein, and nucleotides join to make DNA or RNA, but ATP is singular and works alone. Whether you go skiing, take an aerobics class, or just hang out, ATP molecules provide the energy needed for nerve conduction, muscle contraction, and any other cellular process that requires energy. Cellular respiration, by which cells harvest the energy of organic compounds and convert it to ATP molecules, is the topic of this chapter. It's a process that requires many steps and involves the cytoplasm and the mitochondria. Because mitochondria are involved, they are called the powerhouses of the cell.

Tourists marching through a prickly pear cactus grove on the Galápagos Islands.

concepts

8.1 Cellular Respiration

Cellular respiration is the process by which cells acquire energy by breaking down nutrient molecules produced by photosynthesizers. Its very name implies that cellular respiration requires oxygen (O_2) and gives off carbon dioxide (CO_2). In fact, it is the reason any animal, such as an ocelot or human, breathes (Fig. 8.1) and why plants also require a supply of oxygen. Most often, cellular respiration involves the complete breakdown of glucose to carbon dioxide and water (H_2O):

Oxidation

$$\underset{\text{glucose}}{C_6H_{12}O_6} + 6\,O_2 \longrightarrow 6\,CO_2 + 6\,H_2O + \text{energy}$$

Reduction

This equation points out that cellular respiration is an oxidation-reduction reaction. Recall that oxidation is the loss of electrons, and reduction is the gain of electrons; therefore, glucose has been oxidized and O_2 has been reduced. But, remember that a hydrogen atom consists of a hydrogen ion plus an electron ($H^+ + e^-$). Therefore, when hydrogen atoms are removed from glucose, so are electrons, and similarly, when hydrogen atoms are added to oxygen, so are electrons.

Glucose is a high-energy molecule, and its breakdown products, CO_2 and H_2O, are low-energy molecules. Therefore, as the equation shows, energy is released. This is the energy that will be used to produce ATP molecules. The cell carries out cellular respiration in order to build up ATP molecules!

The pathways of cellular respiration allow the energy within a glucose molecule to be released slowly so that ATP can be produced gradually. Cells would lose a tremendous amount of energy if glucose breakdown occurred all at once—much energy would become nonusable heat. The step-by-step breakdown of glucose to CO_2 and H_2O usually realizes a maximum yield of 36 or 38 ATP molecules, dependent on conditions to be discussed later. The energy in these ATP molecules is equivalent to about 39% of the energy that was available in glucose. This conversion is more efficient than many others; for example, only between 20% and 30% of the energy within gasoline is converted to the motion of a car.

NAD^+ and FAD

Cellular respiration involves many individual metabolic reactions, each one catalyzed by its own enzyme. Enzymes of particular significance are those that use **NAD^+**, a coenzyme of oxidation-reduction sometimes called a redox coenzyme. When a metabolite is oxidized, NAD^+ accepts two electrons plus a hydrogen ion (H^+), and NADH results. The electrons received by NAD^+ are high-energy electrons that are usually carried to the electron transport chain (see Fig. 6.12):

$$NAD^+ + 2\,e^- + H^+ \longrightarrow NADH$$

NAD^+ can oxidize a metabolite by accepting electrons and can reduce a metabolite by giving up electrons. Only a small amount of NAD^+ need be present in a cell, because each NAD^+ molecule is used over and over again. **FAD,** another coenzyme of oxidation-reduction, is sometimes used instead of NAD^+. FAD accepts two electrons and two hydrogen ions (H^+) to become $FADH_2$.

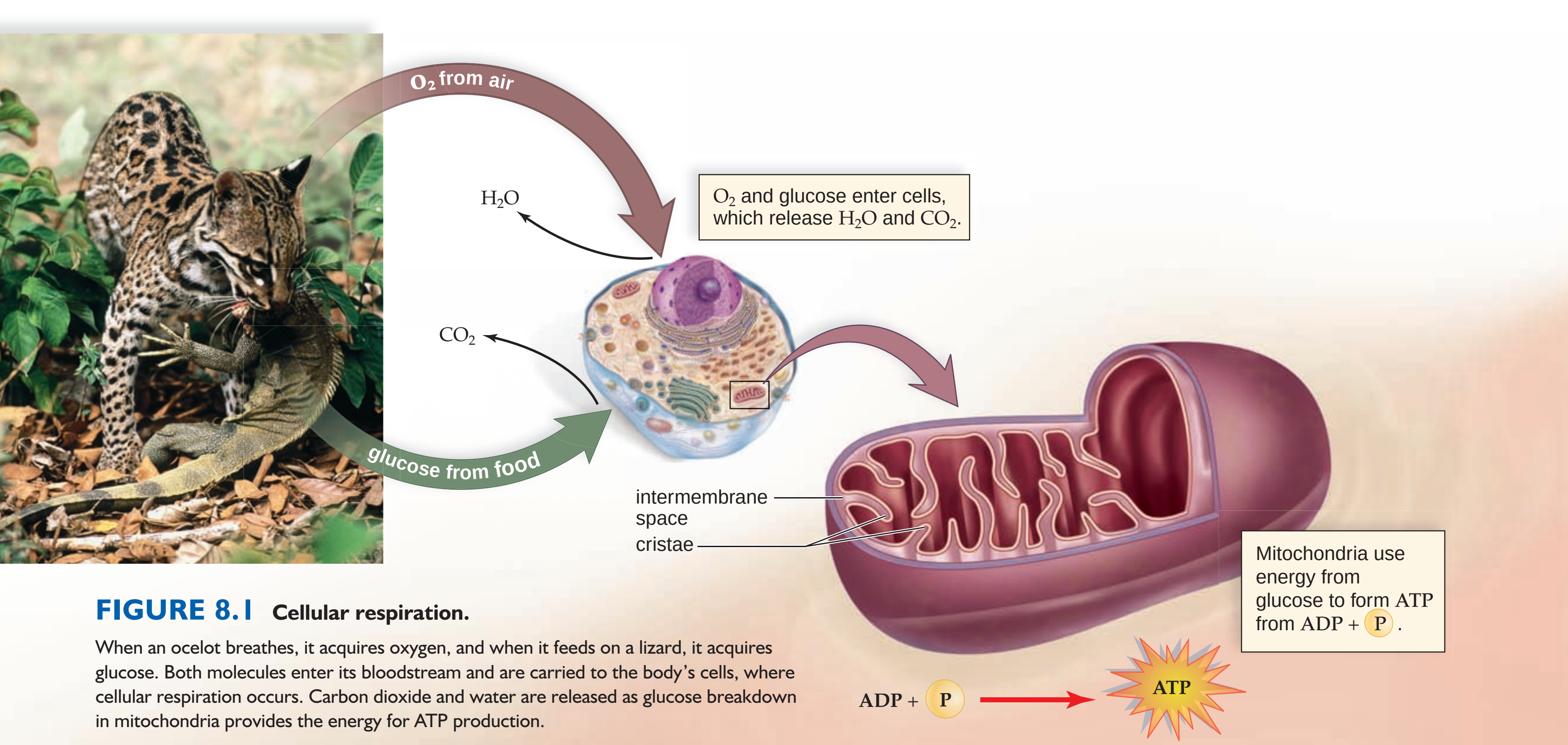


FIGURE 8.1 Cellular respiration.

When an ocelot breathes, it acquires oxygen, and when it feeds on a lizard, it acquires glucose. Both molecules enter its bloodstream and are carried to the body's cells, where cellular respiration occurs. Carbon dioxide and water are released as glucose breakdown in mitochondria provides the energy for ATP production.

Phases of Cellular Respiration

Cellular respiration involves four phases: glycolysis, the preparatory reaction, the citric acid cycle, and the electron transport chain (Fig. 8.2). Glycolysis takes place outside the mitochondria and does not require the presence of oxygen. Therefore, glycolysis is **anaerobic.** The other phases of cellular respiration take place inside the mitochondria, where oxygen is the final acceptor of electrons. Because they require oxygen, these phases are called **aerobic.**

During these phases, notice where CO_2 and H_2O, the end products of cellular respiration, and ATP are produced.

- **Glycolysis** [Gk. *glycos*, sugar, and *lysis*, splitting] is the breakdown of glucose to two molecules of pyruvate. Oxidation results in NADH and provides enough energy for the net gain of two ATP molecules.
- The **preparatory (prep) reaction** takes place in the matrix of the mitochondrion. Pyruvate is broken down to a 2-carbon (C_2) acetyl group, and CO_2 is released. Since glycolysis ends with two molecules of pyruvate, the prep reaction occurs twice per glucose molecule.
- The **citric acid cycle** also takes place in the matrix of the mitochondrion. As oxidation occurs, NADH and $FADH_2$ results, and more CO_2 is released. The citric acid cycle is able to produce one ATP per turn. Because two acetyl groups enter the cycle per glucose molecule, the cycle turns twice.
- The **electron transport chain (ETC)** is a series of carriers on the cristae of the mitochondria. NADH and $FADH_2$ give up electrons to the chain. Energy is released and captured as the electrons move from a higher-energy to a lower-energy state. Later, this energy will be used for the production of ATP by chemiosmosis. After oxygen receives electrons, it combines with hydrogen ions (H^+) and becomes water (H_2O).

Pyruvate, the end product of glycolysis, is a pivotal metabolite; its further treatment is dependent on whether oxygen is available. If oxygen is available, pyruvate enters a mitochondrion and is broken down completely to CO_2 and H_2O. If oxygen is not available, pyruvate is further metabolized in the cytoplasm by an anaerobic process called **fermentation.** Fermentation results in a net gain of only two ATP per glucose molecule.

Check Your Progress 8.1

1. Explain the benefit of slow glucose breakdown rather than rapid breakdown during cellular respiration.
2. List the four phases of complete glucose breakdown. Tell which ones release CO_2 and which produces H_2O.

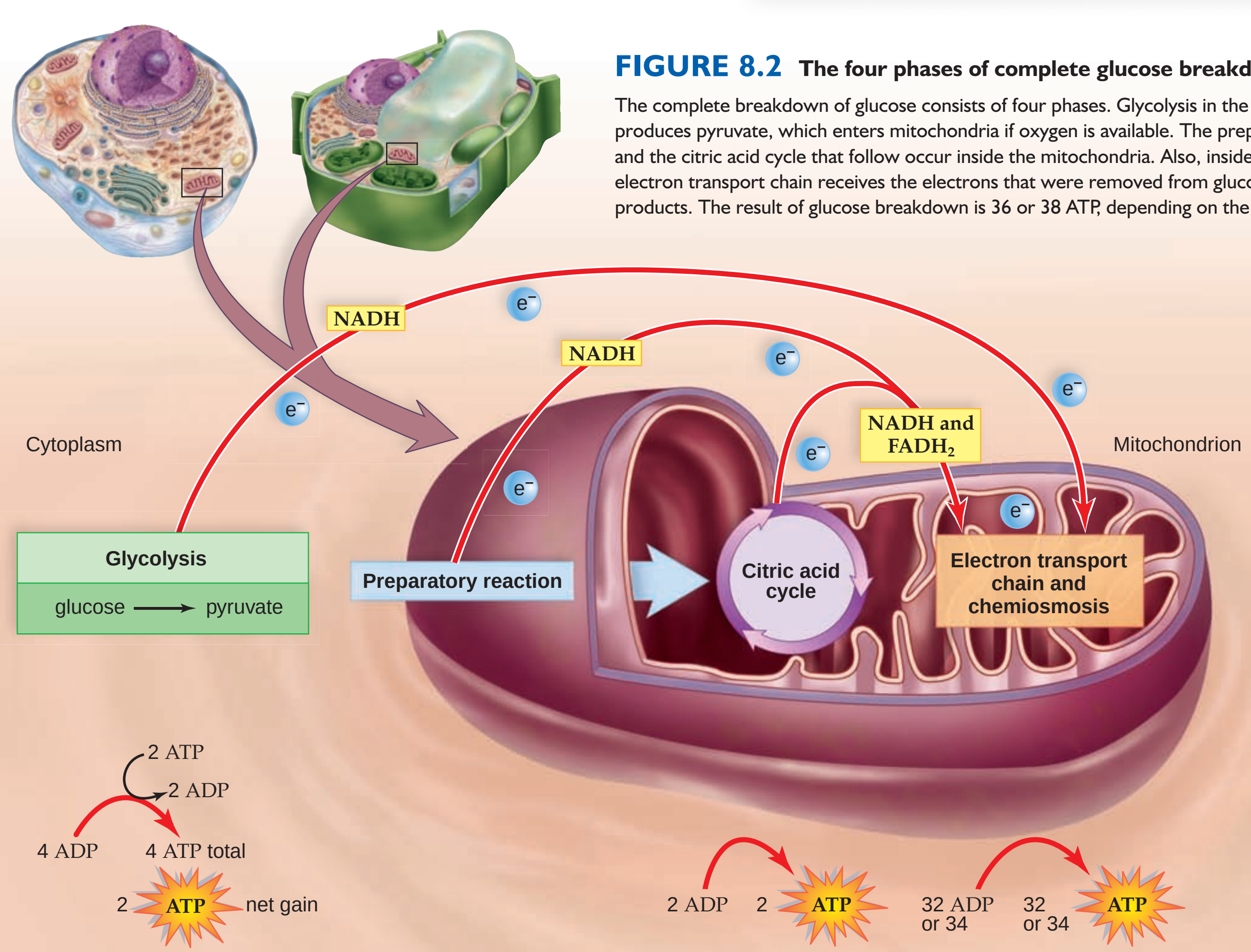


FIGURE 8.2 **The four phases of complete glucose breakdown.**

The complete breakdown of glucose consists of four phases. Glycolysis in the cytoplasm produces pyruvate, which enters mitochondria if oxygen is available. The preparatory reaction and the citric acid cycle that follow occur inside the mitochondria. Also, inside mitochondria, the electron transport chain receives the electrons that were removed from glucose breakdown products. The result of glucose breakdown is 36 or 38 ATP, depending on the particular cell.

8.2 Outside the Mitochondria: Glycolysis

Glycolysis, which takes place within the cytoplasm outside the mitochondria, is the breakdown of glucose to two pyruvate molecules. Since glycolysis occurs universally in organisms, it most likely evolved before the citric acid cycle and the electron transport chain. This may be why glycolysis occurs in the cytoplasm and does not require oxygen. There was no free oxygen in the early atmosphere of the Earth.

Glycolysis is a long series of reactions, and just as you would expect for a metabolic pathway, each step has its own enzyme. The pathway can be conveniently divided into the energy-investment step and the energy-harvesting steps. During the energy-investment step, ATP is used to "jump-start" glycolysis. During the energy-harvesting steps, more ATP is made than was used to get started.

Energy-Investment Step

As glycolysis begins, two ATP are used to activate glucose, a C_6 (6-carbon) molecule that splits into two C_3 molecules known as G3P. Each G3P has a phosphate group. From this point on, each C_3 molecule undergoes the same series of reactions.

Energy-Harvesting Step

Oxidation of G3P now occurs by the removal of electrons accompanied by hydrogen ions. In duplicate reactions, electrons are picked up by coenzyme NAD^+, which becomes NADH:

$$2\,NAD^+ + 4\,e^- + 2\,H^+ \longrightarrow 2\,NADH$$

When O_2 is available, each NADH molecule will carry two high-energy electrons to the electron transport chain and become NAD^+ again. Only a small amount of NAD^+ need be present in a cell, because like other coenzymes, it is used over and over again.

The addition of inorganic phosphate result in a high-energy phosphate group per C_3 molecule. These phosphate groups are used to synthesize two ATP. This is called **substrate-level ATP synthesis** (sometimes called substrate-level phosphorylation) because an enzyme passes a high-energy phosphate to ADP, and ATP results (Fig. 8.3). Notice that this is an example of coupling: An energy-releasing reaction is driving forward an energy-requiring reaction on the surface of the enzyme.

Oxidation occurs again but by the removal of H_2O. Substrate-level ATP synthesis occurs again per C_3, and two molecules of pyruvate result. Subtracting the two ATP that were used to get started, there is a net gain of two ATP from glycolysis (Fig. 8.4).

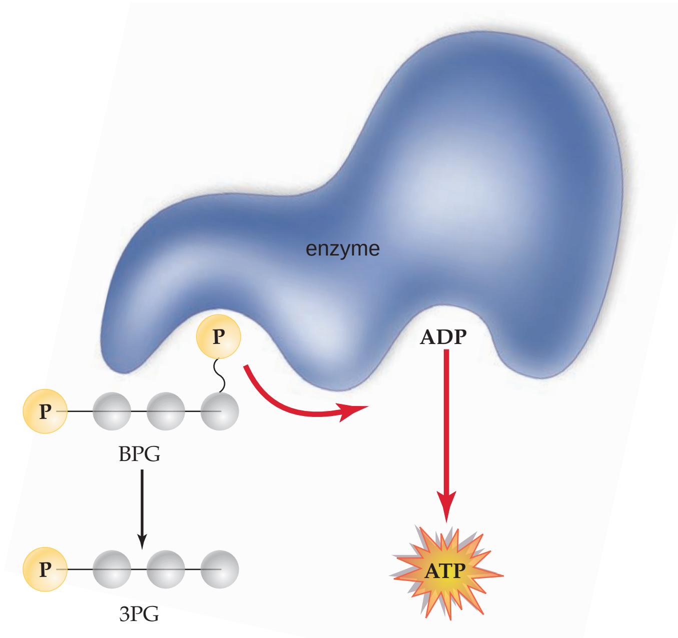
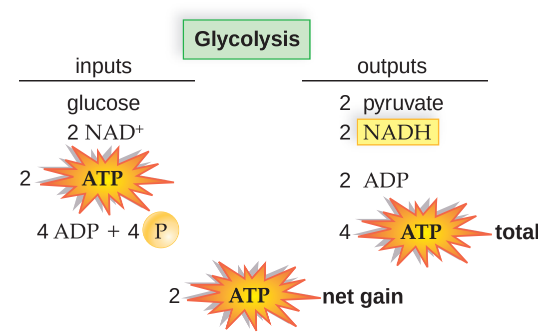


FIGURE 8.3 **Substrate-level ATP synthesis.**

Substrates participating in the reaction are oriented on the enzyme. A phosphate group is transferred to ADP, producing one ATP molecule. During glycolysis (see Fig. 8.4), BPG is a C_3 substrate (each gray ball is a carbon atom) that gives up a phosphate group to ADP. This reaction occurs twice per glucose molecule.

Inputs and Outputs of Glycolysis

Altogether, the inputs and outputs of glycolysis are as follows:



Notice that, so far, we have accounted for only two out of a possible 36 or 38 ATP per glucose when completely broken down to CO_2 and H_2O. When O_2 is available, the end product of glycolysis, pyruvate, enters the mitochondria, where it is metabolized. If O_2 is not available, fermentation, which is discussed next, will occur.

Check Your Progress 8.2

1. Contrast the energy-investment step of glycolysis with the energy-harvesting steps.
2. What happens to pyruvate when oxygen is not available in a cell? When it is available?

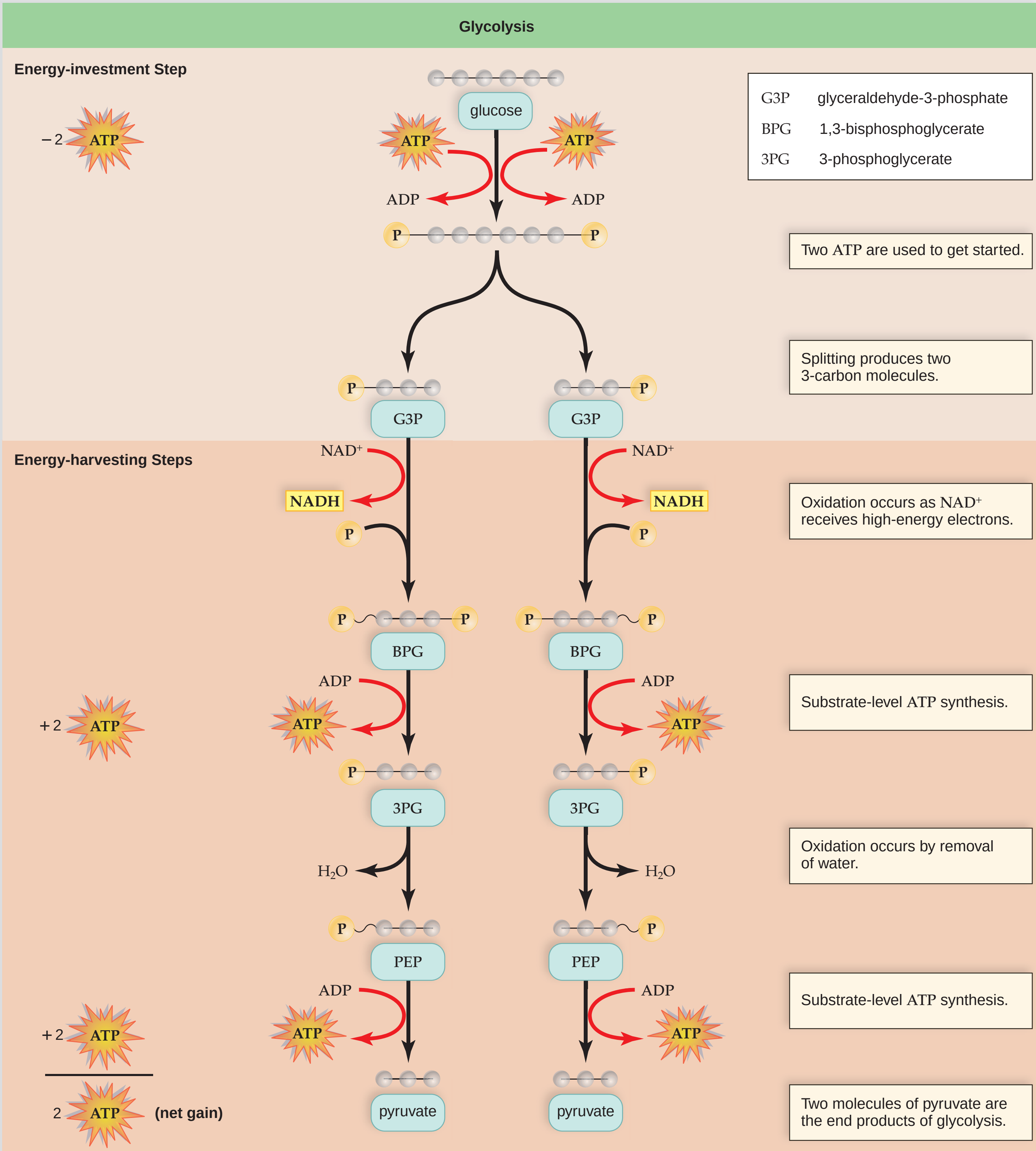


FIGURE 8.4 Glycolysis.

This metabolic pathway begins with C_6 glucose (each gray ball is a carbon atom) and ends with two C_3 pyruvate molecules. Net gain of two ATP molecules can be calculated by subtracting those expended during the energy-investment step from those produced during the energy-harvesting steps.

8.3 Fermentation

Complete glucose breakdown requires an input of oxygen to keep the electron transport chain working. **Fermentation** is anaerobic, and it produces a limited amount of ATP in the absence of oxygen. In animal cells, including human cells, pyruvate, the end product of glycolysis, is reduced by NADH to lactate (Fig. 8.5). Depending on their particular enzymes, bacteria vary as to whether they produce an organic acid, such as lactate, or an alcohol and CO_2. Yeasts are good examples of organisms that generate ethyl alcohol and CO_2 as a result of fermentation.

Why is it beneficial for pyruvate to be reduced when oxygen is not available? This reaction regenerates NAD^+, which is required for the first step in the energy-harvesting phase of glycolyis. This NAD^+ is now "free" to return to the earlier reaction (see return arrow in Figure 8.5) and become reduced once more. In this way, glycolysis and substrate-level ATP synthesis continue to occur, even though oxygen is not available and the ETC is not working.

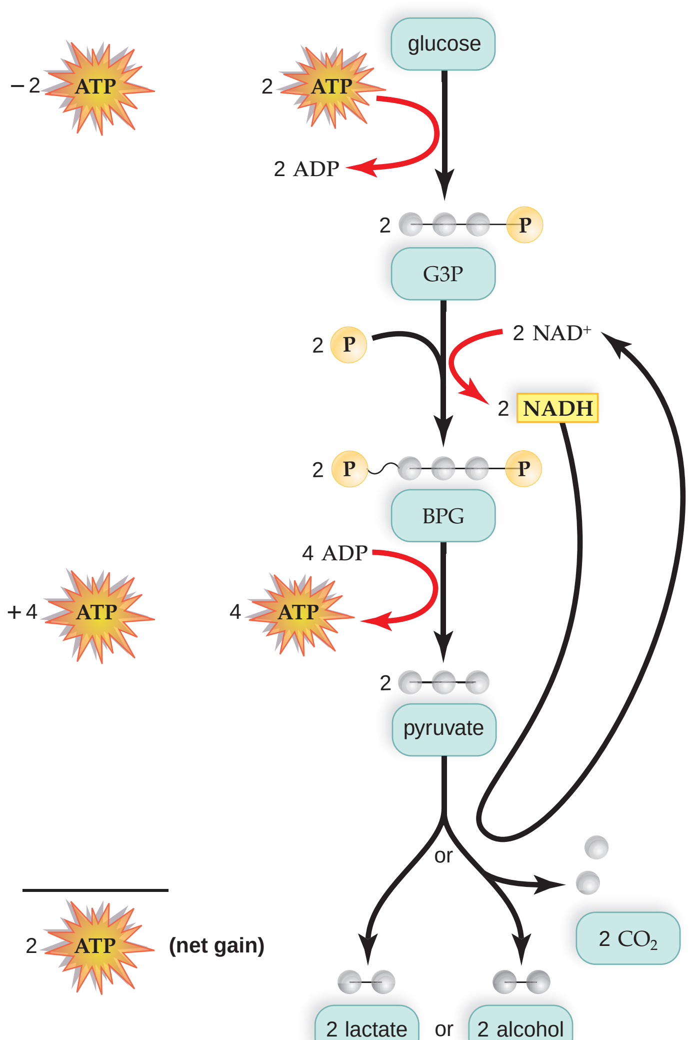


FIGURE 8.5 Fermentation.

Fermentation consists of glycolysis followed by a reduction of pyruvate. This "frees" NAD^+ and it returns to the glycolytic pathway to pick up more electrons.

Advantages and Disadvantages of Fermentation

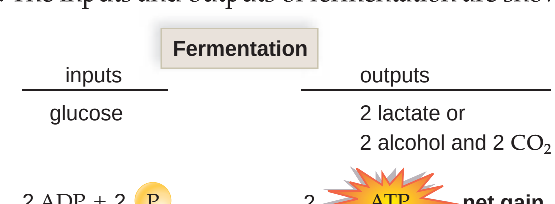
As discussed in the Science Focus on page 139, anaerobic bacteria that produce lactate are used by humans in the production of cheese, yogurt, and sauerkraut. Other bacteria produce chemicals of industrial importance, including isopropanol, butyric acid, proprionic acid, and acetic acid when they ferment. Yeasts, of course, are used to make breads rise. In addition, alcoholic fermentation is utilized to produce wine, beer, and other alcoholic beverages.

Despite its low yield of only two ATP made by substrate-level ATP synthesis, lactic acid fermentation is essential to certain animals and/or tissues. Typically, animals use lactic acid fermentation for a rapid burst of energy. Also, when muscles are working vigorously over a short period of time, lactic acid fermentation provides them with ATP, even though oxygen is temporarily in limited supply.

Fermentation products are toxic to cells. At first, blood carries away all the lactate formed in muscles. Yeasts die from the alcohol they produce. In humans, when lactate begins to build up, pH changes occur that can possibly be harmful. After running for a while, our bodies are in **oxygen debt,** a term that refers to the amount of oxygen needed to rid the body of lactate. Oxygen debt is evidenced when we continue breathing heavily for a time after exercise. Recovery involves transporting most of the lactate to the liver, where it is converted back to pyruvate. Some of the pyruvate is respired completely, and the rest is converted back to glucose.

Efficiency of Fermentation

The two ATP produced per glucose during alcoholic fermentation and lactic acid fermentation are equivalent to 14.6 kcal. Complete glucose breakdown to CO_2 and H_2O represents a possible energy yield of 686 kcal per molecule. Therefore, the efficiency of fermentation is only 14.6 kcal/686 kcal $\times$ 100, or 2.1% of the total possible for the complete breakdown of glucose. The inputs and outputs of fermentation are shown here:



The two ATP produced by fermentation fall far short of the 36 or 38 ATP molecules produced by cellular respiration. To achieve this number of ATP per glucose molecule, it is necessary to move on to the reactions and pathways that occur in the mitochondria.

Check Your Progress 8.3

1. What are the drawbacks and benefits of fermentation?

science focus

Fermentation Helps Produce Numerous Food Products

At the grocery store, you will find such items as bread, yogurt, soy sauce, pickles, and maybe even wine (Fig. 8A). These are just a few of the many foods that are produced when microorganisms ferment (break down sugar in the absence of oxygen). Foods produced by fermentation last longer because the fermenting organisms have removed many of the nutrients that would attract other organisms. The products of fermentation can even be dangerous to the very organisms that produced them, as when yeasts are killed by the alcohol they produce.

Yeast Fermentation

Baker's yeast, *Saccharomyces cerevisiae,* is added to bread for the purpose of leavening—the dough rises when the yeasts give off CO_2. The ethyl alcohol produced by the fermenting yeast evaporates during baking. The many different varieties of sourdough breads obtain their leavening from a starter composed of fermenting yeasts along with bacteria from the environment. Depending on the community of microorganisms in the starter, the flavor of the bread may range from sour and tangy, as in San Francisco–style sourdough, to a milder taste, such as that produced by most Amish friendship bread recipes.

Ethyl alcohol is desired when yeasts are used to produce wine and beer. When yeasts ferment the carbohydrates of fruits, the end result is wine. If they ferment grain, beer results. A few specialized varieties of beer, such as traditional wheat beers, have a distinctive sour taste because they are produced with the assistance of lactic acid–producing bacteria, such as those of the genus *Lactobacillus.* Stronger alcoholic drinks (e.g., whiskey and vodka) require distillation to concentrate the alcohol content.

The acetic acid bacteria, including *Acetobacter aceti,* spoil wine. These bacteria convert the alcohol in wine or cider to acetic acid (vinegar). Until the renowned nineteenth-century scientist Louis Pasteur invented the process of pasteurization, acetic acid bacteria commonly caused wine to spoil. Although today we generally associate the process of pasteurization with making milk safe to drink, it was originally developed to reduce bacterial contamination in wine so that limited acetic acid would be produced.

Bacterial Fermentation

Yogurt, sour cream, and cheese are produced through the action of various lactic acid bacteria that cause milk to sour. Milk contains lactose, which these bacteria use as a substrate for fermentation. Yogurt, for example, is made by adding lactic acid bacteria, such as *Streptococcus thermophilus* and *Lactobacillus bulgaricus,* to milk and then incubating it to encourage the bacteria to act on lactose. During the production of cheese, an enzyme called rennin must also be added to the milk to cause it to coagulate and become solid.

Old-fashioned brine cucumber pickles, sauerkraut, and kimchi are pickled vegetables produced by the action of acid-producing, fermenting bacteria that can survive in high-salt environments. Salt is used to draw liquid out of the vegetables and aid in their preservation. The bacteria need not be added to the vegetables, because they are already present on the surfaces of the plants.

Soy Sauce Production

Soy sauce is traditionally made by adding a mold, *Aspergillus,* and a combination of yeasts and fermenting bacteria to soybeans and wheat. The mold breaks down starch, supplying the fermenting microorganisms with sugar they can use to produce alcohol and organic acids.

FIGURE 8A Products from fermentation.
Fermentation helps make the products shown on this page.

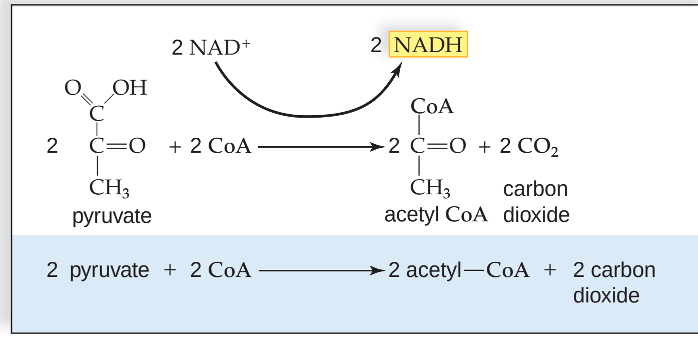
8.4 Inside the Mitochondria

The preparatory (prep) reaction, the citric acid cycle, and the electron transport chain, which are needed for the complete breakdown of glucose, take place within the mitochondria. A **mitochondrion** has a double membrane with an intermembrane space (between the outer and inner membrane). Cristae are folds of inner membrane that jut out into the matrix, the innermost compartment, which is filled with a gel-like fluid (Fig. 8.6). Just like a chloroplast, a mitochondrion is highly structured, and we would expect reactions to be located in particular parts of this organelle.

The enzymes that speed the prep reaction and the citric acid cycle are arranged in the matrix, and the electron transport chain is located in the cristae in a very organized manner. Most of the ATP from cellular respiration is produced in mitochondria; therefore, mitochondria are often called the powerhouses of the cell.

The Preparatory Reaction

The **preparatory (prep) reaction** is so called because it occurs before the citric acid cycle. In this reaction, the C_3 pyruvate is converted to a C_2 acetyl group and CO_2 is given off. This is an oxidation reaction in which electrons are removed from pyruvate by NAD^+, and NADH is formed. One prep reaction occurs per pyruvate, so altogether, the prep reaction occurs twice per glucose molecule:



The C_2 acetyl group is combined with a molecule known as CoA. CoA will carry the acetyl group to the citric acid cycle. The two NADH carry electrons to the electron transport chain. What about the CO_2? In vertebrates, such as ourselves, CO_2 freely diffuses out of cells into the blood, which transports it to the lungs where it is exhaled.

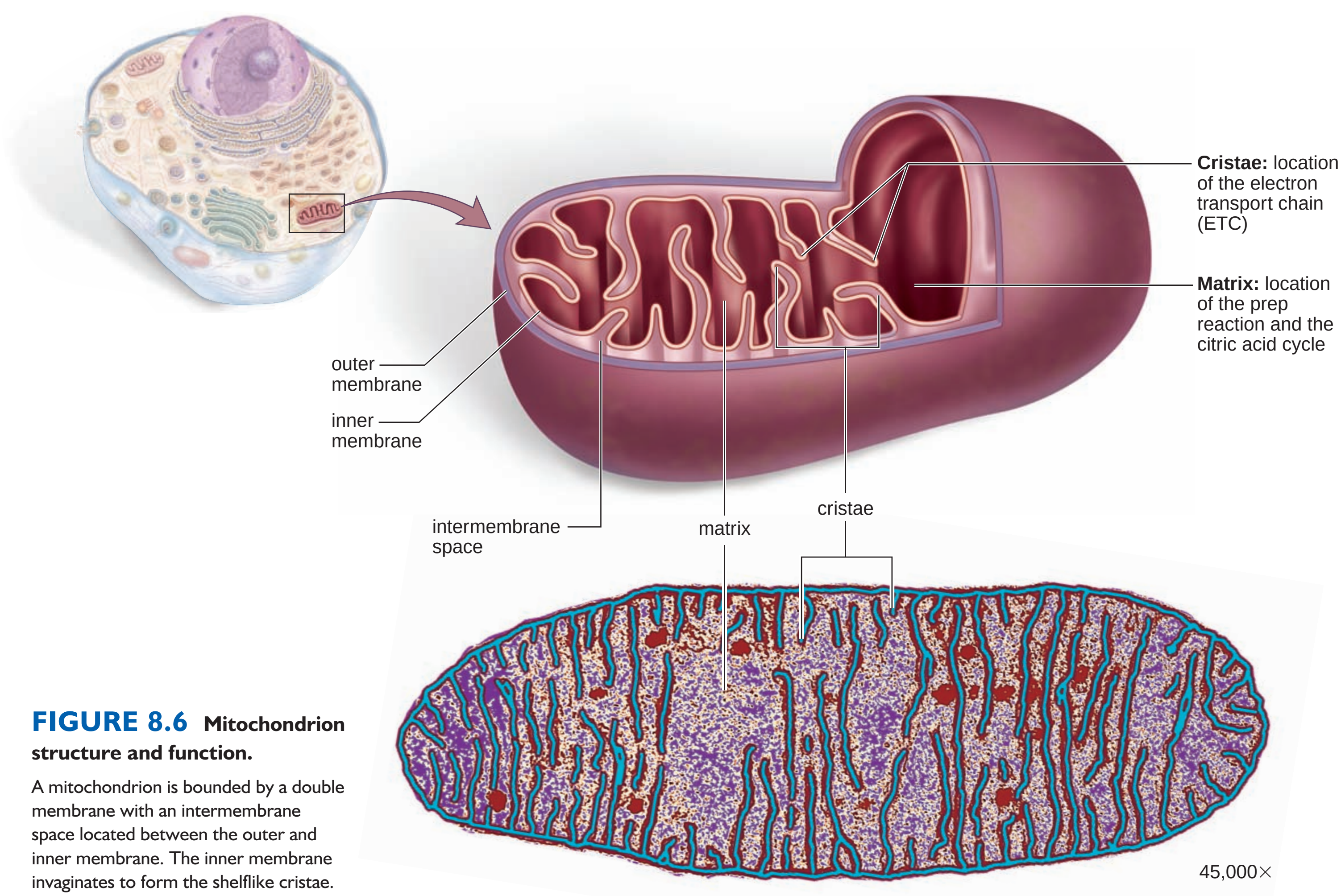


FIGURE 8.6 Mitochondrion structure and function.

A mitochondrion is bounded by a double membrane with an intermembrane space located between the outer and inner membrane. The inner membrane invaginates to form the shelflike cristae.