CHAPTER 6

Cell Energy: Photosynthesis and Respiration



It may seem that little is happening in this peaceful sunny field. However, the trees, flowers, and grasses are actively involved in capturing energy from sunlight and transforming it into energy that can be used by all types of living things.

In contrast to the roar and fury of hurricanes and floods, a gentle sunrise over forest and field seems uneventful. But the movement of sunlight across a landscape is only the first event in the daily struggle of living things to obtain energy. The starting point for that struggle is the energy of sunlight and its conversion to chemical energy.

What kinds of organisms can trap the energy in sunlight? How is that energy changed into a form other organisms can utilize? In this chapter we shall examine these questions and, in so doing, discover one of the most important secrets of life: how organisms capture, store, and transform energy!

CHAPTER OUTLINE

6–1 Photosynthesis: Capturing and Converting Energy
- Photosynthesis
- Requirements for Photosynthesis

6–2 Photosynthesis: The Light and Dark Reactions
- The Light Reactions
- The Dark Reactions

6–3 Glycolysis and Respiration
- Glycolysis—Breaking Down Glucose
- Respiration
- Obtaining Energy from Food
- Breathing and Respiration
- Energy in Balance

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- Lactic Acid Fermentation
- Alcoholic Fermentation

6–1 Photosynthesis: Capturing and Converting Energy

Section Objectives

- Describe the experiments that contributed to the understanding of photosynthesis.
- Discuss the requirements for photosynthesis.

Energy is the ability to do work, and there is always work to be done, even at the level of the cell. In this chapter we will explore some of the ways in which living things capture, convert, store, and use energy. We will concentrate our attention on the way in which energy is used within the individual cell.

Photosynthesis

The study of energy and living things begins with photosynthesis. **In the process of photosynthesis, plants convert the energy of sunlight into the energy in the chemical bonds of carbohydrates—sugars and starches.** Put another way, plants use the energy of sunlight to produce carbohydrates in a process called **photosynthesis**.

An understanding of photosynthesis was first developed from studies of plant growth. For years gardeners had asked a perplexing question about plant growth: When a seedling with a mass of only a few grams grows into a tall tree with a mass of several tons, where does the tree's increase in mass come from? From the soil? From the water? From the air? In the seventeenth century, the Dutch physician Jan van Helmont devised an experiment to find out.

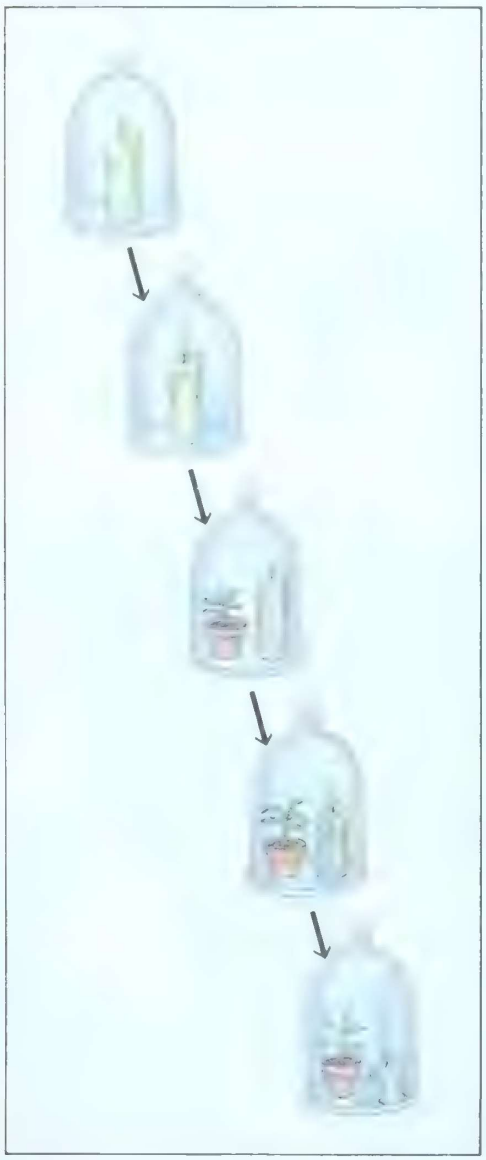


Figure 6–1 *The very culture of a human society may revolve around the way energy is used to heat homes, cook food, light buildings and streets, and provide for other human needs. In nature, as in human societies, some of the most important activities concern the processes in which energy is produced and distributed.*



Figure 6–2 *As a tiny seedling grows into a large tree, it uses water and air to make the chemicals needed for growth.*

Figure 6–3 *A burning candle soon uses up the oxygen in a glass jar and goes out. In the presence of light, a plant placed inside the jar releases oxygen. This allows the candle to be relighted. The candle continues to burn as long as enough oxygen is available.*



Van Helmont carefully found the mass of a pot of dry soil and a small seedling. Then he planted the seedling in the pot of soil. He took care of it and watered it regularly for five years. At the end of five years, the seedling, which by then was a small tree, had gained about 75 kilograms. However, the mass of the soil was almost unchanged. Van Helmont concluded that most of the mass must have come from water because that was the only thing that he had added to the pot.

Van Helmont's experiment accounts for the *hydrate*, or water, portion of the carbohydrate produced by photosynthesis. But where does the carbon of the *carbo* portion come from? Although Van Helmont did not realize it, carbon dioxide in the air made a major contribution to the mass of his tree. And it is the carbon in carbon dioxide that is used to make carbohydrates in photosynthesis. Even though Van Helmont had only part of the story, he had made a major contribution to science.

Almost a hundred years after Van Helmont's experiment, Joseph Priestley performed an experiment that would give another insight into the process of photosynthesis. Priestley took a candle, placed a glass jar over it, and watched as the flame gradually died out. Something in the air, Priestley reasoned, was necessary to keep a candle flame burning. When that substance was used up, the candle went out. Today we call this substance oxygen.

Priestley then found that if he placed a sprig of mint under the jar and allowed a few days to pass, the candle could be relighted and would remain lighted for a while. The mint plant had produced the substance required for burning. In other words, it released oxygen. Later, the Dutch scientist Jan Ingenhousz showed that the effect observed by Priestley occurred only when the plant was exposed to light. This means that light is necessary for plants to produce oxygen.

Requirements for Photosynthesis

The experiments performed by Van Helmont, Priestley, Ingenhousz, and other scientists reveal that in the presence of light, plants transform carbon dioxide and water into carbohydrates and release oxygen. This gives us the basic outline of the process of photosynthesis:

$$CO_2 + H_2O \xrightarrow{\text{light}} (CH_2O)_n + O_2$$

carbon dioxide + water $\xrightarrow{\text{light}}$ carbohydrate + oxygen

Because photosynthesis usually produces a particular carbohydrate—the sugar **glucose** ($C_6H_{12}O_6$)—we can rewrite and balance the equation for photosynthesis as follows:

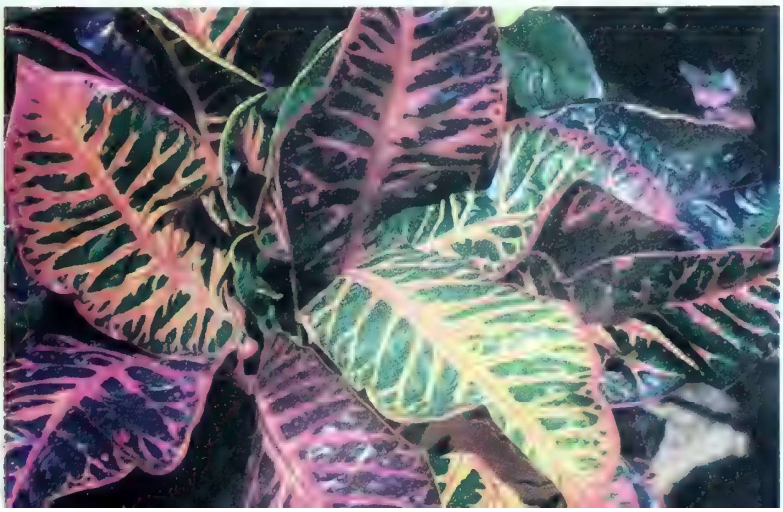
$$6\ CO_2 + 6\ H_2O \xrightarrow{\text{light}} C_6H_{12}O_6 + 6\ O_2$$

carbon dioxide + water $\xrightarrow{\text{light}}$ glucose + oxygen

Do not be fooled by how simple this equation looks. In photosynthesis, a great deal happens between the beginning and the end of the equation. You do not get glucose and oxygen just by putting water and carbon dioxide together. Let us, then, examine some of the other requirements of photosynthesis.

SUNLIGHT Nearly all organisms on Earth depend on the sun for energy. Some organisms, such as green plants, can use the sun's energy directly. As a result, green plants are called **autotrophs** (AW-toh-trohfs). Autotrophs are organisms that are able to use a source of energy, such as sunlight, to produce food directly from simple inorganic molecules in the environment. Other organisms, such as animals, cannot use the sun's energy directly. These organisms, known as **heterotrophs**, (HEHT-er-oh-trohfs) obtain energy from the foods they eat. Heterotrophs may eat autotrophs, other heterotrophs, or both.

The sun bathes the Earth in a steady stream of light. What our eyes perceive as colorless "white" light is actually a mixture of different wavelengths of light. Many of these wavelengths are visible to our eyes and make up what is known as the visible spectrum. Our eyes perceive the different wavelengths of the visible spectrum as different colors.



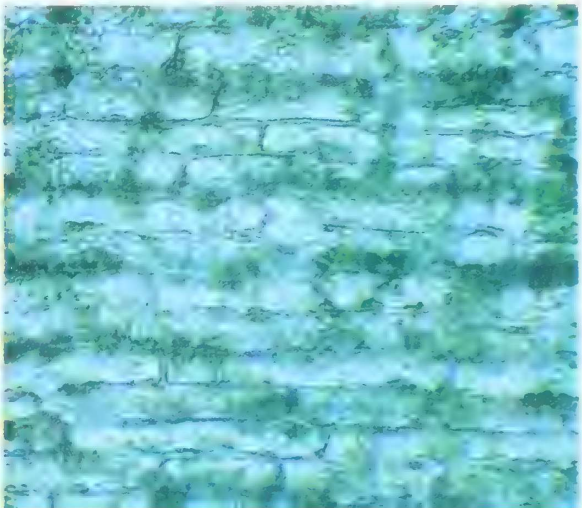


Figure 6–4 *Plant pigments absorb some wavelengths of light and reflect others. Our eyes perceive the reflected wavelengths as different colors (left). Chlorophyll—the principal photosynthetic pigment of green plants—gives the chloroplasts in these plant cells their characteristic color (right).*

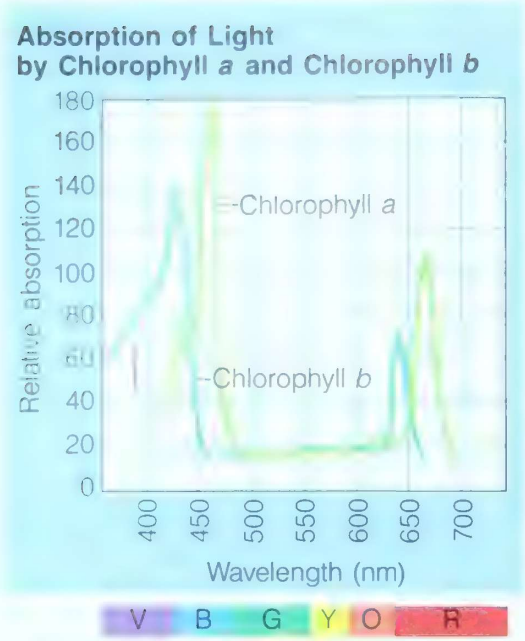


Figure 6–5 *Chlorophyll absorbs red and blue light quite well. Different forms of chlorophyll have their peak absorption at different wavelengths of light.*

PIGMENTS The process of photosynthesis begins when light is absorbed by **pigments** in the plant cell. Pigments are colored substances that absorb or reflect light. The principal pigment of green plants is known as **chlorophyll**. As you can see from the graph in Figure 6–5, chlorophyll absorbs red and blue light but does not absorb light in the middle region of the spectrum very well. Instead, it reflects these wavelengths.

ENERGY-STORING COMPOUNDS Because energy is involved in the formation of chemical bonds, the production of certain compounds can be used to store energy in chemical form. The most important energy-storing compound—one used by every living cell—is **adenosine triphosphate**, or **ATP**. As you can see in Figure 6–6, an ATP molecule consists of a nucleotide called adenine, a 5-carbon sugar called ribose, and three phosphate groups. Energy can be stored when a phosphate group, abbreviated as P, is bonded to adenosine monophosphate (AMP) to produce adenosine diphosphate (ADP). And still more energy can be stored when a third phosphate group is added to ADP to produce ATP. The bonds between the phosphate groups are the key to ATP's energy-storing qualities. Each of these two bonds is capable of storing chemical energy—energy that is released when the bonds are broken.

Some of this stored energy is released when the third phosphate group is split from ATP to produce ADP. Energy is also released when ADP is broken down to AMP.

$$\textbf{ATP} \rightarrow \textbf{ADP} + \textbf{P} + \textbf{energy}$$
$$\textbf{ADP} \rightarrow \textbf{AMP} + \textbf{P} + \textbf{energy}$$

Enzymes control the synthesis and breakdown of ATP within the cell. These enzymes enable ATP to be produced from

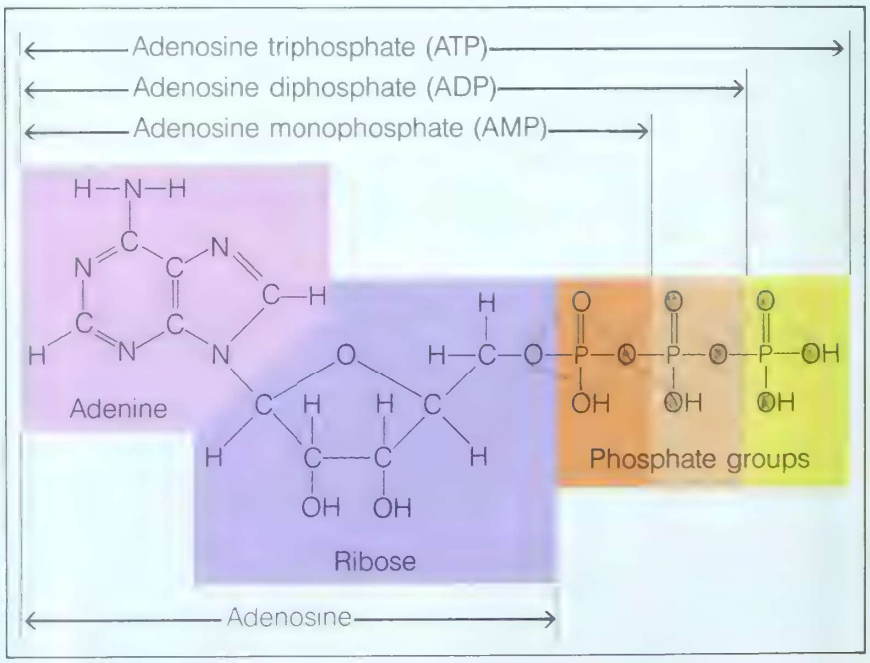


Figure 6–6 *Adenosine triphosphate, or ATP, is the most important energy-storing compound in living things.*

energy-releasing reactions and allow ATP to be used as a source of energy for reactions that require energy. ATP provides energy for a large number of cellular activities, including muscle contraction, protein synthesis, and active transport across cell membranes. During photosynthesis, the ATP produced by the first part of the process is used to provide energy for the second part.

6-1 SECTION REVIEW

1. Define photosynthesis.
2. What did Van Helmont's experiment prove about the source of material for plant growth? What did it not prove?
3. What is ATP?
4. Why is chlorophyll's efficiency in absorbing light energy important for photosynthesis?

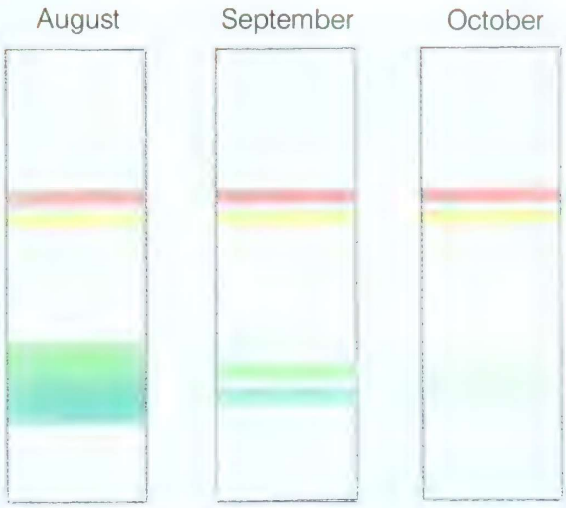
PROBLEM SOLVING IN BIOLOGY

THE COLORS OF AUTUMN

In many parts of the country, the beautiful colors of autumn leaves provide inspiration to artists and poets as the countryside turns into a lovely blaze of red, orange, and yellow. What is the source of these colors? Do plants produce them in response to the changing of the seasons?

The pigments in plant cells, including chlorophyll, can be separated from one another by a technique known as paper chromatography. Study the results of the paper chromotography experiment shown on this page. The green chlorophyll spots, red-orange carotene spots, and yellow xanthophyll spots are labeled on samples taken from the leaves of a single maple tree in August, September, and October.

Using these three chromatographs as evidence, can you explain what seems to happen as the leaves change color as summer ends and autumn begins?



Paper chromatography is based on the fact that different substances (such as plant pigments) in a solvent will move through a piece of paper at different rates.

Section Objectives

- Discuss the light reactions of photosynthesis.
- Relate the dark reactions of photosynthesis to the light reactions.

6–2 Photosynthesis: The Light and Dark Reactions

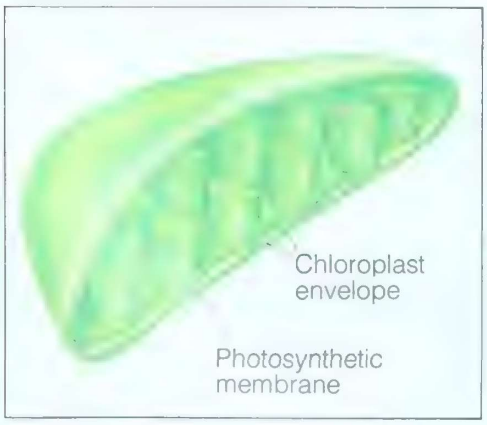
The process of photosynthesis is divided into two parts: the **light reactions** and the **dark reactions**. As their name implies, the light reactions require light. **In the light reactions, the energy of sunlight is captured and used to make energy-storing compounds.** The dark reactions do not require light and thus are also called nonlight or light-independent reactions. However, the dark reactions can—and do—occur in the light. The dark reactions use the energy stored by the light reactions to make glucose.

Photosynthesis takes place in an organelle known as the chloroplast. Within the chloroplast are saclike **photosynthetic membranes** that contain chlorophyll. As you can see in Figure 6–8, the light reactions occur in the photosynthetic membranes, whereas the dark reactions occur outside the photosynthetic membranes.

The Light Reactions

The light reactions absorb the energy of sunlight and convert it to the energy that is stored in chemical bonds. This process occurs very rapidly. However, the light reactions can be divided into four basic processes: light absorption, electron transport, oxygen production, and ATP formation. These processes are closely linked and are dependent on one another. As you examine the light reactions in more detail, keep in mind that these processes occur nonstop in green plants as long as the sun shines.

Figure 6–7 *The chloroplast is the site of photosynthesis. The light reactions take place in the saclike photosynthetic membranes. The dark reactions take place in the areas surrounding the photosynthetic membranes.*



LIGHT ABSORPTION The photosynthetic membrane contains clusters of pigment molecules, or **photosystems**, that are able to capture the energy of sunlight. There are two photosystems in green plants: photosystem I and photosystem II. See Figure 6–8.

Each photosystem contains several hundred chlorophyll molecules, as well as a number of accessory pigments. These accessory pigments absorb light in the regions of the spectrum where chlorophyll does not and thus allow more of the available light energy to be used. The absorption of light causes electrons in a pigment molecule to be raised to a higher level, an "excited" state. This excitation energy is then passed from one pigment molecule to another until it reaches a special pair of chlorophyll molecules. Although all the photosystem pigments can absorb light, only the special pair of chlorophyll molecules can process the light energy. The special pair of chlorophyll molecules are surrounded by an apparatus that enables the excitation energy to be captured in chemical form.

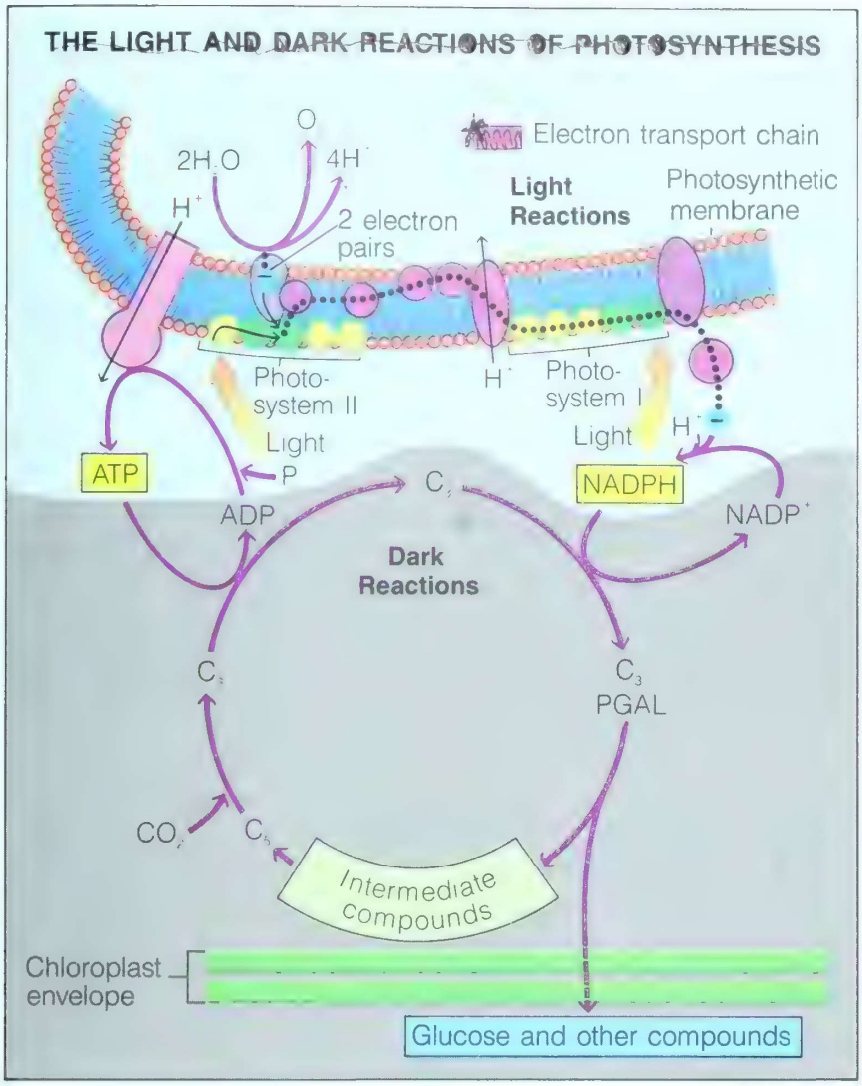


Figure 6–8 *Clusters of pigment molecules known as photosystems are embedded in the photosynthetic membrane. Photosystems capture the energy of sunlight, which is used to make energy-storing compounds. The energy in these compounds, in turn, is used to make biologically important compounds such as glucose.*

ELECTRON TRANSPORT The high-energy electrons produced by light travel from the special pair of chlorophyll molecules to an adjacent molecule called an electron carrier. This begins a process known as **electron transport**.

The high-energy electrons are transferred along a series of electron-carrier molecules in the photosynthetic membrane

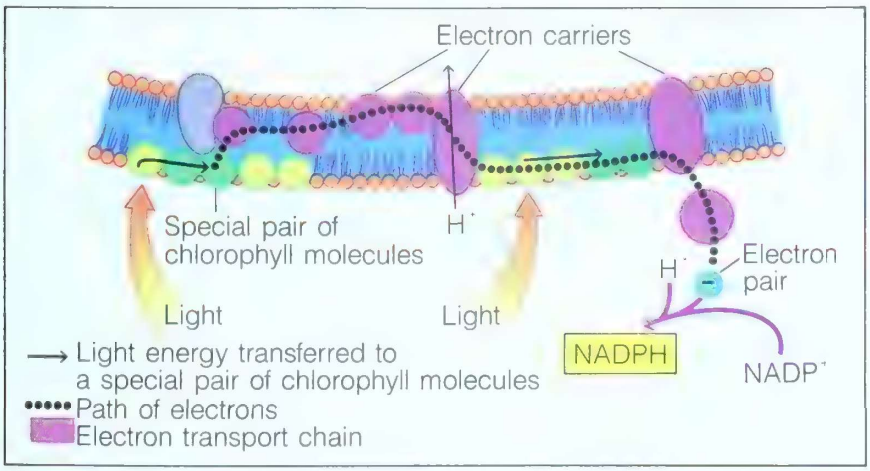


Figure 6–9 *The high-energy electrons produced by light are transferred from chlorophyll to the electron transport chain. The electrons are passed from one carrier in the chain to the next. At the end of the chain, they are used to make the energy-storing compound NADPH.*

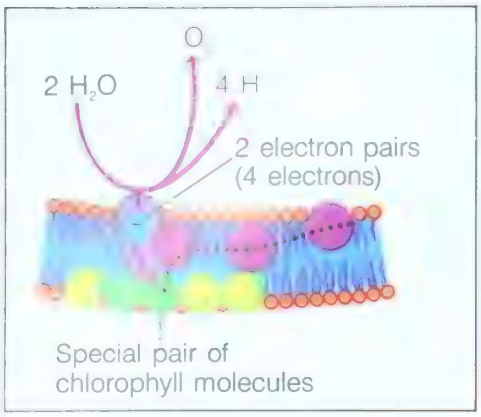


Figure 6–10 *The breakdown of water produces electrons that replace the electrons lost by the special pair of chlorophyll molecules. This process also results in the formation of hydrogen ions and oxygen gas.*

known as the electron transport chain. Electrons are passed from one carrier to another almost as pails of water are passed from one person to the next in a bucket brigade.

At the end of the chain is an enzyme that passes the high-energy electrons to an electron carrier called $NADP^+$, converting it to NADPH. Adding a pair of electrons to this electron carrier requires energy. This is the first way in which part of the energy of sunlight is trapped in chemical bonds. The electrons and energy stored in the bonds of NADPH will be used later on.

OXYGEN PRODUCTION As the light continues to shine, what happens to chlorophyll? Does it run out of electrons? No. The photosynthetic membrane contains a system that provides new electrons to chlorophyll to replace the ones that wound up in NADPH. These electrons are taken from water. Four electrons are removed from 2 water molecules (H_2O), leaving 4 hydrogen ions (H^+) and 2 oxygen atoms (O). The 2 oxygen atoms form a single molecule of oxygen gas (O_2) that leaves the chloroplast and is eventually released into the air.

ATP FORMATION The hydrogen ions left behind when water is "split" are released inside the photosynthetic membrane. In addition, as electrons are passed from chlorophyll to $NADP^+$, more hydrogen ions are pumped across the membrane. After a while, the inside of the membrane fills up with positively charged hydrogen ions. This makes the outside of the photosynthetic membrane negatively charged and the inside positively charged.

The difference in charges across the membrane is a source of energy. An enzyme in the photosynthetic membrane makes use of this energy to attach a phosphate molecule to ADP, forming ATP. This is the second way in which the energy of sunlight is trapped in chemical form.

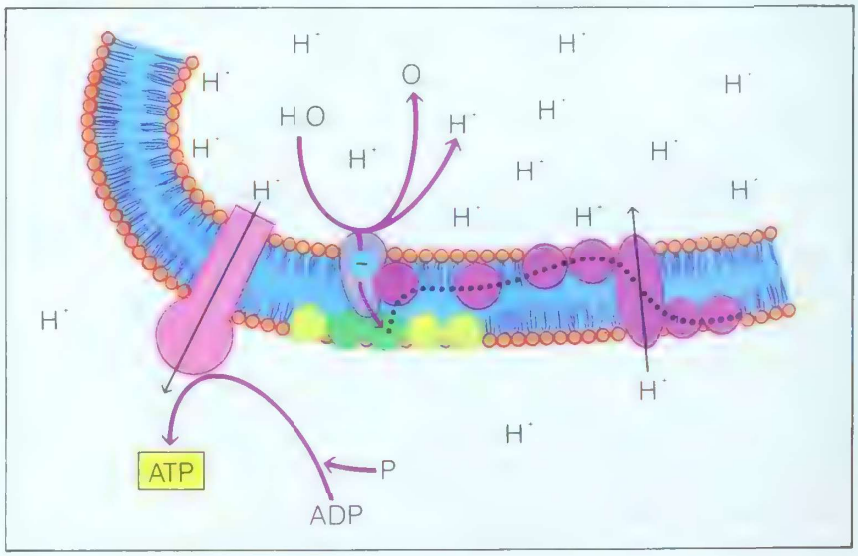


Figure 6–11 *The buildup of hydrogen ions (produced in the breakdown of water) inside the photosynthetic membrane produces a difference in charges across the membrane. This powers the formation of the energy-storing compound ATP.*

A SUMMARY OF THE LIGHT REACTIONS As we have seen, the light reactions use water, ADP, and $NADP^+$; they produce O_2 (which is of no help in photosynthesis but is of great use to us!) and the energy-storing molecules ATP and NADPH. The next stage of photosynthesis, the dark reactions, will convert these energy-storing molecules to a more convenient form.

The Dark Reactions

Do not be confused by the term dark reactions. The dark reactions generally take place in sunlight. However, light does not play a role in the dark reactions. If ATP and NADPH are supplied, the dark reactions can be carried out in a test tube, even in total darkness and without ever being exposed to light!

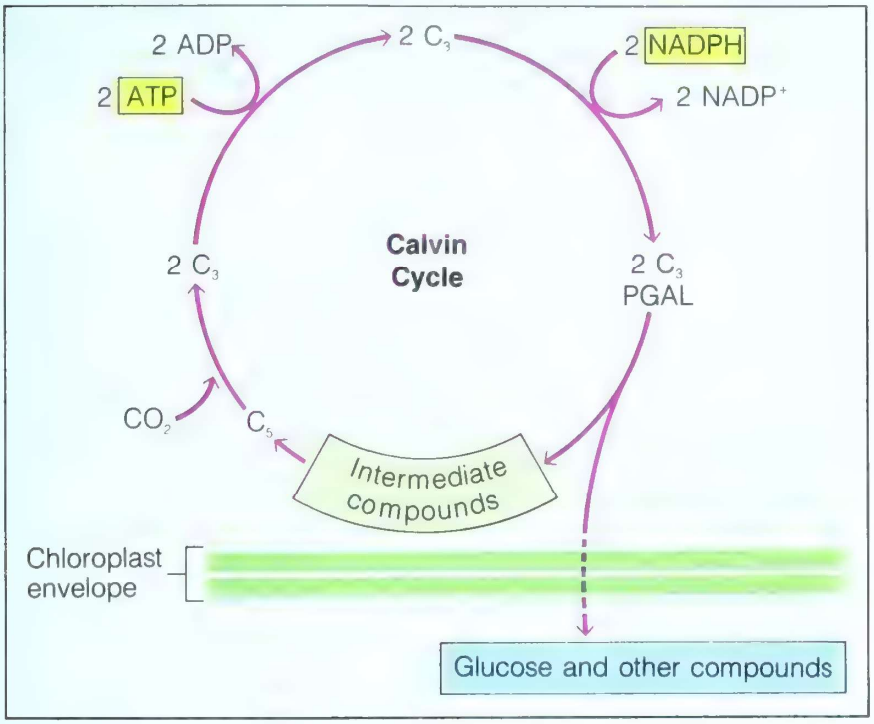


Figure 6–12 *The dark reactions use carbon dioxide and the energy-storing compounds produced in the light reactions to form PGAL. PGAL is a chemical "building block" that can be used to make other organic compounds, such as the sugar glucose.*

The series of chemical changes that make up the dark reactions is particularly critical to living things. In this part of photosynthesis, the simple inorganic molecule carbon dioxide is used to make a complex organic molecule. This molecule can be thought of as a building block that can be used to make other biologically important molecules, including glucose. The dark reactions form a cycle, or circular series of reactions. Because the chemistry of this remarkable cycle was worked out by the American scientist Melvin Calvin, the dark reactions are also known as the **Calvin cycle**.

Throughout this description of the Calvin cycle, you will find it helpful to refer to Figure 6–12. In the first reaction of the Calvin cycle, a 5-carbon sugar (C_5) combines with CO_2 to form two 3-carbon compounds (C_3). The first reaction of the Calvin

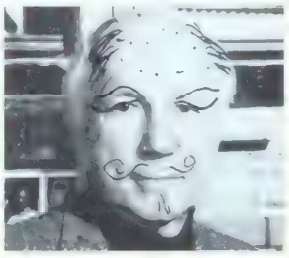
cycle tends to be relatively slow. In order to compensate for this, the chloroplast is loaded with an enzyme that catalyzes this reaction. This enzyme is known as rubisco. There is far more rubisco in an active plant cell than any other protein molecule. Because there are many more plant cells than animal cells on Earth, we can make a remarkable statement about rubisco: It is the most abundant protein in the world!

In the next two reactions of the Calvin cycle, using the chemical energy available in ATP and NADPH, these 3-carbon compounds are converted to PGAL (**phospho**g**lycer**a**l**dehyde). Most PGAL molecules are recycled for the dark reactions, but 1

SCIENCE, TECHNOLOGY, AND SOCIETY **BREAKTHROUGH**

"If at First You Don't Succeed . . ."

In the dark reactions of photosynthesis, simple inorganic molecules are used to form organic molecules—food—that can be used by living things. The process of putting carbon into a form that can be used by living things is known as carbon fixation. Although carbon fixation in photosynthesis is crucial to living things, this process remained a mystery until the late 1940s.



Melvin Calvin worked out the chemistry of the dark reactions of photosynthesis.

It was obvious that the key to understanding the chemical steps of the dark reactions—and carbon fixation—was to find the very first molecule into which CO_2 was fixed, or used to make an organic molecule. But how do you trace the path of a molecule in a chemical reaction? And how can you tell that a particular molecule is really the one you want to observe?

Working at the University of California at Berkeley in 1946, Melvin Calvin and his associates decided to use newly discovered carbon-14, a radioactive isotope of carbon, in their experiments on carbon fixation. They reasoned that the molecule that fixed carbon dioxide would become radioactive when it joined with radioactive carbon dioxide, or carbon dioxide that contained carbon-14. However, when radioactive CO_2 was added to growing plants, within a few minutes nearly every type of carbon-containing molecule in the plant was radioactive. So it was back to the drawing board for the scientists.

Melvin Calvin and his associate John Bassham decided that if carbon was fixed quickly, they would have to act quickly. They put a suspension of green algae into a special flask, injected radioactive CO_2 into it, flashed a bright light at it, and opened a valve at the bottom of the flask. The algae cells dropped suddenly into a beaker of boiling alcohol, which killed the cells and stopped photosynthesis instantly. The molecules associated with carbon fixation, however, were preserved. This approach allowed Calvin and his associates to identify phosphoglyceric acid, a 3-carbon compound, as the product of the first reaction in carbon fixation.

The determination of these scientists to perform a difficult experiment produced the first (and most important) clue in working out the process of carbon fixation. Calvin and his associates continued their work, described the dark reactions, and made a major contribution to our understanding of photosynthesis.

out of every 6 is used to make glucose or other end products. How many times must the Calvin cycle go around to produce 1 molecule of glucose? (Hint: The formula for glucose is $C_6H_{12}O_6$)

Although we have emphasized the production of glucose in the Calvin cycle, the intermediate compounds of the cycle are also important because they can be used by the chloroplast in many ways. Some of the intermediates may be used to form sugars other than glucose; some of them may be used to make amino acids; and some can be converted to lipids. The dark reactions of photosynthesis provide the raw materials to produce almost everything the cell needs.

6-2 SECTION REVIEW

1. What are the products of the light reactions?
2. Where in the cell do the light reactions take place? The dark reactions?
3. Describe the Calvin cycle. Why are the light reactions important to the Calvin cycle?

6-3 Glycolysis and Respiration

Section Objectives

- Discuss the process of glycolysis.
- Describe respiration.
- Explain how breathing is related to respiration.

The ability of autotrophs to produce glucose and other food molecules reflects the fact that photosynthesis is able to trap some of the energy of sunlight in chemical bonds. In a way, the energy stored by photosynthesis is like money deposited in a savings account: It is available for future needs. But organisms—autotrophs and heterotrophs alike—must be capable of making "withdrawals" from that savings account; that is, they must be able to release energy by breaking down food molecules. In this section we will examine two processes used to release energy from glucose.

Glycolysis—Breaking Down Glucose

Glucose ($C_6H_{12}O_6$) is a simple 6-carbon sugar. If glucose is broken down completely in the presence of oxygen, carbon dioxide and water are produced:

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

glucose + oxygen → carbon dioxide + water

This reaction gives off 3811 **calories** per gram of glucose. A calorie is the amount of heat energy required to raise the temperature of 1 gram of water 1 degree Celsius. As you can see, glucose obviously contains a lot of energy. (Those of you who watch your calories should not be alarmed. The Calorie associated with food and diet books is actually a kilocalorie, which is equal to 1000 calories.)

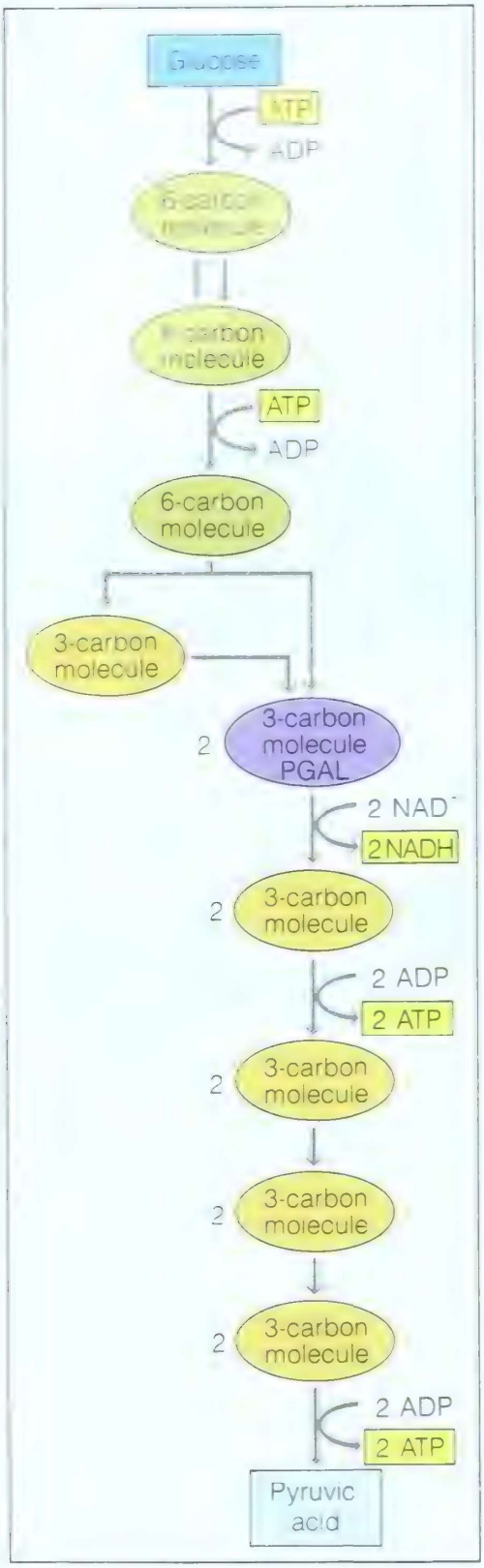


Figure 6–13 *In the process of glycolysis, glucose is broken down and transformed into other molecules. In addition, energy is released in the form of 2 molecules of ATP.*

A cell takes apart glucose slowly and captures the energy a little at a time. Remember, the energy stored in chemical bonds can be used when the bonds are broken. The first stage in this process is known as **glycolysis** (gligh-KAHL-ih-sihs), which means glucose-breaking. Glycolysis takes place in the cytoplasm of a cell. **In glycolysis, a series of enzymes catalyzes chemical reactions that change glucose, one step at a time, into different molecules.**

In the first step, a glucose molecule undergoes several chemical reactions that ultimately split the 6-carbon sugar into two 3-carbon PGAL molecules. See Figure 6–13. Two molecules of ATP are used up in the process. This means that the cell must use up a bit of its stored chemical energy to begin the breakdown of glucose.

Several more chemical steps then occur that transform the 2 PGAL molecules into 2 molecules of pyruvic acid, a 3-carbon compound. The energy from the 2 PGAL molecules is used to make 4 molecules of ADP and 2 molecules of NADH. NADH is an energy-storing compound similar to the NADPH that is formed in the light reactions of photosynthesis.

In the process of glycolysis, 4 molecules of ATP are synthesized from 4 molecules of ADP. Because 2 ATP molecules are used to start the process, we can do a little arithmetic and conclude that there is a net gain of 2 molecules of ATP during glycolysis.

The 2 ATP molecules produced in glycolysis represent no more than 2 percent of the total chemical energy in glucose. What happens to the rest? The answer depends on the presence of oxygen.

Respiration

If oxygen is available, a process known as **respiration** can take place. Because it requires oxygen, respiration is called an **aerobic** process. The word aerobic means with air—specifically, the part of the air called oxygen. **Respiration is the process that involves oxygen and breaks down food molecules to release energy.** Respiration uses the pyruvic acid formed in glycolysis. In breaking down pyruvic acid, respiration captures much of the remaining energy from glucose in the form of 34 additional molecules of ATP.

The term respiration may have a familiar ring. It is often used as a synonym for breathing. Because of this, some biologists use the term cellular respiration instead of respiration to refer to energy-releasing pathways within the cell. The double meaning of respiration points out a crucial connection between cell and organism: The energy-releasing respiratory pathways within the cells require oxygen, which animals take in by breathing—another type of respiration. Although plants do not breathe in the usual sense, they also need to take in oxygen for cellular respiration.

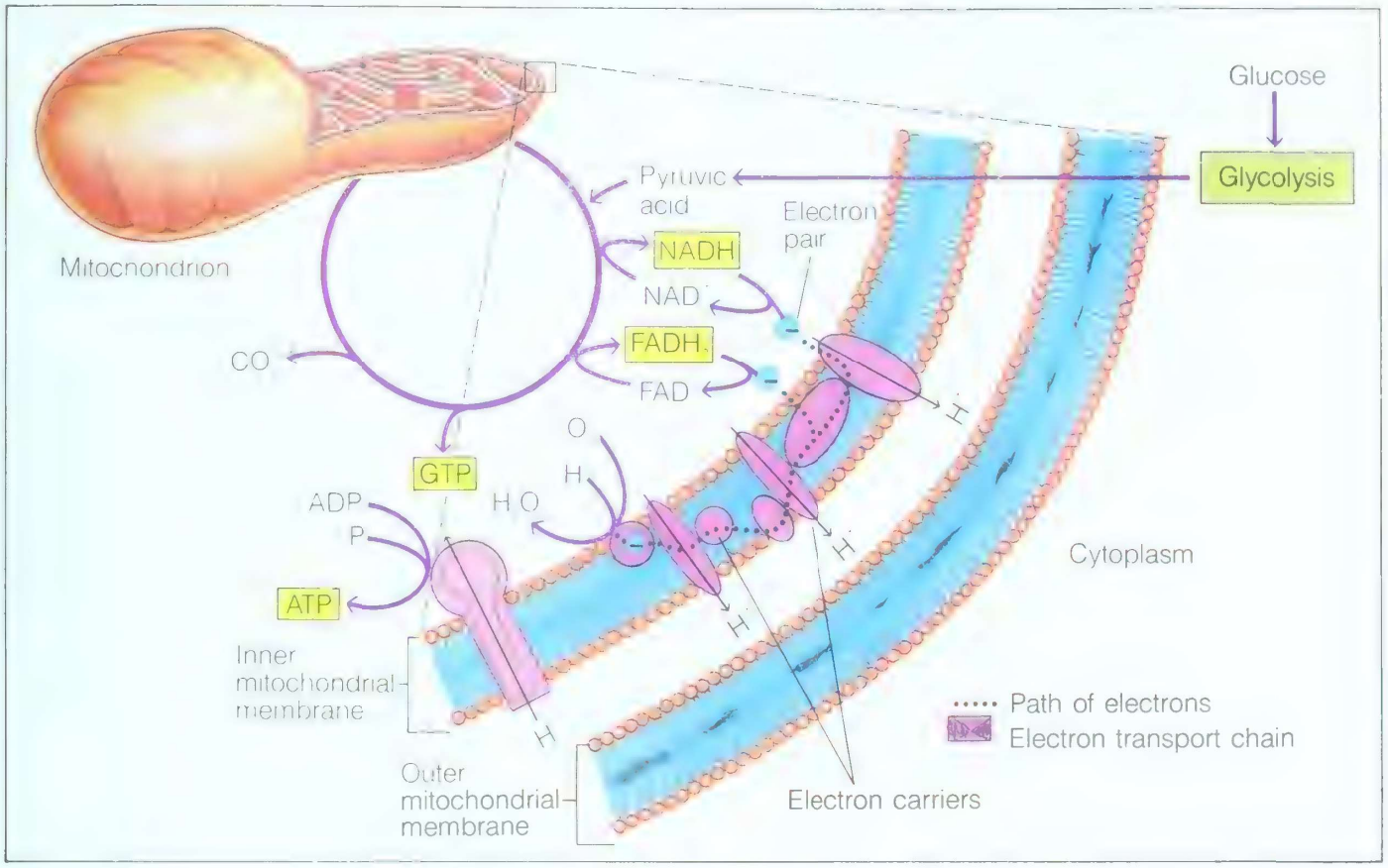


Figure 6–14 *Respiration, an aerobic process, takes place in the mitochondrion. The Krebs cycle takes place in the area enclosed by the inner mitochondrial membrane. Electron transport and ATP formation involve complex molecules embedded in the inner membrane.*

Respiration, like photosynthesis, is associated with a cell organelle. The chemical reactions of respiration take place in a cell's mitochondria. Recall from Chapter 5 that a mitochondrion consists of two membranes, an outer membrane and a folded inner membrane. The first set of reactions in respiration takes place in the area enclosed by the inner membrane. The second set of reactions takes place within the inner membrane itself. See Figure 6–14.

THE KREBS CYCLE The first set of reactions in respiration is the **Krebs cycle**, which is named for its discoverer, Hans Krebs. Unlike glycolysis, the Krebs cycle does not produce a final end product. Instead, it is a continuing series of reactions.

The pyruvic acid produced during glycolysis travels from the cytoplasm to the mitochondrion. In the first reaction of respiration, pyruvic acid is broken down into carbon dioxide and a 2-carbon compound called acetic acid. Acetic acid, bound to a carrier molecule called coenzyme A (CoA), enters the Krebs cycle by reacting with a 4-carbon compound to produce citric acid, a 6-carbon compound. Because citric acid is the first compound formed in this series of reactions, the Krebs cycle is known as the citric acid cycle.

There are nine reactions and nine intermediates in the Krebs cycle. At two places in the cycle, CO_2 is released. At four places in the cycle, a pair of high-energy electrons are

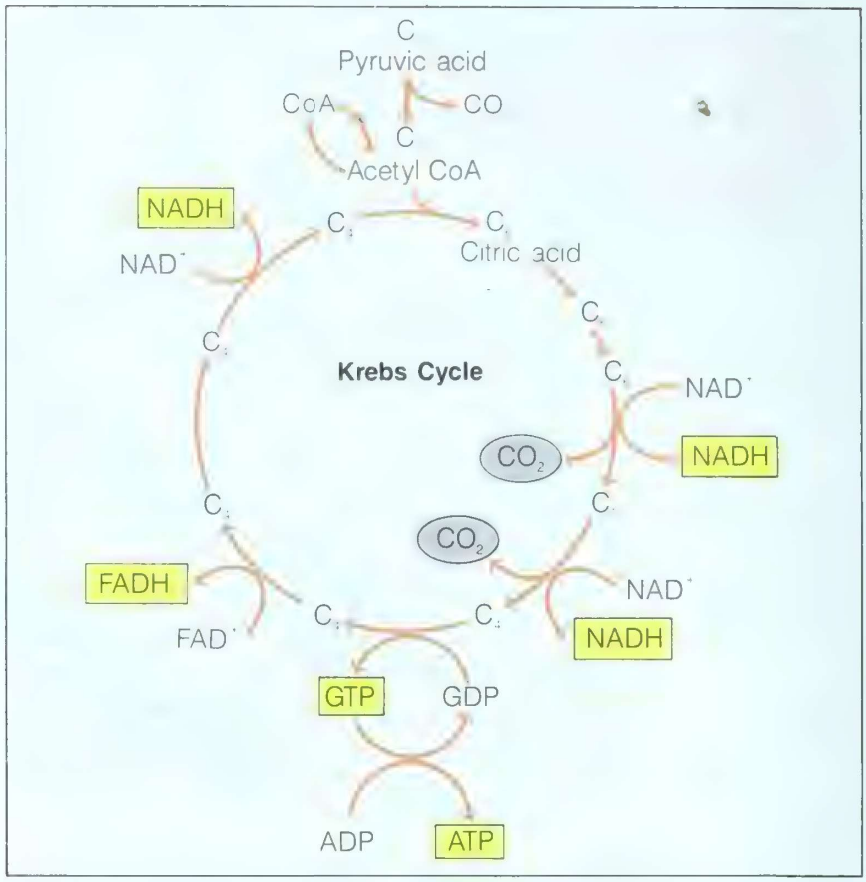


Figure 6–15 *The Krebs cycle, a continuing series of nine reactions involving nine intermediate compounds, produces carbon dioxide and energy-storing compounds.*

accepted by electron carriers, changing NAD^+ to NADH and FAD to $FADH_2$. See Figure 6–15. At one place in the cycle, a molecule of GDP (similar to ADP) is converted to GTP (similar to ATP). The GTP may then used to make ATP from ADP. We can summarize the events in the Krebs cycle as follows:

- **2 carbon atoms added (from the breakdown of pyruvic acid)**
- **2 carbon atoms removed (in 2 molecules of CO_2)**
- **3 molecules of NAD^+ converted to NADH**
- **1 molecule of FAD converted to $FADH_2$**
- **1 molecule of GDP converted to GTP**

Step by step, the carbon atoms in glucose wind up as carbon dioxide. The carbon dioxide produced by the Krebs cycle is a waste product that is released from the cell. But what does the cell do with the other products of the Krebs cycle: NADH and $FADH_2$? And where does oxygen fit into the process?

ELECTRON TRANSPORT IN THE MITOCHONDRION The high-energy electrons from NADH and $FADH_2$ are passed to a series of electron transport enzymes in the inner membrane of the mitochondrion. These enzymes form an electron transport chain along which electrons are passed. At the end of this chain is an enzyme that combines electrons from the electron

transport chain, hydrogen ions (H^+) from the fluid inside the cell, and oxygen (O_2) to form water (H_2O). This is where oxygen comes in. Oxygen is the final electron acceptor in the process of respiration. Thus, oxygen is essential for obtaining energy from both NADH and $FADH_2$.

ATP FORMATION Recall that the photosynthetic electron transport chain was associated with the movement of hydrogen ions (H^+) across the photosynthetic membrane in the chloroplast. Electron transport in the mitochondrion causes a similar movement of hydrogen ions. As they accept electrons, some of the enzymes in the electron transport chain pump a hydrogen ion from the inside of the inner membrane to the outside. As in photosynthesis, the movement of hydrogen ions powers the formation of ATP. On average, the movement of a pair of electrons down the electron transport chain produces enough energy to form 3 ATP molecules from ADP.

Electron transport produces a difference in electric charge across the membrane. There are more hydrogen ions outside the inner membrane of the mitochondrion than inside it. Thus, the outside of the membrane is more positively charged than the inside. The difference in charge created by the imbalance of hydrogen ions supplies the energy to make ATP from ADP.

Like the photosynthetic membrane, the inner mitochondrial membrane has two special properties that make this process work: The electron transport chains in the membrane are arranged so that hydrogen ions are pumped in one direction across the membrane; and the membrane does not allow ions to "leak" back across (otherwise there would not be enough of a charge difference to provide energy for ATP synthesis).

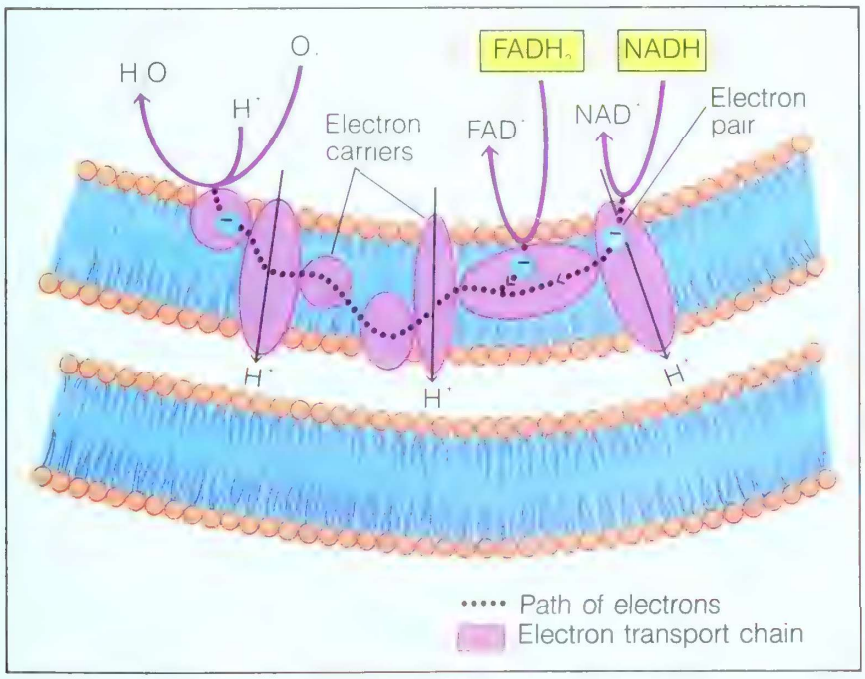


Figure 6–16 *The high-energy electrons in the energy-storing compounds NADH and $FADH_2$ are transferred to the molecules of the electron transport chain, which is located in the inner mitochondrial membrane. At the end of the chain, the electrons react with hydrogen ions and oxygen to form water.*

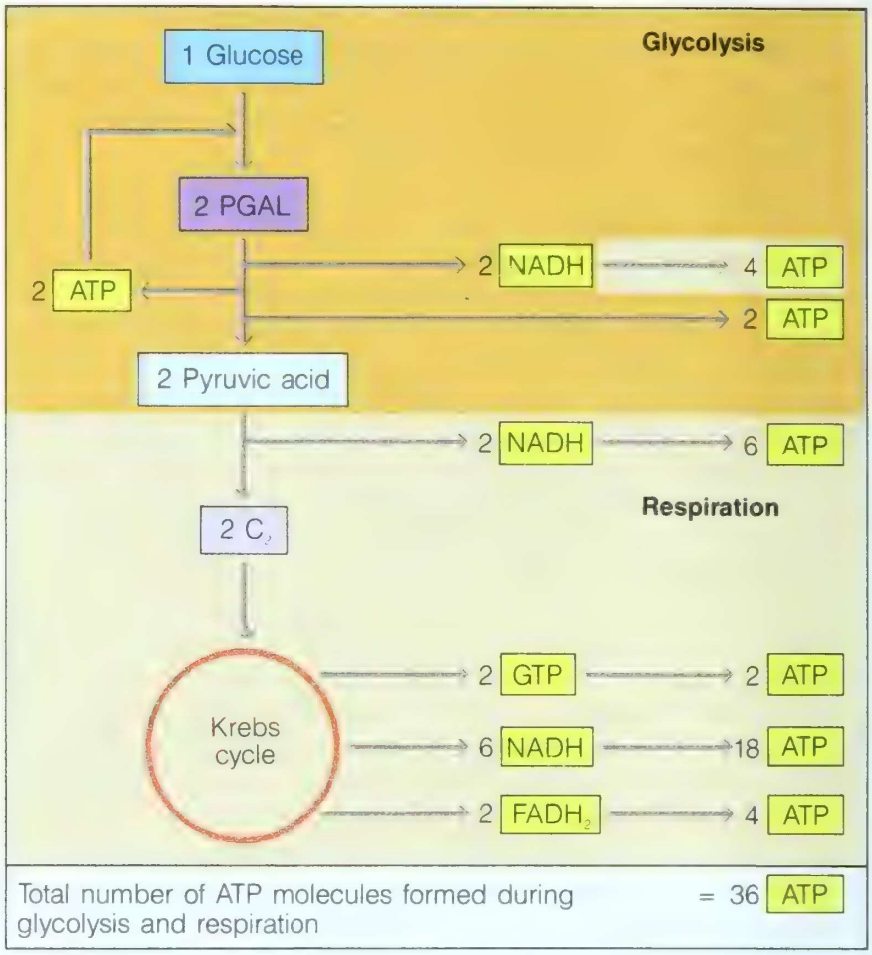


Figure 6–17 *The complete breakdown of glucose through glycolysis and respiration results in the production of chemical energy in the form of 36 molecules of ATP.*

THE TOTALS How much chemical energy is produced by the complete breakdown of glucose? Remember, glycolysis produces a net gain of 2 ATP molecules and passes high-energy electrons to 4 NADH molecules. The energy in these NADH molecules can be used to form 10 ATP molecules. In respiration, 6 more NADH, 2 GTP, and 2 $FADH_2$ molecules are produced in the Krebs cycle. The energy in the 2 GTP molecules can be used to form 2 ATP molecules. The electron transport chain uses the electrons in NADH and $FADH_2$ to produce 22 ATP molecules. See Figure 6–17. When the results of each of these biochemical pathways are considered, we find that a total of 36 molecules of ATP are produced from each glucose molecule. The energy in these 36 ATP molecules is about 37 percent of the total chemical energy available in glucose. That might not sound very impressive. However, the process of respiration is more efficient than the average automobile engine when it comes to converting fuel to usable energy.

Obtaining Energy from Food

Obviously very few of us eat a diet composed exclusively of glucose. But how is energy produced from foods other than glucose?

Complex carbohydrates are broken down into simple sugars that are then converted into glucose. At that point, the pathways we have discussed in this chapter can be used to produce energy. Most lipids and many proteins can be broken down into molecules that can enter glycolysis or the Krebs cycle at one of several places. Like a furnace that can burn wood, coal, or oil, the cell can generate chemical energy in the form of ATP from just about any source.

Breathing and Respiration

After all of this chemical detail, it is reasonable to point out why we have used the term respiration to refer to energy-releasing pathways. Remember that the final acceptor for all electrons produced in respiration is oxygen. Without oxygen, electron transport cannot operate, the Krebs cycle stops, and the synthesis of ATP in the mitochondrion stops. If we are starved for oxygen, our cells will attempt to make the ATP they require by glycolysis alone. But for most cells this is not sufficient.

With each breath we take, air flows into our lungs. Since ancient times, humans have realized that a constant supply of air into the lungs is necessary. But only in this century have we been able to understand why that air is necessary—oxygen has a critical role to play in the mitochondria of every cell!

Energy in Balance

Photosynthesis and respiration can be thought of as opposite processes. Earlier, we compared the chemical energy in glucose to money in a savings account. Photosynthesis is the process that "deposits" energy. Respiration "withdraws" energy. The equations for photosynthesis and for the complete breakdown of glucose (through glycolysis and respiration) are the reverse of each other. The products of photosynthesis are the reactants of glucose breakdown, and the products of glucose breakdown are the reactants of photosynthesis.



Figure 6–18 *As this figure skater breathes, she takes in oxygen. The oxygen is used in the process of respiration, which provides energy in the form of ATP—energy that enables the skater to perform her feats on ice!*

6–3 SECTION REVIEW

1. What is glycolysis?
2. List the products of the Krebs cycle. What happens to each of these products?
3. Why is breathing necessary for cellular respiration in animals?
4. None of the steps of the Krebs cycle involves oxygen. However, the Krebs cycle is considered to be an aerobic process. Explain why.

Section Objectives

- Relate fermentation to glycolysis.
- Compare lactic acid fermentation and alcoholic fermentation.

6–4 Fermentation

If oxygen is present, a cell can use the process of respiration to extract a great amount of energy from glucose. But what happens when no oxygen is available? Does this mean that we can no longer get energy from glucose?

As you may remember, glycolysis produces 2 ATP molecules per molecule of glucose and does not require oxygen.

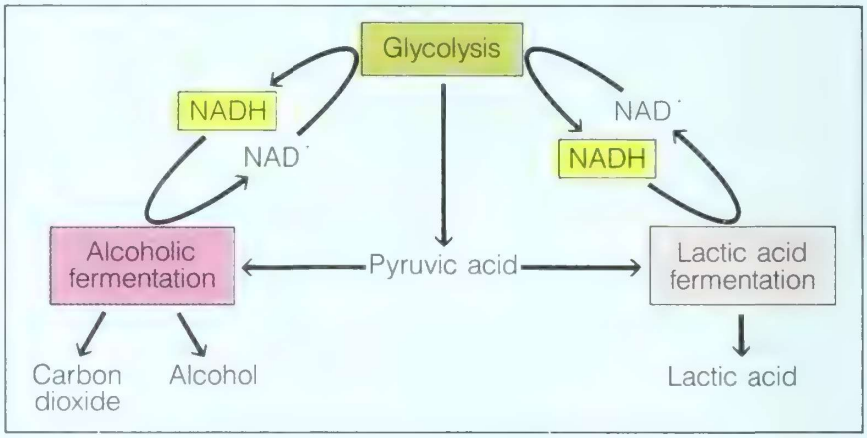


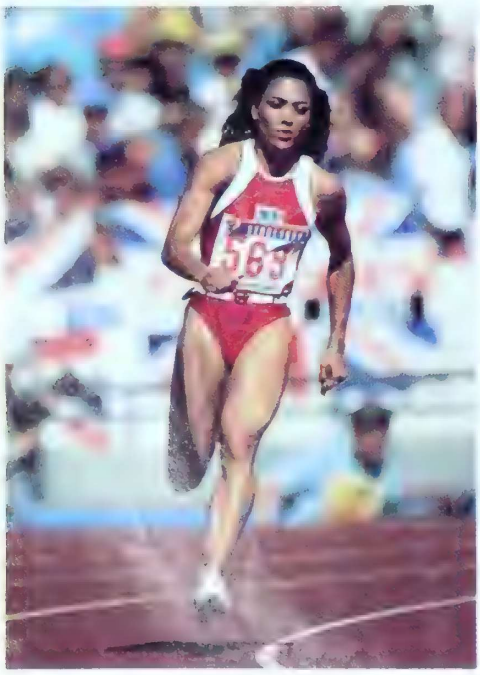
Figure 6–19 *The process of glycolysis produces energy and converts NAD^+ to NADH. Fermentation is an anaerobic process that converts NADH back to NAD^+, thus enabling cells to produce energy under anaerobic conditions.*

This enables cells to produce a limited amount of chemical energy in the form of ATP. Glycolysis also produces high-energy electrons that convert NAD^+ to NADH. In order for glycolysis to continue, NADH must be converted back to NAD^+.

This is where the process of **fermentation** comes in. Fermentation is **anaerobic**, which means that it does not require oxygen. In fermentation, NADH is converted to NAD^+ by adding the extra electrons in NADH to an organic molecule that acts as an electron acceptor. **Thus, fermentation enables cells to carry out energy production in the absence of oxygen.** The combination of glycolysis and fermentation produces 2 ATP molecules from a molecule of glucose.

In bacteria, many different organic molecules can serve as the final electron acceptor in fermentation. However, most eukaryotic cells use one of two fermentation pathways to change NADH to NAD^+. The two pathways are lactic acid fermentation and alcoholic fermentation.

Figure 6–20 *When the body cannot supply enough oxygen to muscles during vigorous exercise, muscle cells begin to produce energy by lactic acid fermentation. Even the best athletes are subject to the aches and pains that result from the buildup of lactic acid in the muscles.*

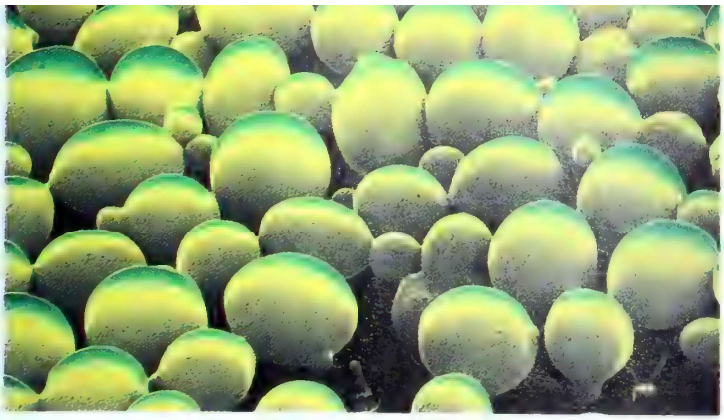


Lactic Acid Fermentation

In many cells, the pyruvic acid that accumulates as a result of glycolysis can be converted to lactic acid. Because this type of fermentation produces lactic acid, it is known as **lactic acid fermentation**. This process regenerates NAD^+ so that glycolysis can continue:

pyruvic acid + NADH → lactic acid + NAD^+

Lactic acid is produced in muscles during rapid exercise when the body cannot supply enough oxygen to the tissues to





produce all of the ATP that is required. The buildup of lactic acid causes a burning, painful sensation that every athlete is familiar with. When you exercise vigorously by running, swimming, or riding a bicycle as fast as you can, the large muscles of your arms and legs quickly run out of oxygen. Your muscle cells rapidly begin to produce ATP by fermentation. During this process, lactic acid is produced. This is why muscles may feel sore after only a few seconds of very rapid activity.

Alcoholic Fermentation

Another type of fermentation occurs in yeasts and a few other microorganisms. In this process, pyruvic acid (which is a 3-carbon compound) is broken down to produce a 2-carbon alcohol and carbon dioxide (CO_2). Because this type of fermentation produces alcohol, it is known as **alcoholic fermentation**. As in lactic acid fermentation, the process that alters pyruvic acid also changes NADH back into NAD^+:

$$\textbf{pyruvic acid} + \textbf{NADH} \rightarrow \textbf{alcohol} + \textbf{CO}_2 + \textbf{NAD}^+$$

Alcoholic fermentation is of particular importance to bakers and brewers. The carbon dioxide produced by yeast during fermentation causes dough to rise and forms the air spaces you see in a slice of bread. The CO_2 released by fermentation is the source of bubbles in beer and sparkling wines. To brewers, alcohol is a welcome byproduct of fermentation. However, it is not desirable from a yeast cell's point of view. Alcohol is toxic. When the level of alcohol reaches about 12 percent, yeast cells die. Thus alcoholic beverages must be processed if higher concentrations of alcohol are desired.

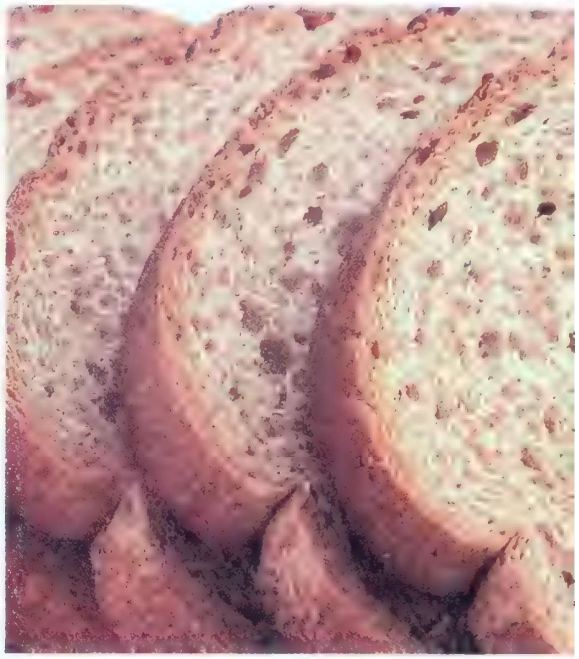


Figure 6–21 *When yeast cells (left) undergo alcoholic fermentation, they produce alcohol and carbon dioxide. The carbon dioxide produces the air spaces in bread and the bubbles in champagne.*

6–4 SECTION REVIEW

1. What is fermentation? What are two types of fermentation?
2. How are respiration and fermentation similar? How are they different?
3. When oxygen is present, yeast cells undergo respiration. Explain why brewers must take special care to prevent air from entering fermentation tanks.

LABORATORY INVESTIGATION

OBSERVING THE RELATIONSHIP BETWEEN PHOTOSYNTHESIS AND RESPIRATION

PROBLEM

What is the relationship between the processes of photosynthesis and respiration?

MATERIALS *(per group)*

2 125-mL flasks
2 #5 rubber stoppers
100-mL graduated cylinder
bromthymol blue solution
2 *Elodea*
light source
drinking straw

PROCEDURE

1. Using a graduated cylinder, measure out 100 mL of bromthymol blue solution for each of the two flasks.
   CAUTION: *Bromthymol blue is a dye and can stain your hands and clothing.*
2. Insert one end of a drinking straw into the bromthymol blue in one of the flasks. Gently blow through the straw. Keep blowing until there is a change in the appearance of the bromthymol blue solution. Repeat this procedure with the other flask.
3. Place a sprig of *Elodea* into each flask. Stopper the flasks.
4. Place one flask in the dark for 24 hours. Place the other flask on a sunny windowsill for the same amount of time. Artificial light may be used to supplement the sunlight.
5. After 24 hours, examine each flask. Note any change in the appearance of the bromthymol blue solution.



OBSERVATIONS

1. What was the color of the bromthymol blue solution before you exhaled into it? After you exhaled into it?
2. What was the color of the bromthymol blue solution in the flask that was placed in the dark for 24 hours? In the flask that was placed in the light for 24 hours?

ANALYSIS AND CONCLUSIONS

1. What substance was released into the bromthymol blue solution when you exhaled into it? How is this substance produced?
2. Explain why the color of the bromthymol blue solution changed after you exhaled into it.
3. Why was *Elodea* placed in both flasks?
4. Which flask is the control? Describe additional controls that you might use for this experiment.
5. Why are the results for the two flasks different?
6. How are photosynthesis and respiration related?

STUDENT STUDY GUIDE

SUMMARIZING THE CONCEPTS

The key concepts in each section of this chapter are listed below to help you review the chapter content. Make sure you understand each concept and its relationship to other concepts and to the theme of this chapter.

6–1 Photosynthesis: Capturing and Converting Energy

- In the process of photosynthesis, green plants capture the energy in sunlight and convert it into chemical energy. The balanced overall equation for photosynthesis is $6\ CO_2 + 6\ H_2O \xrightarrow{\text{light}} C_6H_{12}O_6 + 6\ O_2$.

6–2 Photosynthesis: The Light and Dark Reactions

- The light reactions can be broken down into four parts: light absorption, electron transport, oxygen production, and ATP synthesis.
- The dark reactions occur outside the photosynthetic membrane in the chloroplast. In the Calvin cycle, CO_2 is used to make PGAL, which can then be used to form glucose and other important molecules.

6–3 Glycolysis and Respiration

- Glycolysis is a series of chemical reactions that ultimately produces 2 molecules of ATP and 2 molecules of pyruvic acid.
- Respiration is an aerobic process that breaks down food molecules to release energy. This energy is stored in the form of ATP.

6–4 Fermentation

- Fermentation is an anaerobic process that regenerates NAD^+ for use in glycolysis. In fermentation, organic molecules take electrons from NADH, changing it back to NAD^+
- Photosynthesis stores energy; respiration releases energy. Products of photosynthesis are used in respiration. Products of respiration are raw materials for photosynthesis.

REVIEWING KEY TERMS

Vocabulary terms are important to your understanding of biology. The key terms listed below are those you should be especially familiar with. Review these terms and their meanings. Then use each term in a complete sentence. If you are not sure of a term's meaning, return to the appropriate section and review its definition.

6–1 Photosynthesis: Capturing and Converting Energy
photosynthesis
glucose
autotroph
heterotroph
pigment
chlorophyll
adenosine triphosphate (ATP)

6–2 Photosynthesis: The Light and Dark Reactions
light reactions
dark reactions
photosynthetic membrane
photosystem
electron transport
Calvin cycle

6–3 Glycolysis and Respiration
calorie
glycolysis
respiration
aerobic
Krebs cycle

6–4 Fermentation
fermentation
anaerobic
lactic acid fermentation
alcoholic fermentation

CHAPTER REVIEW

CONTENT REVIEW

Multiple Choice

Choose the letter of the answer that best completes each statement.

1. Which process is anaerobic?
   a. Krebs cycle
   b. mitochondrial electron transport
   c. glycolysis
   d. respiration
2. An experiment that showed that part of a growing plant's mass comes from water was performed by
   a. Priestley.
   b. Van Helmont.
   c. Ingenhousz.
   d. Calvin.
3. Autotrophs include
   a. ferns.
   b. camels.
   c. yeasts.
   d. birds.
4. Photosynthesis produces
   a. carbon dioxide.
   b. alcohol.
   c. water.
   d. glucose.
5. In respiration, the final electron acceptor is
   a. lactic acid.
   b. alcohol.
   c. oxygen.
   d. NAD^+.
6. Which of these is produced by the dark reactions?
   a. PGAL
   b. oxygen
   c. water
   d. ATP
7. A type of pigment found in green plants is
   a. NAD^+.
   b. NADPH.
   c. ATP.
   d. chlorophyll.
8. Which of these is not produced in the light reactions?
   a. NADPH
   b. glucose
   c. ATP
   d. oxygen

True or False

Determine whether each statement is true or false. If it is true, write "true." If it is false, change the underlined word or words to make the statement true.

1. In the dark reactions of photosynthesis, the energy in sunlight is captured and used to make ATP and NADPH.
2. Because they cannot make their own food, autotrophs rely on the food-making ability of green plants.
3. Photosystems are clusters of pigment molecules that are able to capture the energy of sunlight.
4. The light reactions occur outside the photosynthetic membrane.
5. ATP is formed when enzymes move hydrogen ions across a membrane to an area of greater concentration.
6. Glycolysis is an aerobic process that breaks down food molecules to produce energy.
7. When there is no oxygen present, yeast cells break down glucose to form lactic acid and carbon dioxide.
8. Approximately 36 molecules of ATP are formed during glycolysis.

Word Relationships

A. *In each of the following sets of terms, three of the terms are related. One term does not belong. Determine the characteristic common to three of the terms and then identify the term that does not belong.*

1. Calvin cycle, light absorption, electron transport, oxygen production
2. fermentation, respiration, glycolysis, photosynthesis
3. glucose, oxygen, water, energy

B. *An analogy is a relationship between two pairs of words or phrases generally written in the following manner: a:b::c:d. The symbol : is read "is to," and the symbol :: is read "as." For example, cat:animal::rose:plant is read "cat is to animal as rose is to plant."*

In the analogies that follow, a word or phrase is missing. Complete each analogy by providing the missing word or phrase.

4. food and oxygen:respiration::_____:photosynthesis
5. oak tree:autotroph::human:_____
6. PGAL:Calvin cycle::pyruvic acid:_____
7. photosynthesis:chloroplast::respiration:_____

CONCEPT MASTERY

Use your understanding of the concepts developed in the chapter to answer each of the following in a brief paragraph.

1. List the requirements for photosynthesis. Briefly describe how each is involved in the light reactions or the dark reactions.
2. Describe the process of ATP formation.
3. Name ten living things that you see every day. Identify each of these as an autotroph or a heterotroph.
4. What is the relationship between breathing and respiration?
5. How are photosynthesis and respiration related to each other?
6. Compare the reactants and products of two types of fermentation.

CRITICAL AND CREATIVE THINKING

Discuss each of the following in a brief paragraph.

1. **Making comparisons** Compare the chemical steps of the light and dark reactions of photosynthesis with those of glycolysis, the Krebs cycle, and the respiratory electron transport chain.
2. **Making an outline** Outline the process of photosynthesis.
3. **Applying concepts** Some desert animals such as the kangaroo rat never have to drink water. Explain how kangaroo rats can obtain the water they need to survive from the dry seeds they eat.
4. **Making inferences** Some scientists think that the dinosaurs may have become extinct because an asteroid struck the Earth and sent large amounts of dust into the upper atmosphere. The dust remained in the atmosphere a long time. Explain how this would have resulted in the dinosaurs dying off.
5. **Assessing concepts** Which is better: respiration or fermentation? Explain your answer.
6. **Using the writing process** You are a carbon atom. You have just returned to the air as carbon dioxide after being involved in the processes of photosynthesis and respiration. Describe what happened to you on your chemical journey. Where did you go? What other atoms (carbon and otherwise) did you find yourself bonded to? What molecules did you meet along the way, and what were they like?