CHAPTER 7

Cellular Energetics

Exam Weight: 12–16%

IN THIS CHAPTER

Summary: This chapter covers the basics behind the energy-creation processes known as respiration and photosynthesis. This chapter will teach you the difference between aerobic and anaerobic respiration and take you through the steps that convert a glucose molecule into ATP. It will also teach you how plants generate their energy from light in two distinct stages—the light-dependent and the light-independent reactions.

KEY IDEA

Key Ideas

- ✪ Aerobic respiration: glycolysis → Krebs cycle → oxidative phosphorylation → 36 ATP.
- ✪ Anaerobic respiration: glycolysis → regenerate NAD^+ → much less ATP.
- ✪ Oxidative phosphorylation results in the production of large amounts of ATP from NADH and $FADH_2$.
- ✪ Chemiosmosis is the coupling of the movement of electrons down the electron transport chain with the formation of ATP using the driving force provided by the proton gradient.
- ✪ Overall photosynthesis reaction: $H_2O + CO_2$ + light → O_2 + glucose + H_2O.
- ✪ Light-dependent reactions: inputs are water and light; products are ATP, NADPH, and O_2.
- ✪ The oxygen produced in photosynthesis comes from the water.
- ✪ The carbon in the glucose produced in photosynthesis comes from the CO_2.
- ✪ Light-independent reactions (dark reactions): inputs are NADPH, ATP, and CO_2; products are ADP, $NADP^+$, and sugar.

Introduction

In this chapter, we explore how cells obtain energy. It is important that you do not get lost or buried in the details. You should finish this chapter with an understanding of the basic processes.

The AP Biology exam will not ask you to identify by name the enzyme that catalyzes the third step of glycolysis, nor will it require you to name the fourth molecule in the Krebs cycle. But it *will* ask you questions that require an understanding of the respiration process.

The AP Biology exam will not ask you to draw a picture of the thylakoid membrane system. But it will want you to know that photosynthesis is the process by which plants generate their energy from light or that most of plant photosynthesis occurs in the plant's leaves or that the majority of the chloroplasts of a plant are found in mesophyll cells.

It's important to remember that there are two stages to photosynthesis: the light-dependent reactions and the light-independent reactions, commonly called the dark reactions. The simplified equation of photosynthesis is:

$$\mathbf{H_2O + CO_2 + light \rightarrow O_2 + glucose + H_2O}$$

Enzymes

ENE-1
The highly complex organization of living systems requires constant input of energy and the exchange of macromolecules.

Enzymes are proteins that act as organic catalysts and will be encountered often in your review for this exam. **Catalysts** speed up reactions by lowering the energy (activation energy) needed for the reaction to take place, but are not used up in the reaction. The substances that enzymes act on are known as **substrates**.

Enzymes are selective; they interact only with particular substrates. It is the shape of the enzyme that provides the specificity. The part of the enzyme that interacts with the substrate is called the **active site.** The lock and key model describes a substrate's interaction with the enzyme's active sight and suggests that the enzyme and the substrate possess specific complementary geometric shapes that fit perfectly just like a key fighting into a lock. The **induced-fit model** of enzyme-substrate interaction describes the active site of an enzyme as specific for a particular substrate that fits its shape.

When the enzyme and substrate bind together, the enzyme is *induced* to alter its shape for a tighter active site–substrate attachment. This tight fit places the substrate in a favorable position to react, speeding up (accelerating) the rate of reaction. After an enzyme interacts with a substrate, converting it into a product, it is free to find and react with another substrate; thus, a small concentration of enzyme can have a major effect on a reaction.

Each enzyme functions best at an optimal temperature, pH, and salt concentration. If those values stray too far from "optimal," the effectiveness of the enzyme will suffer and the enzyme could **denature**. The weak chemical bonds and interactions within a protein may be destroyed, causing the protein to unravel and lose its shape. The effectiveness of an enzyme can be affected by four things:

1. The temperature
2. The pH
3. The concentration of the substrate involved
4. The concentration of the enzyme involved

You should be able to identify the basic components of an activation energy diagram if you encounter one on the AP exam. The important parts are identified in Figure 7.1.

The last enzyme topic to cover is the difference between competitive and noncompetitive inhibition. In **competitive inhibition** (Figure 7.2), an inhibitor molecule resembling the substrate binds to the active site and physically blocks the substrate from attaching.

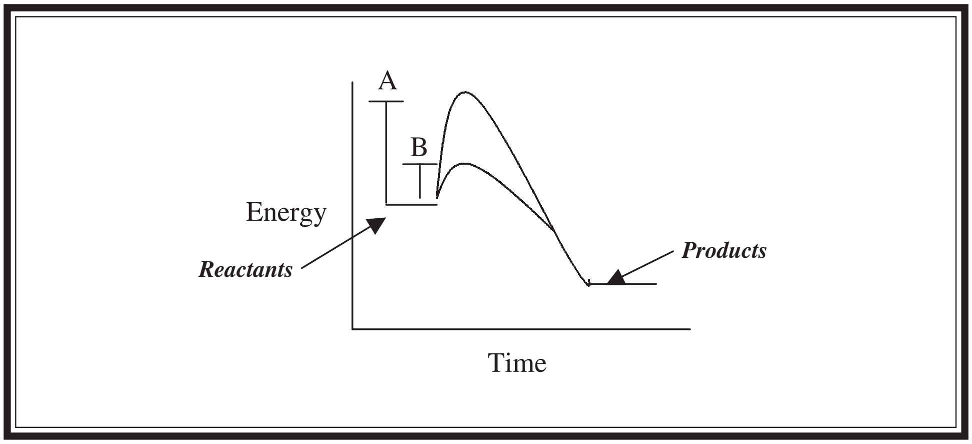


Figure 7.1 Plot showing energy versus time. Height A represents original activation energy; height B represents the lowered activation energy due to the addition of enzyme.

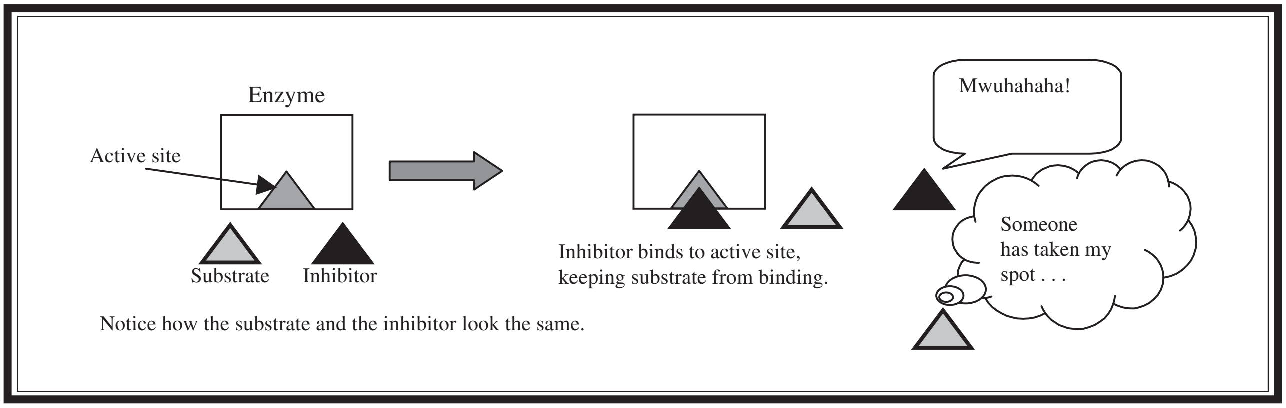


Figure 7.2 Competitive inhibition.

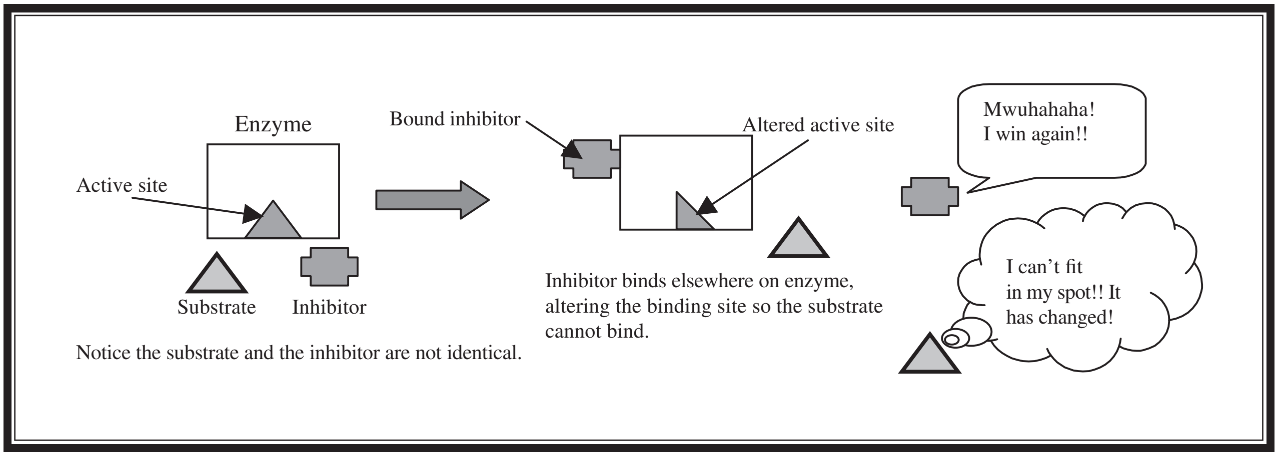


Figure 7.3 Noncompetitive inhibition.

Competitive inhibition can sometimes be overcome by adding a high concentration of substrate to outcompete the inhibitor. In **noncompetitive inhibition** (Figure 7.3), an inhibitor molecule binds to a different part of the enzyme, causing a change in the shape of the active site so that it can no longer interact with the substrate.

Cellular Energy

ENE-1
The highly complex organization of living systems requires constant input of energy and the exchange of macromolecules.

All living organisms rely on a constant input of energy in different forms to survive and thrive. This flow of energy follows the laws of thermodynamics that govern all forms of energy. The first law of thermodynamics states that energy cannot be created or destroyed; it can only change form, and it must be obtained through its environment. The second law of thermodynamics states that life is in a constant movement toward entropy or a "gradual decline of order" in a system and requires a constant input of energy from its environment that can be used to overcome this decline of order. Without the constant input of energy, an organism will die!!!

The constant input of energy to overcome energy and the idea that energy cannot be created or destroyed is the foundation upon which trophic or energy dynamics on Earth rest. The movement energy comes from the coupling of endergonic and exergonic reactions. **Endergonic reactions** are reactions in which energy is absorbed from the surroundings. **Exergonic reactions** are reactions in which free energy is released (See Figure 7.4).

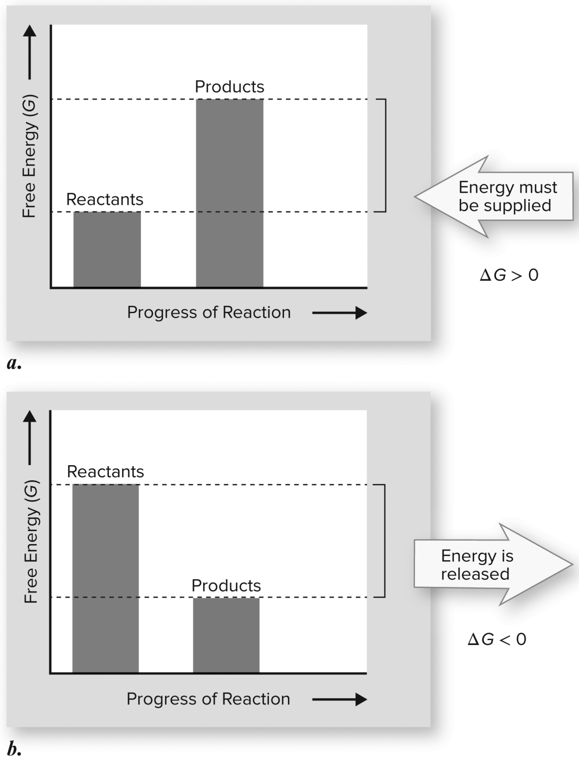


Figure 7.4 Energy in chemical reactions. ***a.*** In an endergonic reaction, the products of the reaction contain more energy than the reactants, and the extra energy must be supplied for the reaction to proceed. ***b.*** In an exergonic reaction, the products contain less energy than the reactants, and the excess energy is released. (*Reproduced with permission from Raven P, Johnson G, Mason K, Losos J, Duncan T;* Biology, *12th ed. New York: McGraw Hill; 2020*)

Image of ATP-ADP – Conversion of ATP to ADP releases energy which is used for many metabolic processes.

This constant exchange of free energy is maintained in living systems through controlled and efficient transfer of energy during the metabolic pathway. The products of one reaction in a metabolic pathway become the reactants for the next step in the pathway. One such reaction is the production of adenosine triphosphate (ATP) in cells. ATP is the energy currency of life. It is the high-energy molecule that stores the energy that life needs to do just about everything. ATP is constructed from an adenosine diphosphate (ADP) and an inorganic phosphate group (Pi) through phosphorylation, a chemical process in which a phosphate group is added using free energy.

Aerobic Respiration

ENE-1
The highly complex organization of living systems requires constant input of energy and the exchange of macromolecules.

Glycolysis

Glycolysis occurs in the cytoplasm of cells and is the beginning pathway for both aerobic and anaerobic respiration. During glycolysis, a glucose molecule is broken down through a series of reactions into two molecules of pyruvate. It is important to remember that oxygen plays no role in glycolysis. This reaction can occur in oxygen-rich and oxygen-poor environments. However, when in an environment lacking oxygen, glycolysis slows because the cells run out (become depleted) of NAD^+. For reasons we will discuss later, a lack of oxygen prevents oxidative phosphorylation from occurring, causing a buildup of NADH in the cells. This buildup causes a shortage of NAD^+. This is bad for glycolysis because it requires NAD^+ to function. Fermentation is the solution to this problem—it takes the excess NADH that builds up and converts it back to NAD^+ so that glycolysis can continue. More to come on fermentation later . . . be patient. ☺

To reiterate, the AP Biology exam will not require you to memorize the various steps of respiration. Your time is better spent studying the broad explanation of respiration, to understand the basic process, and become comfortable with respiration as a whole. Major concepts are the key. We will explain the specific steps of glycolysis because they will help you understand the big picture—but do not memorize them all. Save the space for other facts you have to know from other chapters of this book.

Examine Figure 7.5, which illustrates the general layout of glycolysis. The beginning steps of glycolysis require energy input. The first step adds a phosphate to a molecule of glucose with the assistance of an ATP molecule to produce *glucose-6-phosphate* (G6P). The newly formed G6P rearranges to form a molecule named *fructose-6-phosphate* (F6P). Another molecule of ATP is required for the next step, which adds another phosphate group to produce fructose 1,6-biphosphate. Already, glycolysis has used two of the ATP molecules that it is trying to produce—seems stupid . . . but be patient . . . the genius has yet to show its face. F6P splits into two 3-carbon-long fragments known as **PGAL** (glyceraldehyde phosphate). With the formation of PGAL, the energy-producing portion of glycolysis begins. Each PGAL molecule takes on an inorganic phosphate from the cytoplasm to produce 1,3-diphosphoglycerate. During this reaction, each PGAL gives up two electrons and a hydrogen to molecules of NAD^+ to form the all-important NADH molecules. The next step is a big one, as it leads to the production of the first ATP molecule in the process of respiration—the 1,3-diphosphoglycerate molecules donate one of their two phosphates to molecules of ADP to produce ATP and 3-phosphoglycerate (3PG). You'll notice that there are *two* ATP molecules formed here because before this step, the single molecule of glucose divided into *two* 3-carbon fragments. After 3PG rearranges to form 2-phosphoglycerate, phosphoenolpyruvate (PEP) is formed, which donates a phosphate group to molecules of ADP to form another pair of ATP molecules and pyruvate. This is the final step of glycolysis. In total, two molecules each of ATP, NADH, and pyruvate are formed during this process. Glycolysis produces the same result under anaerobic conditions as it does under aerobic conditions: two ATP molecules. If oxygen is present, more ATP is later made by oxidative phosphorylation.

TIP

If you are going to memorize one fact about glycolysis, remember that one glucose molecule produces two pyruvate, two NADH, and two ATP molecules.

One glucose → 2 pyruvate, 2 ATP, 2 NADH

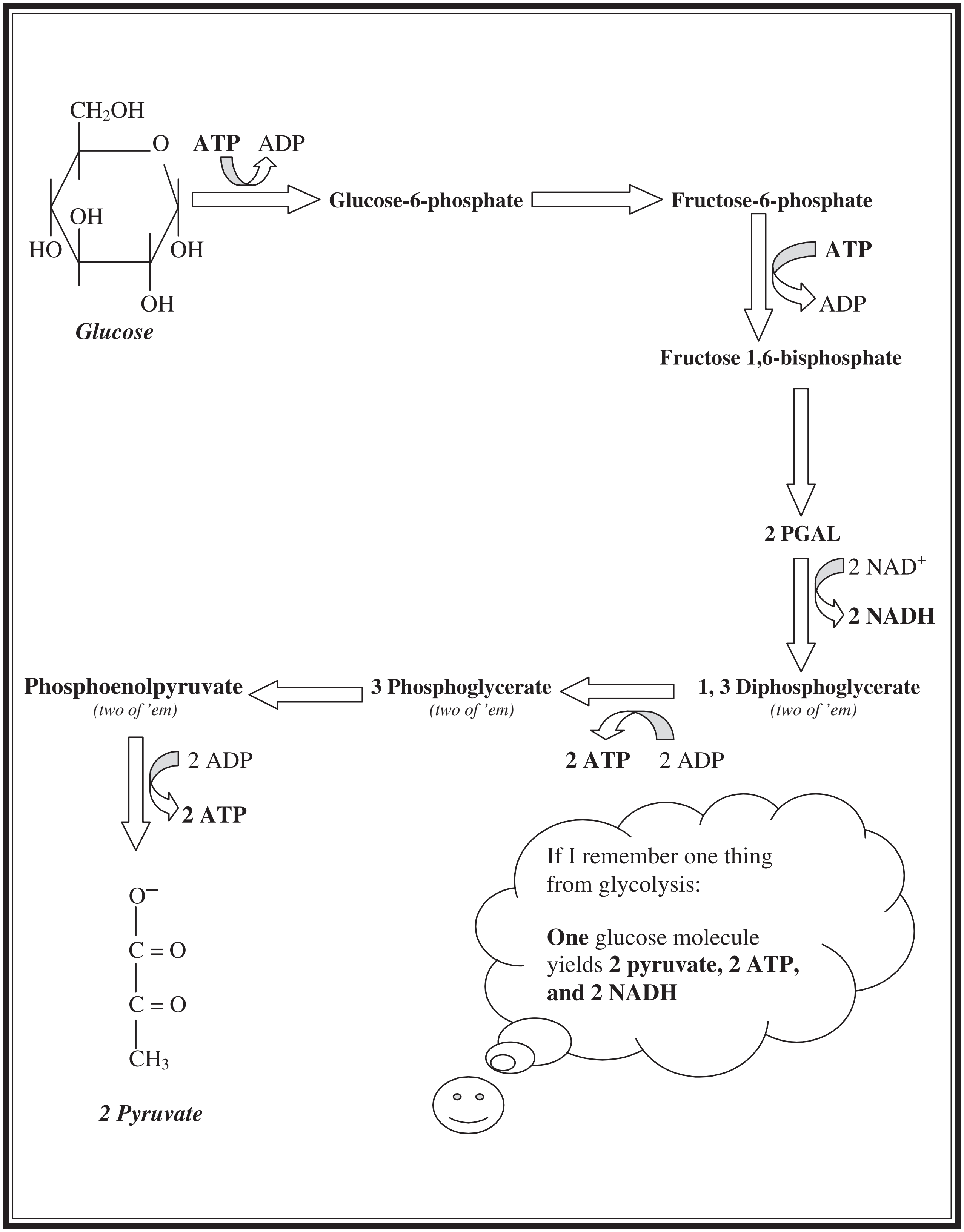


Figure 7.5 Glycolysis.

The Krebs Cycle

The pyruvate formed during glycolysis next enters the **Krebs cycle,** which is also known as the *citric acid cycle.* The Krebs cycle occurs in the matrix of the **mitochondria.** The pyruvate enters the mitochondria of the cell and is converted into acetyl coenzyme A (CoA) in a step that produces an NADH. This compound is now ready to enter the eight-step Krebs cycle, in which pyruvate is broken down completely to H_2O and CO_2. You do not need to memorize the eight steps.

As shown in Figure 7.6, a representation of the Krebs cycle, the 3-carbon pyruvate does not enter the Krebs cycle per se. Rather, it is converted, with the assistance of CoA and NAD^+, into 2-carbon acetyl CoA and NADH. The acetyl CoA dives into the Krebs cycle and reacts with oxaloacetate to form a 6-carbon molecule called *citrate.* The citrate is converted to a molecule named isocitrate, which then donates electrons and a hydrogen to NAD^+ to form 5-carbon α-ketoglutarate, carbon dioxide, and a molecule of NADH. The α-ketoglutarate undergoes a reaction very similar to the one leading to its formation and produces 4-carbon succinyl CoA and another molecule each of NADH and CO_2. The succinyl CoA is converted into succinate in a reaction that produces a molecule of ATP. The succinate then transfers electrons and a hydrogen atom to FAD to form $FADH_2$ and fumarate. The next-to-last step in the Krebs cycle takes fumarate and rearranges it to another 4-carbon molecule: malate. Finally, in the last step of the cycle, the malate donates electrons and a hydrogen atom to a molecule of NAD^+ to form the final NADH molecule of the Krebs cycle, at the same time regenerating the molecule of oxaloacetate that helped kick off the cycle. One turn of the Krebs cycle takes a single pyruvate and produces one ATP, four NADH, and one $FADH_2$.

TIP

If you are going to memorize one thing about the Krebs cycle, remember that for each glucose dropped into glycolysis, the Krebs cycle occurs twice. Each pyruvate dropped into the Krebs cycle produces

4 NADH, 1 $FADH_2$, 1 ATP, and 2 CO_2

Therefore, the *pyruvate* obtained from the original glucose molecule produces:

8 NADH, 2 $FADH_2$, and 2 ATP

Up to this point, having gone through glycolysis and the Krebs cycle, one molecule of glucose has produced the following energy-related compounds: 10 NADH, 2 $FADH_2$, and 4 ATP. Not bad for an honest day's work . . . but the body wants more and needs to convert the NADH and $FADH_2$ into ATP. This is where the electron transport chain, chemiosmosis, and oxidative phosphorylation come into play.

Oxidative Phosphorylation

After the Krebs cycle comes the largest energy-producing step of them all: **oxidative phosphorylation.** During this aerobic process, the NADH and $FADH_2$ produced during the first two stages of respiration are used to create ATP. Each NADH leads to the production of up to three ATP, and each $FADH_2$ will lead to the production of up to two ATP molecules. This is an inexact measurement—those numbers represent the

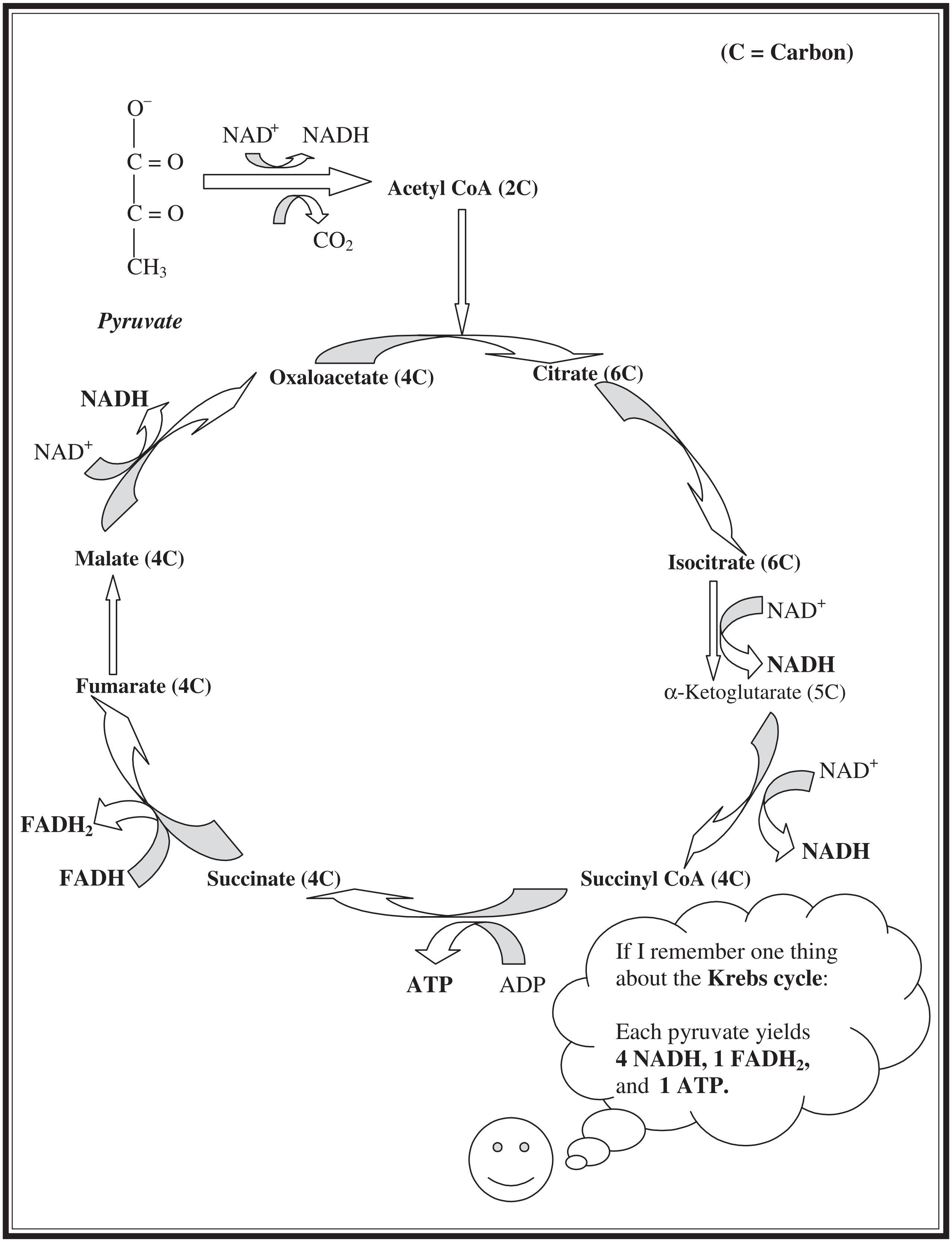


Figure 7.6 The Krebs cycle.

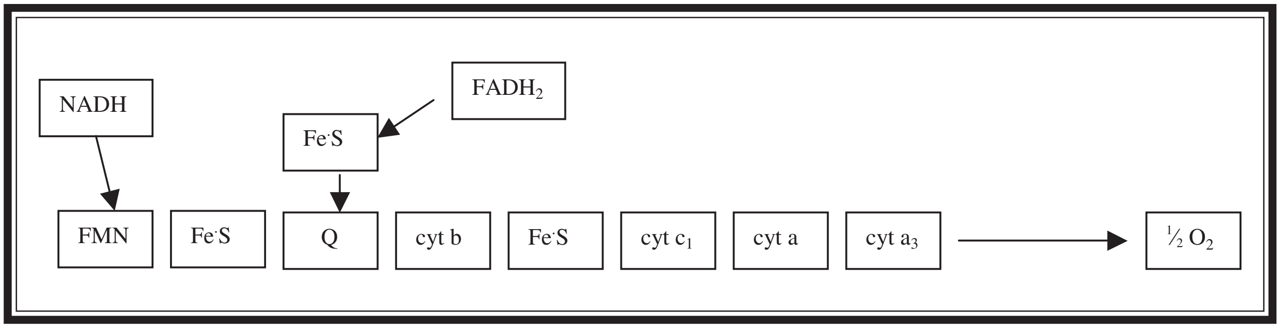


Figure 7.7 Electron transport chain (ETC).

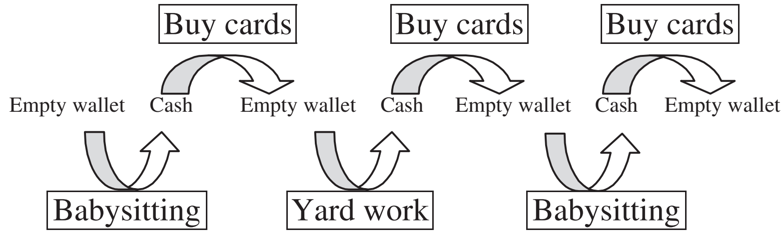
maximum output possible from those two energy components if all goes smoothly. For each molecule of glucose, up to 30 ATP can be produced from the NADH molecules and up to 4 ATP from the $FADH_2$. Add to this the 4 total ATP formed during glycolysis and the Krebs cycle for a grand total of 38 ATP from *each glucose.* Two of these ATP are used during aerobic respiration to help move the NADH produced during glycolysis into the mitochondria. All totaled, during aerobic respiration, each molecule of glucose can produce up to 36 ATP.

Do not panic when you see the illustration for the **electron transport chain** (Figure 7.7). Once again, the big picture is the most important thing to remember. Do not waste your time memorizing the various cytochrome molecules involved in the steps of the chain. Remember that the ½ O_2 is the final electron acceptor in the chain, and that without the O_2 (anaerobic conditions), the production of ATP from NADH and $FADH_2$ will be compromised. Remember that each NADH that goes through the chain can produce three molecules of ATP, and each $FADH_2$ can produce two.

The *electron transport chain* (ETC) is the chain of enzyme molecules, located in the mitochondria, that passes electrons along during the process of chemiosmosis to regenerate NAD^+ to form ATP. Each time an electron passes to another member of the chain, the energy level of the system drops. Do not worry about the individual members of this chain—they are unimportant for this exam. When thinking of the ETC, we are reminded of the passing of a bucket of water from person to person until it arrives at and is tossed onto a fire. In the ETC, the various molecules in the chain are the people passing the buckets; the drop in the energy level with each pass is akin to the water sloshed out as the bucket is hurriedly passed along, and the ½ O_2 represents the fire onto which the water is dumped at the end of the chain. As the ½ O_2 (each oxygen atom, or half of an O_2 molecule) accepts a pair of electrons, it actually picks up a pair of hydrogen ions to *produce* water.

KEY IDEA

Chemiosmosis is a very important term to understand. It is defined as the coupling of the movement of electrons down the electron transport chain with the formation of ATP using the driving force provided by a proton gradient. So, what does that mean in English? Well, let's start by first defining what a coupled reaction is. It is a reaction that uses the product of *one* reaction as part of *another* reaction. Thinking back to our baseball card collecting days helps us better understand this coupling concept. We needed money to buy baseball cards. We would babysit or do yardwork for our neighbors and use that money to buy cards. We coupled the money-making reaction of hard labor to the money-spending reaction of buying baseball cards.



Let's look more closely at the reactions that are coupled in chemiosmosis. If you look at Figure 7.8a, a crude representation of a mitochondrion, you will find the ETC embedded within the inner mitochondrial membrane. As some of the molecules in the chain accept and then pass on electrons, they pump hydrogen ions into the space between the inner and outer membranes of the mitochondria (Figure 7.8b). This creates a proton gradient that drives the production of ATP. The difference in hydrogen concentration on the two sides of the membrane causes the protons to flow back into the matrix of the mitochondria through ATP synthase channels (Figure 7.8c). **ATP synthase** is an enzyme that uses the flow of hydrogens to drive the phosphorylation of an ADP molecule to produce ATP. This reaction completes the process of oxidative phosphorylation and chemiosmosis. The proton gradient created by the movement of electrons from molecule to molecule has been used to form the ATP that this process is designed to produce. In other words, the formation of ATP has been coupled to the movement of electrons and protons.

Chemiosmosis is not oxidative phosphorylation per se; rather, it is a major *part* of oxidative phosphorylation. An important fact we want you to take out of this chapter is that chemiosmosis is not unique to the mitochondria. It is the same process that occurs in the

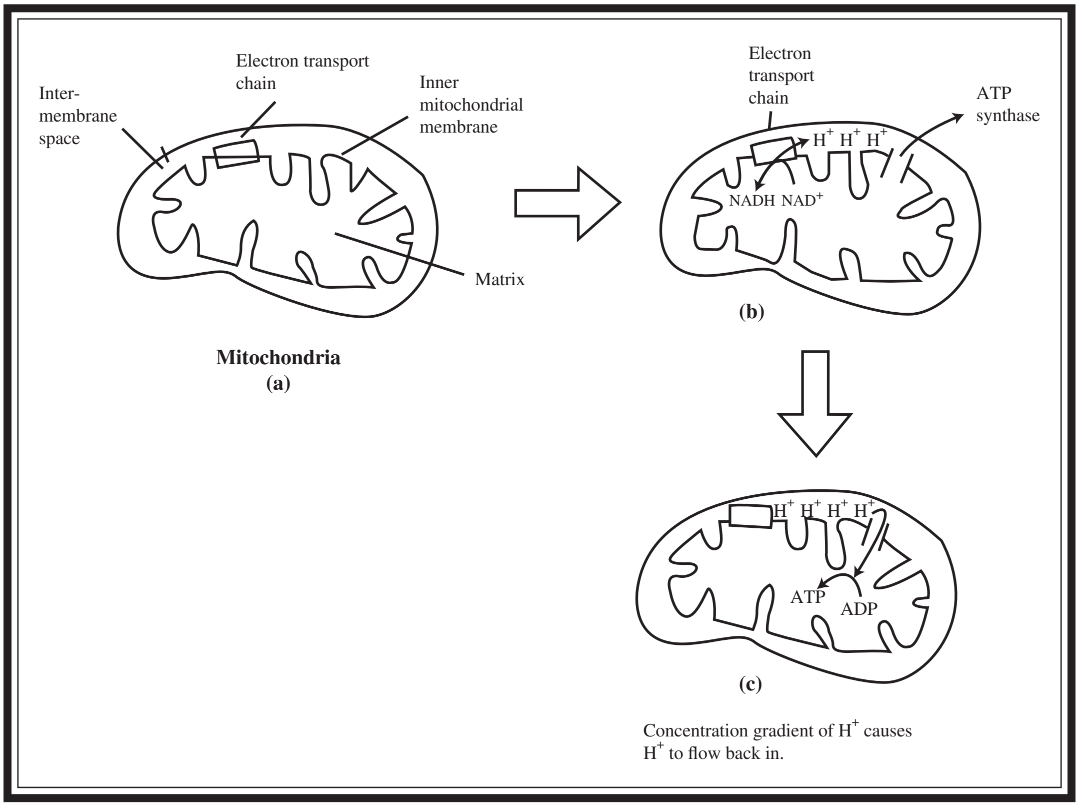


Figure 7.8 Chemiosmosis.

chloroplasts during the ATP-creating steps of photosynthesis. The difference is that light is driving the electrons along the ETC in plants. Remember that chemiosmosis occurs in both mitochondria and chloroplasts.

Remember the following facts about oxidative phosphorylation (Ox-phos):

KEY IDEA

1. Each NADH → 3 ATP.
2. Each $FADH_2$ → 2 ATP.
3. ½ O_2 is the final electron acceptor of the electron transport chain, and the chain will not function in the absence of oxygen.
4. Ox-phos serves the important function of regenerating NAD^+ so that glycolysis and the Krebs cycle can continue.
5. Chemiosmosis occurs in photosynthesis as well as respiration.

Anaerobic Respiration

ENE-1
The highly complex organization of living systems requires constant input of energy and the exchange of macromolecules.

Anaerobic respiration, or *fermentation,* occurs when oxygen is unavailable or cannot be used by the organism. As in aerobic respiration, glycolysis occurs and pyruvate is produced. The pyruvate enters the Krebs cycle, producing NADH, $FADH_2$, and some ATP. The problem arises in the ETC—because there is no oxygen available, the electrons do not pass down the chain to the final electron acceptor, causing a buildup of NADH in the system. This buildup of NADH means that the NAD^+ normally regenerated during oxidative phosphorylation is not produced, and this creates an NAD^+ shortage. This is a problem, because in order for glycolysis to proceed to the pyruvate stage, it needs NAD^+ to help perform the necessary reactions. **Fermentation** is the process that begins with glycolysis and ends when NAD^+ is regenerated. A glucose molecule that enters the fermentation pathway produces two net ATP per molecule of glucose, representing a tremendous decline in the efficiency of ATP production.

Under aerobic conditions, NAD^+ is recycled from NADH by the movement of electrons down the electron transport chain. Under anaerobic conditions, NAD^+ is recycled from NADH by the movement of electrons to pyruvate, namely, fermentation. The two main types of fermentation are **alcohol fermentation** and **lactic acid fermentation.** Refer to Figures 7.9 and 7.10 for the representations of the different forms of fermentation. Alcohol fermentation (Figure 7.9) occurs in fungi, yeast, and some bacteria. The first step involves the conversion of pyruvate into two 2-carbon acetaldehyde molecules. Then, in the all-important step of alcohol fermentation, the acetaldehyde molecules are converted to ethanol, regenerating two NAD^+ molecules in the process.

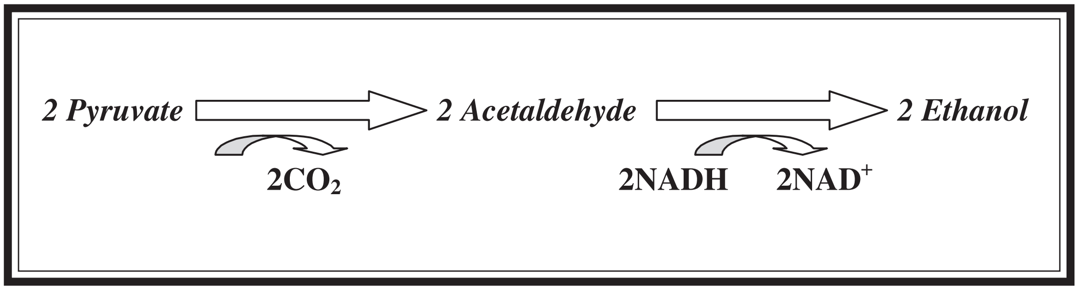


Figure 7.9 Alcohol fermentation.

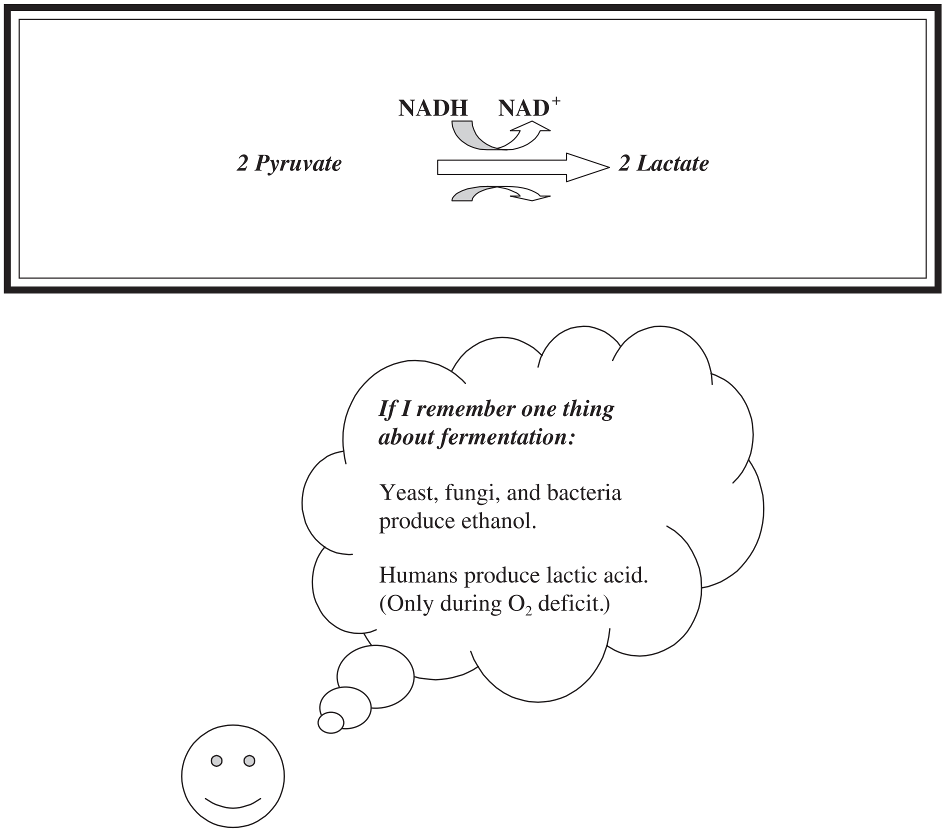


Figure 7.10 Lactic acid fermentation.

Lactic acid fermentation (Figure 7.10) occurs in human and animal muscle cells when oxygen is not available. This is a simpler process than alcoholic fermentation—the pyruvate is directly reduced to lactate (also known as lactic acid) by NADH to regenerate the NAD^+ needed for the resumption of glycolysis. Have you ever had a cramp during exercise? The pain you felt was the result of lactic acid fermentation. Your muscle was deprived of the necessary amount of oxygen to continue glycolysis, and it switched over to fermentation. The pain from the cramp came from the acidity in the muscle.

The Players in Photosynthesis

ENE-1
The highly complex organization of living systems requires constant input of energy and the exchange of macromolecules.

The host organelle for photosynthesis is the **chloroplast,** which is divided into an inner and outer portion. The inner fluid portion is called the **stroma,** which is surrounded by two outer membranes. In Figure 7.11, you can see that winding through the stroma is an inner membrane called the **thylakoid membrane system.** This is where the first stage of photosynthesis occurs. This membrane consists of flattened channels and disks arranged in stacks called **grana.** We always remember the thylakoid system as resembling stacks of poker chips, where each chip is a single thylakoid. It is within these poker chips that the light-dependent reactions of photosynthesis occur.

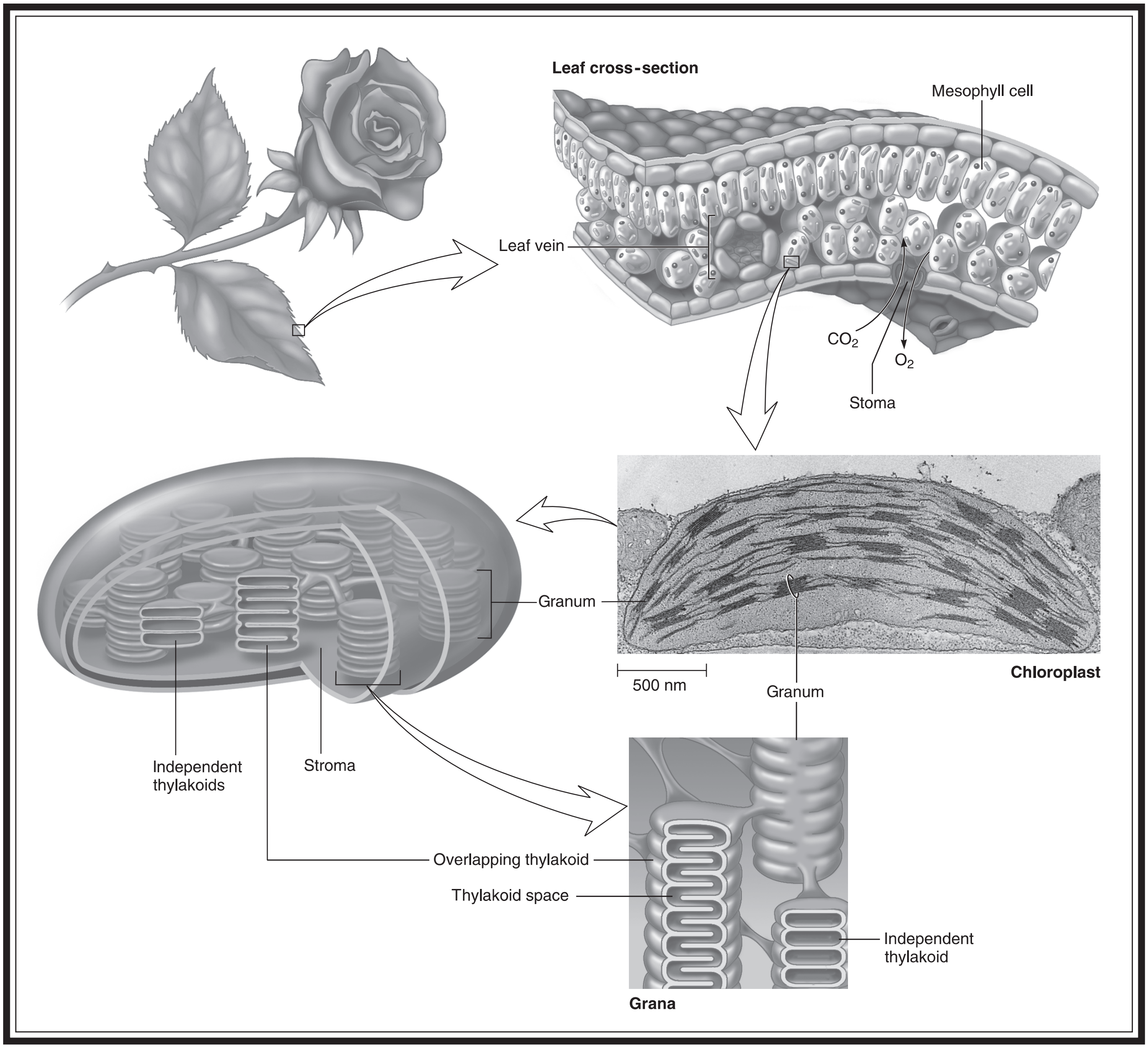


Figure 7.11 An overall view of photosynthesis. (*From* Biology, *8th ed., by Sylvia S. Mader, © 1985, 1987, 1990, 1993, 1996, 1998, 2001, 2004 by the McGraw Hill Companies, Inc. Reproduced with permission of The McGraw Hill Companies.*)

Before we examine the process of photosynthesis, here are some definitions that will make things a bit easier as you read this chapter.

Autotroph: an organism that is self-nourishing. It obtains carbon and energy without ingesting other organisms. Plants and algae are good examples of autotrophic organisms—they obtain their energy from carbon dioxide, water, and light. They are the producers of the world.

Bundle sheath cells: cells that are tightly wrapped around the veins of a leaf. They are the site for the **Calvin cycle** in C_4 plants.

C_4 plant: plant that has adapted its photosynthetic process to more efficiently handle hot and dry conditions.

Heterotroph: organisms that must consume other organisms to obtain nourishment. They are the consumers of the world.

Mesophyll: interior tissue of a leaf.

Mesophyll cells: cells that contain many chloroplasts and host the majority of photosynthesis.

Photolysis: process by which water is broken up by an enzyme into hydrogen ions and oxygen atoms; occurs during the light-dependent reactions of photosynthesis.

Photophosphorylation: process by which ATP is produced during the light-dependent reactions of photosynthesis. It is the chloroplast equivalent of oxidative phosphorylation.

Photorespiration: process by which oxygen competes with carbon dioxide and attaches to RuBP. Plants that experience photorespiration have a lowered capacity for growth.

Photosystem: a cluster of light-trapping pigments involved in the process of photosynthesis. Photosystems vary tremendously in their organization and can possess hundreds of pigments. The two most important are photosystems I and II of the light reactions.

Pigment: a molecule that absorbs light of a particular wavelength. Pigments are vital to the process of photosynthesis and include **chlorophyll, carotenoids,** and **phycobilins.**

Rubisco: an enzyme that catalyzes the first step of the Calvin cycle in C_3 plants.

Stomata: structure through which CO_2 enters a plant and water vapor and O_2 leave.

Transpiration: natural process by which plants lose H_2O via evaporation through their leaves.

The Reactions of Photosynthesis

The process of photosynthesis can be neatly divided into two sets of reactions: the light-dependent reactions and the light-independent reactions. The light-dependent reactions occur first and require an input of water and light. They produce three things: the oxygen we breathe, NADPH, and ATP. These last two products of the light reactions are then consumed during the second stage of photosynthesis: the dark reactions. These reactions, which need CO_2, NADPH, and ATP as inputs, produce sugar and recycle the $NADP^+$ and ADP to be used by the next set of light-dependent reactions.

Now, we would be too kind The process of photosynthesis can be neatly divided into two sets of reactions: the light-dependent reactions and the light-independent reactions. The light-dependent reactions occur first and require an input of water and light. They produce three things: the oxygen we breathe, NADPH, and ATP. These last two products of the light reactions are then consumed during the second stage of photosynthesis: the dark reactions. These reactions, which need CO_2, NADPH, and ATP as inputs, produce sugar and recycle the $NADP^+$ and ADP to be used by the next set of light-dependent reactions. Now, we would be too kind if we left the discussion there. Let's look at the reactions in more detail. Stop groaning . . . you know we have to go there.

Light-Dependent Reactions

Light-dependent reactions occur in the thylakoid membrane system. The thylakoid system is composed of the various stacks of poker chip look-alikes located within the stroma of the chloroplast. Within the thylakoid membrane is a photosynthetic participant termed **chlorophyll.** There are two main types of chlorophyll that you should remember: chlorophyll *a* and chlorophyll *b*. Chlorophyll *a* is the major pigment of photosynthesis, while chlorophyll *b* is considered to be an accessory pigment. The pigments are very similar structurally, but the minor differences are what account for the variance in their absorption of light. Chlorophyll absorbs light of a particular wavelength, and when it does, one of its electrons is elevated to a higher energy level (it is "excited"). Almost immediately, the excited electron drops back down to the ground state, giving off heat in the process. This energy is passed along until it finds chlorophyll *a*, which, when excited, passes its electron to the primary electron acceptor; then, the light-dependent reactions are under way.

The pigments of the thylakoid space organize themselves into groups called *photosystems.* These photosystems consist of varying combinations of chlorophylls *a*, *b*, and others; pigments called **phycobilins;** and another type of pigment called **carotenoids.** The accessory pigments help pick up light when chlorophyll *a* cannot do it as effectively. An example is red algae on the ocean bottom. When light is picked up by the accessory pigments, it is fluoresced and altered so that chlorophyll *a* can use it.

Imagine that the plant represented in Figure 7.12 is struck by light from the sun. This light excites the **photosystem** of the thylakoid space, which absorbs the photon and transmits the energy from one pigment molecule to another. As this energy is passed along, it loses a bit of energy with each step and eventually reaches chlorophyll *a*, which proceeds to kick off the process of photosynthesis. It initiates the first step of photosynthesis by passing the electron to the primary electron acceptor.

Before we continue, there are two major photosystems we want to tell you about—you might want to get out a pen or pencil here to jot this down, because the names for these photosystems may seem confusing. They are photosystem I and photosystem II. The only difference between these two **reaction centers** is that the main chlorophyll of photosystem I absorbs light with a wavelength of 700 nm, while the main chlorophyll of photosystem II absorbs light with a wavelength of 680 nm. By interacting with different thylakoid membrane proteins, they are able to absorb light of slightly different wavelengths.

Now let's get back to the reactions. Let's go through the rest of Figure 7.12 and talk about the light-dependent reactions. For the sole purpose of confusing you, plants start photosynthesis by using photosystem II before photosystem I. As light strikes photosystem II, the energy is absorbed and passed along until it reaches the P680 chlorophyll. When this chlorophyll is excited, it passes its electrons to the primary electron acceptor. This is where the water molecule comes into play. **Photolysis** in the thylakoid space takes electrons from H_2O and passes them to P680 to replace the electrons given to the primary acceptor. With this reaction, a lone oxygen atom and a pair of hydrogen ions are formed from the water. The oxygen atom quickly finds another oxygen atom buddy, pairs up with it, and generates the O_2 that the plants so graciously put out for us every day. This is the first product of the light reactions.

The light reactions do not stop here, however. We need to consider what happens to the electron that has been passed to the primary electron acceptor. The electron is passed to photosystem I, P700, in a manner reminiscent of the electron transport chain. As the

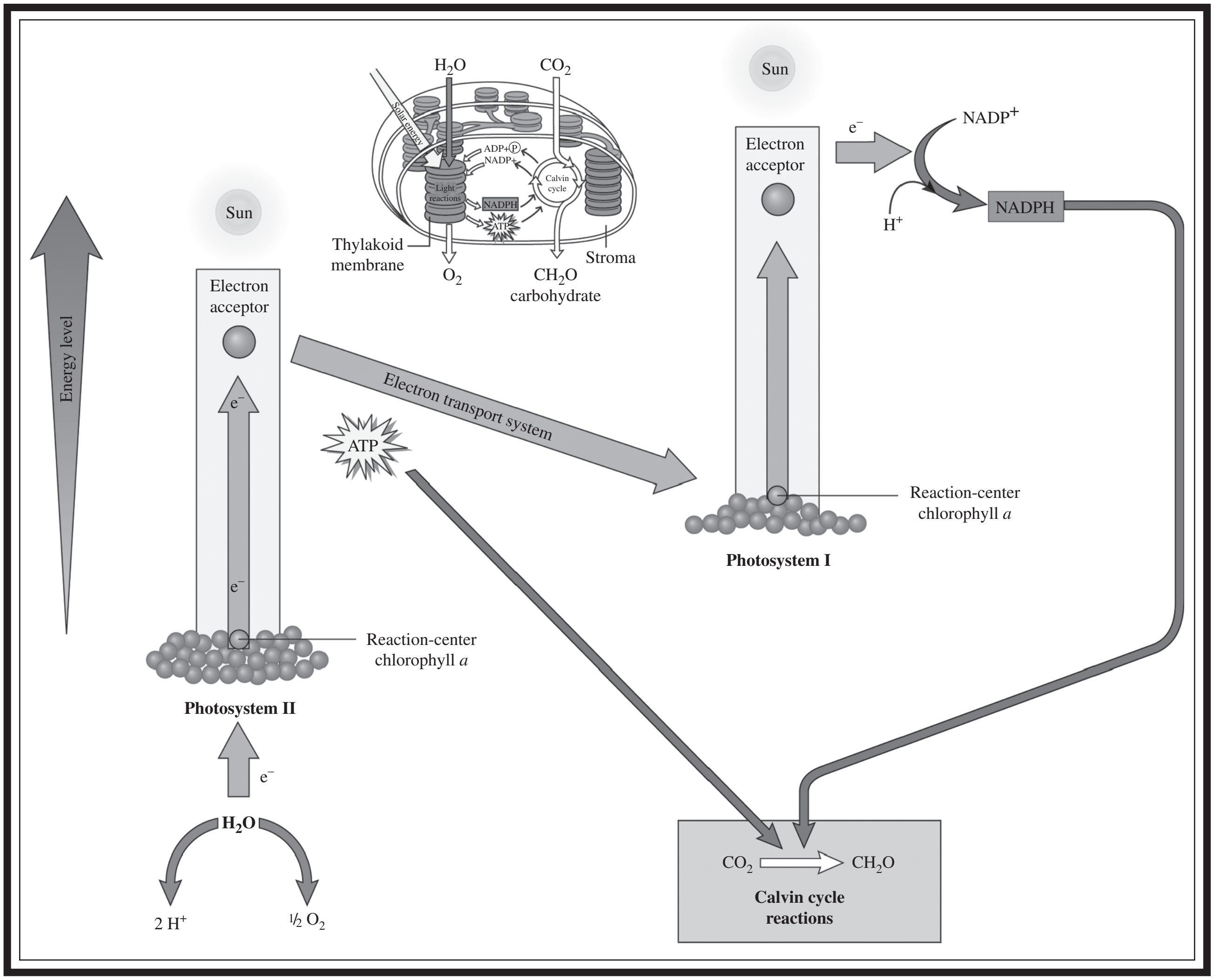


Figure 7.12 Light-dependent reactions. (*From* Biology, *8th ed., by Sylvia S. Mader, © 1985, 1987, 1990, 1993, 1996, 1998, 2001, 2004 by the McGraw Hill Companies, Inc. Reproduced with permission of The McGraw Hill Companies.*)

electrons are passed from P680 to P700, the lost energy is used to produce ATP (remember chemiosmosis). This ATP is the second product of the light reactions and is produced in a manner mechanistically similar to the way ATP is produced during oxidative phosphorylation of respiration. In plants, this process of ATP formation is called **photophosphorylation.**

After the photosystem I electrons are excited, photosystem I passes the energy to its own primary electron acceptor. These electrons are sent down another chain to **ferredoxin,** which then donates the electrons to $NADP^+$ to produce NADPH, the third and final product of the light reactions. (Notice how in photosynthesis, there is NADPH instead of NADH. The symbol P can help you remember that it relates to photosynthesis. ☺)

Remember the following about the light reactions:

KEY IDEA

1. The light reactions occur in the thylakoid membrane.
2. The inputs to the light reactions are water and light.
3. The light reactions produce three products: ATP, NADPH, and O_2.
4. The oxygen produced in the light reactions comes from H_2O, not CO_2.

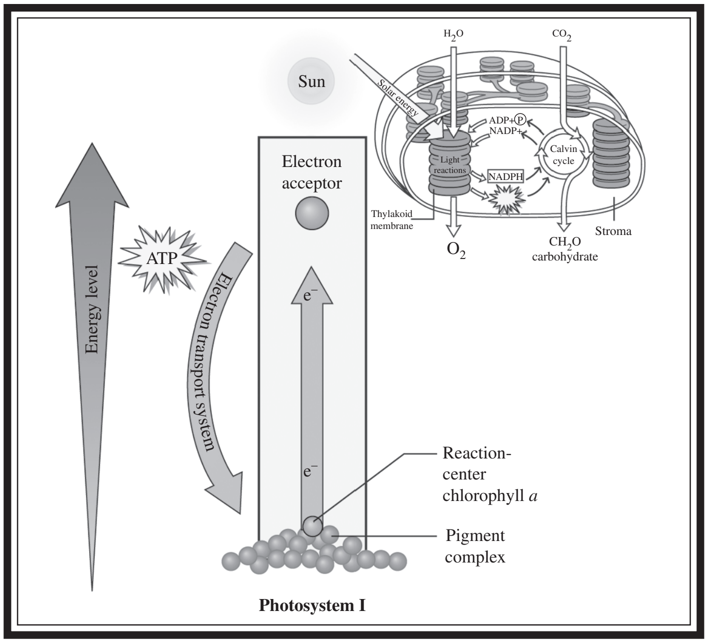


Figure 7.13 Cyclic phosphorylation. (*From* Biology*, 8th ed., by Sylvia S. Mader, © 1985, 1987, 1990, 1993, 1996, 1998, 2001, 2004 by the McGraw Hill Companies, Inc. Reproduced with permission of The McGraw Hill Companies.*)

Two separate light-dependent pathways occur in plants. What we have just discussed is the **noncyclic light reaction** pathway. Considering the name of the first one, it is not shocking to discover that there is also a **cyclic light reaction** pathway (Figure 7.13). One key difference between the two is that in the noncyclic pathway, the electrons taken from chlorophyll *a* are not recycled back down to the ground state. This means that the electrons do not make their way back to the chlorophyll molecule when the reaction is complete. The electrons end up on NADPH. Another key difference between the two is that the cyclic pathway uses only photosystem I; photosystem II is not involved. In the cyclic pathway, sunlight hits P700, thus exciting the electrons and passing them from P700 to its primary electron acceptor. It is called the *cyclic pathway* because these electrons pass down the electron chain and eventually back to P700 to complete the cycle. The energy given off during the passage down the chain is harnessed to produce ATP—the only product of this pathway. Neither oxygen nor NADPH is produced from these reactions.

KEY IDEA

A question that might be forming as you read this is: "Why does this pathway continue to exist?" or perhaps you are wondering "Why do they insist on torturing me by writing about all of this photosynthesis stuff?" We will answer the first question and ignore the second one. The cyclic pathway exists because the Calvin cycle, which we discuss next, uses more ATP than it does NADPH. This eventually causes a problem because the light reactions produce equal amounts of ATP and NADPH. The plant compensates for this disparity by dropping into the cyclic phase when needed to produce the ATP necessary to keep the light-independent reactions from grinding to a halt.

Before moving on to the Calvin cycle, it is important to understand how ATP is formed. We know, we know . . . you thought we were finished . . . but we want you to be an expert in the field of photosynthesis. You never know when these facts might come in handy. For example, just the other day one of us was offered $10,000 by a random person on the street to recount the similarities between photosynthesis and respiration. So, this stuff *is* useful in everyday life. As the electrons are passing from the primary electron acceptor to the next photosystem, hydrogen ions are picked up from outside the membrane and brought back into the thylakoid compartment, creating an H^+ gradient similar to what we saw in oxidative phosphorylation. During the light-dependent reactions, when hydrogen ions are taken from water during photolysis, the proton gradient grows larger, causing some protons to leave, leading to the formation of ATP.

You'll notice that this process in plants is a bit different from oxidative phosphorylation of the mitochondria, where the proton gradient is created by pumping protons from the matrix *out* to the intermembrane space. In the mitochondria, the ATP is produced when the protons move back *in*. But in plants, photophosphorylation creates the gradient by pumping protons in from the stroma to the thylakoid compartment, and the ATP is produced as the protons move back *out*. The opposing reactions produce the same happy result—more ATP for the cells.

Light-Independent Reactions (Calvin Cycle)

After the light reactions have produced the necessary ATP and NADPH, the synthesis phase of photosynthesis is ready to proceed. The inputs into the Calvin cycle are NADPH (which provides hydrogen and electrons), ATP (which provides energy), and CO_2. From here on, just so we don't drive you *insane* switching from term to term, we are going to call the dark reactions of photosynthesis the *Calvin cycle* (Figure 7.14). The Calvin cycle occurs

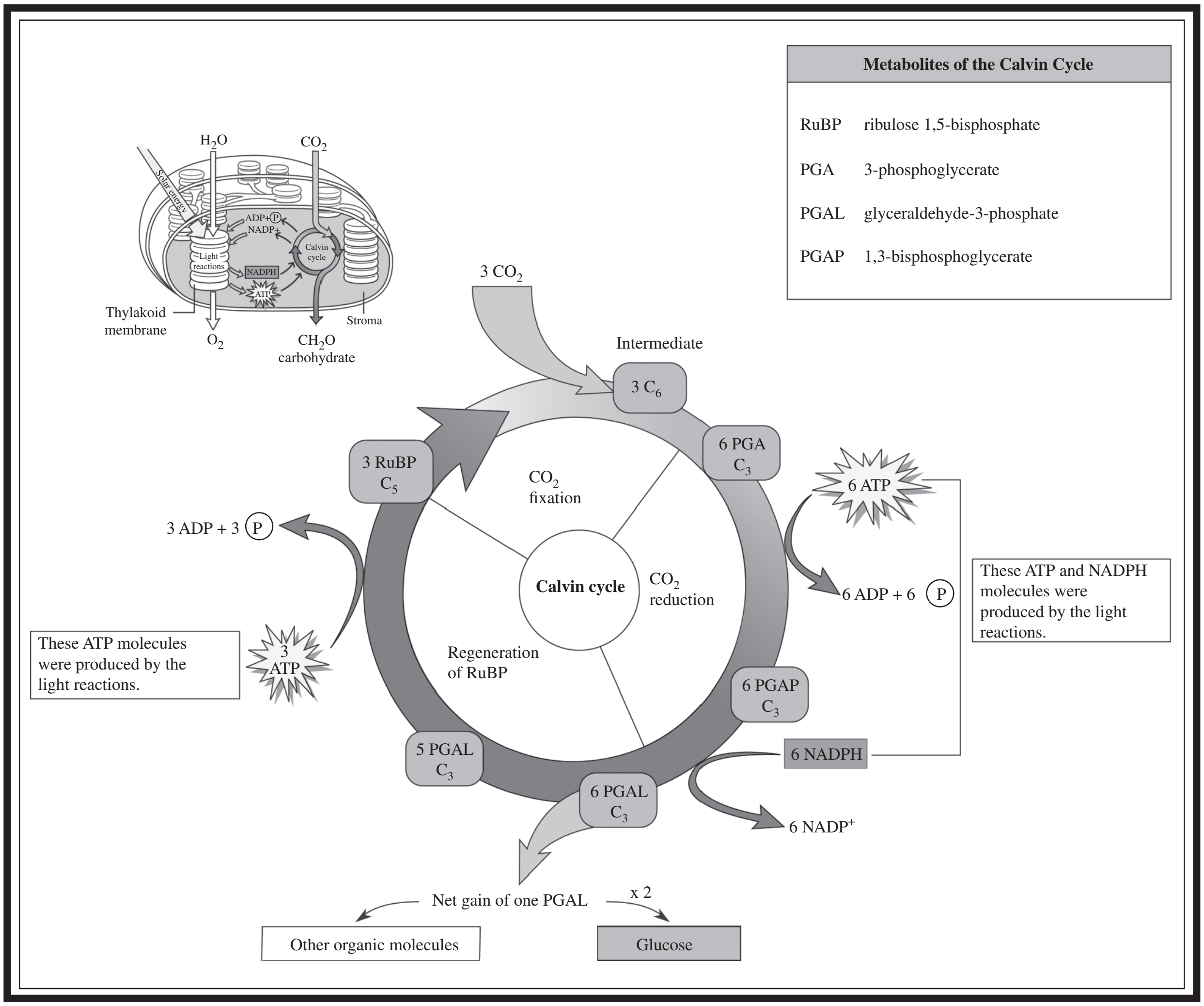


Figure 7.14 The Calvin cycle. (*From* Biology, *8th ed., by Sylvia S. Mader, © 1985, 1987, 1990, 1993, 1996, 1998, 2001, 2004 by the McGraw Hill Companies, Inc. Reproduced with permission of The McGraw Hill Companies.*)

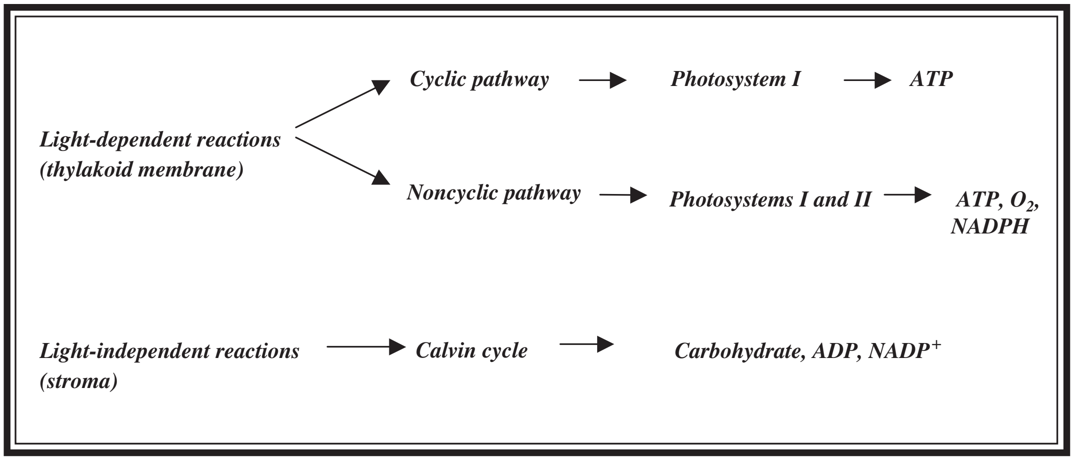


Figure 7.15 Summary of photosynthesis.

in the stroma of the chloroplast, which is the fluid surrounding the thylakoid "poker chips." (For further distinctions among the cyclic pathway, the noncyclic pathway, and the Calvin cycle, see Figure 7.15.)

The Calvin cycle begins with a step called **carbon fixation.** This is a tricky and complex term that makes it sound more confusing than it really is. Basically, carbon fixation is the binding of the carbon from CO_2 to a molecule that is able to enter the Calvin cycle. Usually this molecule is ribulose bis-phosphate, a 5-carbon molecule known to its closer friends as RuBP. This reaction is assisted by the enzyme with one of the cooler names in the business: **rubisco.** The result of this reaction is a 6-carbon molecule that breaks into two 3-carbon molecules named *3-phosphoglycerate* (3PG). ATP and NADPH step up at this point and donate a phosphate group and hydrogen electrons, respectively, to (3PG) to form glyceraldehyde 3-phosphate (G3P). Most of the G3P produced is converted back to RuBP so as to fix more carbon. The remaining G3P is converted into a 6-carbon sugar molecule, which is used to build carbohydrates for the plant. This process uses more ATP than it does NADPH. This is the disparity that makes cyclic photophosphorylation necessary in the light-dependent reactions.

We know that for some of you, the preceding discussion contains many difficult scientific names, strangely spelled words, and esoteric acronyms. So, here's the bottom line—you should remember the following about the Calvin cycle:

KEY IDEA

1. The Calvin cycle occurs in the stroma of the chloroplast.
2. The inputs into the Calvin cycle are NADPH, ATP, and CO_2.
3. The products of the Calvin cycle are $NADP^+$, ADP, and a sugar.
4. More ATP is used than NADPH, creating the need for cyclic photophosphorylation to create enough ATP for the reactions.
5. The carbon of the sugar produced in photosynthesis comes from the CO_2 of the Calvin cycle.

Types of Photosynthesis

Plants do not always live under ideal photosynthetic conditions. Some plants must make changes to the system in order to successfully use light and produce energy. Plants contain a structure called a **stomata,** which consists of pores through which oxygen exits and carbon dioxide enters the leaf to be used in photosynthesis. **Transpiration** is the natural process by which plants lose water by evaporation from their leaves. When the temperature is very high, plants have to worry about excess transpiration. This is a potential problem for plants because they need the water to continue the process of photosynthesis. To combat this evaporation problem, plants must close their stomata to conserve water. But this solution leads to two different problems: (1) how will they bring in the CO_2 required for photosynthesis? and (2) what will the plants do with the excess O_2 that builds up when the stomata are closed?

When plants close their stomata to protect against water loss, they experience a shortage of CO_2, and the oxygen produced from the light reactions is unable to leave the plant. This excess oxygen competes with the carbon dioxide and attaches to RuBP in a reaction called **photorespiration.** This results in the formation of one molecule of PGA and one molecule of phosphoglycolate. This is not an ideal reaction because the sugar formed in photosynthesis comes from the PGA, not phosphoglycolate. As a result, plants that experience photorespiration have a lowered capacity for growth. Photorespiration tends to occur on hot, dry days when the stomata of the plant are closed.

A group of plants called **C_4 plants** combat photorespiration by altering the first step of their Calvin cycle. Normally, carbon fixation produces two 3-carbon molecules. In C_4 plants, the carbon fixation step produces a 4-carbon molecule called **oxaloacetate.** This molecule is converted into malate and sent from the mesophyll cells to the bundle sheath cells, where the CO_2 is used to build sugar. The **mesophyll** is the tissue of the interior of the leaf, and **mesophyll cells** are cells that contain bunches of chloroplasts. **Bundle sheath cells** are cells that are tightly wrapped around the veins of a leaf. They are the site for the Calvin cycle in C_4 plants.

What is the difference between C_3 plants and C_4 plants? One difference is that C_4 plants have two different types of photosynthetic cells: (1) tightly packed bundle sheath cells, which surround the vein of the leaf, and (2) mesophyll cells. Another difference involves the first product of carbon fixation. For C_3 plants, it is PGA, for C_4 plants, it is oxaloacetate. C_4 plants are able to successfully perform photosynthesis in these hot areas because of the presence of an enzyme called PEP (*phosphoenolpyruvate*) *carboxylase*. This enzyme really wants to bind to CO_2 and is not tricked by the devious oxygen into using it instead of the necessary CO_2. PEP carboxylase prefers to pair up with CO_2 rather than O_2, and this cuts down on photorespiration for C_4 plants. The conversion of PEP to oxaloacetate occurs in the mesophyll cells; then, after being converted into malate, PEP is shipped to the bundle sheath cells. These cells contain the enzymes of photosynthesis, including our good pal rubisco. The malate releases the CO_2, which is then used by rubisco to perform the reactions of photosynthesis. This process counters the problem of photorespiration because the shuttling of CO_2 from the mesophyll cells to the bundle sheath cells keeps the CO_2 concentration high enough so that it is not beat out by oxygen for rubisco's love and attention.

One last variation of photosynthesis that we should look at is the function performed by **CAM** (Crassulacean acid metabolizing) plants—water-storing plants, such as cacti, that close their stomata by day and open them by night to avoid transpiration during the hot days, without depleting the plant's CO_2 reserves. The CO_2 taken in during the night is stored as organic acids in the vacuoles of mesophyll cells until daybreak when the stomata close. The Calvin cycle is able to proceed during the day because the stored CO_2 is released, as needed, from the organic acids to be incorporated into the sugar product of the Calvin cycle.

To sum up these two variations of photosynthesis:

KEY IDEA

C_4 photosynthesis: photosynthetic process that first converts CO_2 into a 4-carbon molecule in the mesophyll cells, converts that product to malate, and then shuttles the malate into the bundle sheath cells. There, malate releases CO_2, which reacts with rubisco to produce the carbohydrate product of photosynthesis.

CAM photosynthesis: plants close their stomata during the day, collect CO_2 at night, and store the CO_2 in the form of acids until it is needed during the day for photosynthesis.