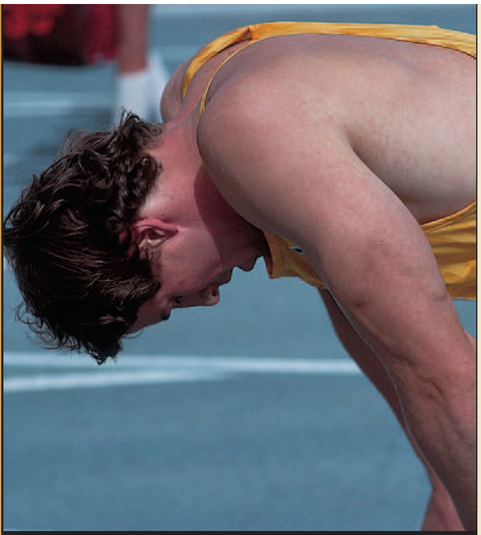


CHAPTER 6

Biochemical Pathways

6

Chapter Outline

Key Concepts	Applications
Recognize the sources of energy for all living things.	• Understand that energy is manipulated to keep organisms alive.
Understand how chemical-bond energy is utilized.	• Know how much food energy it takes to keep an organism alive. • Explain the importance of ATP. • Understand the role coenzymes play in metabolism.
Understand the process of aerobic cellular respiration.	• Explain the role of oxygen in certain organisms.
Understand the process of anaerobic cellular respiration.	• Understand why yeast can make alcohol and carbon dioxide and how these processes differ.
Understand how cells process nutrients.	• Explain what can happen to carbohydrates, fats, and proteins from your diet.
Understand the process of photosynthesis.	• Explain how plants can metabolize and grow using water and carbon dioxide as their basic building materials. • Explain how visible light is converted to chemical-bond energy. • Describe how plants create complex organic molecules. • Explain how pigments are used in photosynthesis by various plants.
Understand how the light-dependent and light-independent reactions work.	• Be able to explain how light can be used to make organic molecules.

6.1 Cellular Respiration and Photosynthesis

All living organisms require energy to sustain life. The source of this energy comes from the chemical bonds of molecules (figure 6.1). Burning wood is an example of a chemical reaction that results in the release of energy by breaking chemical bonds. The organic molecules of wood are broken and changed into the end products of ash, gases (CO_2), water (H_2O), and energy (heat and light). Living organisms are capable of carrying out these same types of reactions but in a controlled manner. By controlling energy-releasing reactions, they are able to use the energy to power activities such as reproduction, movement, and growth. These reactions form a biochemical pathway when they are linked to one another. The products of one reaction are used as the reactants for the next.

Organisms such as green plants, algae, and certain bacteria are capable of trapping sunlight energy and holding it in the chemical bonds of molecules such as carbohydrates. The process of converting sunlight energy to chemical-bond energy, called **photosynthesis,** is a major biochemical pathway. Photosynthetic organisms produce food molecules, such as carbohydrates, for themselves as well as for all the other organisms that feed upon them. **Cellular respiration,** a second major biochemical pathway, is a chain of reactions during which cells release the chemical-bond energy and convert it into other usable forms (figure 6.2). All organisms must carry out cellular respiration if they are to survive. Whether organisms manufacture food or take it in from the environment, they all use chemical-bond energy.

Organisms that are able to make energy-containing organic molecules from inorganic raw materials by using basic energy sources such as sunlight are called **autotrophs** (self-feeders). All other organisms are called **heterotrophs** (feeding on others). Heterotrophs get their energy from the chemical bonds of food molecules such as fats, carbohydrates, and proteins (table 6.1).

Within eukaryotic cells, certain **biochemical pathways** are carried out in specific organelles. Chloroplasts are the site of photosynthesis, and mitochondria are the site of most of the reactions of cellular respiration. Because prokaryotic cells lack mitochondria and chloroplasts, they carry out photosynthesis and cellular respiration within the cytoplasm or on the inner surfaces of the cell or other special membranes (table 6.2).

Generating Energy in a Useful Form: ATP

Photosynthesis and cellular respiration consist of many steps. If the products of a reaction do not have the same amount of energy as the reactants, energy has either been released or added in the reaction. Some chemical reactions—like cellular

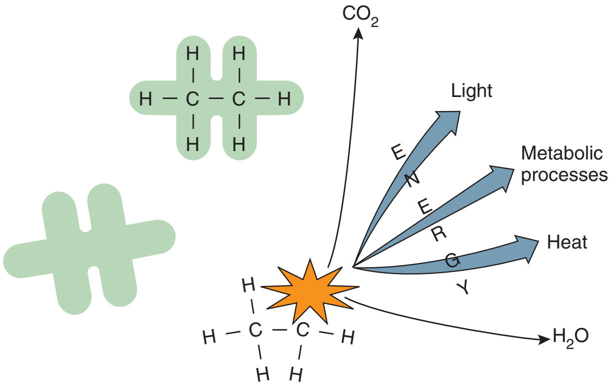


Figure 6.1

Life's Energy: Chemical Bonds
All living things utilize the energy contained in chemical bonds. As organisms break down molecules such as the organic molecule ethane shown in this illustration, the energy released may be used for metabolic processes such as growth and reproduction. Some organisms, such as fireflies and certain bacteria, are able to bioluminesce as some of this chemical-bond energy is released as visible light. In all cases, there is a certain amount of heat freed from the breaking of chemical bonds.

Table 6.1

ENERGY AND ORGANISMS

Organism Type	Building Materials	External Energy Source	Pathways
Autotroph (e.g., algae, maple tree)	Simple inorganic molecules (e.g., CO_2, H_2O, NO_3)	Sunlight	Photosynthesis and cellular respiration
Heterotroph (e.g., fish, human)	Complex organic molecules (e.g., carbohydrates, proteins, lipids)	Complex organic molecules (e.g., carbohydrates, proteins, lipids)	Cellular respiration

respiration—may have a net release of energy, whereas others—like photosynthesis—require an input of energy.

To transfer the right amount of chemical-bond energy from energy-releasing to energy-requiring reactions, cells use the molecule ATP. **Adenosine *tri*phosphate (ATP)** is a handy source of the right amount of usable chemical-bond energy. Each ATP molecule used in the cell is like a rechargeable AAA battery used to power small toys and electronic equipment. Each contains just the right amount of energy to power the job. When the power has been drained, it can be recharged numerous times before it must be recycled. Recharging the AAA battery requires getting a small amount of energy from a source of high energy such as a hydroelectric power plant (figure 6.3). Energy from the electric plant is too powerful to directly run a small flashlight or portable tape recorder. If you plug your recorder directly into the power plant, the recorder would be destroyed. However, the recharged AAA battery delivers just the right amount of

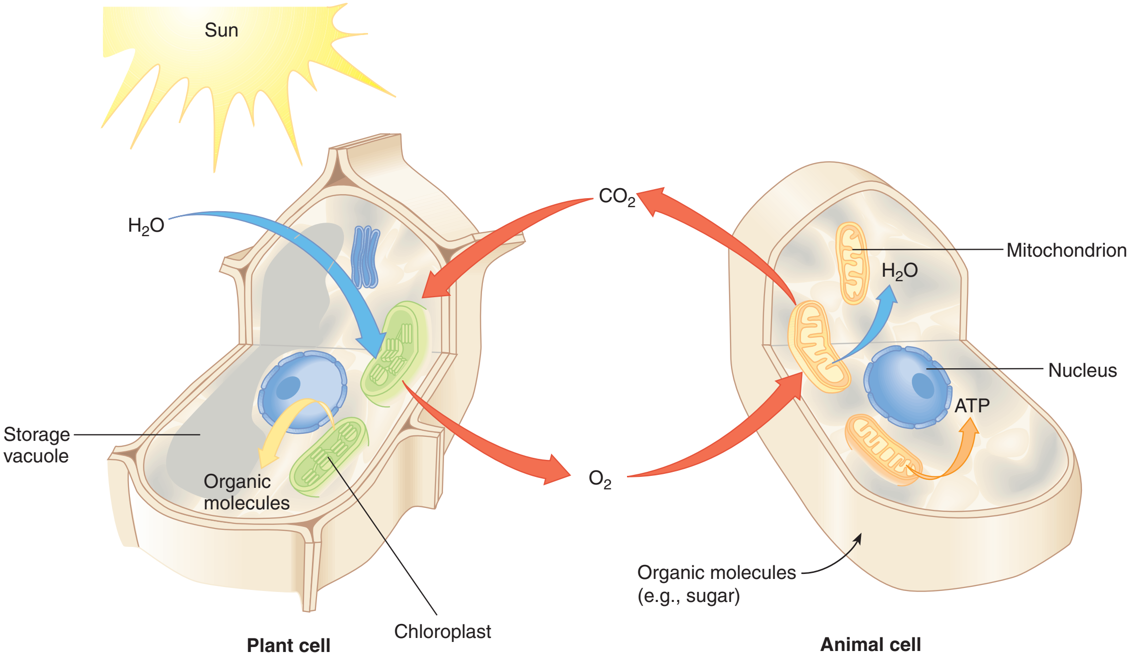


Figure 6.2

Biochemical Pathways that Involve Energy Transformation
Photosynthesis and cellular respiration are series of chemical reactions that control the flow of energy in many organisms. Organisms that contain photosynthetic machinery are capable of using light, water, and carbon dioxide to produce organic molecules such as sugars, proteins, lipids, and nucleic acids. The molecules, along with oxygen, are used by all organisms during cellular respiration to provide the energy to sustain life.

Table 6.2

METABOLIC PATHWAYS

Reaction	Cell Type	Organisms Capable of Pathway	Location of Pathway in Cell
Photosynthesis	Prokaryotic	Certain types of bacteria	Cytoplasmic membranes
	Eukaryotic	Algae and green plants	Inner membranes of chloroplasts
Cellular respiration	Prokaryotic	All	Inner surface of cell membrane and in cytoplasm
	Eukaryotic	All	Cytoplasm and inner membranes of mitochondria

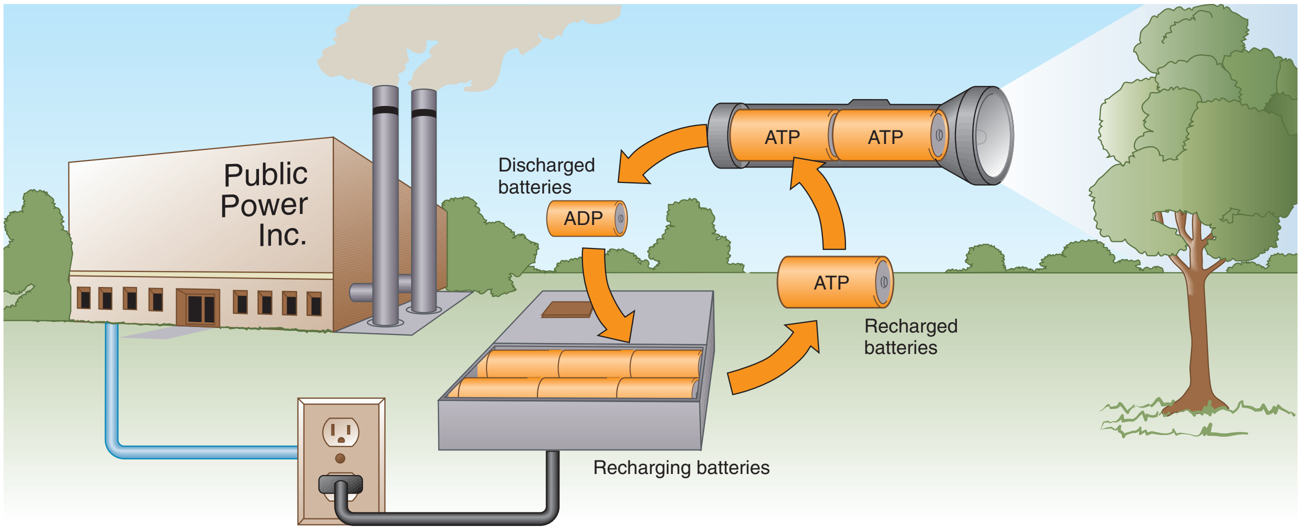
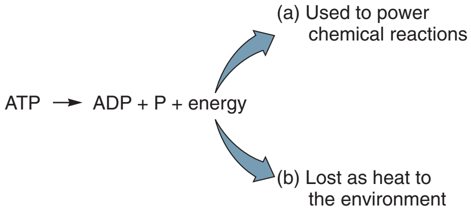


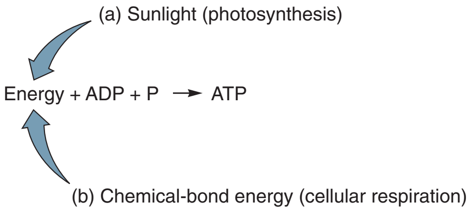
Figure 6.3

Just the Right Amount of Power for the Job
When rechargeable batteries in a flashlight have been drained of their power, they can be recharged by placing them in a specially designed battery charger. This enables the right amount of power from a power plant to be packed into the batteries for reuse. Cells operate in much the same manner. When the cell's "batteries," ATP, are drained while powering a job like muscle contraction, the discharged "batteries," ADP, can be recharged back to full ATP power.

energy at the right time and place. ATP functions in much the same manner. After the chemical-bond energy has been drained by breaking one of its bonds:



the discharged molecule (ADP) is recharged by "plugging it in" to a high-powered energy source. This source may be (1) sunlight (photosynthesis) or (2) chemical-bond energy (released from cellular respiration):



An ATP molecule is formed from adenine (nitrogenous base), ribose (sugar), and phosphates (figure 6.4). These three are chemically bonded to form AMP, *a*denosine *mono*phosphate (one phosphate). When a second phosphate

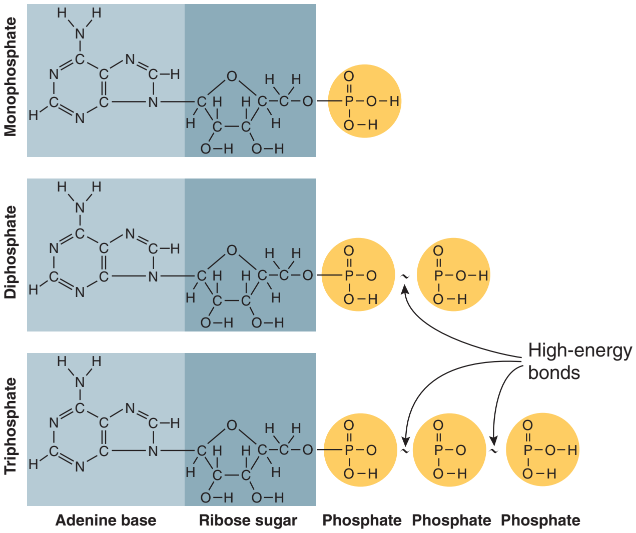


Figure 6.4

Adenosine Triphosphate (ATP)
A macromolecule of ATP consists of a molecule of adenine, a molecule of ribose, and three phosphate groups. The two end phosphate groups are bonded together by high-energy bonds. When these bonds are broken, they release an unusually great amount of energy; therefore, they are known as high-energy bonds. These bonds are represented by curved, solid lines. The ATP molecule is considered an energy carrier.

group is added to the AMP, a molecule of ADP (diphosphate) is formed. The ADP, with the addition of more energy, is able to bond to a third phosphate group and form ATP. (The addition of phosphate to a molecule is called a *phosphorylation reaction*.) The covalent bond that attaches the second phosphate to the AMP molecule is easily broken to release energy for energy-requiring cell processes. Because the energy in this bond is so easy for a cell to use, it is called a **high-energy phosphate bond.** ATP has two high-energy phosphate bonds represented by curved solid lines. Both ADP and ATP, because they contain high-energy bonds, are very unstable molecules and readily lose their phosphates. When this occurs, the energy held in the high-energy bonds of the phosphate can be transferred to another molecule or released to the environment. Within a cell, enzymes speed this release of energy as ATP is broken down to ADP and P.

6.2 Understanding Energy Transformation Reactions

Oxidation-Reduction and Cellular Respiration

This equation summarizes the chemical reactions humans and many other organisms use to extract energy from the carbohydrate glucose:

$$C_6H_{12}O_6 + 6\,O_2 + 6\,H_2O^* \rightarrow 6\,CO_2 + 12\,H_2O + \text{energy (ATP + heat)}$$

This is known as aerobic cellular respiration, an oxidation-reduction reaction process. **Aerobic cellular respiration** is a specific series of chemical reactions involving the use of molecular oxygen (O_2) in which chemical-bond energy is released to the cell in the form of ATP. **Oxidation-reduction (redox) reactions** are electron transfer reactions in which the molecules losing electrons become oxidized and those gaining electrons become reduced (Outlooks 6.1). This process is not difficult to understand if you think about it in simple terms. The molecule that loses the electron loses energy and the molecule that gains the electron gains energy.

Covalent bonds in the sugar glucose contain potential energy. Because this molecule contains more bonds than any of the other molecules listed in the equation, it contains the greatest amount of potential energy. That is, a single molecule of sugar contains more potential energy than single molecules of oxygen, water, or carbon dioxide. (Which would you rather have for lunch?) The covalent bonds of glucose are formed by sharing pairs of fast-moving, energetic electrons. Of all the covalent bonds in glucose (H–O, H–C, C–C), those easiest to get at are on the outside of the molecule. If we could get the hydrogen electrons off glucose, their energy could be used to phosphorylate ADP molecules, producing higher energy ATP molecules. The ATP could be used to power the metabolic activities of the cell. The chemical reaction that results in the loss of electrons from this molecule is the *oxidation* part of this reaction. However, problems could occur with removing the hydrogen electrons.

First, these high-energy electrons must be controlled because they can be dangerous. If they were allowed to fly about at random, they could combine with other molecules, causing cell death. They must be "handled" carefully! Once energy has been removed for ATP production, the electrons must be placed in a safe location. In *aerobic* cellular respiration, these electrons are ultimately attached to oxygen. Oxygen

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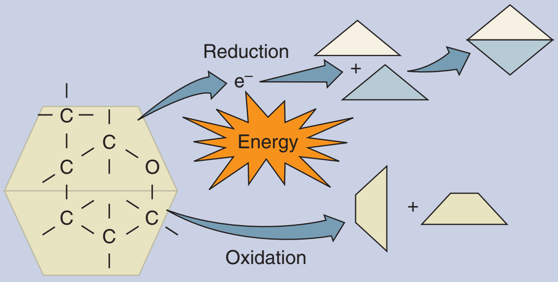
*These water molecules are added at various reaction points from the cytoplasm.

OUTLOOKS 6.1

Oxidation-Reduction (Redox) Reactions in a Nutshell

The most important characteristic of redox (*red*uction + *ox*idation) reactions is that energy-containing electrons are transferred from one molecule to another. Such reactions enable cells to produce useful chemical-bond energy in the form of ATP in cellular respiration, and to synthesize the energy-containing bonds of carbohydrates in photosynthesis. Oxidation means the loss of electrons, and reduction means the gain of electrons. (Do not associate oxidation with oxygen; many different elements may enter into redox reactions.) Molecules that lose electrons (serve as electron donors) usually release this chemical-bond energy and are broken down into more simple molecules. Molecules that gain electrons (serve as electron acceptors) usually gain electron energy and are enlarged, forming a more complex molecule (see figure). Because electrons cannot exist apart from the atomic nucleus for a long period, both oxidation and reduction occur in a redox reaction; whenever an electron is donated, it is quickly gained by another molecule. A simple way to help identify a redox reaction is to use the mnemonic device "LEO the lion says GER." LEO stands for "loss of electrons is oxidation"; and GER stands for "gain of electrons is reduction."



serves as the final resting place of the less energetic hydrogen electrons. When the electrons are added to oxygen, it becomes a negatively charged ion, O^{--}. This is the *reduction* portion of the reaction. Reduction occurs when a molecule gains electrons. *So, in the aerobic cellular respiration of glucose, glucose is oxidized and oxygen is reduced.* One cannot occur without the other (figure 6.5). If something is oxidized (loses electrons), something else must be reduced (gains electrons). A molecule cannot simply lose its electrons; they have to go someplace!

The second problem that occurs when electrons are removed from the glucose relates to what is left of the hydrogen atoms, that is, the protons (H^+). As more and more electrons are removed from the glucose (oxidized) to power the phosphorylation of ADP (charge batteries), unless they are controlled there could be an increase in the hydrogen ion concentration. This would result in a decrease in the pH of the cytoplasm which could also be fatal to the cell. The pH is controlled, however, because these H^+ ions can easily combine with the O^{--} ions to form molecules of harmless water (H_2O) with a pH of 7.

What happens to what is left of the molecule of glucose? Once the hydrogens have all been stripped off, the remaining carbon and oxygen atoms are rearranged to form individual molecules of CO_2. The oxidation-reduction reaction is complete. All the hydrogen originally a part of the glucose has been moved to the oxygen to form water. All the remaining carbon and oxygen atoms of the original glucose are now in the form of CO_2. The total amount of energy released from this process is enough to theoretically generate 38 ATPs in prokaryotic cells and 36 ATPs in eukaryotic cells.

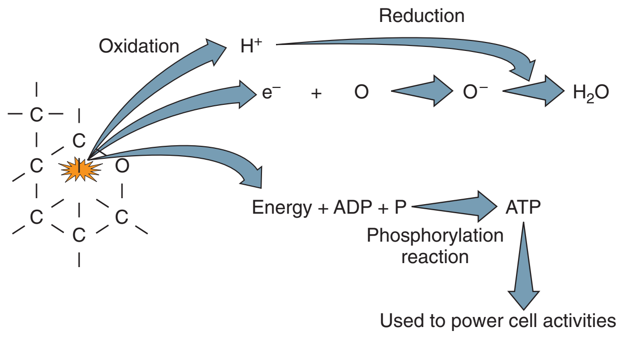


Figure 6.5

Oxidation-Reduction (Redox) Reactions

During an oxidation-reduction reaction, a large molecule loses electrons. This is the "oxidation" portion of the reaction. When the electrons are removed, the large molecule is unable to stay together and breaks into smaller units. The energy released during oxidation can be used to power cell activities such as the manufacture of sugars, fats, and nucleic acids. It may also be used to move molecules through cell membranes or contract muscle fibers. The reduction part of the reaction occurs when the removed electrons are picked up and attached to another molecule. When they are acquired, these electrons can become involved in the formation of new chemical bonds. Thus, during the reduction part of the reaction, new large molecules are formed.

The section on aerobic cellular respiration and the section on photosynthesis are divided into three levels: Basic Description, Intermediate Description, and Detailed Description. Ask your instructor which level is required for your course of study.

6.3 Aerobic Cellular Respiration

Basic Description

In eukaryotic cells the process of releasing energy from food molecules begins in the cytoplasm and is completed in the mitochondrion. The major parts of the cellular respiration process are listed:

1. **Glycolysis** (*glyco* = carbohydrate; *lys* = splitting; *sis* = the process of) breaks the 6-carbon sugar (glucose) into two smaller 3-carbon molecules of pyruvic acid; ATP is produced. Hydrogens and their electrons are sent to the electron-transport system (ETS) for processing.
2. The **Krebs cycle** removes the remaining hydrogen, electrons, and carbon from pyruvic acid. ATP is produced for cell use. The hydrogens and their electrons are sent to the ETS for processing.
3. The **electron-transport system (ETS)** converts the kinetic energy of hydrogen electrons received from glycolysis and the Krebs cycle to the high-energy phosphate bonds of ATP, as the hydrogen ions and electrons are ultimately bonded with oxygen to form water (figure 6.6).

Intermediate Description

Glycolysis takes place in the cytoplasm. During glycolysis, a 6-carbon sugar molecule (glucose) is encouraged to break down by being energized by two ATP molecules. Adding this energy makes some of the bonds unstable. The broken bonds ultimately release enough chemical-bond energy to recharge four ATP molecules. Enzymes lower the activation energy and speed these oxidation-reduction reactions. Because two ATP molecules were used to start the reaction and four were produced, there is a *net gain* of two ATPs from the glycolytic pathway. The sugar is broken down (oxidized) into two 3-carbon molecules of **pyruvic acid** ($CH_3COCOOH$) (figure 6.7). During glycolysis the hydrogen electrons and protons are not added to oxygen to form water. Because O_2 is not used as a hydrogen ion and electron acceptor in glycolysis, this pathway is called **anaerobic cellular respiration.** Instead, the hydrogen electrons and protons are picked up by special carrier molecules (coenzymes) known as **NAD**$^+$ (**n**icotinamide

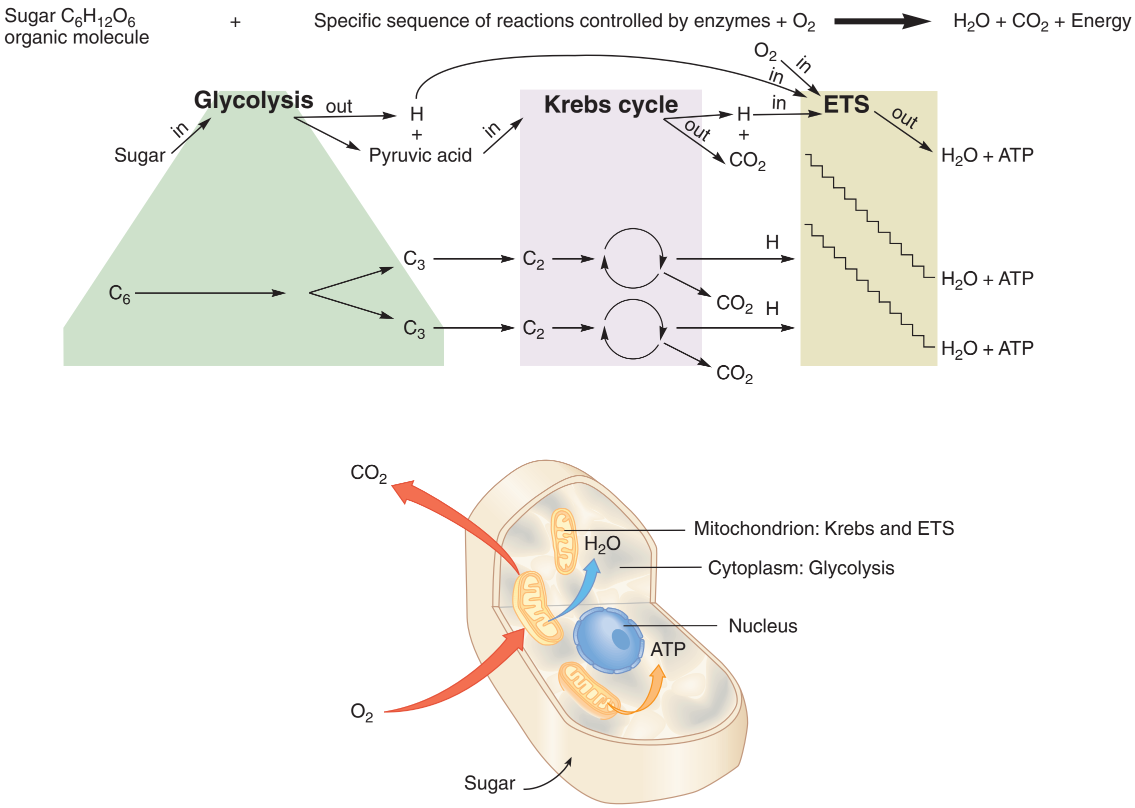


Figure 6.6

Aerobic Cellular Respiration: Basic Description

This sequence of reactions in the aerobic oxidation of glucose is an overview of the energy-yielding reactions of a cell. The first line presents the respiratory process in its most basic form. The next two lines expand on the generalized statement and illustrate how sugar (glucose) moves through a complex series of reactions to produce usable energy (ATP). Note that both CO_2 and H are products of the citric acid cycle, but only the H enters the ETS. The bottom illustration notes where these important biochemical pathways occur in an animal cell.

adenine **d**inucleotide). The reduced molecules of NAD^+ (NADH)* contain a large amount of potential energy that can be used to make ATP in the ETS. The job of the coenzyme NAD^+ is to safely transport these energy-containing electrons and protons to their final resting place, oxygen. Once they have dropped off their load in the electron-transport system, the oxidized NAD^+ returns to repeat the job.

In summary, the process of glycolysis takes place in the cytoplasm of a cell, where glucose ($C_6H_{12}O_6$) enters a series of reactions that:

1. Requires the use of two ATPs
2. Ultimately results in the formation of four ATPs
3. Results in the formation of two NADHs
4. Results in the formation of two molecules of pyruvic acid ($CH_3COCOOH$)

Because two molecules of ATP are used to start the process and a total of four ATPs are generated, each glucose molecule that undergoes glycolysis produces a net yield of two ATPs. Furthermore, the process of glycolysis does not require the presence of oxygen molecules (O_2).

After glucose has been broken down into two pyruvic acid molecules, those hydrogen-containing molecules are converted into two smaller molecules called acetyl. During the Krebs cycle (figure 6.8), the acetyl is completely oxidized inside the mitochondrion of eukaryotic cells. In prokaryotic cells, this occurs in the cytoplasm. The rest of the hydrogens on the acetyl molecule are removed and sent to the electron-transport system. The remaining carbon and oxygen atoms are combined to form CO_2. As in glycolysis, enough energy is released to generate two ATP molecules, and the hydrogen ions and electrons are carried to the ETS on NAD^+ and

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*NADH is really NADH + H^+ but we will use NADH for convenience.

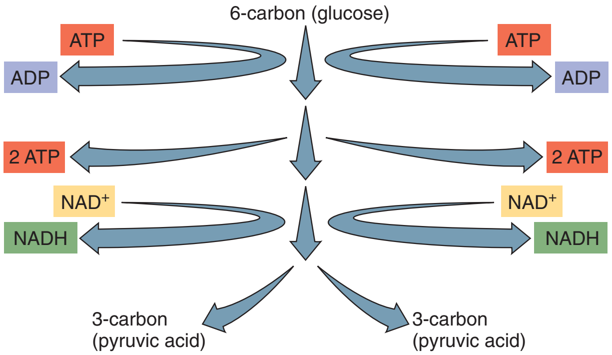


Figure 6.7

Glycolysis: Intermediate Description
Glycolysis is the biochemical pathway many organisms use to oxidize glucose. During this sequence of chemical reactions, the 6-carbon molecule of glucose is oxidized.

$$\mathbf{C_6H_{12}O_6\ (glucose) \rightarrow 2\ CH_3COCOOH\ (pyruvic\ acid) + 2\ NADH + energy\ (2\ ATP + heat)}$$

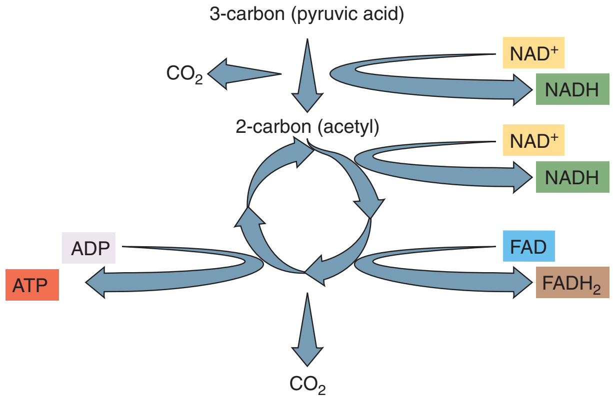


Figure 6.8

Krebs Cycle: Intermediate Description
The Krebs cycle is the biochemical pathway performed by most cells to complete the oxidation of glucose. During this sequence of chemical reactions, a pyruvic acid molecule produced from glycolysis is stripped of its hydrogens. The hydrogens are picked up by NAD^+ and FAD for transport to the ETS. The remaining atoms are reorganized into molecules of carbon dioxide. Enough energy is released during the Krebs cycle to charge two ADP molecules to form two ATPs. Because two pyruvic acid molecules were produced from glycolysis, the Krebs cycle must be run twice in order to complete their oxidation, i.e., once for each pyruvic acid.

$$\mathbf{2\ CH_3COCOOH\ (pyruvic\ acid) \rightarrow 6\ CO_2 + 8\ NADH + 2\ FADH_2 + energy\ (2\ ATP + heat)}$$

another coenzyme called **FAD** (**f**lavin **a**denine **d**inucleotide). At the end of the Krebs cycle, the acetyl has been completely broken down (oxidized) to CO_2. The energy in the molecule has been transferred to either ATP, NADH, or $FADH_2$. Also, some of the energy has been released as heat.

In summary, the Krebs cycle takes place within the mitochondria. For each pyruvic acid molecule that enters a mitochondrion and changed to acetyl that is processed through the Krebs cycle:

1. The three carbons of the pyruvic acid are released as carbon dioxide (CO_2)
2. Five pairs of hydrogens become attached to hydrogen carriers (four NADH and one $FADH_2$)
3. One ATP is generated

Cells generate the greatest amount of ATP from the electron-transport system (figure 6.9). During this stepwise sequence of oxidation-reduction reactions, the energy from the NADH and $FADH_2$ molecules generated in glycolysis and the Krebs cycle is used to recharge the cells' batteries. In a process called **chemiosmosis,** the energy needed to form the high-energy phosphate bonds of ATP comes from electrons that are rich in kinetic energy. The process of chemiosmosis results in the formation of ATP and occurs on the membranes of the mitochondrion. Iron-containing *cytochrome* (*cyto* = cell; *chrom* = color) molecules are located on these membranes. The energy-rich electrons are passed (*transported*) from one cytochrome to another, and the energy is used to pump hydrogen ions from one side of the membrane to the other. The result of this is a higher concentration of hydrogen ions on one side of the membrane. As the concentration of hydrogen ions increases on one side, a concentration gradient is established and a "pressure" builds up. This pressure is released when a membrane channel is opened, allowing these hydrogen ions to fly back to the side from which they were pumped. As they streak through the pores, an enzyme, ATPase (a phosphorylase), speeds the formation of an ATP molecule by bonding a phosphate to an ADP molecule (phosphorylation).

In summary, the electron-transport system takes place within the mitochondrion where:

1. Oxygen is used up as the oxygen atoms receive the hydrogens from NADH and $FADH_2$ to form water (H_2O)
2. NAD^+ and FAD are released to be used over again
3. 32 ATPs are produced

Detailed Description

Glycolysis

The first stage of the cellular respiration process takes place in the cytoplasm. This first step, known as glycolysis, consists

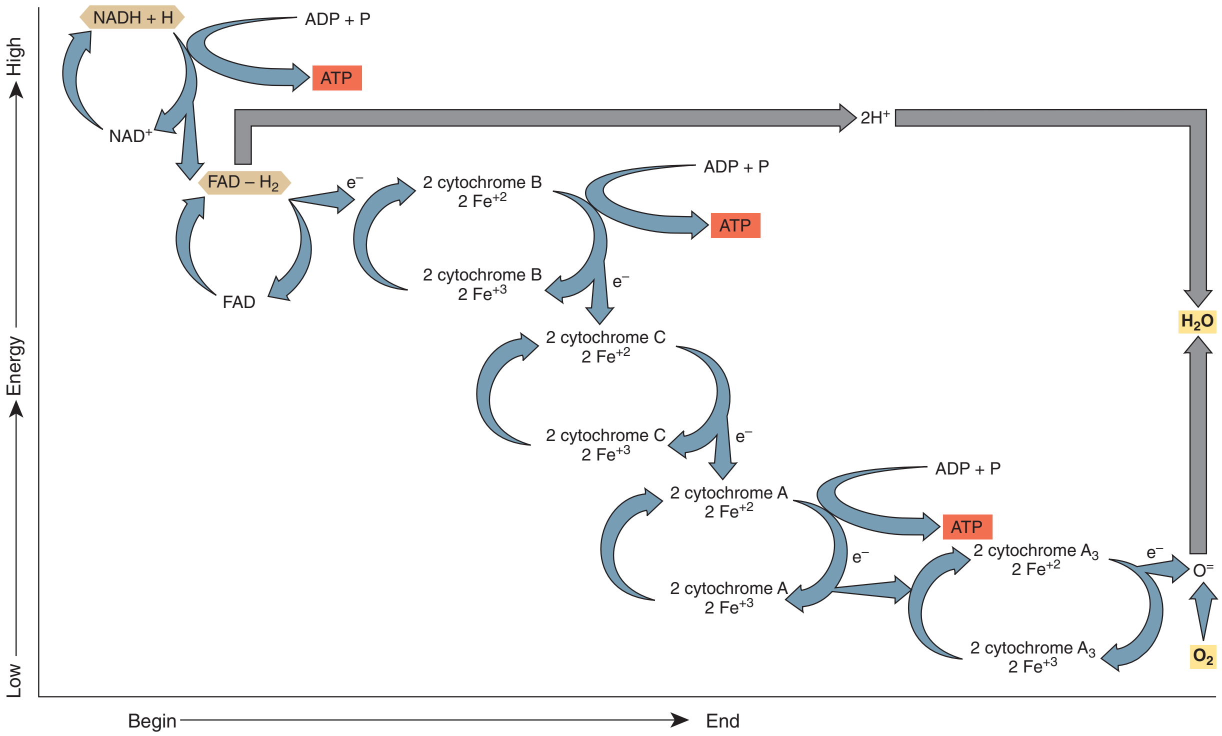


Figure 6.9

The Electron-Transport System: Intermediate Description
The electron-transport system (ETS) is a series of oxidation-reduction reactions also known as the cytochrome system. The movement of electrons down this biochemical "wire" establishes a kind of electrical current that drives H^+ protons to atmospheric oxygen. As the electrons flow through the system in mitochondria, ATPs may be produced.

$$8\ \mathrm{NADH} + 4\ \mathrm{FADH_2} + 6\ \mathrm{O_2} \rightarrow 12\ \mathrm{H_2O} + \text{energy}\ (32\ \mathrm{ATP} + \text{heat}) + 8\ \mathrm{NAD^+} + 4\ \mathrm{FAD}$$

of the enzymatic breakdown of a glucose molecule without the use of molecular oxygen (figure 6.10). Metabolic pathways that result in the breakdown of compounds are generally referred to as **catabolism.** The opposite types of reactions are those that result in the synthesis of new compounds known as **anabolism.** Because no oxygen is required, glycolysis is called an anaerobic process.

Some energy must be put in to start glycolysis because glucose is a very stable molecule and will not automatically break down to release energy. For each molecule of glucose entering glycolysis, two ATP molecules supply this start-up energy. The energy-containing phosphates are released from two ATP molecules and become attached to glucose to form phosphorylated sugar ($P—C_6—P$). This is a phosphorylation reaction. It is controlled by an enzyme named *phosphorylase*. The phosphorylated glucose is then broken down through several other enzymatically controlled reactions into two 3-carbon compounds, each with one attached phosphate ($C_3—P$). These 3-carbon compounds are **PGAL** (**p**hospho**gl**ycer**al**dehyde). Each of the two PGAL molecules acquires a second phosphate from a phosphate supply normally found in the cytoplasm. Each molecule now has two phosphates attached ($P—C_3—P$). A series of reactions follows in which energy is released by breaking chemical bonds, causing each of these 3-carbon compounds to lose their phosphates. These high-energy phosphates combine with ADP to form ATP. In addition, four hydrogen atoms detach from the carbon skeleton (oxidation) and become bonded to two hydrogen-carrier coenzyme molecules (reduction) known as **NAD+** (**n**icotinamide **a**denine **d**inucleotide). The molecules of NADH contain a large amount of potential energy that may be released to generate ATP in the ETS. The 3-carbon molecules that result from glycolysis are called pyruvic acid.

In summary, the process of glycolysis takes place in the cytoplasm of a cell. In this process, glucose undergoes reactions requiring the use of two ATPs, leading to the formation of four molecules of ATP, producing two molecules of NADH and two 3-carbon molecules of pyruvic acid.

The Krebs Cycle

The Krebs cycle is a series of oxidation-reduction reactions that complete the breakdown of pyruvic acid produced by glycolysis (figure 6.11). In order for pyruvic acid to be used

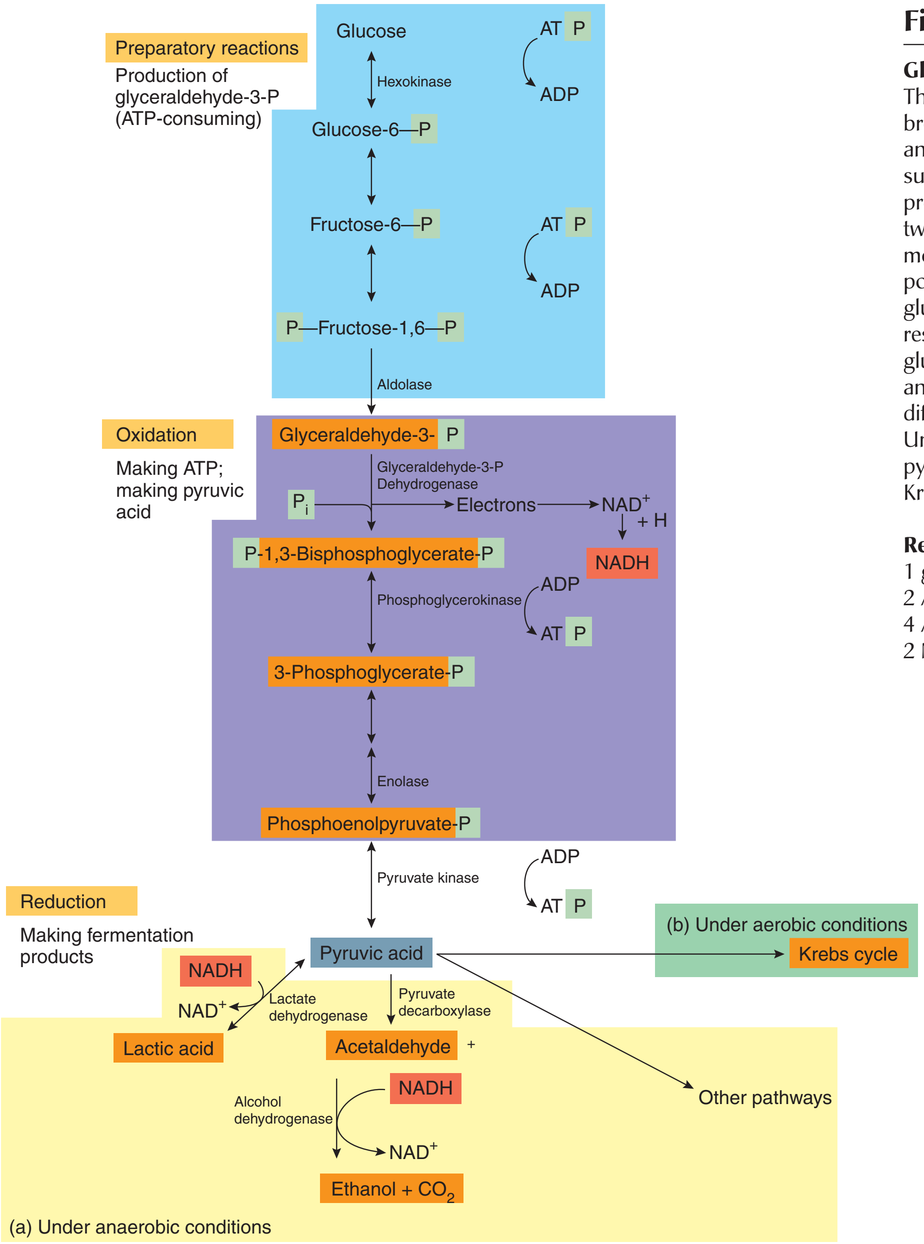


Figure 6.10

Glycolysis: Detailed Description

The glycolytic pathway results in the breakdown of 6-carbon sugars under anaerobic conditions. Each molecule of sugar releases enough energy to produce a profit (net gain) of two ATPs. In addition, two molecules of pyruvic acid and two molecules of NADH are produced. The first portion of the sequence prepares the glucose for oxidation. The second portion results in the oxidation of the original glucose, and the third may be (under anaerobic conditions—part *a*) one of many different types of reduction reactions. Under aerobic conditions (part *b*), the pyruvic acid is further metabolized in the Krebs cycle.

Reactants	**Products**
1 glucose	2 pyruvic acid
2 ATP	2 ADP + 2 P
4 ADP + 4 P	4 ATP
2 NAD^+ + 2 H	2 NADH

as an energy source, it must enter the mitochondrion. Once inside, an enzyme converts the 3-carbon pyruvic acid molecule to a 2-carbon molecule called **acetyl.** When the acetyl is formed, the carbon removed is released as carbon dioxide. In addition to releasing carbon dioxide, each pyruvic acid molecule is oxidized because it loses two hydrogens that become attached to NAD^+ molecules (reduction) to form NADH.

The carbon dioxide is a waste product that is eventually released by the cell into the atmosphere. The 2-carbon acetyl compound temporarily combines with a large molecule called *coenzyme A* (CoA) to form acetyl-CoA and transfers the acetyl to a 4-carbon compound called *oxaloacetic acid* to become part of a 6-carbon molecule. This new 6-carbon compound is broken down in a series of reactions to regenerate oxaloacetic acid in this cyclic pathway. The series of compounds formed during this cycle are called *keto acids* (not to be confused with ketone bodies). In the process of breaking down pyruvic acid, three molecules of carbon dioxide are formed. In addition, five pairs of hydrogens are removed and become attached to hydrogen-carrying coenzymes. Four pairs become attached to NAD^+ and one pair becomes attached to a different hydrogen carrier known as **FAD** (flavin adenine

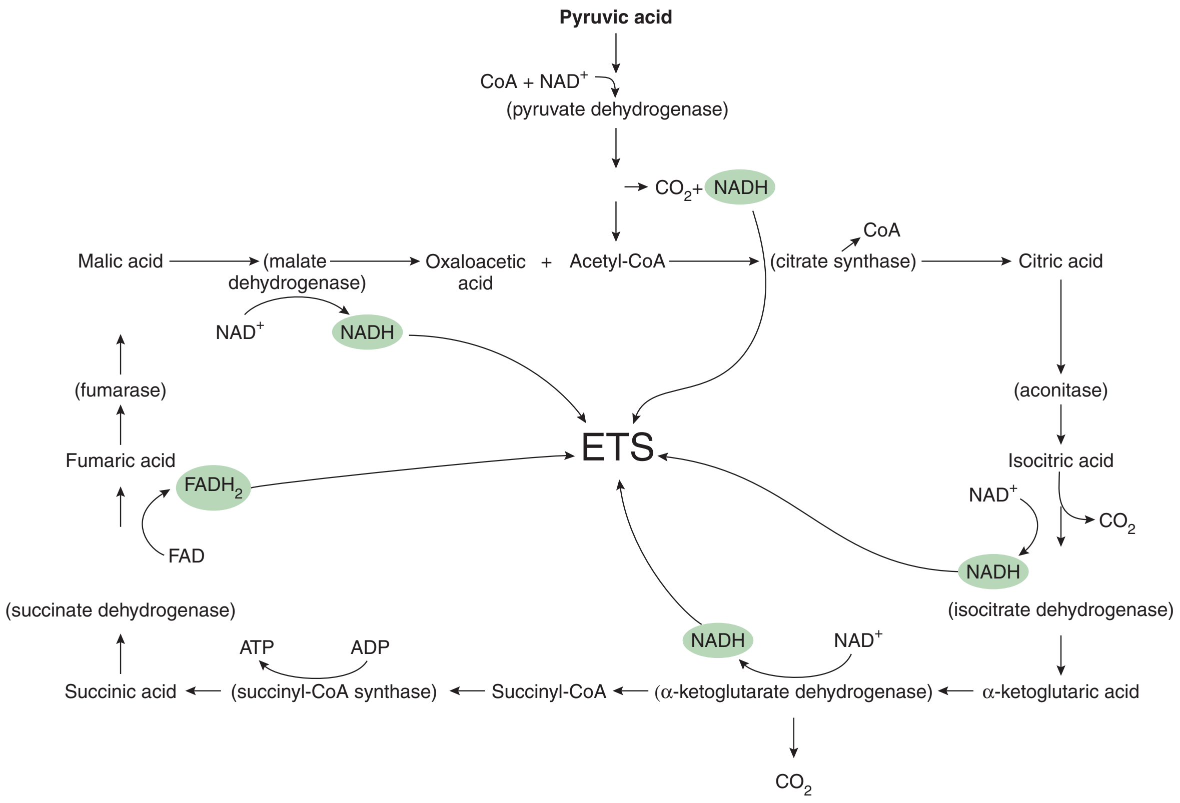


Figure 6.11

Krebs Cycle: Detailed Description	**Reactants**	**Products**
During the Krebs cycle, the pyruvic acid from glycolysis is broken down. The carbon ends up in carbon dioxide and the hydrogens are carried away to the electron-transport system as NADH and $FADH_2$. One ATP molecule is produced during this cycle. Remember that this cycle occurs twice for each mole of sugar oxidized to the two moles of pyruvic acid during glycolysis.	2 pyruvic acid 2 ADP + 2 P 8 NAD^+ + 8 H 2 FAD + 4 H	6 CO_2 2 ATP 8 NADH 2 $FADH_2$

dinucleotide). As the molecules move through the Krebs cycle, enough energy is released to allow the synthesis of one ATP molecule for each acetyl that enters the cycle. The ATP is formed from ADP and a phosphate already present in the mitochondria.

For each pyruvic acid molecule that enters a mitochondrion and is processed through the Krebs cycle, three carbons are released as three carbon dioxide molecules, five pairs of hydrogen atoms are removed and become attached to hydrogen carriers, and one ATP molecule is generated. When both pyruvic acid molecules have been processed through the Krebs cycle, (1) all the original carbons from the glucose have been released into the atmosphere as six carbon dioxide molecules, (2) all the hydrogen originally found on the glucose has been transferred to either NAD^+ or FAD to form NADH or $FADH_2$, and (3) two ATPs have been formed from the addition of phosphates to ADPs.

The Electron-Transport System

The series of reactions in which energy is removed from the hydrogens carried by NAD^+ and FAD is known as the electron-transport system (ETS) (figure 6.12). The process by which this happens is called **chemiosmosis.** This is the final stage of aerobic cellular respiration and is dedicated to generating ATP. The reactions that make up the electron-transport system are a series of oxidation-reduction reactions in which the electrons from the hydrogen atoms are passed from one electron-carrier molecule to another until they ultimately are accepted by oxygen atoms. The negatively charged oxygen combines with the hydrogen ions to form water. It is this step that makes the process aerobic. Keep in mind that potential energy increases whenever things experiencing a repelling force are pushed together, such as adding the third phosphate to an ADP molecule. Potential energy also increases whenever things that attract each

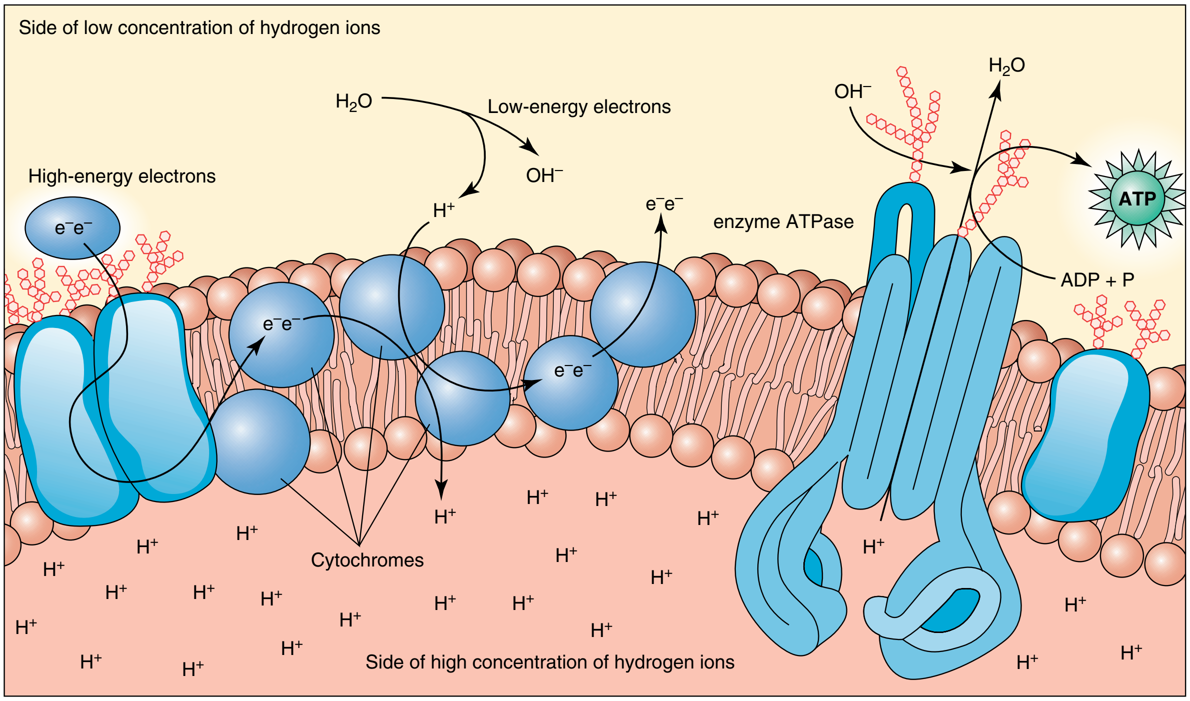


Figure 6.12

The Electron-Transport System: Detailed Description

The most detailed explanation of the ETS is known as chemiosmosis. It is the process of producing ATP by using the energy of hydrogen electrons and protons removed from glucose in glycolysis and the Krebs cycle. These electrons and protons are carried to the electron-transport system in the form of NADH and $FADH_2$. The process takes place in the thousands of mitochondria of a cell and requires electron-transport molecules, the cytochromes and a variety of oxidase enzymes. Cytochromes are located on the cristae, the inner folded membrane of the mitochondrion. Each time a pair of electrons is transported from one cytochrome to another, their energy is used to move H^+s into the space between the inner and outer mitochondrial membranes. This establishes an H^+ concentration gradient; i.e., there are more H^+s on one side of the membrane than the other. When these hydrogen ions fly back through the membrane, energy is released and used to synthesize ATP. The enzyme responsible for the phosphorylation (ATP synthetase) is located on the cristae. The electrons used in this process are added to oxygen to form negatively charged O^{--}, which combines with the H^+ to form H_2O.

Reactants	**Products**
8 NADH + 24 ADP + 24 P	8 NAD^+ + 24 ATP + 16 H
4 $FADH_2$ + 8 ADP + 8 P	4 FAD + 8 ATP + 8 H
6 O_2 + 24 H	12 H_2O

other are pulled apart, as in the separating of the protons from the electrons.

Let's now look at the hydrogen and its carriers in just a bit more detail to account for the energy that theoretically becomes available to the cell.

- At three points in the series of oxidation reductions in the ETS, sufficient energy is released from the NADHs to produce an ATP molecule. Therefore, 24 ATPs are released from these eight pairs of hydrogen electrons carried on NADH.
- In eukaryotic cells, the two pairs of hydrogen electrons released during glycolysis are carried as NADH and converted to $FADH_2$ in order to shuttle them into the mitochondria. Once they are inside the mitochondria, they follow the same pathway as the other $FADH_2$s. The four pairs of hydrogen electrons carried by FAD are lower in energy. When these hydrogen electrons go through the series of oxidation-reduction reactions, they release enough energy to produce ATP at only two points. They produce a total of 8 ATPs; therefore, we have a grand total of 32 ATPs produced from the hydrogen electrons that enter the ETS.

Figure 6.13 summarizes and compares theoretical ATP generation for eukaryotic and prokaryotic aerobic cellular respiration (How Science Works 6.1).

Cellular Respiration Stage	Prokaryotic Cells ATP Theoretically Generated	Eukaryotic Cells ATP Theoretically Generated
Glycolysis	Net gain 2 ATP	Net gain 2 ATP
Krebs cycle	2 ATP	2 ATP
ETS	34 ATP	32 ATP
Total	38 ATP	36 ATP

Figure 6.13

Aerobic ATP Production: Prokaryotic versus Eukaryotic Cells
The total net number of ATPs theoretically generated by the complete, aerobic cellular respiration of a mole of glucose is determined by adding the number of ATPs produced directly in the glycolytic pathways and Krebs cycle and those produced from the conversion of NADH and $FADH_2$. When the potential energy in one NADH is converted in the ETS, it results in the formation of three ATPs. When the potential energy in one $FADH_2$ is converted in the ETS, it results in the formation of two ATPs. The majority of ATPs are produced as a result of performing this reaction in the ETS.

HOW SCIENCE WORKS 6.1

Mole Theory—It's Not What You Think!

In real life it is unreasonable to follow a chemical reaction on an atom-by-atom basis. Therefore, the formulas for reactions represent not individual numbers of molecules but considerably larger amounts. The whole number that appears before the chemical formula in an equation describes how many *moles* of the compound are involved in the reaction. A mole is 6.023×10^{23} objects, or

602,300,000,000,000,000,000,000!

Think of a "mole" as you would think of a "dozen." A dozen eggs is 12 eggs. Two dozen eggs are 24 eggs. A mole of eggs is 6.023×10^{23} eggs. A mole of pencils would contain 6.023×10^{23} pencils. Two moles of bananas would be $2 \times (6.023 \times 10^{23})$ bananas.

In a chemical reaction, this number is equal to the atomic or molecular mass in grams. For example, a mole of hydrogen atoms (H) contains 6.023×10^{23} atoms of hydrogen. A mole of glucose contains 6.023×10^{23} molecules of glucose. The number 6.023×10^{23} is known as Avogadro's number after its discoverer, Italian chemist and physicist Amedeo Avogadro. With respect to aerobic cellular respiration in humans,

$$C_6H_{12}O_6 + 6\ O_2 + 6\ H_2O \rightarrow 6\ CO_2 + 12\ H_2O + 36\ ATP + heat$$

the number preceding each formula tells the number of moles of each substance. Therefore, we are talking not about the number of individual molecules being respired but the number of moles of each substance being respired. In this case there are

$1 \times 6.023 \times 10^{23}$ **molecules of** $C_6H_{12}O_6$
$6 \times 6.023 \times 10^{23}$ **molecules of** O_2
$6 \times 6.023 \times 10^{23}$ **molecules of** H_2O
$6 \times 6.023 \times 10^{23}$ **molecules of** CO_2

being metabolized to theoretically produce 36 moles of ATP.

How does this measure up on a scale? It amounts to:

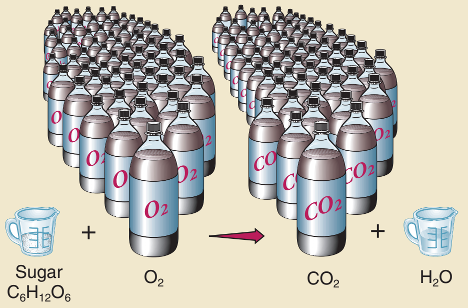
180 grams of $C_6H_{12}O_6$ = molecular weight of $C_6H_{12}O_6$ × 1 mole
= 0.5 cup

192 grams of O_2 = molecular weight of O_2 × 6 moles
= 67 2-liter pop bottles of oxygen!

108 grams of H_2O (net) = molecular weight of H_2O × 6 moles
= 0.45 cup

264 grams of CO_2 = molecular weight of CO_2 × 6 moles
= 67 2-liter pop bottles

These are sizable amounts of food and water! How do these numbers compare to those noted on the nutrition labels of some of your snack foods?



6.4 Alternatives: Anaerobic Cellular Respiration

Not all organisms use O_2 as their ultimate hydrogen acceptor. Certain cells do not or cannot produce the enzymes needed to run aerobic cellular respiration. Other cells have the enzymes but cannot function aerobically if O_2 is not available. These organisms must use a different biochemical pathway to generate ATP. Some are capable of using other inorganic or organic molecules for this purpose. An organism that uses something other than O_2 as its final hydrogen acceptor is called anaerobic (*an* = without; *aerob* = air) and performs **anaerobic cellular respiration.** The acceptor molecule could be sulfur, nitrogen, or other inorganic atoms or ions. It could also be an organic molecule such as pyruvic acid ($CH_3COCOOH$). Anaerobic pathways that oxidize glucose to generate ATP energy using an organic molecule as the ultimate hydrogen acceptor are called **fermentation.** Anaerobic cellular respiration results in the release of less ATP and heat energy than aerobic cellular respiration. Anaerobic respiration is the incomplete oxidation of glucose.

$$C_6H_{12}O_6 + (H^+ \text{ \& } e^- \text{ acceptor}) \rightarrow \textbf{smaller hydrogen-containing molecules + energy (ATP + heat)}$$

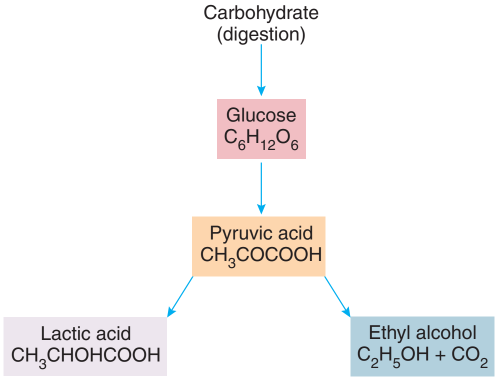
Many fermentations include glycolysis but are followed by reactions that vary depending on the organism involved and its enzymes. Some organisms are capable of returning the hydrogens removed from sugar to pyruvic acid, forming the products ethyl alcohol and carbon dioxide.

$$C_6H_{12}O_6 + \textbf{pyruvic acid + hydrogen \& electrons from glucose} \rightarrow \textbf{ethyl alcohol} + CO_2 + \textbf{energy (ATP + heat)}$$

Other organisms produce enzymes that enable the hydrogens to be bonded to pyruvic acid, changing it to lactic acid, acetone, or other organic molecules (figure 6.14).

Although many different products can be formed from pyruvic acid, we will look at only two anaerobic pathways. **Alcoholic fermentation** is the anaerobic respiration pathway that, for example, yeast cells follow when oxygen is lacking in their environment. In this pathway, the pyruvic acid is converted to ethanol (a 2-carbon alcohol, C_2H_5OH) and carbon dioxide. Yeast cells then are able to generate only four ATPs from glycolysis. The cost for glycolysis is still two ATPs; thus, for each glucose a yeast cell oxidizes, it profits by two ATPs. The products carbon dioxide and ethanol are useful to humans. In making bread, the carbon dioxide is the important end product; it becomes trapped in the bread dough and makes it rise. When this happens we say the bread is *leavened.* Dough that has not undergone this process is called unleavened. The alcohol evaporates during the baking process. In the brewing industry, ethanol is the desirable product produced by yeast cells. Champagne, other sparkling wines, and beer are products that contain both carbon dioxide and alcohol. The alcohol accumulates, and the carbon dioxide in the bottle makes them sparkling (bubbly) beverages. In the manufacture of many wines, the carbon dioxide is allowed to escape so they are not sparkling but "still" wines.

Certain bacteria are unable to use oxygen even though it is available, and some bacteria are killed in the presence of



Fermentation product	Possible source	Importance
Lactic acid	Bacteria: *Lactobacillus bulgaricus*	Aids in changing milk to yogurt
	Homo sapiens Muscle cells	Produced when O_2 is limited; results in pain and muscle inaction
Ethyl alcohol +CO_2	Yeast: *Saccharomyces cerevisiae*	Brewing and baking

Figure 6.14

A Variety of Fermentations
This biochemical pathway illustrates the digestion of a complex carbohydrate to glucose followed by the glycolytic pathway forming pyruvic acid. Depending on the genetic makeup of the organisms and the enzymes they are able to produce, different end products may be synthesized from the pyruvic acid. The synthesis of these various molecules is the organism's particular way of oxidizing NADH to NAD^+ and reducing pyruvic acid to a new end product.

O_2. The pyruvic acid ($CH_3COCOOH$) that results from glycolysis is converted to lactic acid ($CH_3CHOHCOOH$) by the addition of the hydrogens that had been removed from the original glucose.

$C_6H_{12}O_6$ + pyruvic acid + hydrogen & electrons from glucose → lactic acid + energy (ATP + heat)

In this case, the net profit is again only two ATPs per glucose. The lactic acid buildup eventually interferes with normal metabolic functions and the bacteria die. We use the lactic acid waste product from these types of anaerobic bacteria when we make yogurt, cultured sour cream, cheeses, and other fermented dairy products. The lactic acid makes the milk protein coagulate and become puddinglike or solid. It also gives the products their tart flavor, texture, and aroma.

In the human body, different cells have different metabolic capabilities. Red blood cells lack mitochondria and must rely on lactic acid fermentation to provide themselves with energy. Nerve cells can use glucose only aerobically. As long as oxygen is available to skeletal muscle cells, they function aerobically. However, when oxygen is unavailable—because of long periods of exercise, or heart or lung problems that prevent oxygen from getting to the skeletal muscle cells—the cells make a valiant effort to meet energy demands by functioning anaerobically.

While skeletal muscle cells are functioning anaerobically, they are building up an *oxygen debt.* These cells produce lactic acid as their fermentation product. Much of the lactic acid is transported by the bloodstream to the liver, where about 20% is metabolized through the Krebs cycle and 80% is resynthesized into glucose. Even so, there is still a buildup of lactic acid in the muscles. It is the lactic acid buildup that makes the muscles tired when exercising (figure 6.15). When the lactic acid concentration becomes great enough, lactic acid fatigue results. Its symptoms are cramping of the muscles and pain. Because of the pain, we generally stop the activity before the muscle cells die. As a person cools down after a period of exercise, breathing and heart rate stay high until the oxygen debt is repaid and the level of oxygen in muscle cells returns to normal. During this period, the lactic

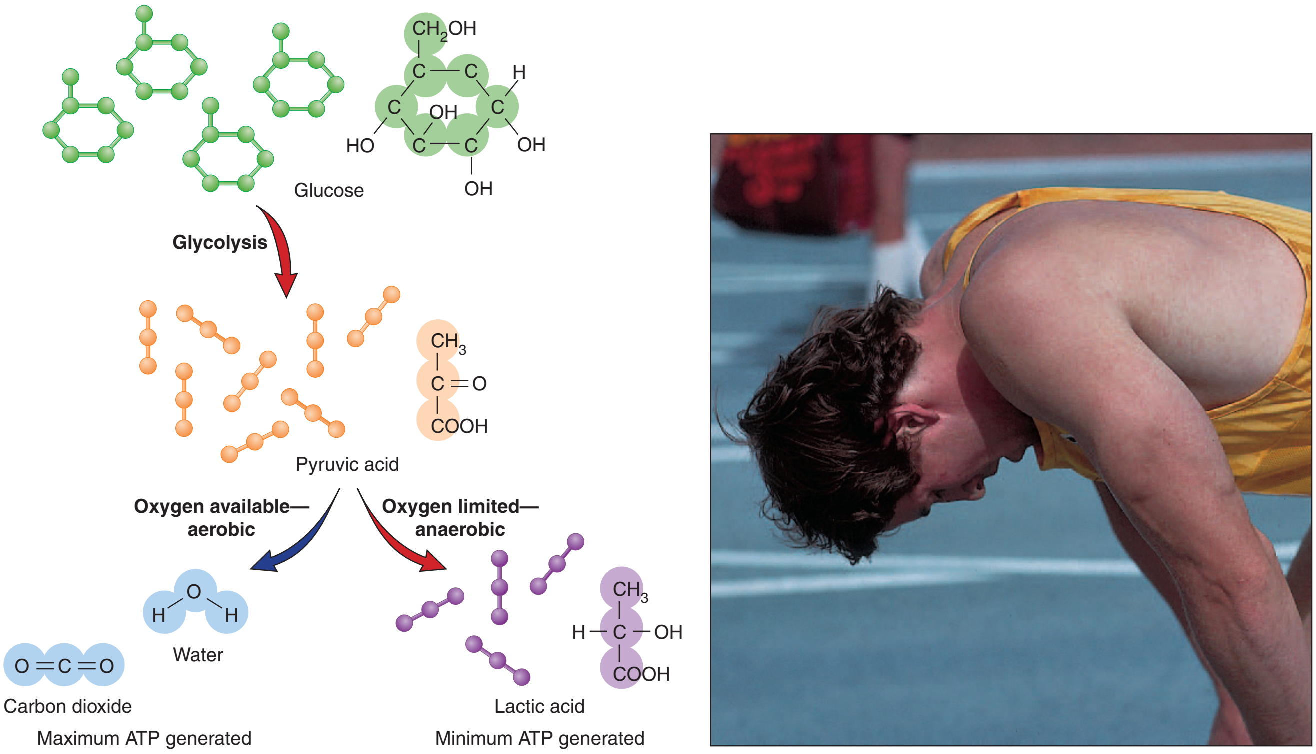


Figure 6.15

Oxygen Debt

When oxygen is available to all cells, the pyruvic acid from glycolysis is converted into acetyl-CoA, which is sent to the Krebs cycle, and the hydrogens pass through the electron-transport system. When oxygen is not available in sufficient quantities (because of a lack of environmental oxygen or a temporary inability to circulate enough oxygen to cells needing it), some of the pyruvic acid from glycolysis is converted to lactic acid. The lactic acid builds up in cells when this oxygen debt occurs. It is the presence of this lactic acid that results in muscle fatigue and a burning sensation.

acid that has accumulated is being converted back into pyruvic acid. The pyruvic acid can now continue through the Krebs cycle and the ETS as oxygen becomes available. In the genetic abnormality sickle-cell anemia, lactic acid accumulation becomes so great that people experiencing this condition may suffer from many severe symptoms (see chapters 7, 10, and 11).

6.5 Metabolism of Other Molecules

Up to this point we have described the methods and pathways that allow organisms to release the energy tied up in carbohydrates. Frequently, cells lack sufficient carbohydrates but have other materials from which energy can be removed. Fats and proteins, in addition to carbohydrates, make up the diet of many organisms. These three foods provide the building blocks for the cells, and all can provide energy. The pathways that organisms use to extract this chemical-bond energy are summarized here.

Fat Respiration

A molecule of true or neutral fat (triglyceride) consists of a molecule of glycerol with three fatty acids attached to it. Before fats can undergo catabolic oxidation and release energy, they must be broken down into glycerol and fatty acids. The 3-carbon glycerol molecule can be converted into PGAL (phosphoglyceraldehyde), which can then enter the glycolytic pathway (figure 6.16). However, each of the fatty acids must be processed before it can enter the pathway. Each long chain of carbons that makes up the carbon skeleton is hydrolyzed into 2-carbon fragments. Next, each of the 2-carbon fragments is converted into acetyl. The acetyl molecules are carried into the Krebs cycle by coenzyme A molecules.

By following the glycerol and each 2-carbon fragment through the cycle, you can see that each molecule of fat has the potential to release several times as much ATP as does a molecule of glucose. Each glucose molecule has six pairs of hydrogen, whereas a typical molecule of fat has up to 10 times that number. This is why fat makes such a good long-term energy storage material. It is also why the removal of fat on a weight-reducing diet takes so long! It takes time to use all the energy contained in the hydrogen of fatty acids. On a weight basis, there are twice as many calories in a gram of fat as there are in a gram of carbohydrate.

Notice in figure 6.16 that both carbohydrates and fats can enter the Krebs cycle and release energy. Although people require both fats and carbohydrates in their diets, they need not be in precise ratios; the body can make some interconversions. This means that people who eat excessive amounts of carbohydrates will deposit body fat. It also means that people who starve can generate glucose by breaking down fats and using the glycerol to synthesize glucose.

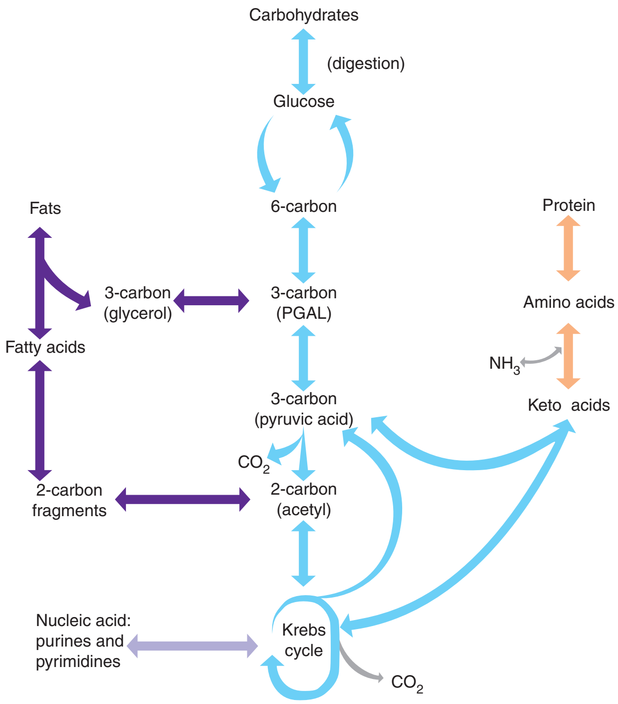


Figure 6.16

The Interconversion of Fats, Carbohydrates, and Proteins
Cells do not necessarily utilize all food as energy. One type of food can be changed into another type to be used as raw materials for construction of needed molecules or for storage. Notice that many of the reaction arrows have two heads, i.e., these reactions can go in either direction. For example, glycerol can be converted into PGAL and PGAL can become glycerol.

Protein Respiration

Proteins can also be catabolized and interconverted just as fats and carbohydrates are. The first step in utilizing protein for energy is to digest the protein into individual amino acids. Each amino acid then needs to have the amino group (—NH_2) removed. The remaining carbon skeleton, a keto acid, is changed and enters the respiratory cycle as pyruvic acid or as one of the other types of molecules found in the Krebs cycle. These acids have hydrogens as part of their structure. As the acids progress through the Krebs cycle and the ETS, the hydrogens are removed and their energy is converted into the chemical-bond energy of ATP. The amino group that was removed is converted into ammonia. Some organisms excrete ammonia directly; others convert ammonia into other nitrogen-containing compounds, such as urea or uric acid. All of these molecules are toxic and must be eliminated. They are transported in the blood to the kidneys, where they are eliminated. In the case of a high-protein diet, increasing fluid intake will allow the kidneys to efficiently remove the urea or uric acid.

When proteins are eaten, they are able to be digested into their component amino acids. These amino acids are then available to be used to construct other proteins. If there is no need to construct protein, the amino acids are metabolized to provide energy, or they can be converted to fat for long-term storage. One of the most important concepts you need to recognize from this discussion is that carbohydrates, fats, and proteins can all be used to provide energy. The fate of any type of nutrient in a cell depends on the momentary needs of the cell.

An organism whose daily food-energy intake exceeds its daily energy expenditure will convert only the necessary amount of food into energy. The excess food will be interconverted according to the enzymes present and the needs of the organism at that time. In fact, glycolysis and the Krebs cycle allow molecules of the three major food types (carbohydrates, fats, and proteins) to be interconverted.

As long as a person's diet has a certain minimum of each of the three major types of molecules, the cell's metabolic machinery can interconvert molecules to satisfy its needs. If a person is on a starvation diet, the cells will use stored carbohydrates first. Once the carbohydrates are gone (about two days), cells will begin to metabolize stored fat. When the fat is gone (a few days to weeks), the proteins will be used. A person in this condition is likely to die.

If excess carbohydrates are eaten, they are often converted to other carbohydrates for storage or converted into fat. A diet that is excessive in fat results in the storage of fat. Proteins cannot be stored. If they or their component amino acids are not needed immediately, they will be converted into fat, carbohydrates, or energy. This presents a problem for individuals who do not have ready access to a continuous source of amino acids (i.e., individuals on a low-protein diet). They must convert important cellular components into protein as they are needed. This is the reason why protein and amino acids are considered an important daily food requirement.

6.6 Photosynthesis

Basic Description

Ultimately the energy to power all organisms comes from the sun. Chlorophyll-containing plants, algae, and certain bacteria have the ability to capture and transform light energy through the process of photosynthesis. They transform light energy to chemical-bond energy in the form of ATP and then use ATP to produce complex organic molecules such as glucose. It is these organic molecules that organisms use as an energy source through the process of cellular respiration. In algae and the leaves of green plants, the process occurs in cells that contain structures called chloroplasts (figure 6.17).

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

$$\textbf{Light energy} + 6\ CO_2 + 12\ H_2O \rightarrow C_6H_{12}O_6 + 6\ H_2O + 6\ O_2$$

There are three stages in the photosynthetic pathway (figure 6.18):

1. **Light-capturing stage.** In eukaryotic cells photosynthetic pigments such as chlorophyll are clustered together on chloroplasts membranes. When enough of the right kind of light is available, the pigment electrons absorb extra energy and become "excited." With this added energy they are capable of entering into the chemical reactions responsible for the production of ATP. Light-capturing reactions take place on the thylakoid membranes.

$$\textbf{Light energy + photosynthetic pigments} \rightarrow \textbf{excited electrons}$$

2. **Light-dependent reaction stage.** Since this stage depends on the presence of light, it is also called light dependent or the *light reaction.* During this stage "excited" electrons from the light-capturing stage are used to make ATP. In addition, water is broken down to hydrogen and oxygen. The oxygen is released to the environment as O_2 and the hydrogens are transferred to electron carrier coenzymes, **NADP$^+$** (**n**icotinamide **a**denine **d**inucleotide **p**hosphate). (NADP$^+$ is similar to NAD that was discussed in the section on cellular respiration.) Light-dependent reactions also take place on the thylakoid membranes.

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

3. **Light-independent reaction stage.** This stage is also known as the dark reaction since light is not needed for the reactions to take place. During these reactions, ATP and NADPH from the light-dependent reaction stage are used to attach CO_2 to five carbon starter molecules (already present in the cell) to manufacture new larger organic molecules, for example, glucose ($C_6H_{12}O_6$) (figure 6.18). These reactions take place in the light or dark as long as substrates are available from the light-dependent stage. These reactions take place in the stroma of the chloroplast.

$$ATP + NADPH + CO_2 + 5\ \text{carbon starter} \rightarrow \text{larger organic molecules, e.g., glucose}$$

Intermediate Description

Light energy is used to drive photosynthesis during the light-capturing stage. About 40% of the Sun's energy is visible light and plant leaves absorb about 80% of the visible light that falls on them. Visible light is a combination of many different wavelengths of light seen as different colors. Some of these colors are seen when white light is separated to form a rainbow. The colors of the electromagnetic spectrum that provide the energy for photosynthesis are correlated with different kinds of light-energy-absorbing pigments. The green

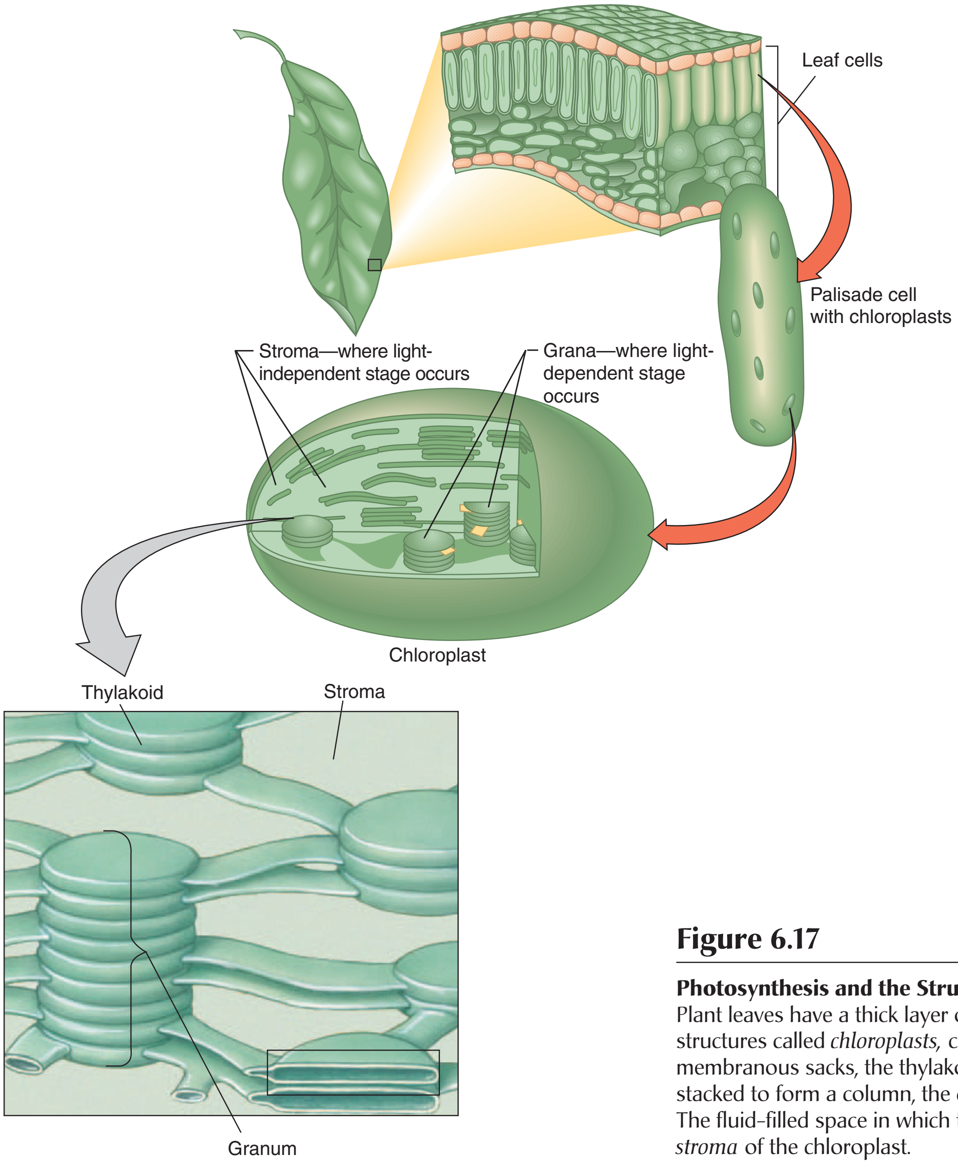


Figure 6.17

Photosynthesis and the Structure of a Leaf
Plant leaves have a thick layer of chlorophyll-containing cells. Within structures called *chloroplasts,* chlorophyll is located on individual membranous sacks, the thylakoids. When many thylakoid sacks are stacked to form a column, the column is called *granum* (pl., grana). The fluid-filled space in which the grana are located is called the *stroma* of the chloroplast.

chlorophylls are the most familiar and abundant. There are several types of this pigment. The two most common types are chlorophyll *a* and chlorophyll *b*. Chlorophyll *a* absorbs red light and chlorophyll *b* absorbs blue-green light (figure 6.19). These pigments reflect green light. That is why we see chlorophyll-containing plants as predominantly green. Other pigments, called **accessory pigments,** include the *carotenoids* (yellow, red, and orange), and the *phycobilins* (i.e., *phycoerythrins*—red and *phycocyanin*—blue). They absorb mostly blue and green light while reflecting the oranges and yellows. Accessory pigments, usually masked by chlorophyll, are responsible for the brilliant colors of vegetables such as carrots, tomatoes, eggplant, and peppers. Having a combination of all these pigments enables an organism to utilize more colors of the electromagnetic spectrum for photosynthesis.

For most plants, the entire process of photosynthesis takes place in the leaf, in cells containing large numbers of chloroplasts (refer to figure 6.17). Recall from chapter 4 that chloroplasts are membranous, saclike organelles containing many thin flat disks. These disks, called **thylakoids,** contain chlorophylls, accessory pigments, electron-transport molecules, and enzymes. They are stacked in groups, called **grana** (singular, granum). The fluid-filled spaces between the grana are called the **stroma** of the chloroplast. The structure of the chloroplast is directly related to both the light-capturing and the energy-conversion steps of photosynthesis. In the

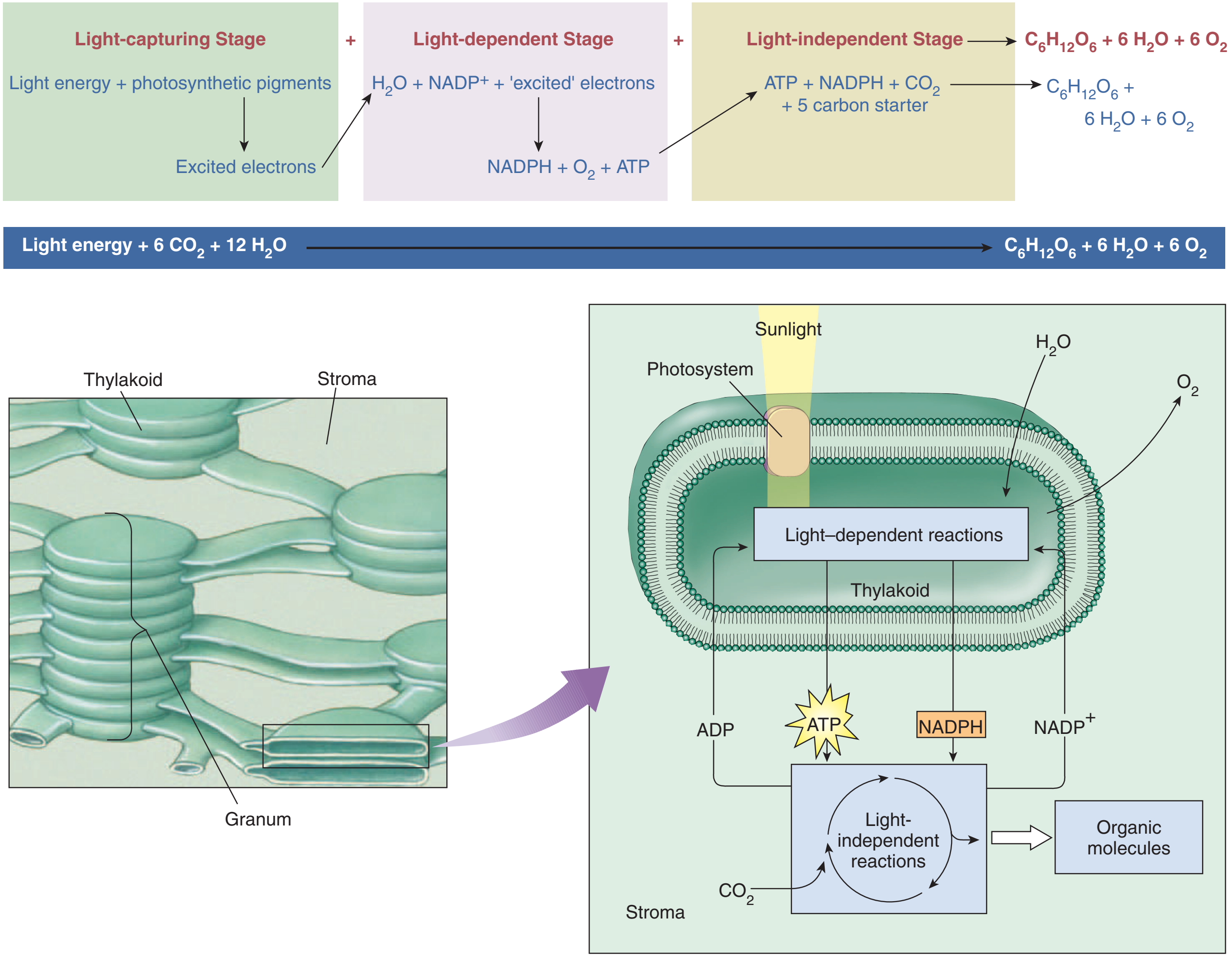


Figure 6.18

Photosynthesis: Basic Description

Photosynthesis is a complex biochemical pathway in plants, algae, and certain bacteria. The upper portion of this figure shows the overall process. Sunlight, along with CO_2 and H_2O, is used to make organic molecules such as sugar. The lower portion illustrates the three parts to the process: (1) the light-capturing stage, (2) the light-dependent reaction stage, and (3) the light-independent reaction stage. Notice that the end products of the light-dependent reaction, NADPH and ATP, are necessary to run the light-independent stage while the water and carbon dioxide are supplied from the environment.

light-capturing process, the electrons of pigments (e.g., chlorophyll) imbedded in the thylakoid membranes absorb light energy. The pigments and other molecules involved in trapping sunlight energy are arranged into clusters called **photosystems.** By clustering the pigments, they serve as energy-gathering or -concentrating mechanisms that allow light to be collected more efficiently, that is, "exciting" the electrons to higher energy levels (figure 6.20).

The light-dependent reaction stage of photosynthesis takes place in the thylakoid membranes. The "excited" or energized electrons from the light-capturing stage are passed to protein molecules in the thylakoid. From here the energy is used to phosphorylate ADP molecules (ADP + P $\rightarrow$ ATP), or, in other words, charge the cells' batteries. This system is similar to the ETS of aerobic cellular respiration. During the light-dependent reactions, water molecules are split, resulting in the production of hydrogen ions, electrons, and oxygen gas, O_2. The coenzyme, $NADP^+$ picks up the electrons, and becomes reduced to NADPH. The oxygen remaining from the water molecules is released into the atmosphere or can be used by the aerobic cellular respiration process that also takes place in plant cells.

The light-independent reaction stage is a series of reactions that occurs outside the grana, in the stroma. This stage is a series of oxidation-reduction reactions that combine hydrogen from water (carried by NADPH) with carbon

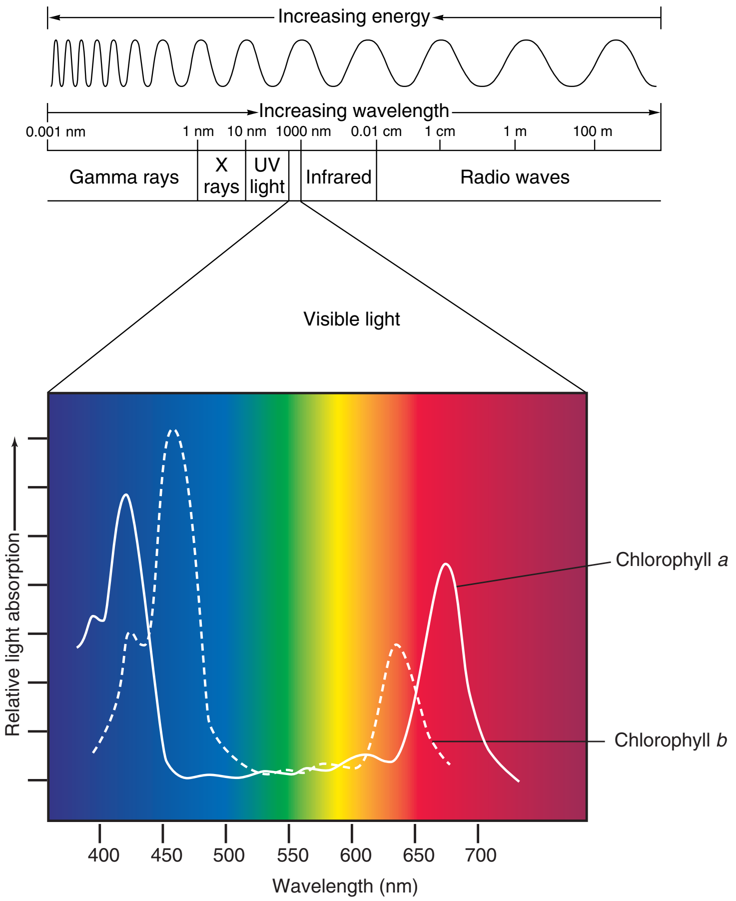


Figure 6.19

The Visible Light Spectrum and Chlorophyll
Light is a form of electromagnetic energy that can be thought of as occurring in waves. The shorter the wavelength the greater the energy it contains. Humans are capable of only seeing waves that are between about 400 and 740 nm (nanometers) long. Chlorophyll *a* (the solid graph line) and chlorophyll *b* (the dotted graph line) absorb different wavelengths of light energy.

dioxide from the atmosphere to form simple organic molecules such as sugar. As CO_2 diffuses into the chloroplasts the enzyme, **ribulose bisphosphate carboxylase (RuBisCo)** speeds the combining of the CO_2 with an already-present, 5-carbon carbohydrate, **ribulose.** NADPH then donates its hydrogens and electrons to complete the reduction of the molecule. The resulting 6-carbon molecule is immediately split into two 3-carbon molecules of **phosphoglyceraldehyde, PGAL.** PGAL can then be used by the plant for the synthesis of numerous other types of organic molecules such as starch. The plant can construct a wide variety of other organic molecules (e.g., proteins, nucleic acids), provided there are a few additional raw materials, such as minerals and nitrogen-containing molecules (figure 6.21).

Detailed Description

The Light-Capturing Stage of Photosynthesis

The green pigment, chlorophyll, which is present in chloroplasts, is a complex molecule with many loosely attached electrons. When struck by units of light energy called *photons,* the electrons of the chlorophyll absorb the energy and transfer it to other adjacent pigments. When the right amount of energy has been trapped and transferred to a key protein molecule, the energy of this "excited" electron can be used for other purposes. The various molecules involved in these reactions are referred to as photosystems. A photosystem is composed of two portions: (1) an *antenna complex* and (2) a *reaction center.* The antenna complex is a network of hundreds of chlorophyll and accessory pigment molecules whose role is to capture photons of light energy and transfer the energy to the reaction center. When light shines on the antenna and strikes a chlorophyll molecule, an electron becomes excited. The energy of the excited electron is passed from one pigment to another through the network. This series of excitations continues until the combined energies are transferred to the reaction center which consists of a chlorophyll *a*/protein complex. The reaction center protein forms a channel through the thylakoid membrane. The excited electron passes through the channel to a primary electron acceptor molecule, oxidizing the chlorophyll

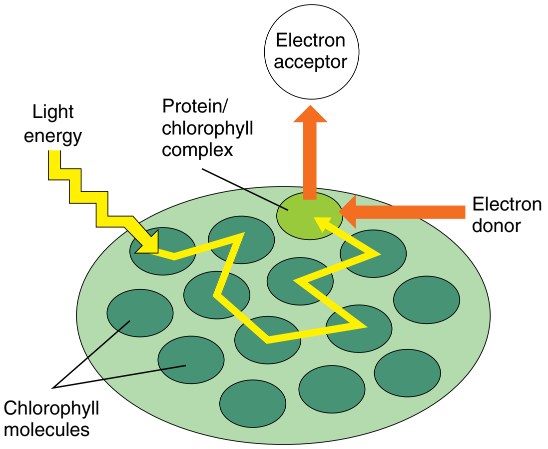


Figure 6.20

How a Photosystem Works: Intermediate Description
On the surface of the thylakoid membranes are large numbers of clusters of photosynthetic pigments. When light strikes one of the pigments, it excites the electrons and transmits that additional energy to adjacent pigments until it reaches a key protein/chlorophyll complex. This final high-energy electron acceptor transmits the electron out of the photosystem to the light-independent reactions.

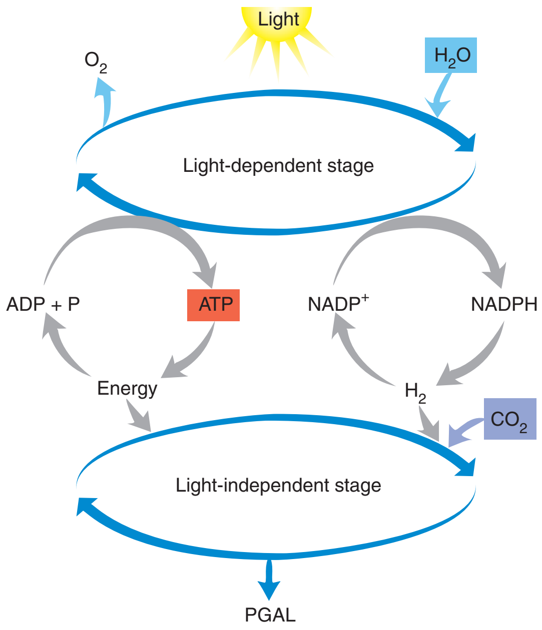


Figure 6.21

Photosynthesis: Intermediate Description—Light-Dependent and -Independent Stages
The process of photosynthesis is composed of the interrelated stages of light-dependent reaction and light-independent reaction. The light-independent reaction stage requires the ATP and NADPH produced in the light-dependent reaction stage. The light-dependent reaction stage, in turn, requires the ADP and $NADP^+$ released from the light-independent reaction stage. Therefore, each stage is dependent on the other.

and reducing the acceptor. The oxidized chlorophyll then has its electron replaced with another electron from a different electron donor. Exactly where this hole-filling electron comes from is the basis upon which two different photosystems have been identified—photosystems II and I.

The Light-Dependent Reaction Stage of Photosynthesis

In actuality, photosystem II occurs first and feeds electrons to photosystem I. In *photosystem II,* an enzyme on the thylakoid is responsible for splitting water molecules ($H_2O \rightarrow 2H + O$). The oxygen is released into the environment as O_2 and the electrons of the hydrogens are transferred to the chlorophyll of the reaction center that previously had lost electrons. The high-energy electrons from the reaction center do not move directly to the chlorophyll but are moved through a series of electron-transport molecules (cytochromes, in an electron-transport system). The protons from water (H^+—hydrogens that had lost their electrons) are pumped across the thylakoid membrane producing a H^+ gradient. This gradient is then used as the source of energy to phosphorylate ADP forming ATP (ADP + P → ATP). This *chemiosmotic* process in the chloroplast takes the energy from the excited electrons and uses it to bind a phosphate to an ADP molecule, forming ATP. This energy-conversion process begins with sunlight energy exciting the electrons of chlorophyll to a higher energy level and ends when the electron energy is used to make ATP.

The chlorophyll electrons from photosystem II eventually replace the electrons lost from the chlorophyll molecules in photosystem I. In *photosystem I* light has been trapped and the energy absorbed in the same manner as occurred in photosystem II. However this system does not have the enzyme involved in hydrolyzing water into oxygen, protons, and electrons; therefore no O_2 is released from photosystem I. The high-energy electrons leaving the reaction center of photosystem I make their way through a different series of oxidation-reduction reactions. During these reactions, $NADP^+$ is reduced to NADPH (figure 6.22).

The Light-Independent Reaction Stage of Photosynthesis

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

CO_2 is said to undergo *carbon fixation* through the **Calvin cycle** (named after its discoverer, Melvin Calvin). In the Calvin cycle, CO_2 and H (carried from NADPH) are synthesized into complex organic molecules. The Calvin cycle uses large amounts of ATP (manufactured by chemiosmosis) to bond hydrogen from NADPH, along with carbon dioxide, to ribulose in order to immediately form two C_3 compounds, PGAL. Because PGAL contains three carbons and is formed as the first compound in this type of photosynthesis, it is sometimes referred to as the C_3 pathway (figure 6.23).

The carbon dioxide molecule does not become PGAL directly; it is first attached to the 5-carbon starter molecule, ribulose, to form an unstable 6-carbon molecule. This reaction is carried out by the enzyme ribulose bisphosphate carboxylase (RuBisCo), reportedly the most abundant protein on the planet. The newly formed 6-carbon molecule immediately breaks down into two 3-carbon molecules, which then undergo a series of reactions that involve a transfer from ATP and a transfer of hydrogen from NADPH. This series of reactions produces PGAL molecules. The general chemical equation for the CO_2 conversion stage is as follows:

$$\mathbf{CO_2 + ATP + NADPH + \underset{\text{(ribulose)}}{\underset{\text{starter}}{\text{5-carbon}}} \rightarrow PGAL + NADP^+ + ADP + \textcircled{P}}$$

PGAL: The Product of Photosynthesis

The 3-carbon phosphoglyceraldehyde (PGAL) is the actual product of the process of photosynthesis. However, many textbooks show the generalized equation for photosynthesis as

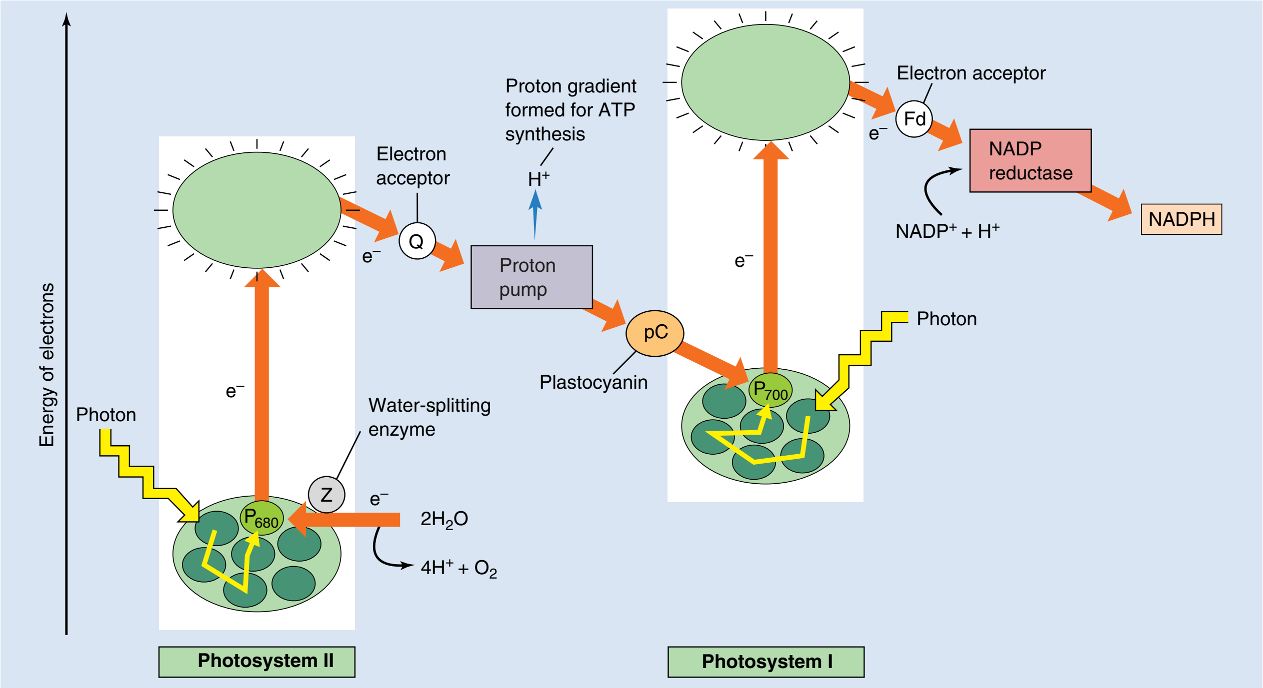


Figure 6.22

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

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

making it appear as if a 6-carbon sugar (hexose) is the end product. The reason a hexose ($C_6H_{12}O_6$) is usually listed as the end product is simply because, in the past, the simple sugars were easier to detect than was PGAL. If a plant goes through photosynthesis and produces 12 PGALs, 10 of the 12 are rearranged by a series of complex chemical reactions to regenerate the molecules needed to operate the light-independent reaction stage. The other two PGALs can be considered profit from the process. As the PGAL profit accumulates, it is frequently changed into a hexose. So those who first examined photosynthesis chemically saw additional sugars as the product and did not realize that PGAL is the initial product.

There are a number of things the cell can do with the PGAL profit from photosynthesis in addition to manufacturing hexose (figure 6.24). Many other organic molecules can be constructed using PGAL as the basic construction unit. PGAL can be converted to glucose molecules, which can be combined to form complex carbohydrates, such as starch for energy storage or cellulose for cell wall construction. In addition, other simple sugars can be used as building blocks for ATP, RNA, DNA, or other carbohydrate-containing materials.

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

6.7 Plant Metabolism

Earlier in this chapter we considered the conversion of carbon dioxide and water into PGAL through the process of photosynthesis. We described PGAL as a very important molecule because of its ability to be used as a source of energy. Plants and other autotrophs obtain energy from food molecules in the same manner that animals and other heterotrophs do.

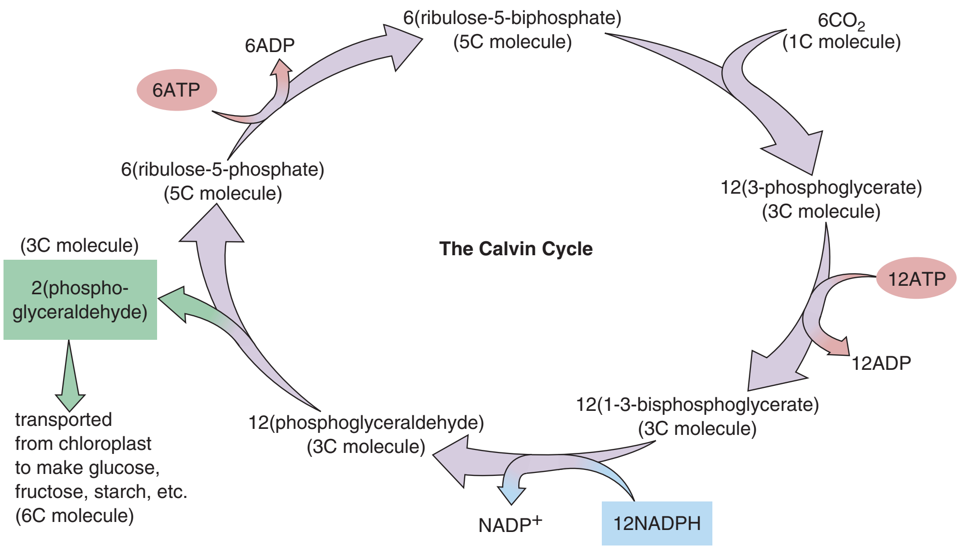


Figure 6.23

The Calvin Cycle: Detailed Description

During the Calvin cycle, CO_2 is fixed into ribulose. The cycle must turn six times to incorporate a new carbon from CO_2. The 6-carbon dioxides are eventually used to synthesize glucose or some other carbohydrate, fat, amino acid, nucleotides, or any other organic molecule found in living things. The glucose may also be respired by the plant cell as an energy source through cellular respiration.

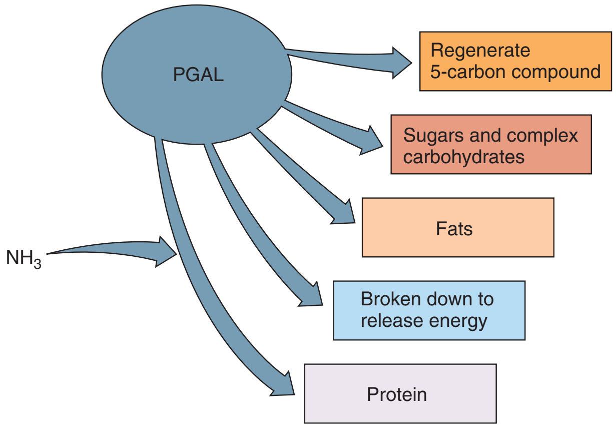


Figure 6.24

Uses of PGAL

The PGAL that is produced as the end product of photosynthesis is used for a variety of things. The plant cell can make simple sugars, complex carbohydrates, or even the original 5-carbon starter from it. It can also serve as an ingredient of lipids and amino acids (proteins). In addition, it provides a major source of metabolic energy when it is sent through the respiratory pathway.

They process the food through the respiratory pathways. This means that plants, like animals, require oxygen for the ETS portion of aerobic cellular respiration. Many people believe that plants only give off oxygen and never require it. This is incorrect! Plants do give off oxygen in the light-dependent reaction stage of photosynthesis, but in aerobic cellular respiration they use oxygen as does any other organism. During their life spans, green plants give off more oxygen to the atmosphere than they take in for use in respiration.

The surplus oxygen given off is the source of oxygen for aerobic cellular respiration in both plants and animals. Animals are not only dependent on plants for oxygen, but are ultimately dependent on plants for the organic molecules necessary to construct their bodies and maintain their metabolism (figure 6.25).

By a series of reactions, plants produce the basic foods for animal life. To produce PGAL, which can be converted into carbohydrates, proteins, and fats, plants require carbon dioxide and water as raw materials. The carbon dioxide and water are available from the environment, where they have been deposited as waste products of aerobic cellular respiration. To make the amino acids that are needed for proteins, plants require a source of nitrogen. This is available in the waste materials from animals.

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

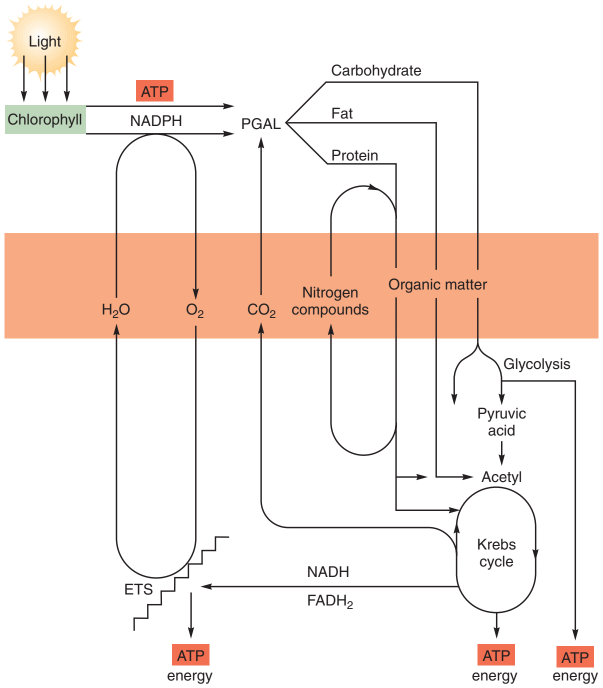


Figure 6.25

The Interdependency of Photosynthesis and Respiration
Plants use the end products of plant and animal respiration—carbon dioxide, water, and nitrogen compounds—to produce various foods. Plants and animals use the end products of plant photosynthesis—food and oxygen—as sources of energy. Therefore, plants are dependent on animals and animals are dependent on plants. The materials that link the two processes are seen in the colored bar.

SUMMARY

In the process of respiration, organisms convert foods into energy (ATP via chemiosmosis) and waste materials (carbon dioxide, water, and nitrogen compounds). Organisms that have oxygen (O_2) available can employ the Krebs cycle and electron-transport system (ETS), which yield much more energy per sugar molecule than does fermentation; fermenters must rely entirely on glycolysis. Glycolysis and the Krebs cycle serve as a molecular interconversion system: fats, proteins, and carbohydrates are interconverted according to the needs of the cell. Plants, in turn, use the waste materials of respiration. Therefore, there is a constant cycling of materials between plants and animals. Sunlight supplies the essential initial energy for making the large organic molecules necessary to maintain the forms of life we know.

In the light-capturing reaction stage of photosynthesis, plants use chlorophyll to trap the energy of sunlight using photosystems. During the light-dependent stage they manufacture a source of chemical energy, ATP, and a source of hydrogen, NADPH. Atmospheric oxygen is released in this stage. In the light-independent reaction stage of photosynthesis, the ATP energy is used in a series of reactions (the Calvin cycle) to join the hydrogen from the NADPH to a molecule of carbon dioxide and form a simple carbohydrate, PGAL. In subsequent reactions, plants use the PGAL as a source of energy and raw materials to make complex carbohydrates, fats, and other organic molecules. With the addition of ammonia, plants can form proteins.

THINKING CRITICALLY

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

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

CONCEPT MAP TERMINOLOGY

Construct a concept map to show relationships among the following concepts.

aerobic cellular respiration
anabolism
anaerobic cellular respiration
catabolism
fermentation
hydrogen ion and electron acceptor
oxidation-reduction
photosynthesis

KEY TERMS

accessory pigments
acetyl
adenosine triphosphate (ATP)
aerobic cellular respiration
alcoholic fermentation
anabolism
anaerobic cellular respiration
autotrophs
biochemical pathway
Calvin cycle
catabolism
cellular respiration
chemiosmosis
chlorophyll
electron-transport system (ETS)
FAD (**f**lavin **a**denine **d**inucleotide)
fermentation
glycolysis
grana
heterotrophs
high-energy phosphate bond
Krebs cycle
light-capturing stage
light-dependent reaction stage
light-independent reaction stage
NAD$^+$ (**n**icotinamide **a**denine **d**inucleotide)
NADP$^+$ (**n**icotinamide **a**denine **d**inucleotide **p**hosphate)
oxidation-reduction (redox) reactions
PGAL (**p**hospho**g**lycer**al**dehyde)
photosynthesis
photosystem
pyruvic acid
ribulose
ribulose bisphosphate carboxylase (RuBisCo)
stroma
thylakoids

e—LEARNING CONNECTIONS *www.mhhe.com/enger10*

Topics	Questions	Media Resources
6.1 Cellular Respiration and Photosynthesis	1. What is a biochemical pathway? Give two examples. 2. Even though animals do not photosynthesize, they rely on the sun for their energy. Why is this so? 3. In what way does ATP differ from other organic molecules? 4. Which cellular organelles are involved in the processes of photosynthesis and respiration?	**Quick Overview** • The idea of a chemical pathway **Key Points** • Biochemical pathways: Cellular respiration and photosynthesis **Interactive Concept Maps** • Text concept map
6.2 Understanding Energy Transformation Reactions		**Quick Overview** • Using one reaction to drive another **Key Points** • Understanding energy transformation reactions
6.3 Aerobic Cellular Respiration	5. Why does aerobic respiration yield more energy than anaerobic respiration? 6. Explain the importance of each of the following: $NADP^+$ in photosynthesis; PGAL in photosynthesis and in respiration; oxygen in aerobic cellular respiration; hydrogen acceptors in aerobic cellular respiration. 7. Pyruvic acid can be converted into a variety of molecules. Name three. 8. Aerobic cellular respiration occurs in three stages. Name these and briefly describe what happens in each stage.	**Quick Overview** • Three different stages **Key Points** • Aerobic cellular respiration **Interactive Concept Maps** • Cellular respiration
6.4 Alternatives: Anaerobic Cellular Respiration		**Quick Overview** • When oxygen is not present . . . **Key Points** • Alternatives: Anaerobic cellular respiration
6.5 Metabolism of Other Molecules		**Quick Overview** • Fats and amino acids have energy too **Key Points** • Metabolism of other molecules
6.6 Photosynthesis	9. List four ways in which photosynthesis and aerobic respiration are similar. 10. Photosynthesis is a biochemical pathway that occurs in three stages. What are the three stages and how are they related to each other?	**Quick Overview** • Two basic stages **Key Points** • Oxidation-reduction and photosynthesis
6.7 Plant Metabolism		**Quick Overview** • Do plants respire? **Key Points** • Plant metabolism