CHAPTER 4

Is the Earth Warming?

The Greenhouse Effect, Cellular Respiration, and Photosynthesis

Inhabitants of the Nation of Tuvalu . . .

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will have to leave their tiny island communities.

High tides are eroding and flooding these Pacific islands.

Many scientists agree that increased sea levels are caused by global warming.

A nine-island chain in the South Pacific, located between Australia and Hawaii, comprises the nation of Tuvalu. Each of the tropical islands that is part of the chain is an atoll—a circular column of coral rising up from the sea floor and extending above sea level. Many of the islands are covered with coconut trees and sandy beaches; together, they have close to 10 square miles of land above sea level but not very far above sea level—13 feet at the highest point.

The 10,000 or so people inhabiting these islands farm and fish in order to feed themselves and their families. Crops produced on the islands include coconuts, taro, and bananas. Each of the inhabited islands has a cooperative market where goods are sold or traded.

Tuvaluans live peaceful lives in a nation where crime is virtually unheard of; in fact, most residents sleep with their doors open to allow in the cooling night breezes. The islands have no television service, and the lone bank closes at 1:00 p.m. each day; no one takes credit cards. Soccer is the most popular sport, but Tuvaluans consider it bad sportsmanship to tackle an opponent aggressively enough to cause him or her to fall down. Transportation is largely via bicycle or motor scooter.

But there is one big problem in this seemingly idyllic island paradise—the islands of Tuvalu are disappearing. The storm surges and high tides that have become more common in recent years are eroding protective offshore barriers and beaches, destroying roads, and flooding homes and plantations. Recently, a record high tide submerged much of the country, causing week-long telephone service outages and flooding Tuvalu's only airport. Some roads have been moved inland as the Pacific eats away asphalt closer to the shore. The flooding of plantations with salty seawater kills the crops, forcing citizens to grow crops in metal containers filled with compost. Many people have simply left the island nation altogether. Nearly 3,000 native Tuvaluans have relocated, and a government program is moving its citizens at the rate of 75 per year.

What is causing the sudden rise in sea levels of the Tuvaluan islands? The prime minister of Tuvalu believes that global warming, which is causing the polar ice caps to melt and deposit water into the seas, is at fault. Concern that the tides will soon be high enough to submerge the nation and force the exodus of its remaining residents has led the prime minister to attempt to sue those he believes to be responsible—namely, the United States. Per capita, this country is producing more of the gasses associated with global warming than any other country.

4.1 The Greenhouse Effect

Global warming is the progressive increase of Earth's average temperature that has been occurring over the past century. The prime minister of Tuvalu is not alone in his belief that global warming is caused by increased emissions of certain gases. Most scientists agree that global warming is caused by recent increases in the concentrations of particular atmospheric gases including methane, nitrous oxide, water vapor, and carbon dioxide. Because increases in carbon dioxide seem to be the major source of problems related to global warming, we will focus mainly on that gas for the rest of this discussion.

The presence of carbon dioxide in the atmosphere leads to a phenomenon called the **greenhouse effect**. The greenhouse effect works like this: Warmth from the sun heats Earth's surface, which then radiates the heat energy absorbed outward. Most of this heat is radiated back into space, but some of the heat is retained in the atmosphere. The retention of heat is facilitated by carbon dioxide molecules, which act like a blanket to trap the heat radiated by Earth's surface (Figure 4.1). When you sleep under a blanket at night, your body heat is trapped and helps keep you warm. When the levels of greenhouse gases in the atmosphere increase, the effect is similar to sleeping under too many blankets—the temperature increases. The trapping of this warmth radiating from Earth is known as the greenhouse effect.

This is not exactly how panes of glass in a greenhouse function, that is, by allowing radiation from the sun to penetrate into the greenhouse and then trapping the heat that radiates from the warmed-up surfaces inside the greenhouse. But the overall effect is the same—the air temperature increases.

The greenhouse effect is not in itself a dangerous or unhealthy phenomenon. If Earth's atmosphere did not have some greenhouse gases, too much heat would be lost to space, and Earth would be too cold to support life. It is the excess warming due to more and more carbon dioxide accumulating in the atmosphere as a result of coal, oil, and natural gas burning that is causing problems.

In the absence of excess greenhouse gases, water vapor and carbon dioxide work together to keep temperatures on Earth hospitable for life.

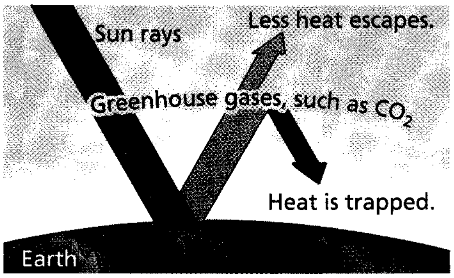


Figure 4.1 The greenhouse effect. Heat from the sun is trapped in the atmosphere by water vapor, carbon dioxide, and other greenhouse gases. Increased levels of carbon dioxide contribute to the greenhouse effect.

Water, Heat, and Temperature

Bodies of water absorb heat and help maintain stable temperatures on Earth. Heat and temperature are measures of energy. **Heat** is the total amount of energy associated with the movement of atoms and molecules in a substance. **Temperature** is a measure of the intensity of heat—for example, how fast the molecules in the substance are moving.

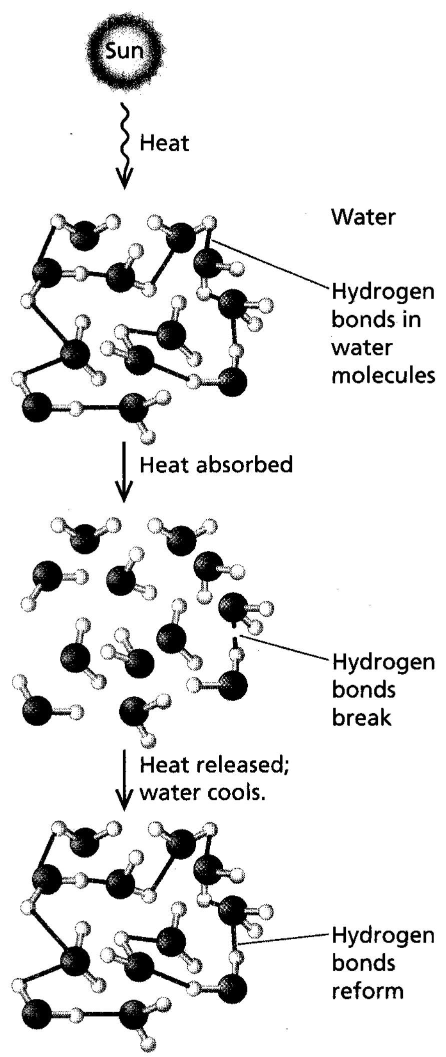


Figure 4.2 Hydrogen bonding in water. Hydrogen bonds break as they absorb heat and reform as water releases heat. Water remains in the liquid form because not all the hydrogen bonds are broken at any one time.

Water molecules are attracted to each other, resulting in the formation of weak chemical bonds, called hydrogen bonds, between neighboring molecules. When water is heated, the heat energy disrupts the hydrogen bonds. Only after the hydrogen bonds have been broken can heat cause individual water molecules to move faster, thus increasing the temperature. In other words, the initial input of heat used to break hydrogen bonds between water molecules does not immediately raise the temperature of water; instead, it breaks hydrogen bonds. Therefore, water can absorb and store a large amount of heat while warming up only a few degrees in temperature. When water cools, hydrogen bonds re-form between adjacent molecules, releasing heat into the atmosphere. Water can release a large amount of heat into the surroundings while not decreasing the temperature of the body of water very much (Figure 4.2).

Water's high heat-absorbing capacity has important effects on Earth's climate. The vast amount of water contained in Earth's oceans and lakes moderates temperatures by storing huge amounts of heat radiated by the sun and giving off heat that warms the air during cooler times. Therefore, the balance between releasing and maintaining heat energy is vital to the maintenance of climate conditions on Earth. This balance can be disrupted when increasing levels of carbon dioxide cause more heat to be trapped.

Carbon Dioxide

Many of the atoms found in complex molecules of living organisms are broken down into simpler molecules and recycled for use in different capacities. Carbon dioxide (CO_2) is no different. The carbon dioxide you exhale is released into the atmosphere, where it can absorb heat, diffuse into the oceans, or be absorbed by forests and soil. Volcanic eruptions return carbon dioxide trapped within Earth's surface to the atmosphere. As you can see in Figure 4.3, carbon dioxide naturally flows back and forth between living organisms, the atmosphere, bodies of water, and soil.

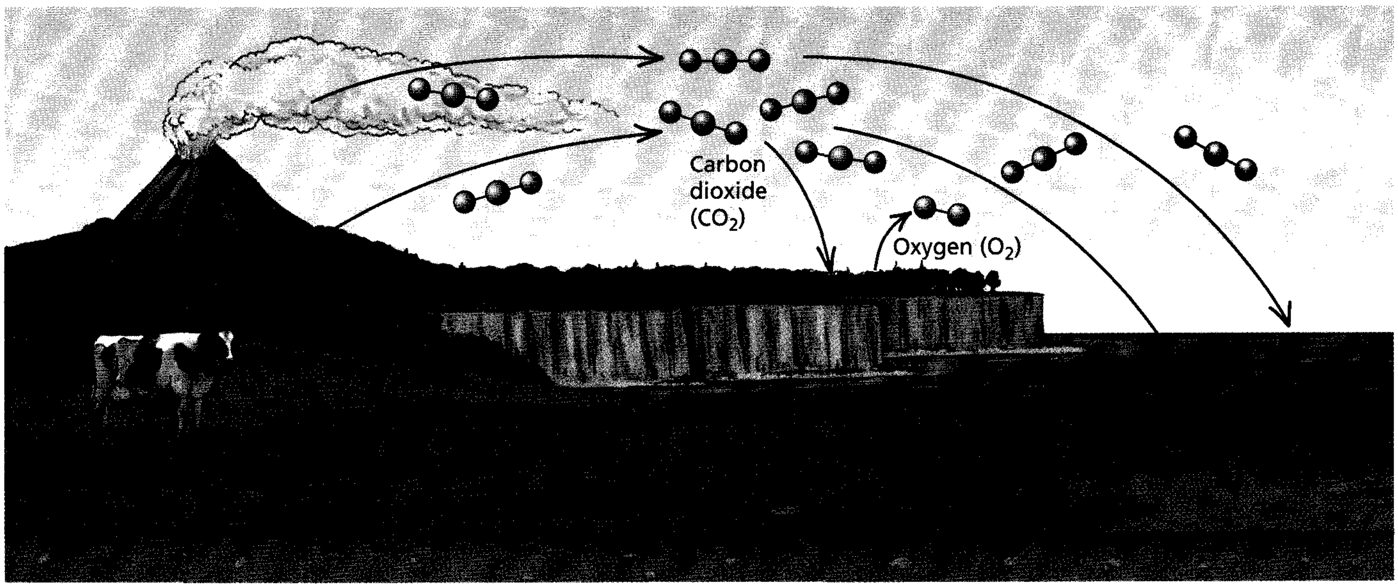


Figure 4.3 The flow of carbon. All living organisms and volcanoes produce CO_2. Forests, oceans, and soil absorb CO_2 from the air.

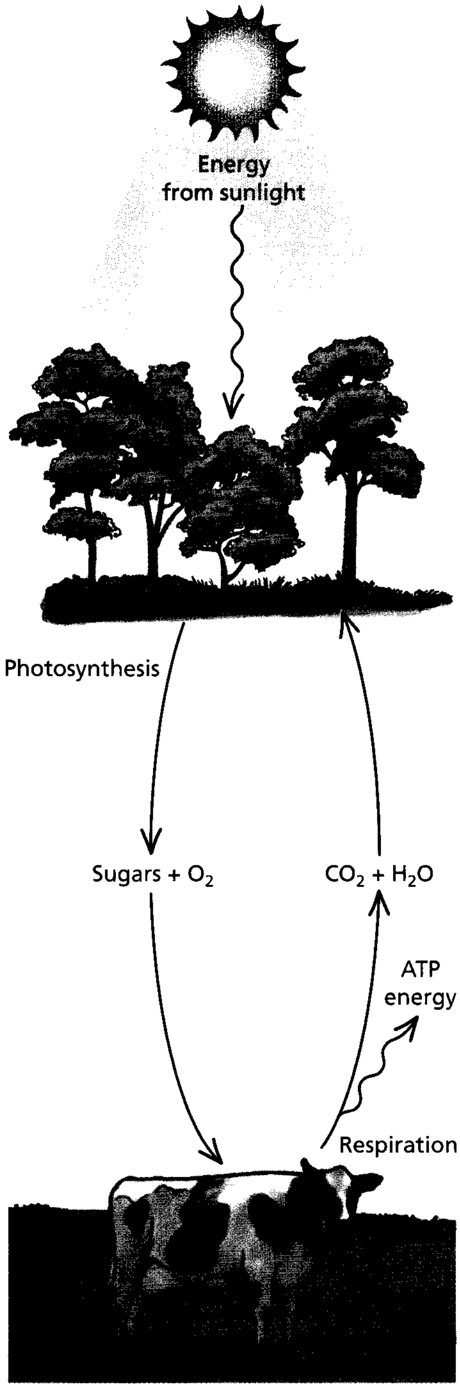


Figure 4.4 The flow of chemicals and energy. Energy enters biological systems in the form of sunlight, which is used to convert carbon dioxide and water into sugars during photosynthesis. The products of photosynthesis are broken down during cellular respiration to produce carbon dioxide and water and release energy.

It is not just carbon that flows between plants and other organisms—energy does also. Plants use energy from the sun to produce sugars and other organic molecules that other organisms consume. The energy is stored in the bonds of these organic molecules and can be used to produce energy for the cell. When plants use energy from sunlight to produce organic molecules, by a process called **photosynthesis**, they also release oxygen (O_2) into the atmosphere. The metabolism of organic molecules by **cellular respiration** produces not only energy but also carbon dioxide and water (Figure 4.4).

The carbon dioxide produced by respiration is taken up by plants during the process of photosynthesis, is absorbed by both chemicals and organisms in the ocean, or accumulates in the atmosphere. The ocean has served as Earth's largest carbon dioxide and heat reservoir, but oceanic and atmospheric scientists are very concerned about the ocean's ability to absorb carbon dioxide at the rate that it is being emitted into the atmosphere. This is because human activities have rapidly increased the rate of carbon dioxide release into the atmosphere, largely by burning fossil fuels (Figure 4.5).

Fossil fuels are the buried remains of ancient plants and microorganisms that have been transformed by heat and pressure into coal, oil, and natural gas. These fuels are rich in carbon because plants remove carbon from the atmosphere during photosynthesis; consequently, plant structures are rich in organic carbon. Dead plant materials that are buried before they decompose, and thus before their carbon is released in the form of carbon dioxide, can produce fossil fuels. Humans combust this stored organic carbon to produce energy. The plants that made up the majority of fossil fuels lived from 362 to 290 million years ago, during a geological period called the Carboniferous period.

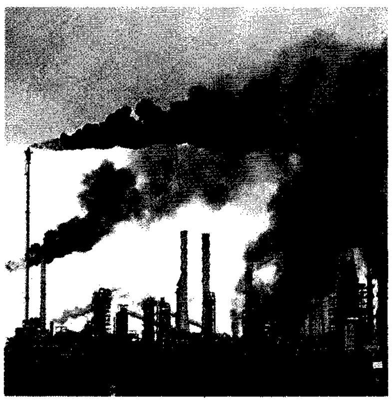


Figure 4.5 Burning fossil fuels. The burning of fossil fuels by industrial plants and automobiles adds more carbon dioxide to the environment.

Burning these fossil fuels to generate electricity, power our cars, and heat our homes releases carbon dioxide into the atmosphere. Increases in carbon dioxide are well documented by direct measurements of the atmosphere over the past 50 years (Figure 4.6).

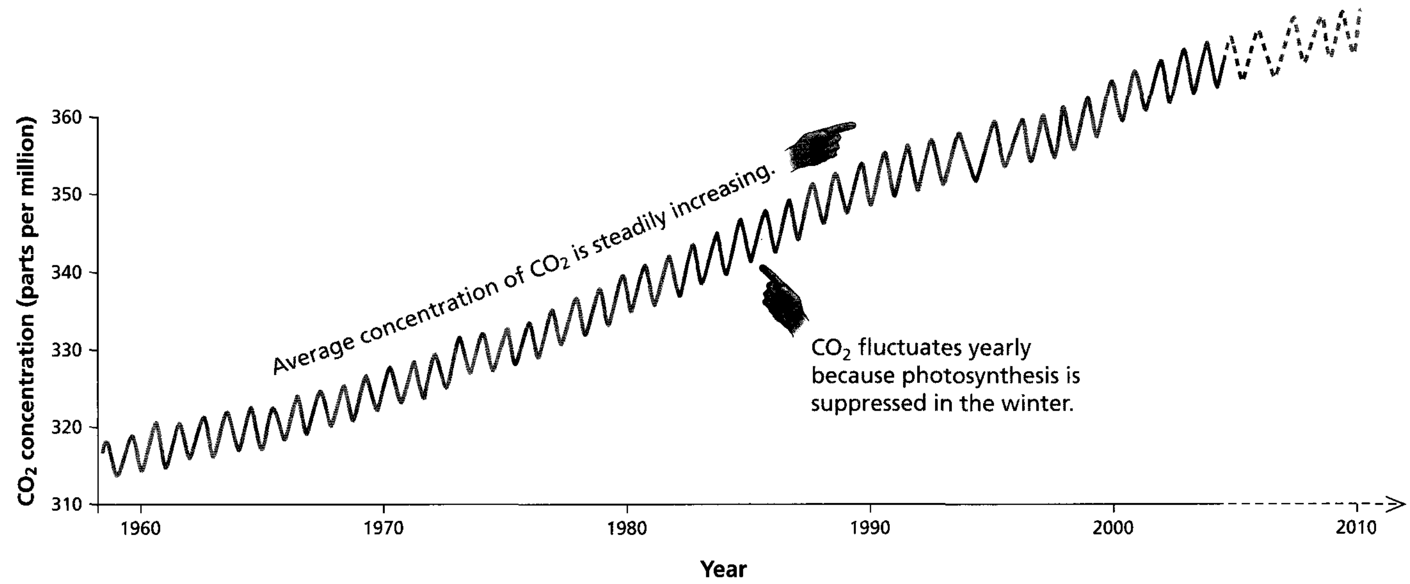


Figure 4.6 Increases in atmospheric carbon dioxide. Carbon dioxide levels have increased over the years.

Scientists can also directly measure the amount of carbon dioxide that was present in the atmosphere in the past by examining cores of ice sheets that have existed for thousands of years. This is because snow near the surface of ice traps air. As more snow accumulates, the underlying snow is compressed into ice that contains air bubbles. Cores can be removed from long-lived ice sheets and analyzed to determine the concentration of carbon dioxide trapped in air bubbles. These bubbles are actual samples of the atmosphere from up to hundreds of thousands of years ago (Figure 4.7). In addition, certain characteristics of gases trapped in the bubbles of ice cores can provide indirect information about temperatures at the time the bubbles formed. Ice core data from Antarctica, shown in Figure 4.8 (shown on page 76), indicate that the concentration of carbon dioxide in the atmosphere is much higher now than at any time in the past 400,000 years and that increased levels of carbon dioxide are correlated with increased temperatures.

Although Earth has gone through temperature cycles many times in the past, the concerns regarding current warming trends are that human activities are inflating the rate of increase and that these increases may persist for thousands of years. Many scientists believe that the effects of increased temperatures will be far reaching. Even now, the Tuvaluans and their Pacific islands are not the only organisms and environments being affected.

Figure 4.7 Ice core. By analyzing ice cores, scientists can measure the concentration of carbon dioxide that was present in early atmospheres.

The Greenhouse Effect, Organisms, and Their Environments

Several million tourists visit Glacier National Park, located in the northwest corner of Montana, every year. With each passing year, the glaciers in this park decrease in size and number. As the glaciers shrink, they take with them natural habitat set aside for protection in this national park. Some of the park's glaciers have already shrunk to half their original size, and the total number of glaciers has decreased from approximately 150 in 1850 to around 35 today.

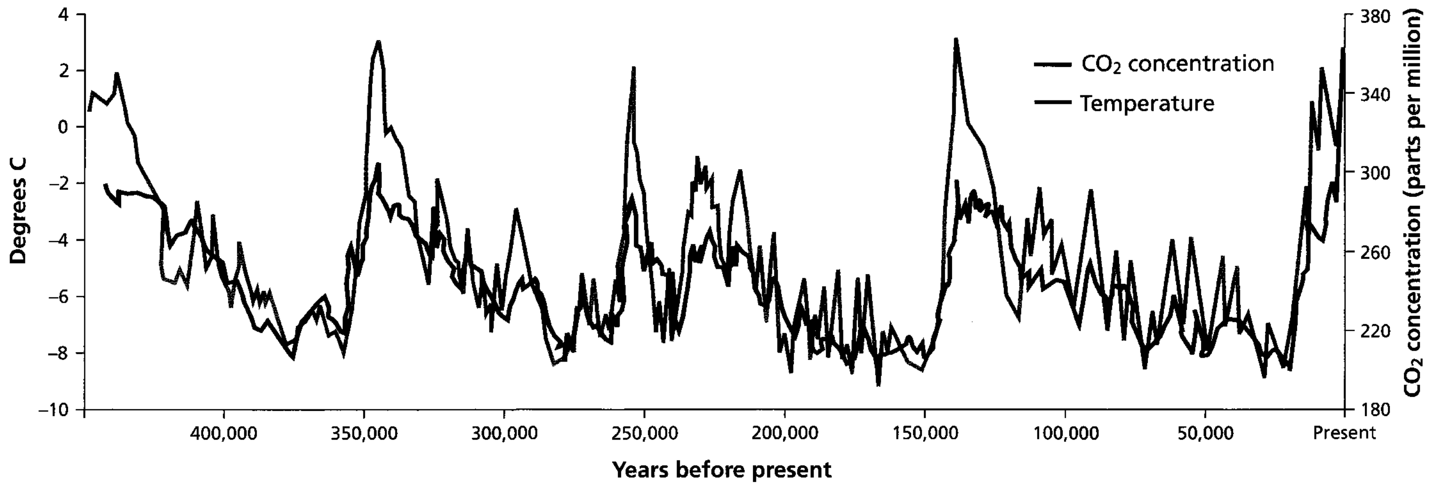


Figure 4.8 Records of temperature and atmospheric carbon dioxide concentration from Antarctic ice cores. These data indicate that increases in carbon dioxide levels are correlated with higher temperatures.

Like ice masses all over the world, these glaciers are slowly succumbing to warmer temperatures. According to the U.S. National Climate Data Center, the entire planet has warmed by 0.25°C (0.5°F) during the twentieth century. If this trend continues, scientists predict that by the year 2030, not a single glacier will be left in the park.

Melting glaciers are not confined to this park; in fact, they are melting worldwide. Mountain glaciers are receding from their peaks as far away as Tanzania, where Mount Kilimanjaro has lost 82% of its ice cap since 1912. The Greenland ice sheet is becoming thinner at its margins every year. Alpine glaciers contain half as much ice as they did in the mid-nineteenth century, when climbers first hiked to their peaks. In Antarctica, rising temperatures have led to the collapse of massive ice shelves. In the past 3 years, two massive chunks of ice, each about the size of Rhode Island, have fallen into the ocean.

The loss of ice has been a problem for the polar bear population in Hudson Bay. Seals, the bears' main food source, live on the ice of Hudson Bay, but this ice is breaking up earlier and earlier. The amount of time ice exists on western Hudson Bay has decreased by 3 weeks over the last 20 years. Rising temperatures thin the ice pack, making it too fragile to support seals and the bears that hunt them and driving the bears to shore in poor condition for hibernation. The average weight of polar bears in this region is declining, and fewer cubs are being born.

Sea levels have risen by 10 to 20 cm (4–8 inches) in the twentieth century. Increased ocean volumes due to the addition of water from melted ice can also lead to changes in climate. Worldwide rain and snowfall over land has increased by about 1%, and rain storms, as seen in Tuvalu, are expected to become more frequent and more severe. In addition to its impact on the humans who live there, flooding of tropical oceanic islands disturbs some of the most unique and diverse habitats on the planet.

A review published in the journal *Nature* in March 2002 described various species that have been affected by climate change. Many of these species are temperature sensitive, and they must move closer to the poles or to higher elevations to find regions with the proper climate. Arctic foxes are retreating northward and being replaced by the less cold-hardy red fox. Edith's checkerspot butterfly is now found 124 meters higher in elevation and 92 kilometers north of its range in 1900, and a wide variety of corals have experienced a dramatic increase in the frequency and extent of damage resulting from increased ocean temperatures.

It is not just animals that need to migrate along with changing temperatures. Plant species with specific temperature requirements will have to move as well. Those that cannot migrate quickly enough will likely become extinct. One example of a plant that will need to undergo this forced migration is the sugar maple, the source of maple syrup.

New England risks losing its profitable maple syrup industry along with its leaf-watching tourists as the cool-weather-adapted sugar maple population declines in a warming climate. Turning the maples' sugar into syrup requires nighttime temperatures that are below freezing and daytime temperatures in the mid-forties. Warmer temperatures overall have led to tapping seasons that start earlier, end sooner, and produce syrup of a lesser quality. A report by the U.S. Office of Science and Technology Policy indicates that the ideal range of the sugar maple is now close to 300 miles north of New England. The effects of warming temperatures on species of less commercial importance are not as well documented, and these species are less likely to receive human aid in making the transition.

The cost of global warming to Tuvaluans is even more dramatic. While migrating to drier climes would not mean extinction of the Tuvaluan people, it might well mean the extinction of their culture, since its members would likely disperse to many different countries. Reducing the biological, economic, and social losses caused by global warming will require not only slowing the rate of warming but also mediating the effects of increasing temperatures that are inevitable given current atmospheric carbon dioxide levels. Before they can effectively mediate these effects, scientists need to understand how warming temperatures affect not only climate factors such as average temperature, rainfall, and storm intensity and frequency but also biological processes. For the remainder of the chapter, we will focus on the effects of increased carbon dioxide and increased temperatures on the physiology of living organisms.

4.2 Cellular Respiration

Increasing temperatures can change an organism's energy needs and can affect how rapidly it grows, develops, and reproduces. For some organisms, increasing energy needs associated with higher temperatures can cause them to be outcompeted for resources by other organisms; this is ultimately what requires many of the species described earlier to move toward the poles or higher in elevation. For other organisms, higher temperatures allow them to go through their life cycles more rapidly, leading to increased populations. In both cases, the process that causes these effects is cellular respiration.

The main function of cellular respiration is to convert the energy stored in chemical bonds of food into energy that cells can use. Energy is stored in the electrons of chemical bonds, and when bonds are broken, electrons can be moved from one molecule to another. Cells use a chemical called **adenosine triphosphate**, or **ATP**, as their energy source. ATP can supply energy to cells because it stores energy obtained from the movement of electrons that originated in food into its own bonds.

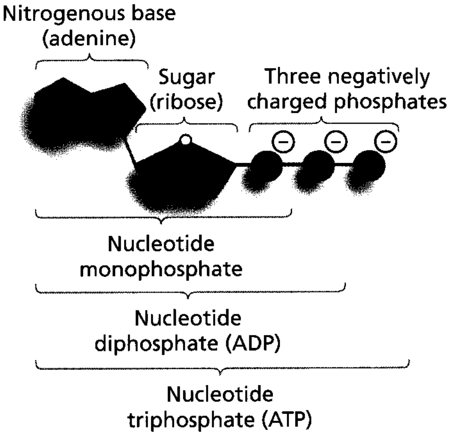


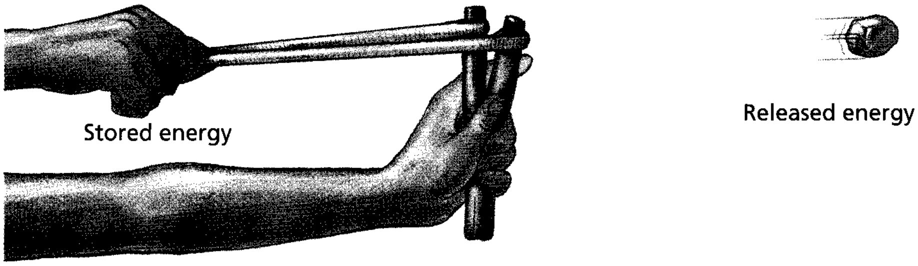
Figure 4.9 The structure of ATP. ATP is a nucleotide (sugar + phosphate + nitrogenous base) with a total of 3 phosphates. Notice that the phosphates are all negatively charged.

Structure and Function of ATP

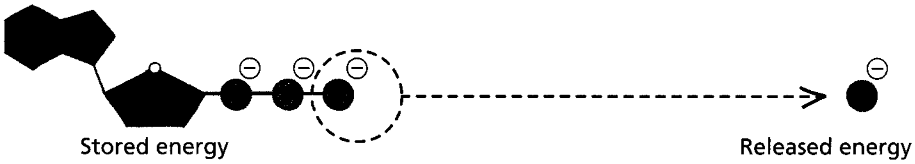
As described in Chapter 2, nucleic acids are one of the four main categories of biological molecules required by cells (the other three are carbohydrates, lipids, and proteins). Nucleic acids are polymers of nucleotides. Nucleotides consist of a nitrogenous, or nitrogen-containing, base—adenine (A), guanine (G), cytosine (C), or thymine (T)—plus a sugar and a phosphate group (made up of the elements phosphorus and oxygen). ATP is a nucleotide *tri*phosphate. It contains the nitrogenous base adenine, a sugar, and not one but three phosphates (Figure 4.9). Each phosphate in the series of three is negatively charged.

Figure 4.10 Stored energy. (a) A slingshot uses energy stored in the rubber band, supplied by arm muscles, to perform the work of propelling an object such as a rock. (b) ATP uses energy stored in its bonds to perform cellular work.

(a) Released energy can be used to perform work.



(b) Releasing a phosphate group from ATP generates released energy.



These negative charges repel each other, which contributes to the stored energy in this molecule. ATP behaves in a manner similar to a stretched rubber band. Think about using a slingshot. Pulling back the rubber band on the slingshot requires energy from your arm muscles, and much of the energy you use will be stored in the stretched band (Figure 4.10a). When you release the rubber band, the energy is released and is used to perform some work—in this case, sending a projectile through the air. Likewise, releasing a phosphate group from ATP liberates stored energy that can be used by cells to perform work (Figure 4.10b). After the removal of a phosphate group, ATP is converted into **adenosine diphosphate (ADP)**, which has two phosphates (hence *di*phosphate instead of *tri*phosphate).

The phosphate group that is removed from ATP can be transferred to another molecule. Thus, one way for ATP to energize other compounds is through **phosphorylation**, which means that it adds a phosphate. You can think of the donated phosphate as a little bag of energy. When a molecule, say an enzyme, needs energy, the phosphate group is transferred from ATP to the enzyme, and the enzyme now has the energy it needs to perform its job (Figure 4.11). The energy released by the removal of the outermost phosphate of ATP can be used to help cells perform many different kinds of work. ATP helps power *mechanical work* such as the movement of proteins in muscles,

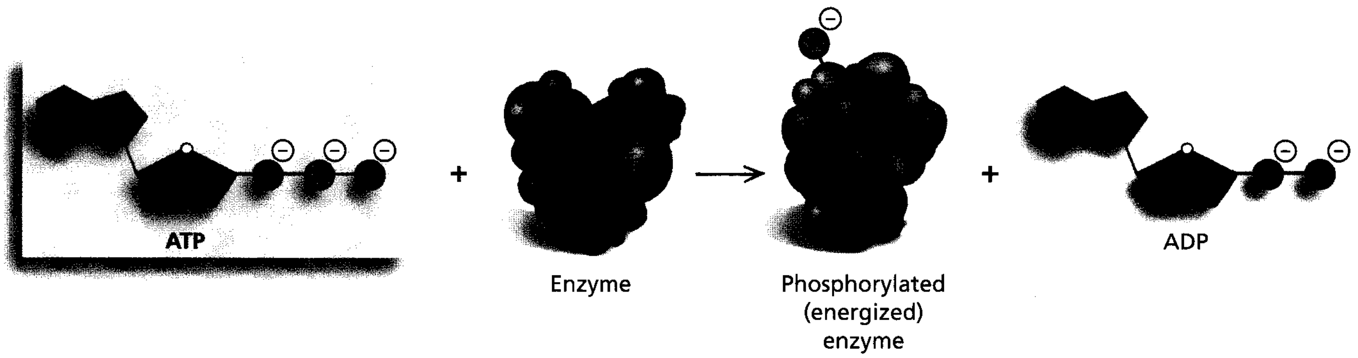


Figure 4.11 Phosphorylation. The terminal phosphate group of an ATP molecule can be transferred to another molecule, in this case an enzyme, to energize it. When ATP loses a phosphate, it becomes ADP. The enzyme that gained the phosphate group becomes energized.

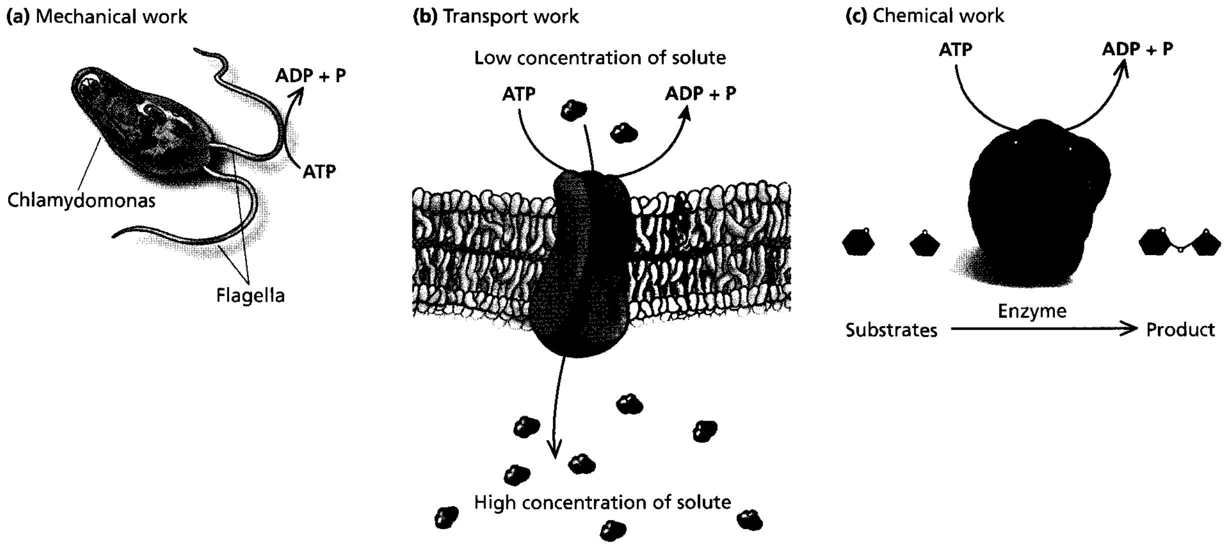


Figure 4.12 ATP and cellular work. ATP powers (a) mechanical work, such as the moving of the flagella of this single-celled green algae, Chlamydomonas; (b) transport work, such as the active transport of a substance across a membrane from its own low to high concentration; and (c) chemical work, such as the enzymatic conversion of substrates to a product.

transport work such as the movement of substances across membranes during active transport, and *chemical work* such as the making of complex molecules from simpler ones (Figure 4.12).

Cells are continuously using ATP. Exhausting the supply of ATP means that more ATP must be regenerated. ATP is synthesized by adding back a phosphate group to ADP during the process of cellular respiration (Figure 4.13). During this process, cells produce carbon dioxide and use oxygen to produce water. Because some of the steps in cellular respiration require oxygen, they are said to be **aerobic** reactions, and cellular respiration is called **aerobic respiration**. Humans and other animals with lungs breathe in oxygen, which is then delivered to cells. The carbon dioxide that is exhaled during breathing removes this waste product of cellular respiration from your body (Figure 4.14, shown on page 80). Plants and other organisms without lungs can respire and produce carbon dioxide as well.

Most foods can be broken down to produce ATP as they are routed through a complex pathway. Carbohydrate metabolism begins at the beginning of the pathway, while proteins and fats enter at later points.

A General Overview of Cellular Respiration

The equation for carbohydrate breakdown is:

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

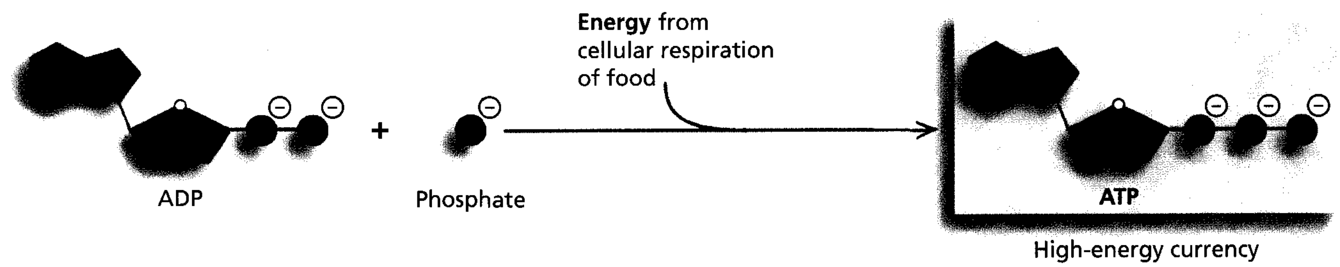


Figure 4.13 Regenerating ATP. ATP is regenerated from ADP and phosphate during the process of cellular respiration.

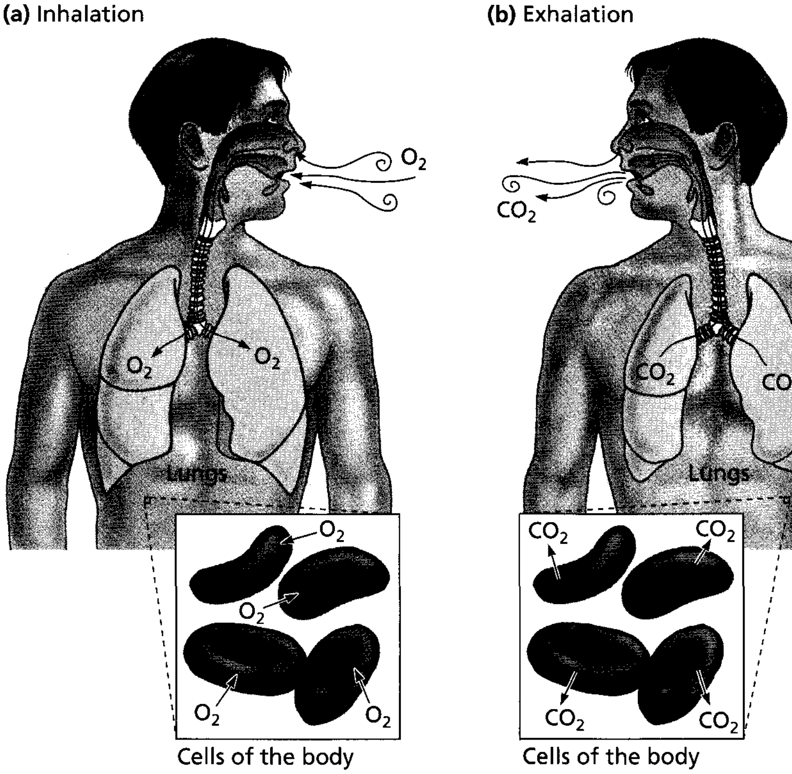


Figure 4.14 Breathing and cellular respiration. (a) When you inhale, you bring oxygen from the atmosphere into your lungs. This oxygen is delivered through the bloodstream to tissues that use it to drive cellular respiration. (b) The carbon dioxide produced by cellular respiration is released from cells and diffuses into the blood and to the lungs. Carbon dioxide is released from the lungs when you exhale.

Glucose is an energy-rich sugar, but the products of its digestion—carbon dioxide and water—are energy poor. The energy released during the conversion of glucose to carbon dioxide and water is used to synthesize ATP. Many of the chemical reactions in this process occur in sausage-shaped organelles called mitochondria through a series of complex reactions that break apart the glucose molecule. In doing so, the carbons and oxygens that make up the original glucose molecule are released from the cell as carbon dioxide. The hydrogens present in the original glucose molecule combine with oxygen to produce water (Figure 4.15). Gaining an appreciation for *how* this happens requires a more in-depth look.

Glycolysis, the Krebs Cycle, and Electron Transport

To harvest energy from glucose, the 6-carbon glucose molecule is first broken down into two 3-carbon **pyruvic acid** molecules. This part of the process of cellular respiration actually occurs outside of any organelle in the fluid cytosol and is called **glycolysis** (Figure 4.16). Glycolysis does not require oxygen but does produce a small amount of ATP. Bacteria on early Earth, which lacked oxygen, may have obtained their energy by glycolysis. Even today, many bacteria and organisms that live in the absence of oxygen, or **anaerobic** environments, rely on glycolysis for energy generation (Essay 4.1 on page 82). After glycolysis, the pyruvic acid is decarboxylated (loses a carbon dioxide molecule), and the 2-carbon fragment that is left is further metabolized inside the mitochondria.

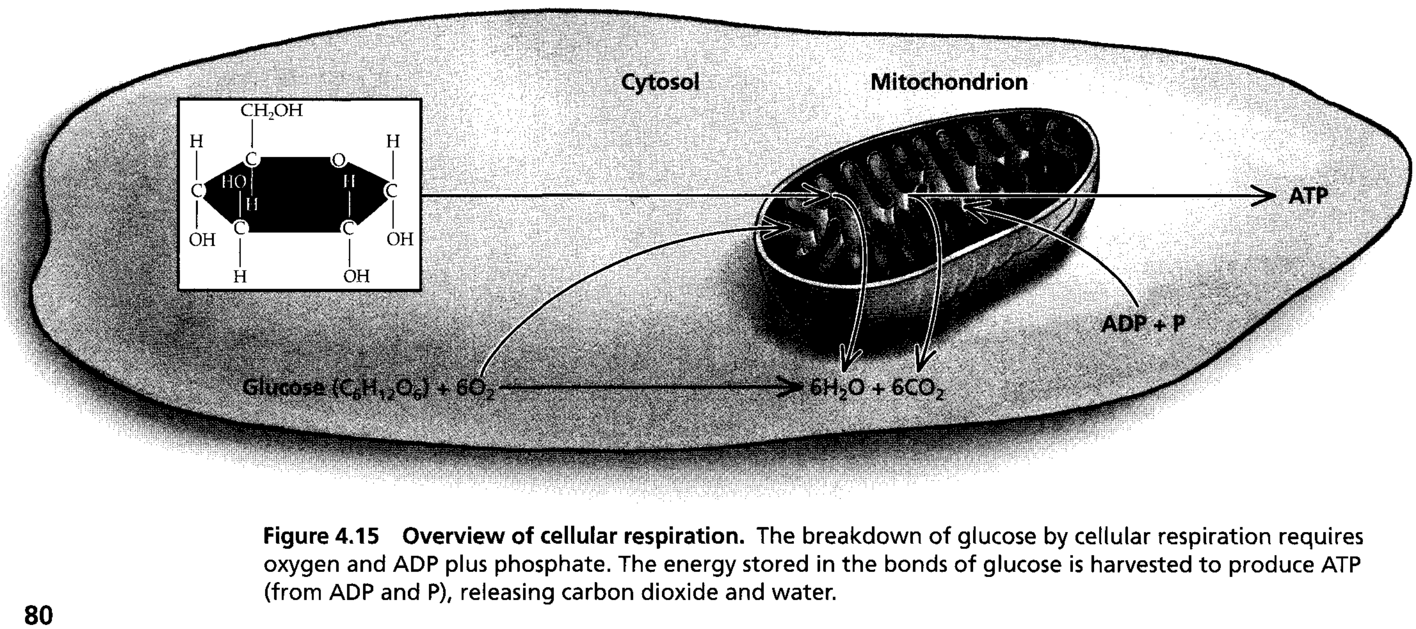


Figure 4.15 Overview of cellular respiration. The breakdown of glucose by cellular respiration requires oxygen and ADP plus phosphate. The energy stored in the bonds of glucose is harvested to produce ATP (from ADP and P), releasing carbon dioxide and water.

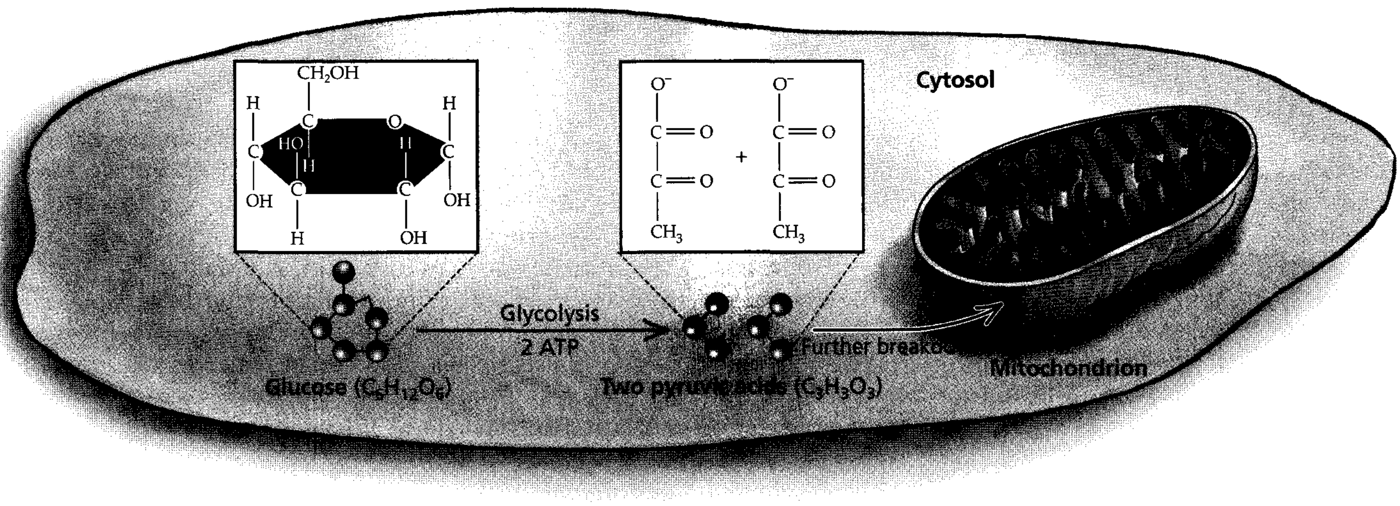


Figure 4.16 Glycolysis. Glycolysis occurs in the cytosol and does not require oxygen. Glycolysis is the enzymatic conversion of glucose into two pyruvic acid molecules. The pyruvic acid molecules are further broken down in the mitochondrion. A very small amount of ATP is made during glycolysis.

Mitochondria (singular: mitochondrion) are organelles found in both plant and animal cells. These organelles are surrounded by an inner and an outer membrane (Figure 4.17). The space between the two membranes is called the intermembrane space. The semifluid medium inside the mitochondrion is called the matrix. Once inside the mitochondrion, the energy stored in the bonds of pyruvic acid is converted into the energy stored in the bonds of ATP. The first step of this conversion is called the Krebs cycle.

Krebs Cycle. The Krebs cycle is a series of reactions catalyzed by eight different enzymes, located in the matrix of each mitochondrion. The Krebs cycle breaks down the remains of a carbohydrate, harvesting its

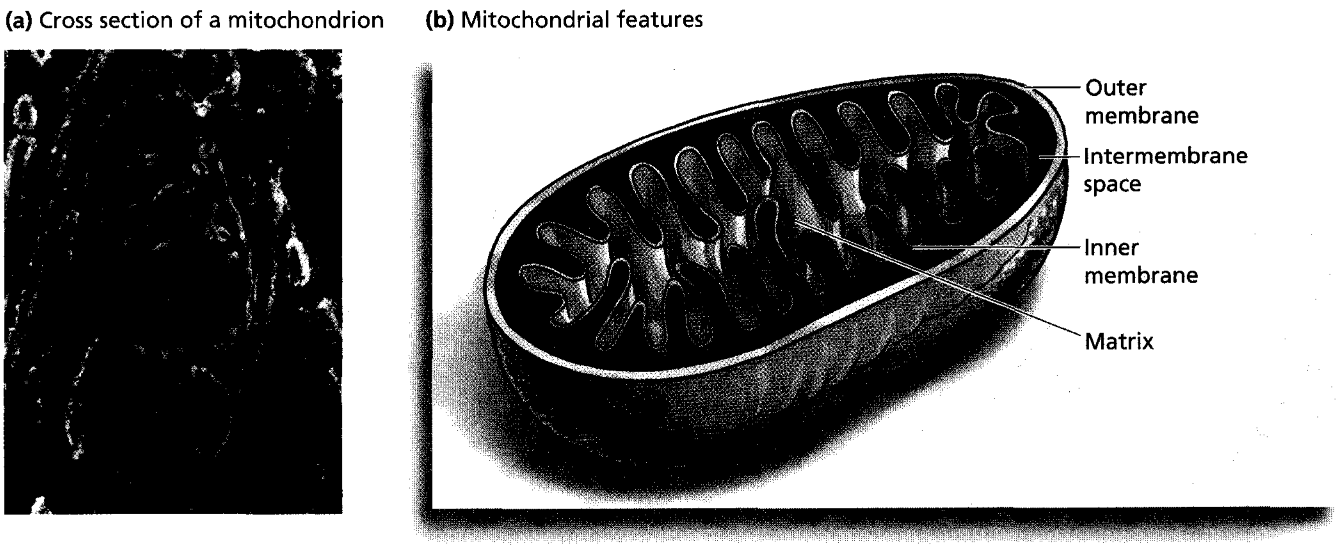


Figure 4.17 Mitochondria. (a) Mitochondria are microscopic organelles. (b) Mitochondria have an inner and an outer membrane. The area enclosed by these two membranes is called the intermembrane space. The fluid enclosed by the inner membrane is called the matrix. Different cell types have different numbers of mitochondria, and energy-requiring cells have more mitochondria than less active cells.

Essay 4.1 Metabolism Without Oxygen: Anaerobic Respiration and Fermentation

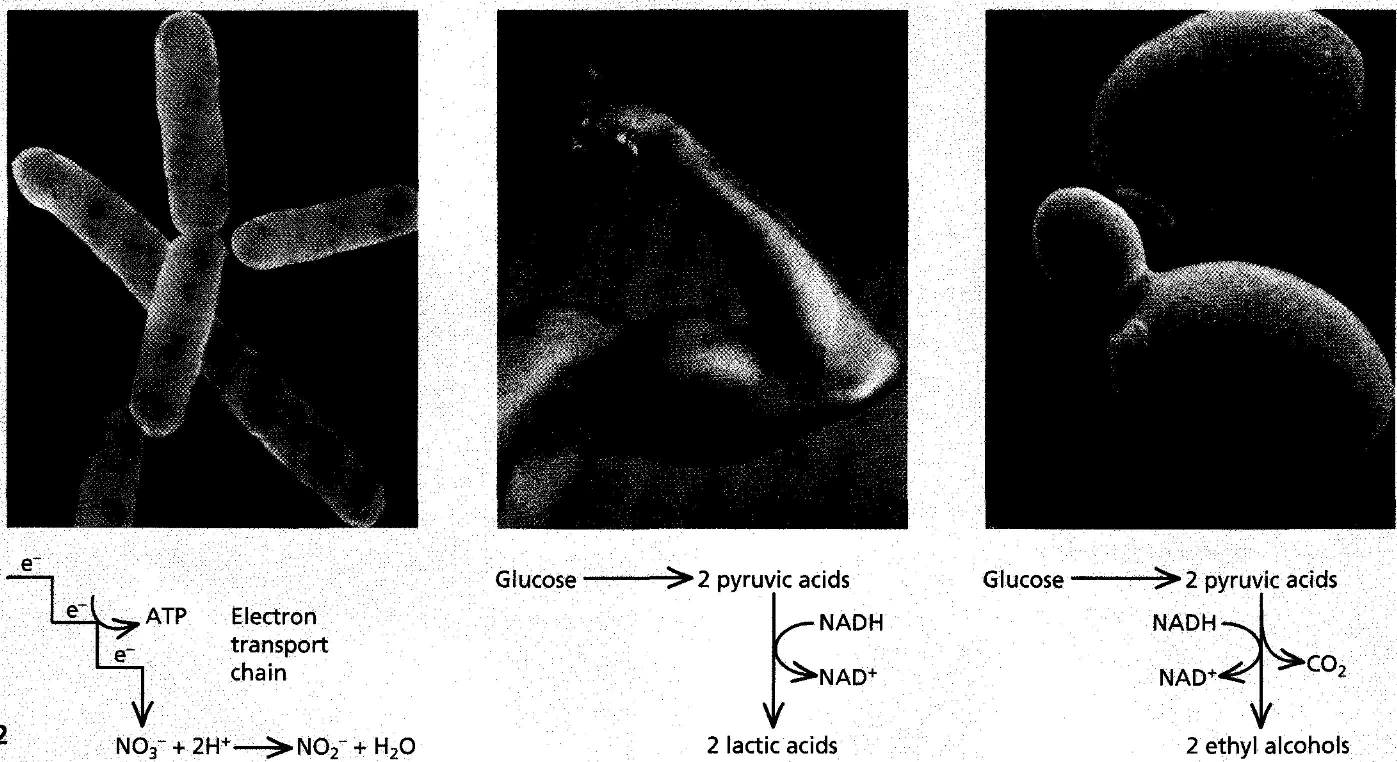
Aerobic respiration is one way for organisms to generate energy. It is also possible for cells to generate energy in the absence of oxygen, by a process called **anaerobic respiration**. Anaerobic organisms do not use oxygen as their final electron acceptor to pull electrons down the electron transport chain; a different molecule must be used. Some bacteria, called nitrate reducers, can transfer electrons to nitrate (NO_3^-), reducing it to nitrite (NO_2^-) (Figure E4.1a). Anaerobic respiration is an ATP-generating process.

Muscle cells normally produce ATP by aerobic respiration. However, oxygen supplies diminish with intense exercise. When muscle cells run low on oxygen, they must get most of their ATP from glycolysis, which does not require oxygen. When glycolysis happens without aerobic respiration, the cells run low on NAD^+, which is converted into NADH by glycolysis. The cells use a process called **fermentation** to regenerate NAD^+. No usable energy is produced by fermentation; fermentation simply recycles NAD^+. Fermentation cannot, however, be used for very long because one of the by-products of this reaction leads to the buildup of a compound called lactic acid. Lactic acid is produced by the actions of the electron acceptor NADH, which has no place to dump its electrons during fermentation since there is no electron transport chain and no oxygen to accept the electrons. Instead, NADH deposits its electrons by giving them to the pyruvic acid produced by glycolysis (Figure E4.1b). Adding electrons to pyruvic acid produces lactic acid that accumulates and causes the muscle burn or cramping you feel after a vigorous workout. Lactic acid is transported to the liver, where liver cells use oxygen to convert it back to pyruvic acid. This requirement for oxygen, to convert lactic acid to pyruvic acid, explains why you continue to breathe heavily even after you have stopped working out. Your body needs to supply oxygen to your liver for this conversion, sometimes referred to as "paying back your oxygen debt." The accumulation of lactic acid also explains the phenomenon called "hitting the wall." Anyone who has ever felt as though their legs were turning to wood while running or biking knows this feeling. When your muscles are producing lactic acid by fermentation for a long time, the oxygen debt becomes too large, and muscles shut down until the rate of oxygen supply outpaces the rate of oxygen utilization.

Some fungi and bacteria also produce lactic acid during fermentation. Certain microbes placed in an anaerobic environment transform the sugars in milk into yogurt, sour cream, and cheese. It is the lactic acid present in these dairy products that gives them their sharp or sour flavor. Yeast in an anaerobic environment produces ethyl alcohol instead of lactic acid. Ethyl alcohol is formed when carbon dioxide is removed from pyruvic acid (Figure E4.1c). The yeast used to help make beer and wine converts sugars present in grains (beer) or grapes (wine) into ethyl alcohol and carbon dioxide. Carbon dioxide produced by baker's yeast helps bread to rise.

Figure E4.1

(a) Bacterial cell **(b)** Human muscle cell **(c)** Yeast cell



electrons and releasing carbon dioxide into the atmosphere (Figure 4.18). These reactions are a cycle because every turn of the cycle regenerates the first reactant in the cycle. Therefore, the first reactant in the cycle, a 4-carbon molecule called oxaloacetate (OAA), is always available to react with carbohydrate fragments entering the Krebs cycle.

In addition to removing carbon dioxide, the Krebs cycle also removes electrons for use in producing ATP. These electrons do not simply float around in a cell; they are carried by molecules called electron carriers. One of the electron carriers utilized by cellular respiration is a chemical called **nicotinamide adenine dinucleotide (NAD)** (Figure 4.19 on page 84). **NAD^+** picks up 2 hydrogen atoms and releases 1 positively charged proton (H^+). Each **hydrogen atom** is composed of 1 negatively charged electron and 1 positively charged proton. When NAD^+ picks up 2 hydrogen atoms (each with 1 proton and 1 electron), it utilizes 1 proton and 2 electrons, releasing the remaining proton.

A careful look back at Figure 4.16 on page 81 shows that the conversion of glucose ($C_6H_{12}O_6$) into 2 pyruvic acid molecules ($2C_3H_3O_3^-$) results in the loss of 6 hydrogens. This is because glycolysis also results in the production of some NADH from NAD^+.

NADH *serves as a sort of taxicab for electrons.* The empty taxicab (NAD^+) picks up electrons. The full taxicab (NADH) carries electrons to their destination, where they are dropped off, and the empty taxicab returns

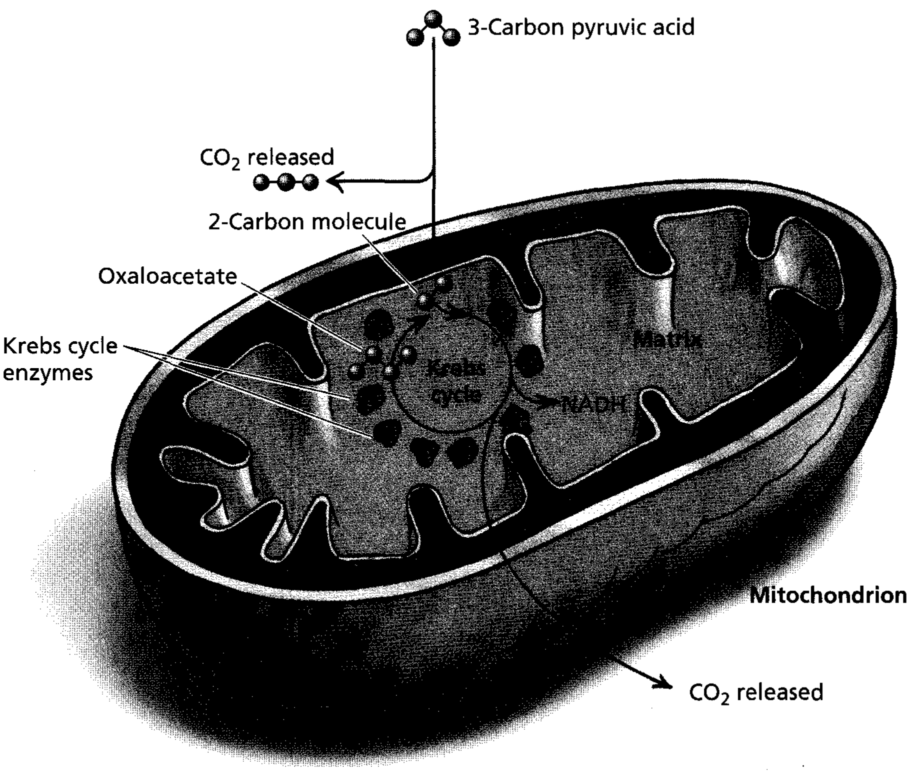


Figure 4.18 The Krebs cycle. The 3-carbon pyruvic acid molecules generated by glycolysis are decarboxylated, leaving a 2-carbon molecule that enters the Krebs cycle within the mitochondrial matrix. The 2-carbon fragment reacts with a 4-carbon OAA molecule and proceeds through a stepwise series of reactions that results in the production of more carbon dioxide and regenerates OAA. NADH is also produced.

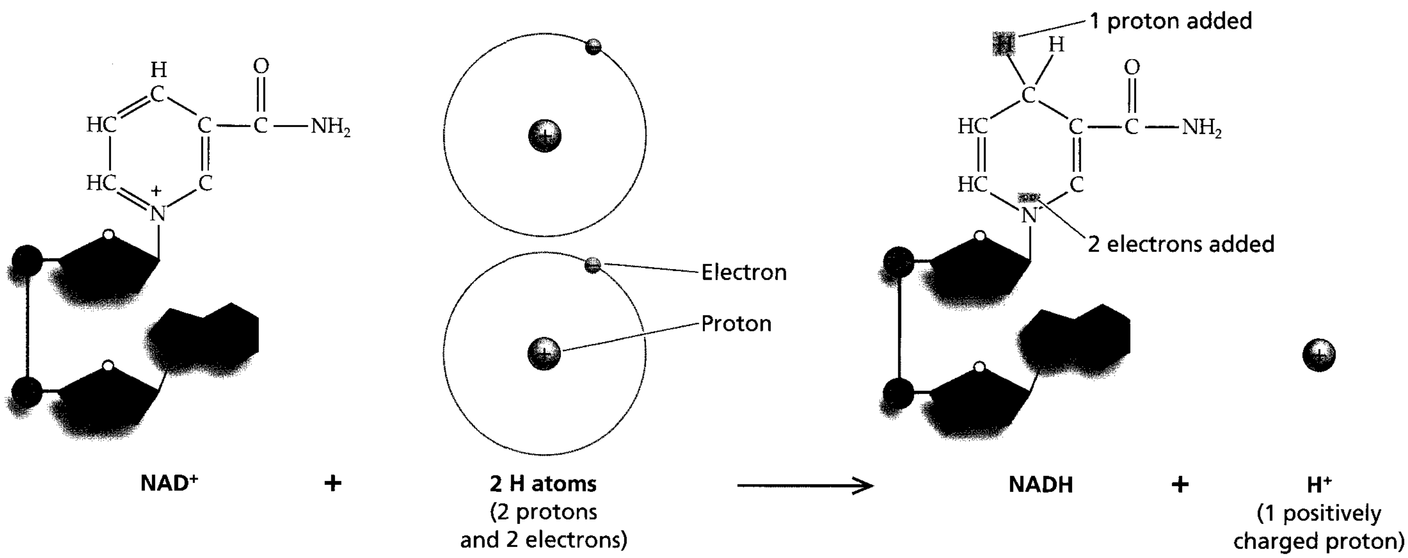


Figure 4.19 Nicotinamide adenine dinucleotide (NAD). Nicotinamide adenine dinucleotide (NAD) is a dinucleotide in the sense that it contains 2 sugars, 2 phosphates, and the nitrogenous base adenine. This molecule can pick up a hydrogen atom along with its electrons. Hydrogen atoms are composed of 1 negatively charged electron that circles around the 1 positively charged proton. When NAD^+ encounters 2 hydrogen atoms (from food), it utilizes each hydrogen atom's electron and only 1 proton, thus releasing 1 proton.

for more electrons. NADH deposits its electrons at the top of the electron transport chain (Figure 4.20).

The Electron Transport Chain. This series of proteins embedded in the inner mitochondrial membrane functions as a sort of conveyer belt for electrons, moving them from one protein to another. The electrons are

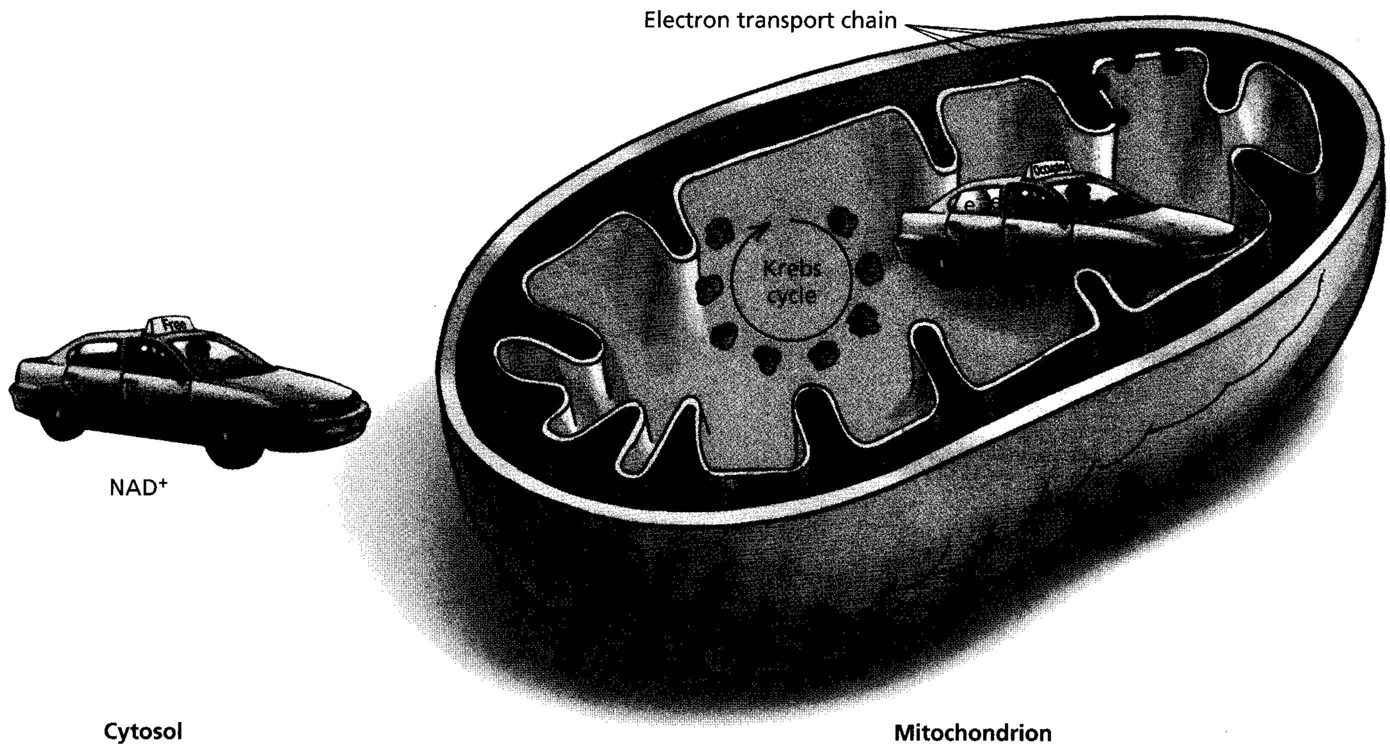
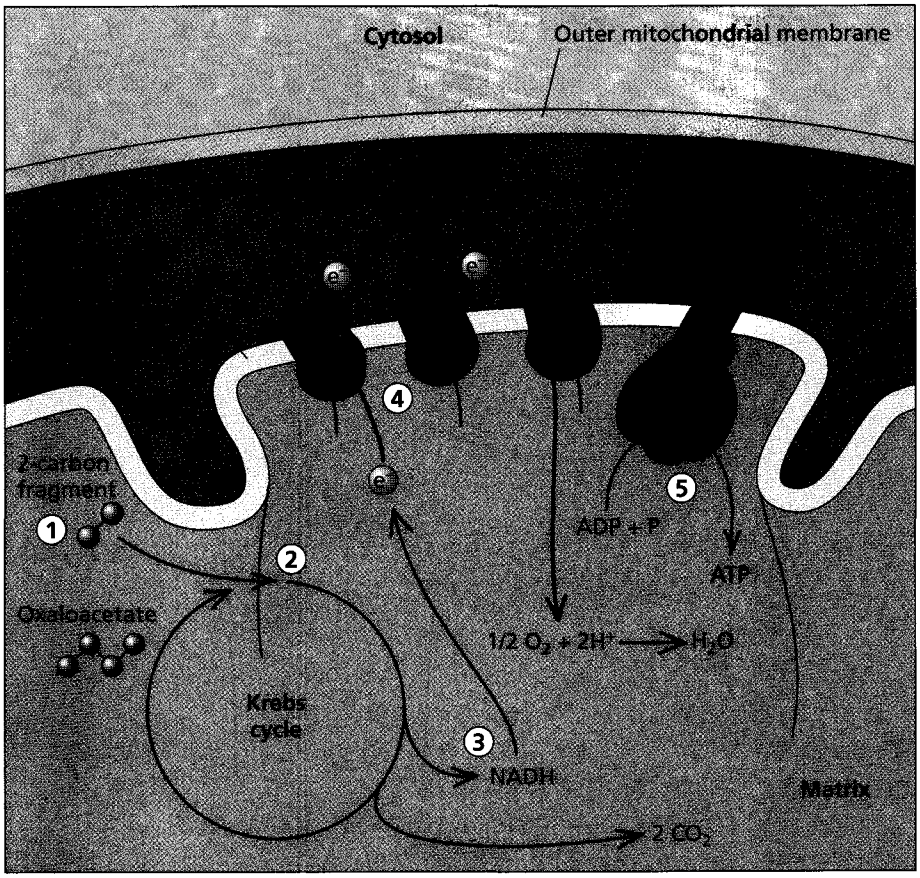


Figure 4.20 Electron carriers. NADH serves as an electron carrier, bringing electrons removed from the original glucose molecule to the electron transport chain. After dropping off its electrons, the electron carrier can be loaded up again and bring more electrons to the electron transport chain.



(1) Glucose is broken down into pyruvic acid by glycolysis. Pyruvic acid is decarboxylated producing a 2-carbon fragment.

(2) The 2-carbon fragment is fed into the Krebs cycle in the matrix of the mitochondrion.

(3) NADH molecules carry electrons from the Krebs cycle to the electron transport chain.

(4) As electrons are moved through the proteins of the electron transport chain, hydrogen ions are pumped into the intermembrane space.

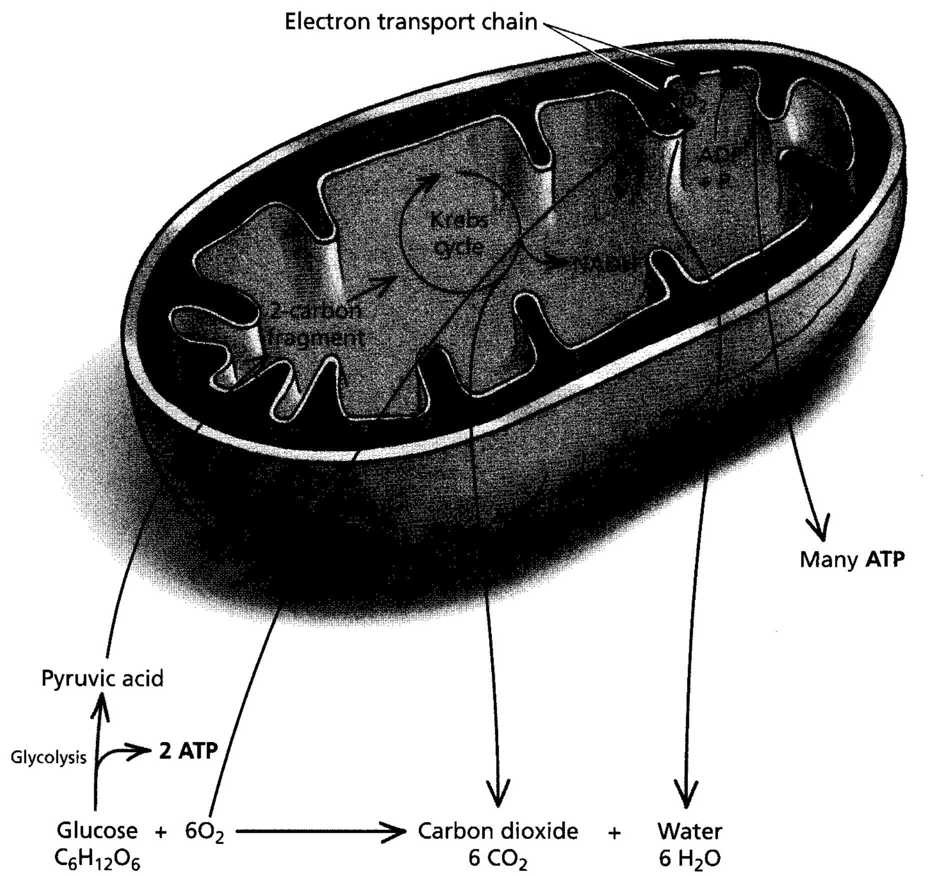
(5) Hydrogen flows back into the matrix through an ATP synthase protein, which converts ADP and P to ATP.

Figure 4.21 The electron transport chain. Energy from electrons added to the top of the electron transport chain is used to produce ATP.

pulled toward the bottom of the electron transport chain by oxygen in the matrix of the mitochondrion. One property of oxygen is that because it is very electronegative, or electron-loving, it pulls electrons toward itself. Each time an electron is picked up by a protein or handed off to another protein, the protein moving it changes shape. This shape change facilitates the movement of protons (H^+) from the matrix of the mitochondrion to the intermembrane space. So, while the proteins in the electron transport chain are moving electrons down the electron transport chain toward oxygen, they are also moving H^+ ions across the inner mitochondrial membrane and into the intermembrane space. This decreases the concentration of H^+ ions in the matrix and increases their concentration within the intermembrane space. As you learned in Chapter 3, whenever a concentration gradient of a molecule exists, molecules will diffuse from an area of high concentration to an area of low concentration. Since charged ions cannot diffuse across the hydrophobic core of the membrane, they escape through a protein channel in the membrane called **ATP synthase**. This enzyme uses the energy generated by the rushing H^+ ions to synthesize ATP from ADP and phosphate in the same manner that water rushing through a mechanical turbine can be used to generate electricity. The electrons that were pulled down the electron transport chain then combine with the oxygen at the bottom of the chain and 2 hydrogens in the matrix to produce water (Figure 4.21).

Overall, the two pyruvic acids produced by the breakdown of glucose during glycolysis are converted into carbon dioxide and water. Carbon dioxide is produced when it is removed from the pyruvic acid molecules during the Krebs cycle, and water is formed when oxygen combines with hydrogens at

Figure 4.22 Summary of cellular respiration. This figure diagrams the inputs and outputs of cellular respiration.



the bottom of the electron transport chain. A summary of the process is shown in Figure 4.22.

Metabolism of Other Nutrients. Proteins and fats are broken down and their subunits merge with the carbohydrate breakdown pathway. Figure 4.23 shows the points of entry for proteins and fats. Protein is broken down into component amino acids, which are then used to synthe-

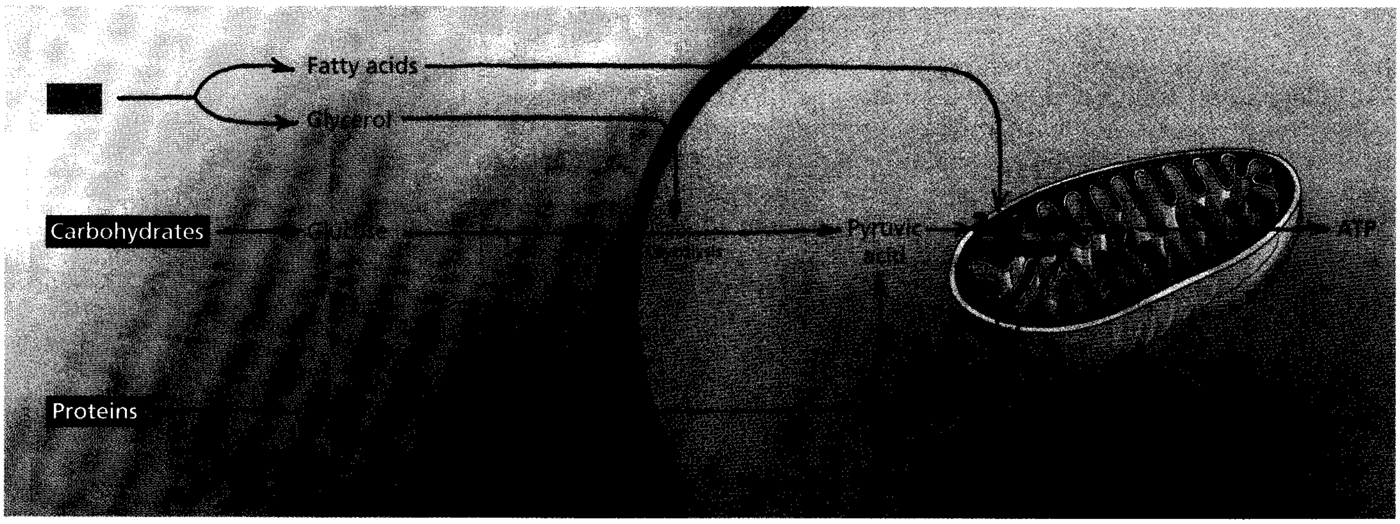
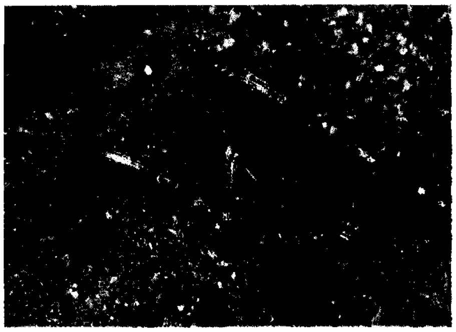


Figure 4.23 Metabolism of other macromolecules. Carbohydrates, proteins, and fats can all undergo cellular respiration; they just feed into different parts of the metabolic pathway.

size new proteins. Most organisms can also break down proteins to supply energy. However, this process takes place only when fats or carbohydrates are unavailable. In humans and other animals, the first step in producing energy from the amino acids of a protein is to remove the nitrogen-containing amino group of the amino acid. Amino groups are then converted to a compound called urea, which is excreted in the urine. The carbon, oxygen, and hydrogen remaining after the amino group is removed undergo further breakdown and eventually enter the mitochondria, where they are fed through the Krebs cycle and produce carbon dioxide, water, and ATP. The subunits of fats (glycerol and fatty acids) also go through the Krebs cycle and produce carbon dioxide, water, and ATP. Most cells will break down fat only when carbohydrate supplies are depleted.

Whether carbohydrate, protein, or fat, these nutrients are used to generate energy. It turns out that this energy generation can be affected by rising temperatures, leading to some devastating effects.

(a) Spruce bark beetle



(b) Spruce tree

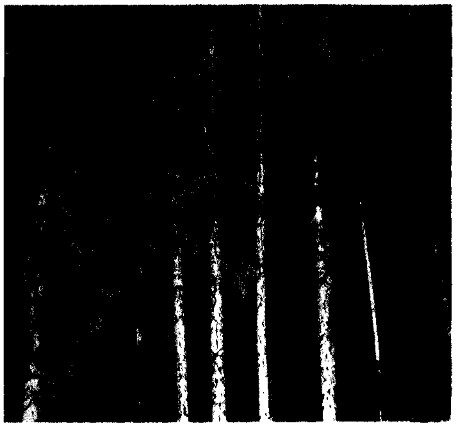


Figure 4.24 Spruce bark infestation. The spruce bark beetle (a) kills spruce trees (b) by blocking water and nutrient flow.

Global Warming and Cellular Respiration

Alaska's Kenai Peninsula is experiencing firsthand some effects of global warming on cellular respiration. Increases in temperature have helped to speed up the life cycle of the spruce bark beetle (Figure 4.24a). These beetles, about the size of a grain of rice, attack spruce trees by boring through the outer bark to the phloem, a thin layer directly beneath the outer bark that transports food manufactured by photosynthesis from the foliage down to the roots. Once inside the phloem, the beetle feeds and lays eggs. The resulting damage and blockage of the phloem prevents nutrient transport to the roots, and the tree dies (Figure 4.24b). Over the past decade, the spruce population has suffered huge losses—close to 4 million acres of trees on southeastern Alaska's Kenai Peninsula; nearly all of the spruce trees there have been killed by infestations of these bark beetles.

Populations of spruce bark beetles are normally kept in check by cool summers and bitterly cold winters. Cooler summers help control the number of beetles because they cannot fly when temperatures are below 60°F. This limits the beetles' ability to colonize other trees. Cold winters can kill beetles and their larvae. The warmer temperatures not only fail to kill beetles in the winter but also speed up this insect's rate of reproduction. Typically it takes a spruce bark beetle 2 years to develop from an egg to an adult. But the warmer summers and winters have allowed the beetle to develop into an adult and lay new eggs during just one summer. More beetles mean more destruction to forests.

The accelerated life cycle of spruce bark beetles can be credited, in part, to the speeding up of cellular respiration. The enzymes that catalyze the reactions of cellular respiration, like all enzymes, are affected by temperature. Warmer temperatures typically speed up the rate at which enzymes catalyze reactions. That is, unless the temperature gets too hot, in which case the enzyme loses its characteristic shape and can no longer perform its job, and then a process called **denaturation** takes place. In a sense, warmer temperatures make the Krebs cycle spin faster, producing more energy, which allows the beetles to grow and reproduce more quickly as well as to fly earlier in the year and thus disperse to a greater number of trees.

As the beetles do their damage, trees drop their dried-out dead needles and limbs on the ground, providing fuel for forest fires. Forest fires release even more carbon dioxide into the atmosphere as the carbohydrate that comprises much of the plant tissue, such as cellulose that makes up the cell wall, is burned. Cellular respiration is a controlled burn of carbohydrates whereby the energy released from breaking the bonds of sugars is used to make ATP.

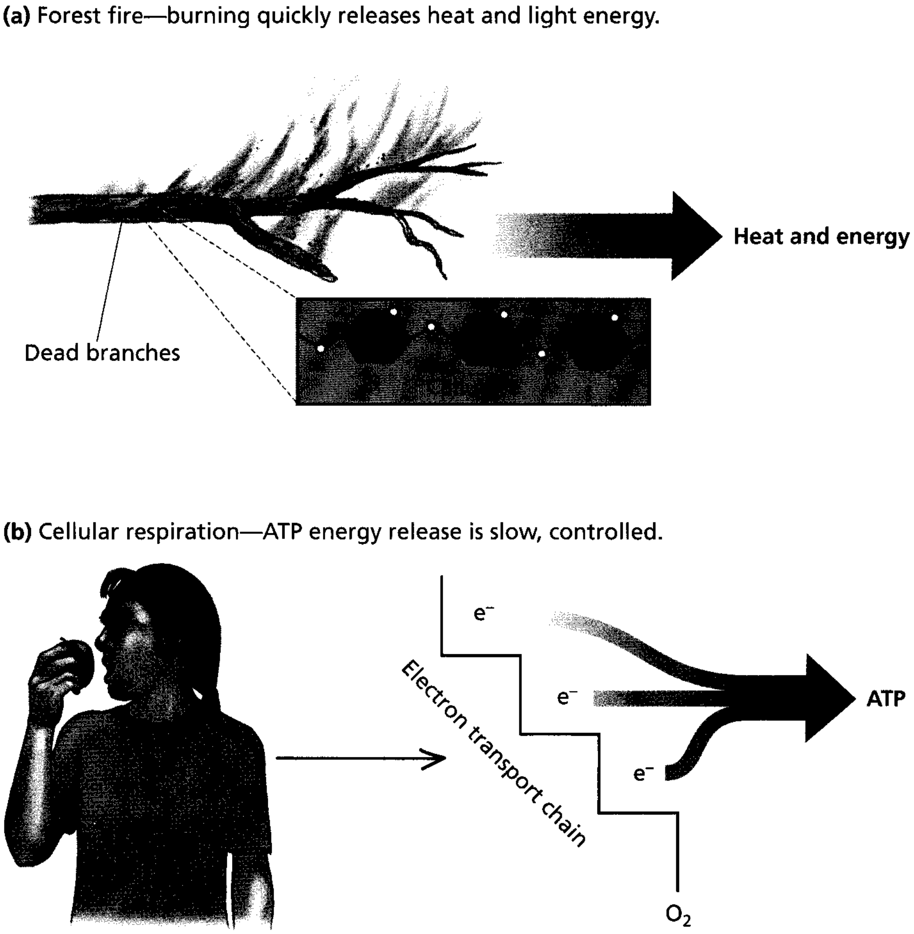


Figure 4.25 Cellular respiration is a controlled burn. Burning carbohydrates releases energy. (a) Plant cells have rigid cell walls composed of cellulose, a polymer of glucose. When carbohydrate burning is uncontrolled, as in a forest fire, energy is released as heat and light. (b) Cellular respiration is a controlled burn. Carbohydrates that are eaten have electrons removed during cellular respiration. As these electrons fall toward oxygen, they release energy that is used to drive the synthesis of ATP.

Combustion by fire releases all the stored energy without harvesting any for ATP production (Figure 4.25).

You have learned that carbon dioxide is released by cellular respiration and that increases in carbon dioxide levels are causing global warming. However, it would be a mistake to assume that cellular respiration is causing global warming. It is the increased carbon dioxide production caused by the burning of enormous amounts of fossil fuels that is shifting the balance of carbon dioxide production and uptake. The effects of carbon dioxide production (due to cellular respiration) on global warming is minimal and is mitigated by carbon dioxide uptake that occurs via photosynthesis.

4.3 Photosynthesis

Plants and other photosynthetic organisms remove carbon dioxide from the atmosphere and use it to make sugars and other macromolecules by the process of photosynthesis. The vast majority of the organic carbon found on Earth is a result of photosynthesis.

A General Overview of Photosynthesis

The equation summarizing photosynthesis follows:

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

The sun is the ultimate source of energy for living organisms. Plants transform energy from the sun into chemical energy through the process of photosynthesis by using light energy to rearrange the atoms present in carbon dioxide and water into energy-rich carbohydrates, producing oxygen as a waste product. In land plants, carbon dioxide enters, and oxygen gas is released through adjustable microscopic structures called **stomata** that are located on the surface of the leaf (Figure 4.26).

Plants use the carbohydrates that they produce by photosynthesis to grow and supply energy to their cells. They, along with the organisms that eat them, liberate the energy stored in the chemical bonds of sugars by undergoing the process of cellular respiration. Both plants and animals perform cellular respiration, but animals cannot perform photosynthesis.

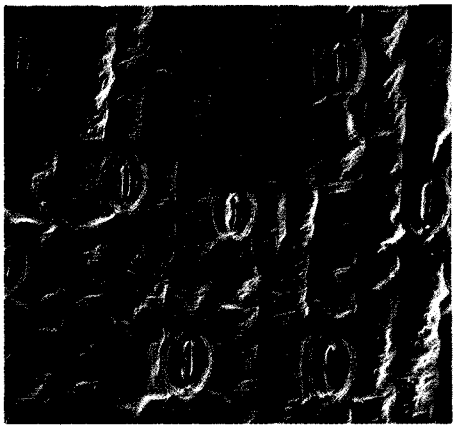


Figure 4.26 Stomata. Stomata are adjustable microscopic pores found on the surface of leaves that allow for gas exchange. Carbon dioxide enters the plant, and oxygen leaves through these openings.

The Light Reactions and Calvin Cycle

Green tissues in plants contain specialized organelles that serve as the sites of photosynthesis. Structurally, **chloroplasts** (Figure 4.27) are surrounded by two membranes. The inner and outer membranes together are called the chloroplast envelope. The chloroplast envelope encloses a compartment filled with **stroma**, a thick fluid that houses some of the enzymes of photosynthesis. Suspended in the stroma are disk-like membranous structures called **thylakoids**. When thylakoids are stacked on top of each other, like pancakes, the stacks are called **grana**. The large amount of membrane inside the chloroplast provides more surface area upon which some of the reactions of photosynthesis can occur. On the surface of the thylakoid membrane are millions of pigment molecules, called **chlorophyll**, that absorb energy from the sun.

It is the chlorophyll molecule that gives leaves and other plant structures their green color. Like all pigments, chlorophyll absorbs light. Light is made up of rays with different colors, or levels of energy, and each energy level has a different wavelength—to the human eye, shorter and middle wavelengths appear violet to green, and longer wavelengths appear yellow to red. Different organisms can perceive different wavelengths of light. For example, bees can see ultraviolet light, which is invisible to humans. Differences in wavelength visibility help bees see colors and patterns in floral structures as an aid to direct them to the sexual organs of the plant, like the landing lights at an airport direct jets to the runway.

Chlorophyll looks green to human eyes because it absorbs the shorter (blue) and longer (red) wavelengths of visible light and reflects the middle

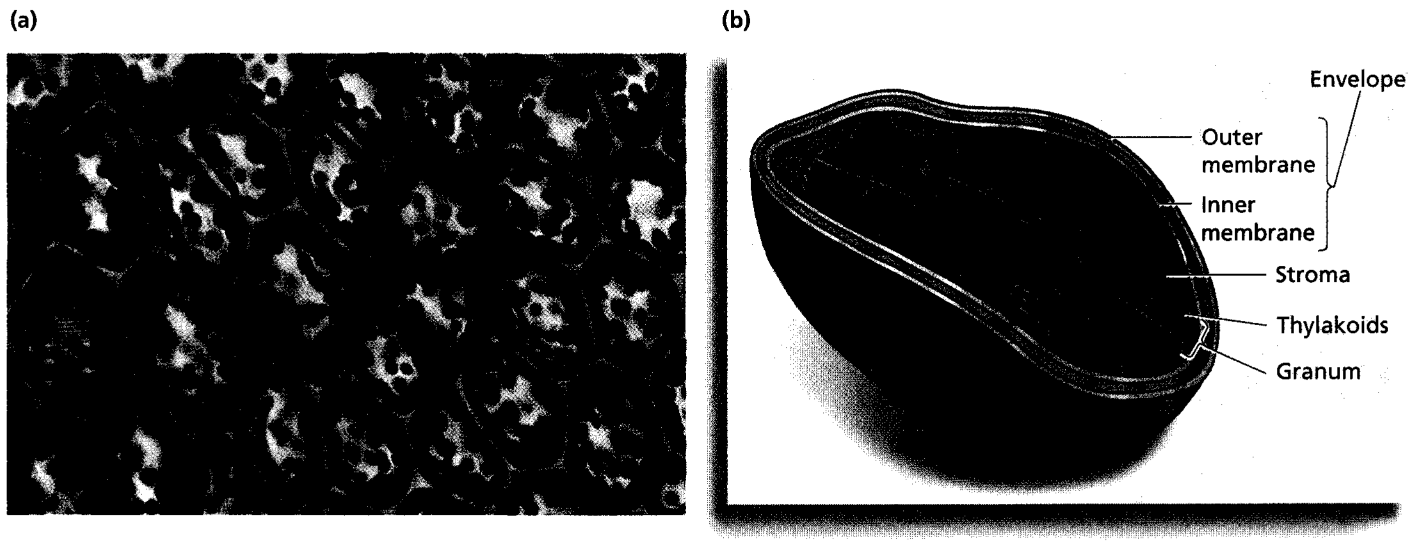


Figure 4.27 Chloroplasts. (a) Chloroplasts are microscopic organelles found in plant cells. (b) The chloroplast is enveloped—it has an inner and an outer membrane. More membranes are found inside the chloroplast housed in the liquid stroma. These membranes are called *thylakoids* when separate and *grana* when stacked.

(green) range of wavelengths. Leaves on deciduous trees change color in the fall because the abundant chlorophyll breaks down, making visible other less-abundant pigments present in the leaf that reflect red, orange, and yellow wavelengths.

Photosynthesis can be broken down into two steps. The first or "photo" step harvests energy from the sun during a series of reactions called the **light reactions**, which occur when there is sunlight. The second or "synthesis" step, called the **Calvin cycle**, uses the harvested energy to synthesize sugars either in the presence or absence of sunlight. For this reason, the Calvin cycle is also sometimes referred to as the dark reactions.

The Light Reactions. When a pigment such as chlorophyll absorbs sunlight, electrons associated with the pigment become excited or increase their energy level. In effect, the light energy is transferred to the chlorophyll and becomes chemical energy. For most pigments, the molecule remains excited for a very brief amount of time before the chemical energy is lost as heat. This is why a surface that looks black (that is, one composed of a pigment that absorbs all visible light wavelengths) heats up quickly in comparison to a surface that looks white (one that absorbs no visible light wavelengths). Inside a chloroplast, however, the chemical energy of the excited chlorophyll molecules is not allowed to be released as heat; instead, the energy is captured.

When sunlight strikes the chlorophyll molecule and electrons are excited, they move to a higher energy level. The electrons are then transferred to other molecules in an electron transport chain located in the thylakoid membrane. As the electrons are handed down the electron transport chain, some ATP is produced. Some of the proteins in the electron transport chain not only move electrons to a lower energy level, they also pump protons into the interior of the thylakoid, setting up a gradient in protons. The protons then rush through an ATP synthase enzyme located in the thylakoid membrane and produce ATP in the same way that mitochondria make ATP. The newly synthesized ATP is released into the stroma, where it can be used by the enzymes of the Calvin cycle to produce sugars and other organic molecules.

During the light reactions, oxygen is produced when water (H_2O) is "split" into 2 H^+ ions and a single oxygen atom (O). Two oxygen atoms combine to produce O_2, which is released from the chloroplast. Since the hydrogen atom usually contains a single proton, around which orbits a single electron, the splitting of water to produce two H^+ ions also releases 2 electrons. These 2 electrons are transferred back to the chlorophyll molecule to replace those passed along the electron transport chain.

At the end of the electron transport chain, electrons are transferred to the electron carrier for plants, which is nicotinamide adenine dinucleotide phosphate, or NADP. Just like the NAD^+ involved in cellular respiration, $NADP^+$ functions as an electron taxicab. The difference between NAD^+ and $NADP^+$ is simply the presence of an extra phosphate group. The $NADP^+$ used during photosynthesis picks up 2 electrons and 1 H^+ ion to become NADPH. NADPH ferries electrons to the stroma, where the enzymes of the Calvin cycle will use the electrons in assembling sugars (Figure 4.28). Thus, the light reactions produce ATP, a source of electrons for the synthesis step, and release oxygen as a by-product.

Calvin Cycle. The Calvin cycle is a series of enzymes located in the stroma that uses the ATP and NADPH produced during photosynthesis to convert carbon dioxide (CO_2) into sugars (CH_2O). CH_2O is the general formula for sugars. For example, glucose is $C_6H_{12}O_6$ or $6(CH_2O)$. A quick comparison of the composition of these molecules makes it obvious that converting CO_2 into CH_2O requires the incorporation of hydrogen atoms and their associated

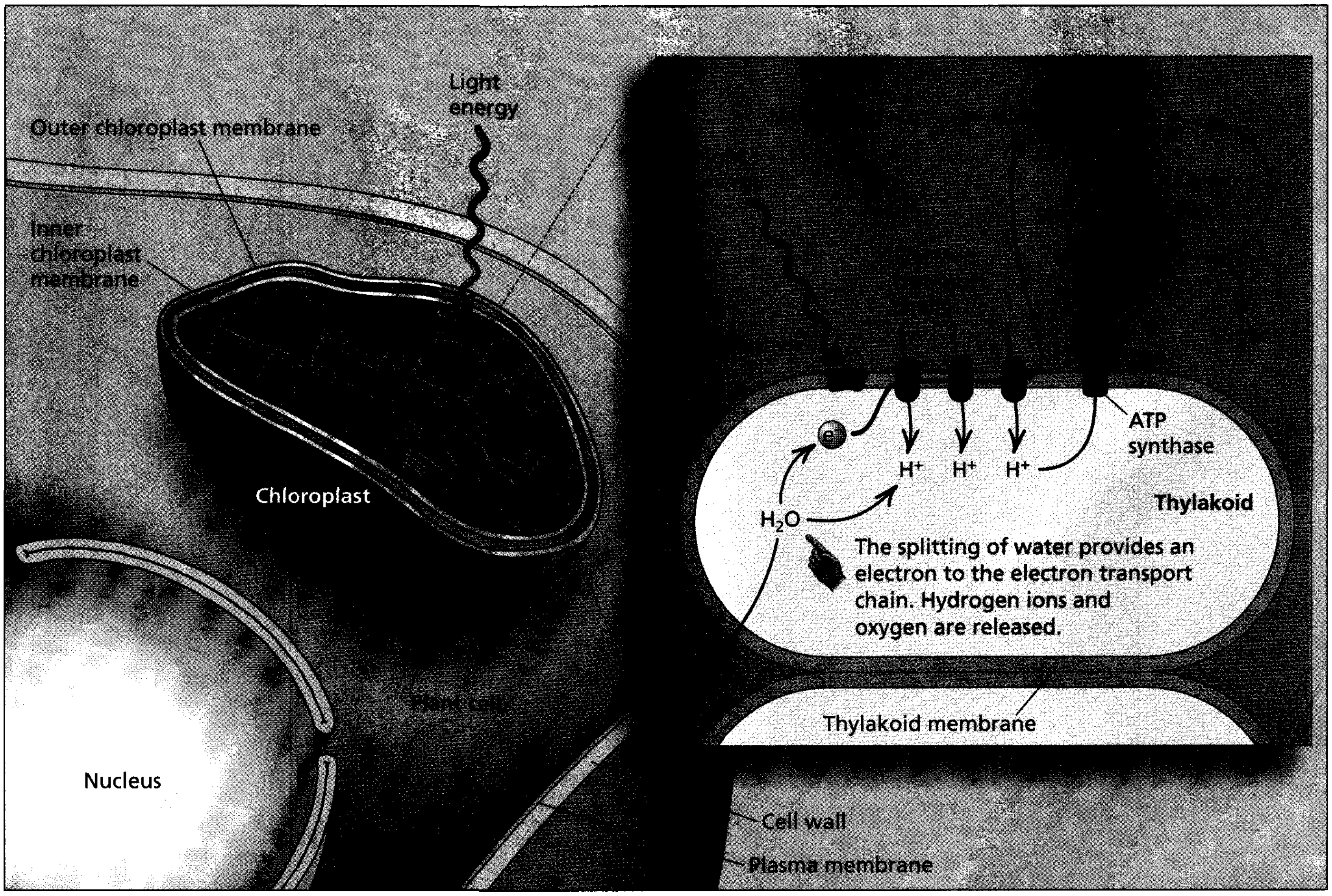


Figure 4.28 The light reactions. During the light reactions of photosynthesis, light strikes chlorophyll molecules located in the thylakoid membrane, exciting electrons that then move to a higher energy level. The energy of the excited electrons is harvested in a stepwise manner as the electrons are handed down an electron transport chain, producing ATP and NADPH that will be used by the Calvin cycle. The proton gradient is generated inside the thylakoid. ATP and NADPH are produced in the stroma where they will be available to the enzymes of the Calvin cycle.

electrons. Hydrogen atoms are removed from NADPH in order to produce sugars, thereby regenerating $NADP^+$.

During the Calvin cycle, carbon dioxide from the environment reacts with a 5-carbon molecule that is generated by the Calvin cycle and called ribulose bisphosphate or RuBP. The enzyme that performs this reaction is ribulose bisphosphate carboxylase oxygenase, or **rubisco**. This reaction produces an unstable 6-carbon molecule that immediately breaks down into two 3-carbon molecules called three-phosphoglyceric acid, or 3-PGA, which is rearranged to produce glyceraldehyde three-phosphate or G3P, a 3-carbon sugar that the cell uses to produce glucose and other compounds. RuBP is regenerated, completing the cycle (Figure 4.29 on page 92).

A careful look at the reactions of photosynthesis and cellular respiration show that the products of photosynthesis are used as reactants in cellular respiration and vice versa. This does not mean that these reactions are simply the reverse of each other. Instead, photosynthesis uses the products of cellular respiration as raw materials for the synthesis of sugars.

Without this reaction in the chloroplasts—when solar energy is transformed into the chemical energy in glucose—cellular respiration could not occur, and glucose would not be used to synthesize ATP. For this reason, *all* living things are dependent on photosynthesis for food, even meat-eating organisms, since they consume organisms that eat plants. In fact, the only two items in the human diet that do not come from plants (either directly or indirectly) are water and salt. Plants and other photosynthetic organisms make all the oxygen in the atmosphere that humans require for respiration.

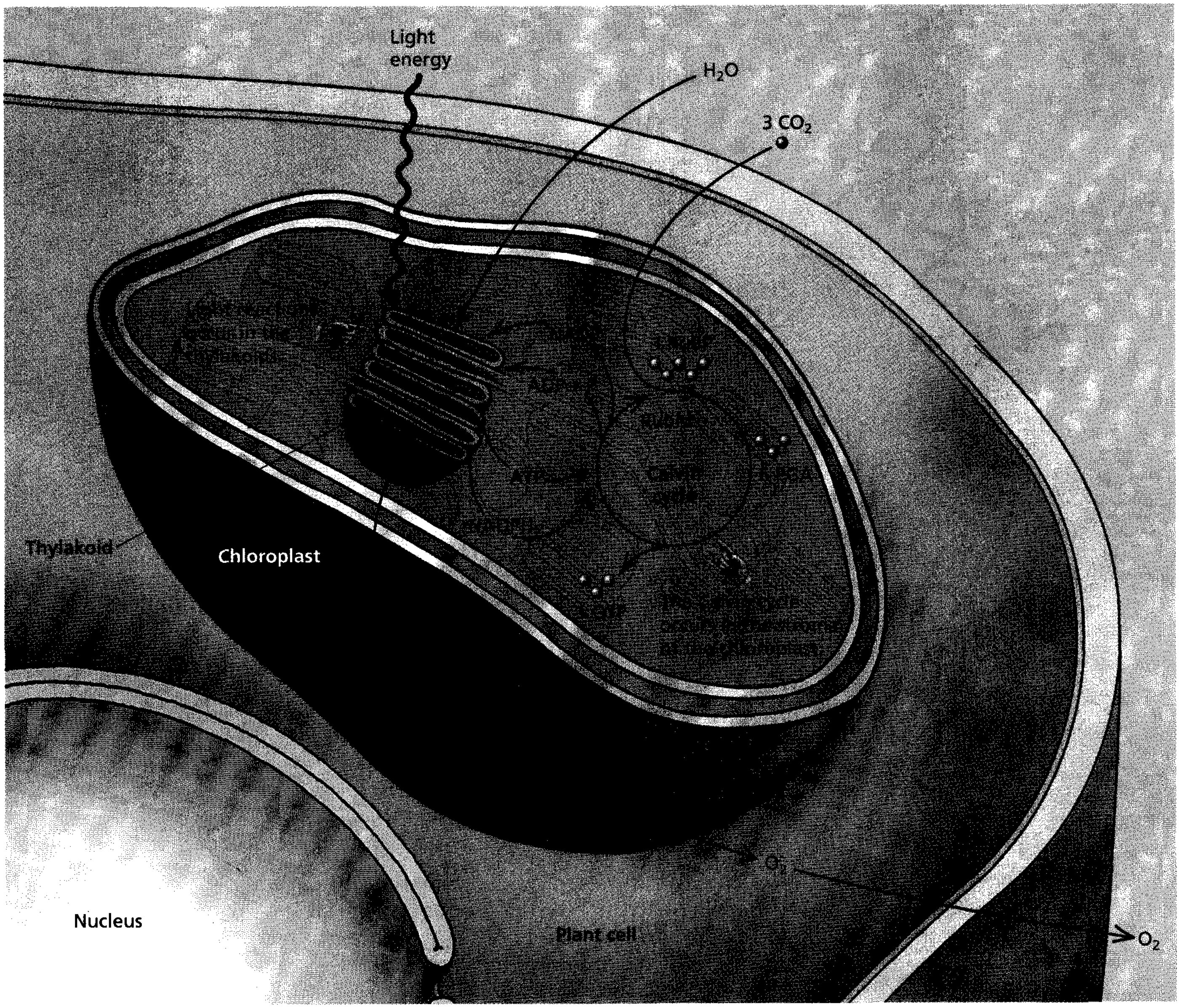


Figure 4.29 The Calvin cycle. Carbon dioxide enters the Calvin cycle. The energy of ATP is used to add hydrogens and electrons from NADPH to produce sugars.

Over time, plants have been able to capture the energy from light to form carbon-rich fossil fuels now buried in the earth. It took over 100 million years to form these nonrenewable resources such as coal, oil, and gas, which are now being consumed at a much faster rate than they were formed. The result is that more carbon dioxide is being released into the atmosphere than can be absorbed via photosynthesis.

Global Warming and Photosynthesis

Global warming is made worse by deforestation and may affect the distribution of plants that undergo different variations of photosynthesis.

Deforestation. The process that occurs when forests are cleared for logging, farming, and ever-expanding human settlements is called **deforestation**. Deforestation contributes directly to the increase in carbon dioxide within the atmosphere. Current estimates are that up to 25% of the carbon dioxide introduced into the atmosphere originates from the cutting and burning of forests in the tropics. The loss of trees as a result of deforestation also indirectly contributes to rising carbon dioxide levels when these forests are replaced by pasture or cropland. Because net rates of photosynthesis (as measured by grams of carbon dioxide removed from the atmosphere per acre per year) in grasslands or agricultural fields are 30% to 60% less than rates in forests, the loss of forests significantly decreases the removal of carbon dioxide from the atmosphere.

Replanting trees in deforested areas may help increase the rate at which carbon dioxide is removed from the atmosphere because young trees have a faster net photosynthetic rate than older trees. This is because older trees have lots of non-photosynthetic, woody tissues that use the products of photosynthesis and that seedlings have yet to develop. In other words, young trees can put more of their organic carbon into storage as wood, while older trees use more of the carbon simply to maintain themselves. However, when these trees are logged, their roots and branches are left behind to decompose. In addition, most of the wood that is harvested is turned into paper, which will decompose after a few years, or fuel, which will be burned. Decomposition and burning result in the release into the environment of carbon compounds that were once part of the trees. Therefore, even though replanting after deforestation helps remove some of the carbon dioxide from the atmosphere, it does not result in a return to previous levels.

C_3, C_4, and CAM Plants. You learned earlier that plants can bring carbon dioxide into leaves through openings called stomata and that the carbon dioxide brought in is used to produce sugars during the Calvin cycle. Stomatal openings are located on the surface of a leaf and are surrounded by two kidney-bean-shaped cells called **guard cells**. When the guard cells are compressed against each other, the stomata are closed, thus restricting the flow of gases into or out of the plant. When the guard cells change shape to create an opening between them, the stomata are open, and carbon dioxide and oxygen gases can be exchanged. In addition to the exchange of gases, water can move out of the plant through the stomatal opening via a process called **transpiration** (Figure 4.30). The transpired water is replaced when water from the soil is brought into the plant, bringing with it minerals that the plant needs to synthesize many compounds.

In most plant species, the Calvin cycle produces 3-carbon sugars, which are converted into the sugars that are either stored as food for the plant or transported to growing leaves, roots, and reproductive structures. Plants that produce the 3-carbon molecule are called **C_3 plants**. C_3 plants are the most abundant type of plant on Earth and include agriculturally important species such as soybeans, wheat, and rice.

Rising temperatures can reduce the rate of photosynthesis because on hot, dry days, plants close their stomata in order to reduce the rate of water lost to transpiration. Closing stomatal openings prevents carbon dioxide from entering the plant, and the rate of photosynthesis declines.

Closing the stomatal openings to prevent water loss causes another series of reactions to occur, called **photorespiration**. During photorespiration, the first enzyme in the Calvin cycle uses oxygen instead of carbon dioxide as its substrate. While most enzymes display a high degree of specificity for their particular substrate, some enzymes have additional substrates to which they have lesser affinities. The enzyme that catalyzes the first step of the Calvin cycle, rubisco, is one such enzyme. The most common protein on Earth, rubisco is the also most common protein in leafy tissue. Carbon dioxide is its preferred substrate, but when carbon dioxide is low, rubisco will also allow oxygen into its active site. That is, it behaves as an oxygenase. When oxygen is high, such as when photosynthesis is occurring but the stomata are closed, oxygen will be used as the substrate of rubicso, and the plant will undergo photorespiration. During photorespiration, the rubisco enzyme catalyzes the incorporation of oxygen into a compound called glycolate. Glycolate cannot be used for food or for the synthesis of structural components. In fact, it must be destroyed by the plant since high levels of glycolate inhibit photosynthesis. The breakdown of glycolate requires ATP and releases carbon dioxide that had been previously incorporated into sugars during the Calvin cycle.

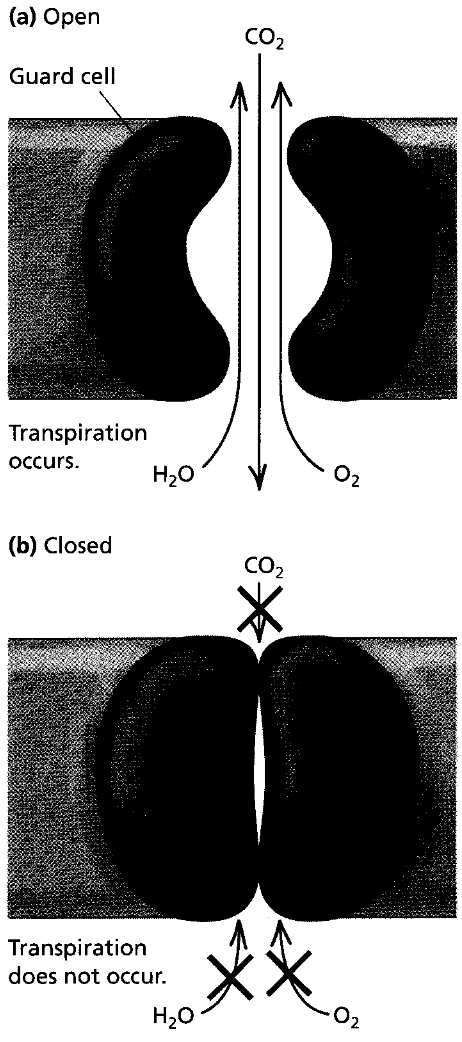


Figure 4.30 Gas exchange and water loss. (a) When the stomata are open, carbon dioxide and oxygen gases can be exchanged. Water can be lost through a process called transpiration. (b) When the guard cells change shape to block the opening, gas exchange and transpiration do not occur.

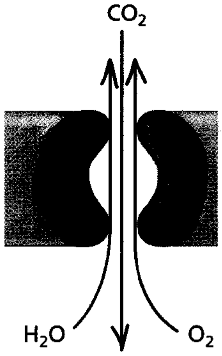
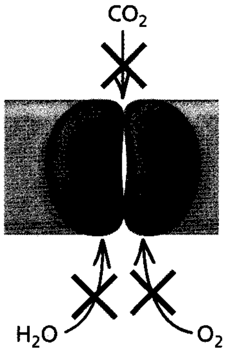
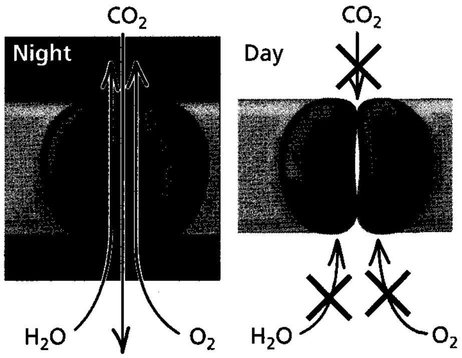
You might wonder why it is that plant cells perform this wasteful process. It has to do with the evolution of photosynthesis on early Earth. Photosynthesis evolved when the atmosphere was largely devoid of oxygen. Under these conditions, the enzyme's affinity for oxygen did not present the problems it does in today's oxygen-rich atmosphere. All descendants of the first photosynthesizers inherited the instructions for producing the same rubisco enzyme, and so modern plants are "stuck" with this somewhat inefficient system. In dry environments, natural selection should favor plants that can minimize photorespiration despite having closed stomata much of the time. Two mechanisms for reducing photorespiration are known as C_4 and CAM photosynthesis.

C_4 plants, like all plants, conserve water during hot, sunny periods by closing their stomata. However, these plants carry an additional enzyme (compared to C_3 plants) that allows them to avoid photorespiration and continue to make sugars even though carbon dioxide levels within the plants are low during these periods. This enzyme is present in cells closest to the stomata and has a much higher affinity for carbon dioxide than does rubisco. It is able to procure carbon dioxide even when the stomata are almost closed. The carbon dioxide is combined with a 3-carbon acceptor molecule to produce a 4-carbon compound, hence the name C_4 plants. The 4-carbon compound then migrates to cells deeper within the leaf, where the carbon dioxide is released and produces a locally high concentration of carbon dioxide that enables rubisco to function as a carboxylase in the Calvin cycle. The 3-carbon acceptor molecule returns to the cells nearest the stomata. Corn and sugar cane are C_4 plants that can keep making sugars even though their stomata are almost closed. However, C_4 photosynthesis carries a cost—C_3 plants require 3 ATP molecules to convert 1 molecule of carbon dioxide into sugar, but C_4 plants require 5 molecules of ATP. The enzymes used in C_4 photosynthesis are also more sensitive to cold temperatures than are the enzymes of the Calvin cycle. Thus, C_3 plants have an advantage in certain environmental situations (cool and shady), and C_4 plants have an advantage in others (hot and sunny).

One other photosynthetic adaptation involves **CAM plants**. *CAM* stands for crassulacean acid metabolism, named for the plant family Crassulaceae, in which this mechanism was first discovered. Members of the Crassulaceae include the jade plant and other succulent (water-storing) plants. A CAM plant conserves water by opening its stomata at night only. The carbon dioxide that comes in during the night cannot immediately be used for photosynthesis because that process requires energy from the sun. During the night, the carbon is stored as an acid that is broken down during the day and releases carbon dioxide while the stomata are closed. This carbon dioxide can then be used for photosynthesis when sunlight becomes available. Therefore, carbon dioxide can enter at night, be stored as an acid, and then be used by the Calvin cycle during the subsequent day, even if the stomata are closed during the day to conserve water. Growth is limited in CAM plants because the amount of carbon dioxide stored in acid during the night is limited; the plants use it all up early in the day and cannot perform any more photosynthesis. Table 4.1 summarizes C_3, C_4, and CAM plant strategies.

Scientists are concerned that increasing temperatures may favor plants with these water-saving adaptations and change the relative percentages of C_3, C_4, and CAM plants in existence. This change could negatively affect some agricultural crops and could change the relative percentages of native plant species in a given region since certain adaptations gain relative advantages as the climate changes. Like the sugar maple, those species that cannot migrate to more appropriate environments or cannot compete with other plants in a changing environment may become extinct. As plant communities change and lose species, many of the animals that depend on these communities may suffer. The disruption of biological communities caused by global warming may prove to be the most damaging of all the changes caused by humans' consumption of fossil fuels.

Table 4.1 C_3, C_4, and CAM plant photosynthesis. Plants have evolved adaptations that prevent water loss.

Type of Plant and Example		Stomata Status	Description
C_3 Soybean			The Calvin cycle converts two 3-carbon sugars into glucose.
C_4 Corn			Enzymes scavenge CO_2 to produce 4-carbon sugars, which donate carbon dioxides to the Calvin cycle.
CAM Jade			Water loss is slowed by opening stomata only at night.

The negative consequences of global warming are substantial and may prove to be too much for many species to adapt to, including humans. The changes that are now threatening the Tuvaluans may eventually threaten all of us.

4.4 Decreasing the Effects of Global Warming

The prime minister of Tuvalu is threatening to sue the United States because this country emits immense amounts of carbon dioxide and has not taken official measures to reduce emissions. While Tuvalu is one of the least polluting countries in the world, the United States is the greatest.

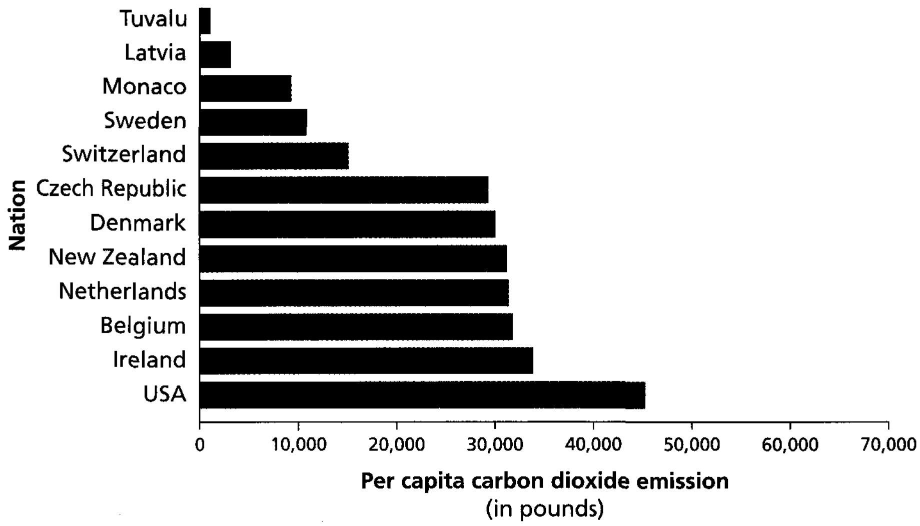


Figure 4.31 Per capita carbon dioxide emissions in pounds (1990–1999). This bar graph shows some of the highest and lowest carbon-dioxide-emitting countries for this time period.

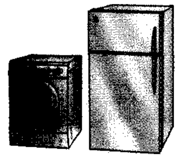
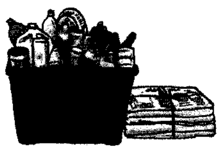
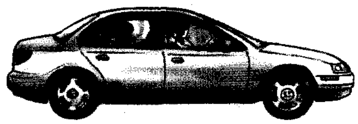
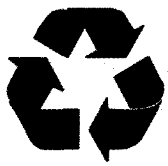
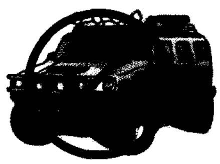
Home to only 4% of the world's population, the U.S. produces close to one-fourth of the carbon dioxide emitted by fossil fuel burning. The per capita emissions rate of carbon dioxide for Americans is twice that of the Japanese or Germans, three times that of the global average, four times that of Swedes, and 20 times that of the average Indian. Figure 4.31 shows average per capita emissions for the highest- and lowest-emitting countries.

The United States has refused to sign the 1997 Kyoto Protocol, an international agreement that sets goals for decreases in emissions of around 5%. To be in compliance with the Kyoto agreement, by the year 2010, the United States would need to decrease its emissions by 24%.

Most of the emissions for an individual country come from industry, followed by transportation and then by commercial, residential, and agricultural emissions. All of us can work to reduce our personal contribution to global warming by decreasing residential and transport emissions. About 2700 pounds of carbon per year come from residential emissions. Most of that is from energy used to heat and cool homes and to power electrical appliances. After residential emissions, transportation is the next highest emitter of carbon dioxide. About 2300 pounds of carbon dioxide per person are released into the atmosphere through personal transportation. Adding to these emissions is the fact that the fuel economy of passenger vehicles has not increased, and the average number of miles traveled has increased. Table 4.2 describes many ways that you can decrease your greenhouse gas emissions and indicates the number of pounds of carbon dioxide that each action would save annually. These reductions may seem trivial in comparison to the scope of the problem, but when they are multiplied by the almost 300 million people in the United States, the savings become significant.

Having an effect on industrial, commercial, and agricultural sectors is difficult for any one individual. Instead, this will take leadership from the policy makers who are committed to reducing emissions. To do so requires that our leaders, and all of us, understand that even though the causes, implications, and solutions of global warming may be open to debate, the fact that it is occurring at an unprecedented rate is not.

Table 4.2 Decreasing your greenhouse gas emissions. Here are some ideas that you can use to help slow the rate of global warming.

Action		Annual decrease in carbon dioxide production
Buy high-efficiency appliances.		400 pounds per appliance
Plant shade trees around your home to decrease energy consumption and to remove carbon dioxide by photosynthesis.		50 pounds
Use a push mower instead of a power mower.		80 pounds
Recycle glass bottles, aluminum cans, plastic, newspapers, and cardboard.		850 pounds
Carpool two days per week.		1590 pounds
Buy food and other products with reusable or recyclable packaging, or reduced packaging, to save the energy required to manufacture new containers.		230 pounds
Drive an energy-efficient vehicle. SUVs average 16 miles per gallon, while smaller cars average 25 miles per gallon.		13,000 pounds
Walk 10 miles per week instead of driving.		590 pounds

CHAPTER REVIEW

Summary

4.1 The Greenhouse Effect

- The planet is warming. This warming will lead to a rise in ocean levels, changes in weather patterns, and the disruption of biological communities (p. 72).
- Greenhouse gases, particularly carbon dioxide, increase the amount of heat retained in Earth's atmosphere, which then leads to increased temperatures (p. 72).
- Water can absorb large amounts of heat without undergoing rapid or drastic changes in temperature because heat must first be used to break hydrogen bonds between adjacent water molecules. A high heat-absorbing capacity is a characteristic of water (p. 73).
- Carbon dioxide cycles between animals, plants, soil, oceans, and the atmosphere (p. 73).
- Carbon dioxide levels in the atmosphere are increasing. This increase is caused by human activities such as the burning of fossil fuels and is leading to global warming (pp. 74–75).
- Glaciers are melting and causing sea levels to rise. This changes habitats for many organisms and forces migrations (pp. 75–76).

4.2 Cellular Respiration

- Cellular respiration converts the energy stored in chemical bonds of food into ATP (p. 77).
- ATP is a nucleotide triphosphate. The nucleotide found in ATP contains a sugar and the nitrogenous base, adenine (p. 77).
- Breaking the terminal phosphate bond of ATP releases energy that can be used to perform cellular work and produces ADP plus a phosphate (p. 78).
- ATP is generated in most organisms by the process of cellular respiration, which consumes carbohydrates and releases water and carbon dioxide as waste products (p. 79).
- Cellular respiration begins in the cytosol, where a 6-carbon sugar is broken down into two 3-carbon pyruvic acid molecules during the anaerobic process of glycolysis (p. 81).
- The pyruvic acid molecules then move across the two mitochondrial membranes where they are decarboxylated. The remaining 2-carbon fragment then moves into the matrix of the mitochondrion, where the Krebs cycle strips them of carbon dioxide and electrons (pp. 81–83).
- The electrons are carried by electron carriers to the inner mitochondrial membrane; there they are added to a series of proteins called the electron transport chain. At the bottom of the electron transport chain, electronegative oxygen pulls the electrons toward itself. As the electrons move down the electron transport chain, the energy that they release is used to drive protons (H^+) into the intermembrane space. Once there, the protons rush through the enzyme ATP synthase and produce ATP from ADP and phosphate (p. 84).
- When electrons reach the oxygen at the bottom of the electron transport chain, they combine with the oxygen and hydrogen ions to produce water (p. 85).
- Increased temperatures lead to an increased rate of cellular respiration, which can then cause increases in the populations of some species and decreases in the populations of others (p. 86).

Web Tutorial 4.1 Glucose Metabolism

4.3 Photosynthesis

- Photosynthesis utilizes carbon dioxide from the atmosphere to make sugars and other substances (p. 87).
- During photosynthesis, energy from sunlight is used to rearrange the atoms of carbon dioxide and water to produce sugars and oxygen (pp. 87–88).
- Photosynthesis occurs in chloroplasts. Sunlight strikes the chlorophyll molecule within chloroplasts, boosting electrons to a higher energy level. These excited electrons are dropped down an electron transport chain located in the thylakoid membrane, and ATP is made (p. 88).
- Electrons are also passed to electron carriers that transport electrons to the Calvin cycle. The electrons that are lost become replaced by electrons acquired during the splitting of water, and oxygen is released. The Calvin cycle utilizes the products of the light reactions (ATP and the electron carrier NADPH) to incorporate carbon dioxide into sugars (pp. 89–90).
- Photosynthesis removes carbon dioxide from the air, potentially reducing the risk of global warming. However, humans are also deforesting Earth's land surface, reducing the global rate of photosynthesis (p. 91).
- Stomata on a plant's surface not only allow in carbon dioxide for photosynthesis but also allow water to escape from the plant. Guard cells surrounding the stomata can change shape to close the stomata and restrict water loss. However, when stomata are closed, carbon dioxide declines in the plant, and the energy-wasting process of photorespiration may occur. C_4 and CAM plants have evolved to perform photosynthesis while reducing the risk of photorespiration in dry conditions (pp. 92–94).
- Global warming may disrupt biological communities as the climate in an area changes and the relative abundance of C_3, C_4, and CAM plants changes (p. 95).

Web Tutorial 4.2 Leaves: The Site of Photosynthesis
Web Tutorial 4.3 Photosynthesis

4.4 Decreasing the Effects of Global Warming

- The effects of global warming will not be as severe if humans can reduce carbon dioxide emissions (pp. 95–97).

Learning the Basics

1. What are the reactants and products of cellular respiration and photosynthesis?

2. Carbon dioxide functions as a greenhouse gas by ______________.

   A. interfering with water's ability to absorb heat; **B.** increasing the random molecular motions of oxygen; **C.** allowing radiation from the sun to reach Earth and absorbing the re-radiated heat; **D.** splitting into carbon and oxygen and increasing the rate of cellular respiration

3. Water has a high heat-absorbing capacity because ______________.

   A. the sun's rays penetrate to the bottom of bodies of water, mainly heating the bottom surface; **B.** the strong covalent bonds that hold individual water molecules together require large inputs of heat to break; **C.** it has the ability to dissolve many heat-resistant solutes; **D.** initial energy inputs are used to break hydrogen bonds between water molecules and then to raise the temperature; **E.** all of the above are true

4. Cellular respiration involves ______________.

   A. the aerobic metabolism of sugars in the mitochondria by a process called glycolysis; **B.** an electron transport chain that releases carbon dioxide; **C.** the synthesis of ATP, which is driven by the rushing of protons through an ATP synthase; **D.** electron carriers that bring electrons to the Krebs cycle; **E.** the production of water during the Krebs cycle

5. The electron transport chain ______________.

   A. is located in the matrix of the mitochondrion; **B.** has the electronegative carbon dioxide at its base; **C.** is a series of nucleotides located in the inner mitochondrial membrane; **D.** is a series of enzymes located in the intermembrane space; **E.** moves electrons from protein to protein and moves protons from the matrix into the intermembrane space

6. Which of the following **does not** occur during the light reactions of photosynthesis?

   A. Oxygen is split, releasing water.; **B.** Electrons from chlorophyll are added to an electron transport chain.; **C.** An electron transport chain drives the synthesis of ATP for use by the Calvin cycle.; **D.** NADPH is produced and will carry electrons to the Calvin cycle.; **E.** Oxygen is produced when water is split.

7. Which of the following is a **false** statement about photosynthesis?

   A. During the Calvin cycle, electrons and ATP from the light reactions are combined with atmospheric carbon dioxide to produce sugars.; **B.** The enzymes of the Calvin cycle are located in the chloroplast stroma.; **C.** Oxygen produced during the Calvin cycle is released into the atmosphere.; **D.** Sunlight drives photosynthesis by boosting electrons found in chlorophyll to a higher energy level.; **E.** Electrons released when sunlight strikes chlorophyll are replaced by electrons from water.

8. Hydrogen atoms are composed of ______________.

   A. 1 electron; **B.** 1 proton; **C.** 2 electrons; **D.** 2 protons; **E.** 1 proton and 1 electron

9. Select the **true** statement regarding metabolism in plant and animal cells.

   A. Plant and animal cells both perform photosynthesis and aerobic respiration.; **B.** Animal cells perform aerobic respiration only, and plant cells perform photosynthesis only.; **C.** Plant cells perform aerobic respiration only, and animal cells perform photosynthesis only.; **D.** Plant cells perform aerobic respiration and photosynthesis, and animal cells perform aerobic respiration only.

Analyzing and Applying the Basics

1. Are sugars the only macromolecules that can be broken down to produce ATP? If not, how are other nutrients metabolized?

2. How do the different strategies employed by C_3, C_4, and CAM plants help them adapt to their environments?

3. Describe the sites of aerobic respiration and photosynthesis. What organelles are involved? Where in each organelle do the different steps of each process occur?

Connecting the Science

1. What can individuals do to slow the effects of global warming?

2. Do you think it is okay for the individuals of one country to produce more greenhouse gases than do individuals of other countries? Why or why not?