

# CHAPTER 3 - PHOTOSYNTHESIS AND CELLULAR RESPIRATION



## CHAPTER OVERVIEW

### Chapter 3 - Photosynthesis and Cellular Respiration

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## 3.1: Energy Enters Ecosystems Through Photosynthesis

Cells run on the chemical energy found mainly in carbohydrate molecules, and the majority of these molecules are produced by one process: photosynthesis. Through photosynthesis, certain organisms convert solar energy (sunlight) into chemical energy, which is then used to build carbohydrate molecules. The energy stored in the bonds to hold these molecules together is released when an organism breaks down food. Cells then use this energy to perform work, such as movement. The energy that is harnessed from photosynthesis enters the ecosystems of our planet continuously and is transferred from one organism to another. Therefore, directly or indirectly, the process of photosynthesis provides most of the energy required by living things on Earth. Photosynthesis also results in the release of oxygen into the atmosphere. In short, to eat and breathe humans depend almost entirely on the organisms that carry out photosynthesis.

### Solar Dependence and Food Production



Figure 3.1.1. (a) Plants, (b) algae, and (c) certain bacteria, called cyanobacteria, are photoautotrophs that can carry out photosynthesis. Algae can grow over enormous areas in water, at times completely covering the surface. (credit a: Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: “eutrophication&hypoxia”/Flickr; credit c: NASA; scale-bar data from Matt Russell)

Some organisms can carry out photosynthesis, whereas others cannot. An **autotroph** is an organism that can produce its own food. The Greek roots of the word autotroph mean “self” (auto) “feeder” (troph). Plants are the best-known autotrophs, but others exist, including certain types of bacteria and algae (Figure 3.1.1). Oceanic algae contribute enormous quantities of food and oxygen to global food chains. More specifically, plants are **photoautotrophs**, a type of autotroph that uses sunlight and carbon from carbon dioxide to synthesize chemical energy in the form of carbohydrates. All organisms carrying out photosynthesis require sunlight.



Figure 3.1.2. The energy stored in carbohydrate molecules from photosynthesis passes through the food chain. The predator that eats these deer is getting energy that originated in the photosynthetic vegetation that the deer consumed. (credit: Steve VanRiper, U.S. Fish and Wildlife Service)

**Heterotrophs** are organisms incapable of photosynthesis that must therefore obtain energy and carbon from food by consuming other organisms. The Greek roots of the word *heterotroph* mean “other” (*hetero*) “feeder” (*troph*), meaning that their food comes from other organisms. Even if the organism being consumed is another animal, it traces its stored energy back to autotrophs and the process of photosynthesis. Humans are heterotrophs, as are all animals and fungi. Heterotrophs depend on autotrophs, either directly or indirectly. For example, a deer obtains energy by eating plants. A wolf eating a deer obtains energy that originally came from the plants eaten by that deer (Figure 3.1.2). Using this reasoning, all food eaten by humans can be traced back to autotrophs that carry out photosynthesis.

### Summary of Photosynthesis

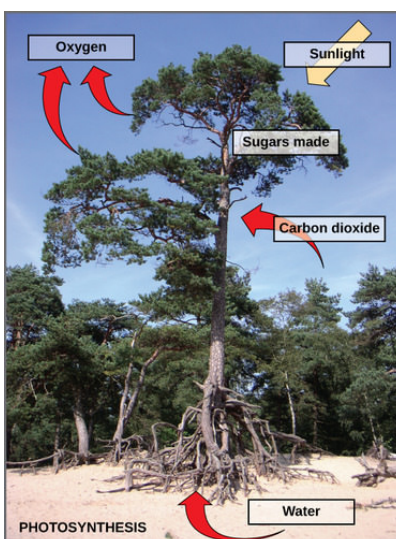


Figure 3.1.3. Photosynthesis uses solar energy, carbon dioxide, and water to release oxygen and to produce energy-storing sugar molecules.

**Photosynthesis** requires sunlight, carbon dioxide, and water as starting reactants (Figure 3.1.3). After the process is complete, photosynthesis releases oxygen and produces carbohydrate molecules, most commonly glucose. These sugar molecules contain the energy that living things need to survive. The complex reactions of photosynthesis can be summarized by the chemical equation shown in Figure 3.1.4 below.

Although the equation looks simple, the many steps that take place during photosynthesis are actually quite complex. In plants, photosynthesis takes place primarily in the chloroplasts of leaves. Chloroplasts have a double (inner and outer) membrane. Within the chloroplast is a third membrane that forms stacked, disc-shaped structures called thylakoids. Embedded in the thylakoid membrane are molecules of **chlorophyll**, a pigment (a molecule that absorbs light) through which the entire process of photosynthesis begins.

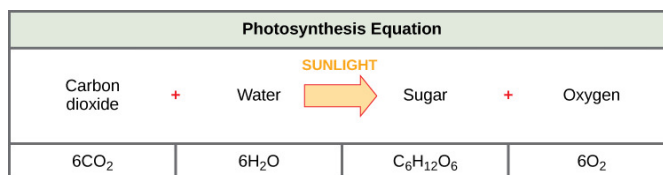


Figure 3.1.4. This equation means that six molecules of carbon dioxide ( $\text{CO}_2$ ) combine with six molecules of water ( $\text{H}_2\text{O}$ ) in the presence of sunlight. This produces one molecule of glucose ( $\text{C}_6\text{H}_{12}\text{O}_6$ ) and six molecules of oxygen ( $\text{O}_2$ ).

### The Two Parts of Photosynthesis

Photosynthesis takes place in two stages: the light-dependent reactions and the Calvin cycle. In the **light-dependent reactions** chlorophyll absorbs energy from sunlight and then converts it into chemical energy with the aid of water. The light-dependent reactions release **oxygen** as a byproduct from the splitting of water. In the **Calvin cycle**, the chemical energy derived from the light-dependent reactions drives both the capture of carbon in **carbon dioxide** molecules and the subsequent assembly of sugar molecules.

### The Global Significance of Photosynthesis

The process of photosynthesis is crucially important to the biosphere for the following reasons:

1. It creates  $\text{O}_2$ , which is important for two reasons. The molecular oxygen in Earth's atmosphere was created by photosynthetic organisms; without photosynthesis there would be no  $\text{O}_2$  to support cellular respiration (see [chapter 3.2](#)) needed by complex, multicellular life. Photosynthetic bacteria were likely the first organisms to perform photosynthesis, dating back 2-3 billion years ago. Thanks to their activity, and a diversity of present-day photosynthesizing organisms, Earth's atmosphere is currently about 21%  $\text{O}_2$ . Also, this  $\text{O}_2$  is vital for the creation of the ozone layer (see [chapter 10.2](#)), which protects life from harmful ultraviolet radiation emitted by the sun. Ozone ( $\text{O}_3$ ) is created from the breakdown and reassembly of  $\text{O}_2$ .
2. It provides energy for nearly all ecosystems. By transforming light energy into chemical energy, photosynthesis provides the energy used by organisms, whether those organisms are plants, grasshoppers, wolves, or fungi. The only exceptions are found in

very rare and isolated ecosystems, such as near deep sea hydrothermal vents where organisms get energy that originally came from minerals, not the sun.

3. It provides the carbon needed for organic molecules. Organisms are primarily made of two things: water and organic molecules, the latter being carbon based. Through the process of **carbon fixation**, photosynthesis takes carbon from  $\text{CO}_2$  and converts it into sugars (which are organic). Carbon in these sugars can be re-purposed to create the other types of organic molecules that organisms need, such as lipids, proteins, and nucleic acids. For example, the carbon used to make your DNA was once  $\text{CO}_2$  used by photosynthetic organisms (see section 3.1 for more information on food webs).

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## 3.2: Photosynthesis

### What you'll learn to do: Identify the basic components and steps of photosynthesis

No matter how complex or advanced a machine, such as the latest cellular phone, the device cannot function without energy. Living things, similar to machines, have many complex components; they too cannot do anything without energy, which is why humans and all other organisms must “eat” in some form or another. That may be common knowledge, but how many people realize that every bite of every meal ingested depends on the process of photosynthesis?



Figure 1. This sage thrasher’s diet, like that of almost all organisms, depends on photosynthesis. (credit: modification of work by Dave Menke, U.S. Fish and Wildlife Service)

#### Learning Objectives

- Summarize the process of photosynthesis
- Describe how the wavelength of light affects its energy and color
- Describe the light-dependent reactions that take place during photosynthesis
- Describe the steps and processes in the Calvin Cycle

### An Overview of Photosynthesis

All living organisms on earth consist of one or more cells. Each cell runs on the chemical energy found mainly in carbohydrate molecules (food), and the majority of these molecules are produced by one process: photosynthesis. Through photosynthesis, certain organisms convert solar energy (sunlight) into chemical energy, which is then used to build carbohydrate molecules. The energy used to hold these molecules together is released when an organism breaks down food. Cells then use this energy to perform work, such as cellular respiration.

The energy that is harnessed from photosynthesis enters the ecosystems of our planet continuously and is transferred from one organism to another. Therefore, directly or indirectly, the process of photosynthesis provides most of the energy required by living things on earth.

Photosynthesis also results in the release of oxygen into the atmosphere. In short, to eat and breathe, humans depend almost entirely on the organisms that carry out photosynthesis.

[Learn more about photosynthesis](#)

### Solar Dependence and Food Production

Some organisms can carry out photosynthesis, whereas others cannot. An autotroph is an organism that can produce its own food. The Greek roots of the word *autotroph* mean “self” (*auto*) “feeder” (*troph*). Plants are the best-known autotrophs, but others exist,

including certain types of bacteria and algae (Figure 2). Oceanic algae contribute enormous quantities of food and oxygen to global food chains. Plants are also photoautotrophs, a type of autotroph that uses sunlight and carbon from carbon dioxide to synthesize chemical energy in the form of carbohydrates. All organisms carrying out photosynthesis require sunlight.

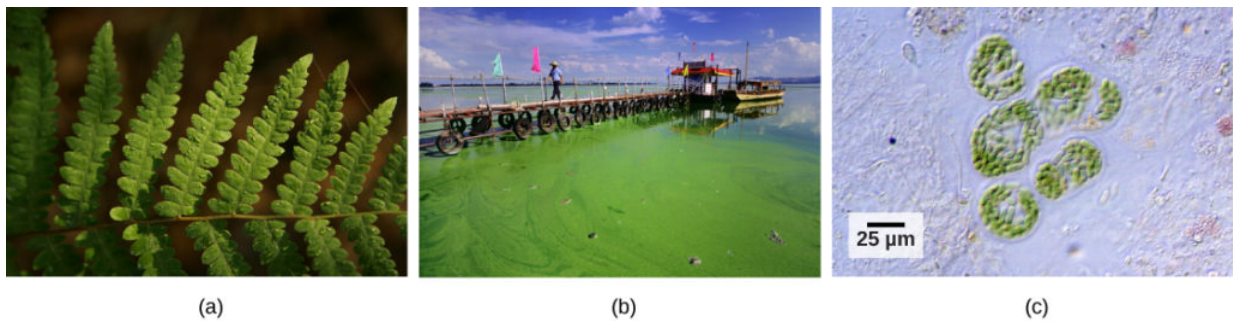


Figure 2. (a) Plants, (b) algae, and (c) certain bacteria, called cyanobacteria, are photoautotrophs that can carry out photosynthesis. Algae can grow over enormous areas in water, at times completely covering the surface. (credit a: Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: “eutrophication&hypoxia”/Flickr; credit c: NASA; scale-bar data from Matt Russell)



Figure 3. The energy stored in carbohydrate molecules from photosynthesis passes through the food chain. The predator that eats these deer is getting energy that originated in the photosynthetic vegetation that the deer consumed. (credit: Steve VanRiper, U.S. Fish and Wildlife Service)

Heterotrophs are organisms incapable of photosynthesis that must therefore obtain energy and carbon from food by consuming other organisms. The Greek roots of the word *heterotroph* mean “other” (*hetero*) “feeder” (*troph*), meaning that their food comes from other organisms. Even if the food organism is another animal, this food traces its origins back to autotrophs and the process of photosynthesis. Humans are heterotrophs, as are all animals. Heterotrophs depend on autotrophs, either directly or indirectly. Deer and wolves are heterotrophs. A deer obtains energy by eating plants. A wolf eating a deer obtains energy that originally came from the plants eaten by that deer. The energy in the plant came from photosynthesis, and therefore it is the only autotroph in this example (Figure 3). Using this reasoning, all food eaten by humans also links back to autotrophs that carry out photosynthesis.

Photosynthesis is a multi-step process that requires sunlight, carbon dioxide (which is low in energy), and water as substrates (Figure 4). After the process is complete, it releases oxygen and produces glyceraldehyde-3-phosphate (GA3P), simple carbohydrate molecules (which are high in energy) that can subsequently be converted into glucose, sucrose, or any of dozens of other sugar molecules. These sugar molecules contain energy and the energized carbon that all living things need to survive.

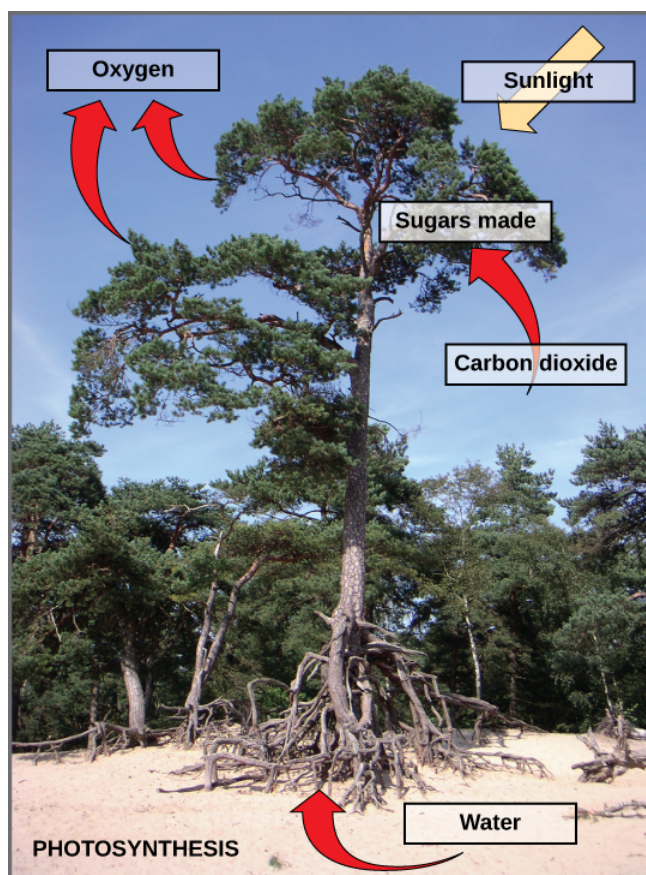


Figure 4. Photosynthesis uses solar energy, carbon dioxide, and water to produce energy-storing carbohydrates. Oxygen is generated as a waste product of photosynthesis.

The following is the chemical equation for photosynthesis (Figure 5):

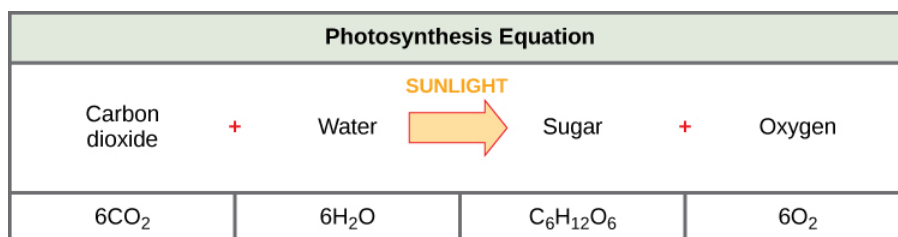


Figure 5. The basic equation for photosynthesis is deceptively simple. In reality, the process takes place in many steps involving intermediate reactants and products. Glucose, the primary energy source in cells, is made from two three-carbon GA3Ps.

Although the equation looks simple, the many steps that take place during photosynthesis are actually quite complex. Before learning the details of how photoautotrophs turn sunlight into food, it is important to become familiar with the structures involved.

In plants, photosynthesis generally takes place in leaves, which consist of several layers of cells. The process of photosynthesis occurs in a middle layer called the **mesophyll**. The gas exchange of carbon dioxide and oxygen occurs through small, regulated openings called **stomata** (singular: stoma), which also play roles in the regulation of gas exchange and water balance. The stomata are typically located on the underside of the leaf, which helps to minimize water loss. Each stoma is flanked by guard cells that regulate the opening and closing of the stomata by swelling or shrinking in response to osmotic changes.

In all autotrophic eukaryotes, photosynthesis takes place inside an organelle called a **chloroplast**. For plants, chloroplast-containing cells exist in the mesophyll. Chloroplasts have a double membrane envelope (composed of an outer membrane and an inner membrane). Within the chloroplast are stacked, disc-shaped structures called **thylakoids**. Embedded in the thylakoid membrane is chlorophyll, a **pigment** (molecule that absorbs light) responsible for the initial interaction between light and plant material, and numerous proteins that make up the electron transport chain. The thylakoid membrane encloses an internal space called the **thylakoid lumen**. As shown in Figure 6, a stack of thylakoids is called a **granum**, and the liquid-filled space surrounding the granum is called **stroma** or “bed” (not to be confused with stoma or “mouth,” an opening on the leaf epidermis).



? Practice Question

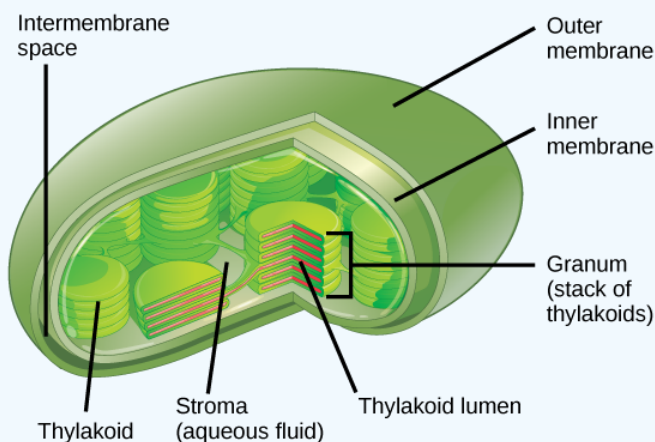


Figure 6. Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. Stacks of thylakoids called grana form a third membrane layer.

On a hot, dry day, plants close their stomata to conserve water. What impact will this have on photosynthesis?

**Show Answer**

Levels of carbon dioxide (a necessary photosynthetic substrate) will immediately fall. As a result, the rate of photosynthesis will be inhibited.

### The Two Parts of Photosynthesis

Photosynthesis takes place in two sequential stages: the light-dependent reactions and the light independent-reactions. In the **light-dependent reactions**, energy from sunlight is absorbed by chlorophyll and that energy is converted into stored chemical energy. In the **light-independent reactions**, the chemical energy harvested during the light-dependent reactions drive the assembly of sugar molecules from carbon dioxide. Therefore, although the light-independent reactions do not use light as a reactant, they require the products of the light-dependent reactions to function. In addition, several enzymes of the light-independent reactions are activated by light. The light-dependent reactions utilize certain molecules to temporarily store the energy: These are referred to as energy carriers. The energy carriers that move energy from light-dependent reactions to light-independent reactions can be thought of as “full” because they are rich in energy. After the energy is released, the “empty” energy carriers return to the light-dependent reaction to obtain more energy. Figure 7 illustrates the components inside the chloroplast where the light-dependent and light-independent reactions take place.

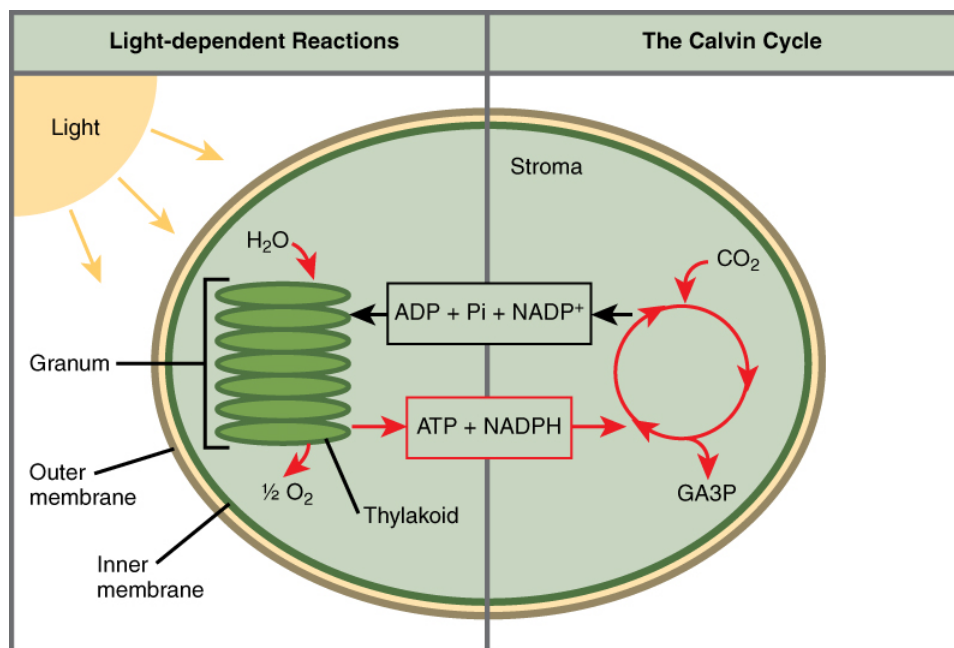


Figure 7. Photosynthesis takes place in two stages: light dependent reactions and the Calvin cycle. Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. The Calvin cycle, which takes place in the stroma, uses energy derived from these compounds to make GA3P from CO<sub>2</sub>.

[Click the link to learn more about photosynthesis.](#)

**? Try It**



Figure 8. Foods that humans consume originate from photosynthesis. (credit: Associação Brasileira de Supermercados)

Major grocery stores in the United States are organized into departments, such as dairy, meats, produce, bread, cereals, and so forth. Each aisle (Figure 8) contains hundreds, if not thousands, of different products for customers to buy and consume.

Although there is a large variety, each item links back to photosynthesis. Meats and dairy link because the animals were fed plant-based foods. The breads, cereals, and pastas come largely from starchy grains, which are the seeds of photosynthesis-dependent plants. What about desserts and drinks? All of these products contain sugar—sucrose is a plant product, a disaccharide, a carbohydrate molecule, which is built directly from photosynthesis. Moreover, many items are less obviously derived from plants: for instance, paper goods are generally plant products, and many plastics (abundant as products and packaging) can be derived from algae or from oil, the fossilized remains of photosynthetic organisms. Virtually every spice and flavoring in the spice aisle was produced by a plant as a leaf, root, bark, flower, fruit, or stem. Ultimately, photosynthesis connects to every meal and every food a person consumes.

**🧠 Learning Objectives**

The process of photosynthesis transformed life on Earth. By harnessing energy from the sun, photosynthesis evolved to allow living things access to enormous amounts of energy. Because of photosynthesis, living things gained access to sufficient energy that allowed them to build new structures and achieve the biodiversity evident today.

Only certain organisms, called photoautotrophs, can perform photosynthesis; they require the presence of chlorophyll, a specialized pigment that absorbs certain portions of the visible spectrum and can capture energy from sunlight. Photosynthesis uses carbon dioxide and water to assemble carbohydrate molecules and release oxygen as a waste product into the atmosphere. Eukaryotic autotrophs, such as plants and algae, have organelles called chloroplasts in which photosynthesis takes place, and starch accumulates. In prokaryotes, such as cyanobacteria, the process is less localized and occurs within folded membranes, extensions of the plasma membrane, and in the cytoplasm.

## Light Energy



Figure 9. Autotrophs can capture light energy from the sun, converting it into chemical energy used to build food molecules. (credit: modification of work by Gerry Atwell, U.S. Fish and Wildlife Service)

How can light be used to make food? It is easy to think of light as something that exists and allows living organisms, such as humans, to see, but light is a form of energy. Like all energy, light can travel, change form, and be harnessed to do work. In the case of photosynthesis, light energy is transformed into chemical energy, which autotrophs use to build carbohydrate molecules. However, autotrophs only use a specific component of sunlight (Figure 9).

### What Is Light Energy?

The sun emits an enormous amount of electromagnetic radiation (solar energy). Humans can see only a fraction of this energy, which is referred to as “visible light.” The manner in which solar energy travels can be described and measured as waves. Scientists can determine the amount of energy of a wave by measuring its wavelength, the distance between two consecutive, similar points in a series of waves, such as from crest to crest or trough to trough (Figure 10).

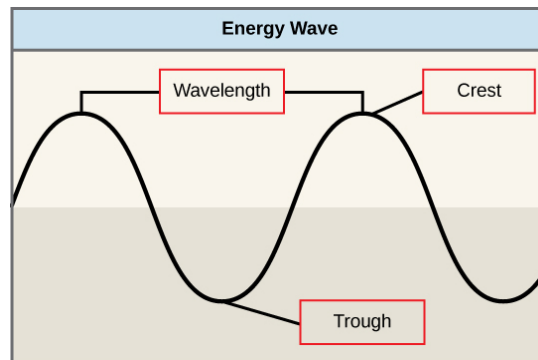


Figure 10. The wavelength of a single wave is the distance between two consecutive points along the wave.

Visible light constitutes only one of many types of electromagnetic radiation emitted from the sun. The electromagnetic spectrum is the range of all possible wavelengths of radiation (Figure 11). Each wavelength corresponds to a different amount of energy carried.

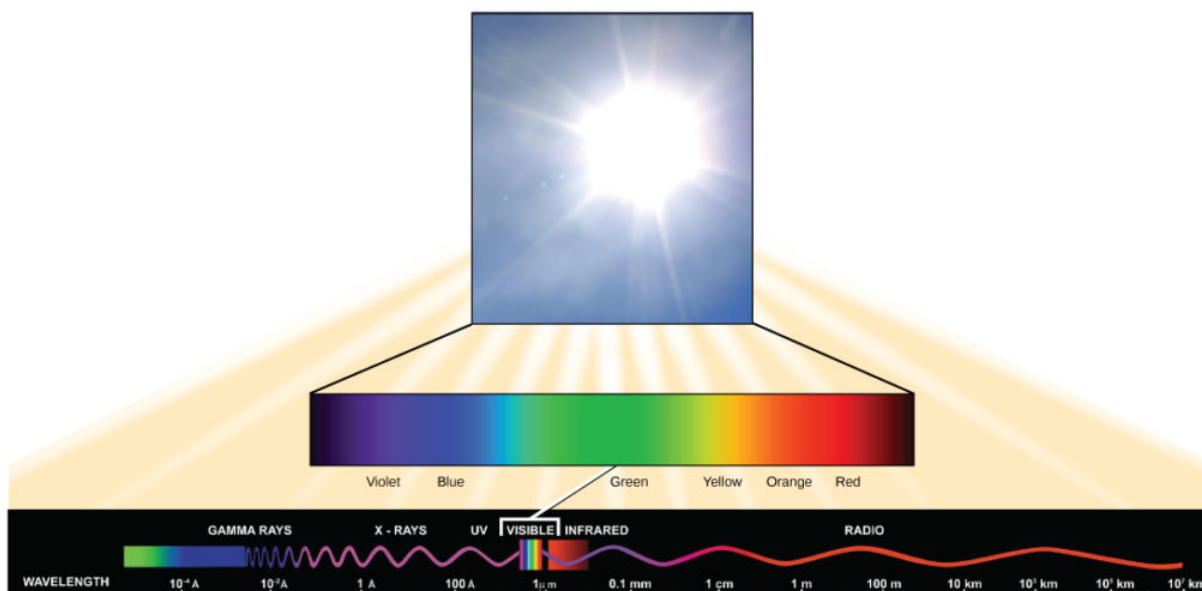


Figure 11. The sun emits energy in the form of electromagnetic radiation. This radiation exists in different wavelengths, each of which has its own characteristic energy. Visible light is one type of energy emitted from the sun.

Each type of electromagnetic radiation has a characteristic range of wavelengths. The longer the wavelength (or the more stretched out it appears), the less energy is carried. Short, tight waves carry the most energy. This may seem illogical, but think of it in terms of a piece of moving rope. It takes little effort by a person to move a rope in long, wide waves. To make a rope move in short, tight waves, a person would need to apply significantly more energy.

The sun emits (Figure 11) a broad range of electromagnetic radiation, including X-rays and ultraviolet (UV) rays. The higher-energy waves are dangerous to living things; for example, X-rays and UV rays can be harmful to humans.

### Absorption of Light

Light energy enters the process of photosynthesis when pigments absorb the light. In plants, pigment molecules absorb only visible light for photosynthesis. The visible light seen by humans as white light actually exists in a rainbow of colors. Certain objects, such as a prism or a drop of water, disperse white light to reveal these colors to the human eye. The visible light portion of the electromagnetic spectrum is perceived by the human eye as a rainbow of colors, with violet and blue having shorter wavelengths and, therefore, higher energy. At the other end of the spectrum toward red, the wavelengths are longer and have lower energy.

### Understanding Pigments

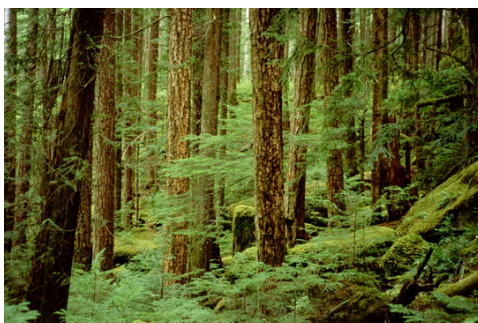


Figure 12. Plants that commonly grow in the shade benefit from having a variety of light-absorbing pigments. Each pigment can absorb different wavelengths of light, which allows the plant to absorb any light that passes through the taller trees. (credit: Jason Hollinger)

Different kinds of pigments exist, and each absorbs only certain wavelengths (colors) of visible light. Pigments reflect the color of the wavelengths that they cannot absorb.

All photosynthetic organisms contain a pigment called chlorophyll *a*, which humans see as the common green color associated with plants. Chlorophyll *a* absorbs wavelengths from either end of the visible spectrum (blue and red), but not from green. Because green is reflected, chlorophyll appears green.

Other pigment types include chlorophyll *b* (which absorbs blue and red-orange light) and the carotenoids. Each type of pigment can be identified by the specific pattern of wavelengths it absorbs from visible light, which is its absorption spectrum.

Many photosynthetic organisms have a mixture of pigments; between them, the organism can absorb energy from a wider range of visible-light wavelengths. Not all photosynthetic organisms have full access to sunlight. Some organisms grow underwater where light intensity decreases with depth, and certain wavelengths are absorbed by the water. Other organisms grow in competition for light. Plants on the rainforest floor must be able to absorb any bit of light that comes through, because the taller trees block most of the sunlight (Figure 12).

## The Light-Dependent Reactions of Photosynthesis

The overall purpose of the light-dependent reactions is to convert light energy into chemical energy. This chemical energy will be used by the Calvin cycle to fuel the assembly of sugar molecules.

The light-dependent reactions begin in a grouping of pigment molecules and proteins called a photosystem. Photosystems exist in the membranes of thylakoids. A pigment molecule in the photosystem absorbs one photon, a quantity or “packet” of light energy, at a time.

A photon of light energy travels until it reaches a pigment molecule, such as chlorophyll. The photon causes an electron in the chlorophyll to become “excited.” The energy given to the electron then travels from one pigment molecule to another until it reaches a pair of chlorophyll *a* molecules called the reaction center. This energy then excites an electron in the reaction center causing it to break free and be passed to the primary electron acceptor. The reaction center is therefore said to “donate” an electron to the primary electron acceptor (Figure 13).

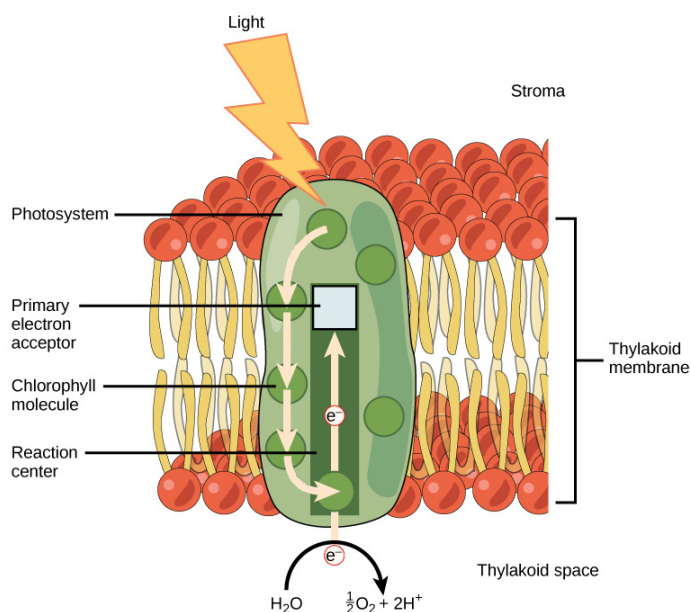


Figure 13. Light energy is absorbed by a chlorophyll molecule and the photon is passed along a pathway to other chlorophyll molecules. The energy culminates in a molecule of chlorophyll found in the reaction center. The energy “excites” one of its electrons enough to leave the molecule and be transferred to a nearby primary electron acceptor. A molecule of water splits to release an electron, which is needed to replace the one donated. Oxygen and hydrogen ions are also formed from the splitting of water.

To replace the electron in the reaction center, a molecule of water is split. This splitting releases an electron and results in the formation of oxygen ( $O_2$ ) and hydrogen ions ( $H^+$ ) in the thylakoid space. Technically, each breaking of a water molecule releases a pair of electrons, and therefore can replace two donated electrons.

The replacing of the electron enables the reaction center to respond to another photon. The oxygen molecules produced as byproducts find their way to the surrounding environment. The hydrogen ions play critical roles in the remainder of the light-dependent reactions.

Keep in mind that the purpose of the light-dependent reactions is to convert solar energy into chemical carriers that will be used in the Calvin cycle. In eukaryotes, two photosystems exist, the first is called photosystem II, which is named for the order of its discovery rather than for the order of function.

After the photon hits, photosystem II transfers the free electron to the first in a series of proteins inside the thylakoid membrane called the electron transport chain. As the electron passes along these proteins, energy from the electron fuels membrane pumps that actively move hydrogen ions against their concentration gradient from the stroma into the thylakoid space. This is quite analogous to the process that occurs in the mitochondrion in which an electron transport chain pumps hydrogen ions from the mitochondrial stroma across the inner membrane and into the intermembrane space, creating an electrochemical gradient. After the energy is used, the electron is accepted by a pigment molecule in the next photosystem, which is called photosystem I (Figure 14).

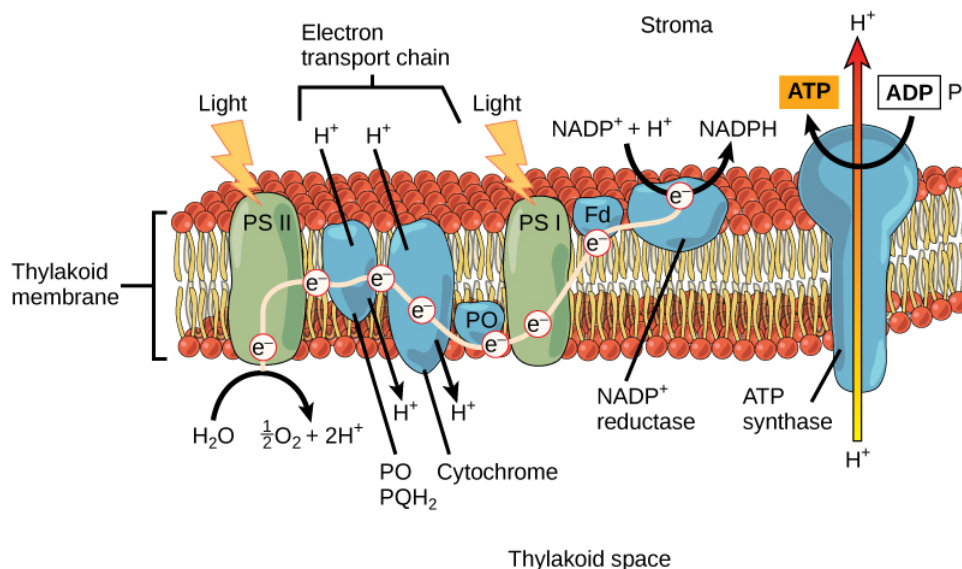


Figure 14. From photosystem II, the excited electron travels along a series of proteins. This electron transport system uses the energy from the electron to pump hydrogen ions into the interior of the thylakoid. A pigment molecule in photosystem I accepts the electron.

### Generating an Energy Carrier: ATP

In the light-dependent reactions, energy absorbed by sunlight is stored by two types of energy-carrier molecules: ATP and NADPH. The energy that these molecules carry is stored in a bond that holds a single atom to the molecule. For ATP, it is a phosphate atom, and for NADPH, it is a hydrogen atom. NADH will be discussed further in relation to cellular respiration, which occurs in the mitochondrion, where it carries energy from the citric acid cycle to the electron transport chain. When these molecules release energy into the Calvin cycle, they each lose atoms to become the lower-energy molecules ADP and  $\text{NADP}^+$ .

The buildup of hydrogen ions in the thylakoid space forms an electrochemical gradient because of the difference in the concentration of protons ( $\text{H}^+$ ) and the difference in the charge across the membrane that they create. This potential energy is harvested and stored as chemical energy in ATP through chemiosmosis, the movement of hydrogen ions down their electrochemical gradient through the transmembrane enzyme ATP synthase, just as in the mitochondrion.

The hydrogen ions are allowed to pass through the thylakoid membrane through an embedded protein complex called ATP synthase. This same protein generated ATP from ADP in the mitochondrion. The energy generated by the hydrogen ion stream allows ATP synthase to attach a third phosphate to ADP, which forms a molecule of ATP in a process called photophosphorylation. The flow of hydrogen ions through ATP synthase is called chemiosmosis, because the ions move from an area of high to low concentration through a semi-permeable structure.

### Generating Another Energy Carrier: NADPH

The remaining function of the light-dependent reaction is to generate the other energy-carrier molecule, NADPH. As the electron from the electron transport chain arrives at photosystem I, it is re-energized with another photon captured by chlorophyll. The energy from this electron drives the formation of NADPH from  $\text{NADP}^+$  and a hydrogen ion ( $\text{H}^+$ ). Now that the solar energy is stored in energy carriers, it can be used to make a sugar molecule.

## Learning Objectives

In the first part of photosynthesis, the light-dependent reaction, pigment molecules absorb energy from sunlight. The most common and abundant pigment is chlorophyll *a*. A photon strikes photosystem II to initiate photosynthesis. Energy travels through the electron transport chain, which pumps hydrogen ions into the thylakoid space. This forms an electrochemical gradient. The ions flow through ATP synthase from the thylakoid space into the stroma in a process called chemiosmosis to form molecules of ATP, which are used for the formation of sugar molecules in the second stage of photosynthesis. Photosystem I absorbs a second photon, which results in the formation of an NADPH molecule, another energy carrier for the Calvin cycle reactions.

## ? Practice Question

Describe the pathway of energy in light-dependent reactions.

### Show Answer

The energy is present initially as light. A photon of light hits chlorophyll, causing an electron to be energized. The free electron travels through the electron transport chain, and the energy of the electron is used to pump hydrogen ions into the thylakoid space, transferring the energy into the electrochemical gradient. The energy of the electrochemical gradient is used to power ATP synthase, and the energy is transferred into a bond in the ATP molecule. In addition, energy from another photon can be used to create a high-energy bond in the molecule NADPH.

## The Calvin Cycle

After the energy from the sun is converted and packaged into ATP and NADPH, the cell has the fuel needed to build food in the form of carbohydrate molecules. The carbohydrate molecules made will have a backbone of carbon atoms. Where does the carbon come from? The carbon atoms used to build carbohydrate molecules comes from carbon dioxide, the gas that animals exhale with each breath. The Calvin cycle is the term used for the reactions of photosynthesis that use the energy stored by the light-dependent reactions to form glucose and other carbohydrate molecules. This process may also be called the light-independent reaction, as it does not directly require sunlight (but it does require the products produced from the light-dependent reactions).

### The Innerworkings of the Calvin Cycle

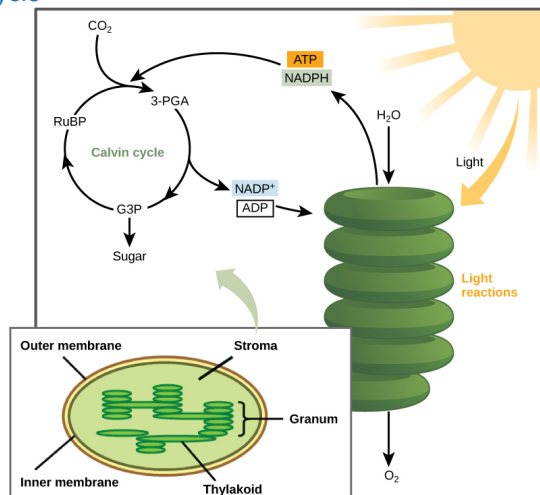


Figure 15. Light-dependent reactions harness energy from the sun to produce ATP and NADPH. These energy-carrying molecules travel into the stroma where the Calvin cycle reactions take place.

In plants, carbon dioxide ( $\text{CO}_2$ ) enters the chloroplast through the stomata and diffuses into the stroma of the chloroplast—the site of the Calvin cycle reactions where sugar is synthesized. The reactions are named after the scientist who discovered them, and reference the fact that the reactions function as a cycle. Others call it the Calvin-Benson cycle to include the name of another scientist involved in its discovery (Figure 15).

The Calvin cycle reactions (Figure 16) can be organized into three basic stages: fixation, reduction, and regeneration. In the stroma, in addition to  $\text{CO}_2$ , two other chemicals are present to initiate the Calvin cycle: an enzyme abbreviated RuBisCO, and the molecule ribulose biphosphate (RuBP). RuBP has five atoms of carbon and a phosphate group on each end.

RuBisCO catalyzes a reaction between  $\text{CO}_2$  and RuBP, which forms a six-carbon compound that is immediately converted into two three-carbon compounds. This process is called carbon fixation, because  $\text{CO}_2$  is “fixed” from its inorganic form into organic molecules.

ATP and NADPH use their stored energy to convert the three-carbon compound, 3-PGA, into another three-carbon compound called G3P. This type of reaction is called a reduction reaction, because it involves the gain of electrons. A reduction is the gain of an electron by an atom or molecule. The molecules of ADP and  $\text{NAD}^+$ , resulting from the reduction reaction, return to the light-dependent reactions to be re-energized.

One of the G3P molecules leaves the Calvin cycle to contribute to the formation of the carbohydrate molecule, which is commonly glucose ( $\text{C}_6\text{H}_{12}\text{O}_6$ ). Because the carbohydrate molecule has six carbon atoms, it takes six turns of the Calvin cycle to make one carbohydrate molecule (one for each carbon dioxide molecule fixed). The remaining G3P molecules regenerate RuBP, which enables the system to prepare for the carbon-fixation step. ATP is also used in the regeneration of RuBP.

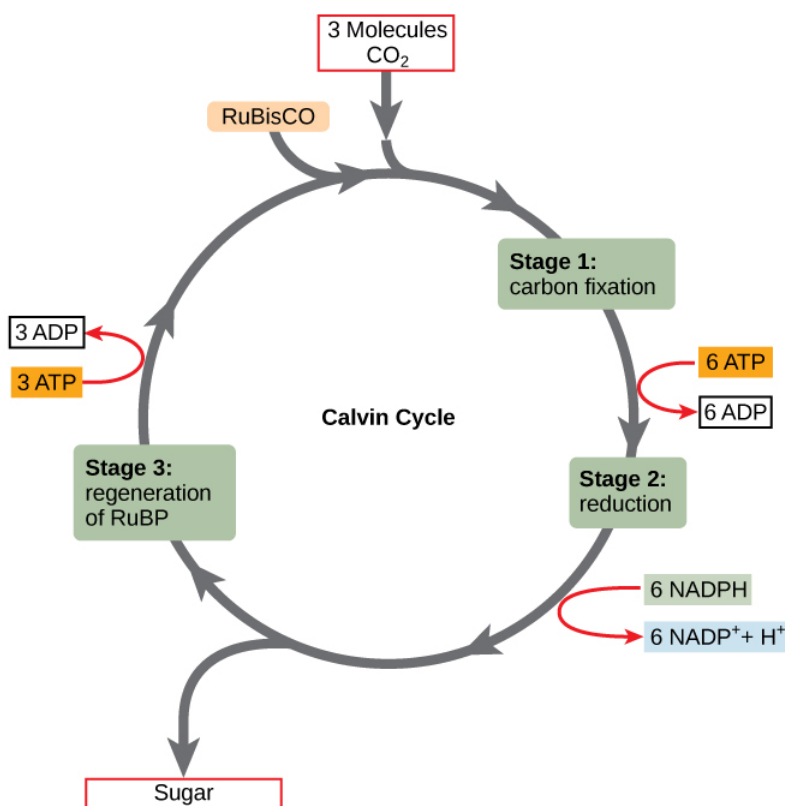


Figure 16. The Calvin cycle has three stages. In stage 1, the enzyme RuBisCO incorporates carbon dioxide into an organic molecule. In stage 2, the organic molecule is reduced. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue.

In summary, it takes six turns of the Calvin cycle to fix six carbon atoms from  $\text{CO}_2$ . These six turns require energy input from 12 ATP molecules and 12 NADPH molecules in the reduction step and 6 ATP molecules in the regeneration step.

Check out this [animation of the Calvin cycle](#). Click Stage 1, Stage 2, and then Stage 3 to see G3P and ATP regenerate to form RuBP.

? Try It





Figure 17. Living in the harsh conditions of the desert has led plants like this cactus to evolve variations in reactions outside the Calvin cycle. These variations increase efficiency and help conserve water and energy. (credit: Piotr Wojtkowski)

The shared evolutionary history of all photosynthetic organisms is conspicuous, as the basic process has changed little over eras of time. Even between the giant tropical leaves in the rainforest and tiny cyanobacteria, the process and components of photosynthesis that use water as an electron donor remain largely the same. Photosystems function to absorb light and use electron transport chains to convert energy. The Calvin cycle reactions assemble carbohydrate molecules with this energy.

However, as with all biochemical pathways, a variety of conditions leads to varied adaptations that affect the basic pattern. Photosynthesis in dry-climate plants (Figure 17) has evolved with adaptations that conserve water. In the harsh dry heat, every drop of water and precious energy must be used to survive. Two adaptations have evolved in such plants. In one form, a more efficient use of  $\text{CO}_2$  allows plants to photosynthesize even when  $\text{CO}_2$  is in short supply, as when the stomata are closed on hot days. The other adaptation performs preliminary reactions of the Calvin cycle at night, because opening the stomata at this time conserves water due to cooler temperatures. In addition, this adaptation has allowed plants to carry out low levels of photosynthesis without opening stomata at all, an extreme mechanism to face extremely dry periods.

### Photosynthesis in Prokaryotes

The two parts of photosynthesis—the light-dependent reactions and the Calvin cycle—have been described, as they take place in chloroplasts. However, prokaryotes, such as cyanobacteria, lack membrane-bound organelles. Prokaryotic photosynthetic autotrophic organisms have infoldings of the plasma membrane for chlorophyll attachment and photosynthesis (Figure 18). It is here that organisms like cyanobacteria can carry out photosynthesis.

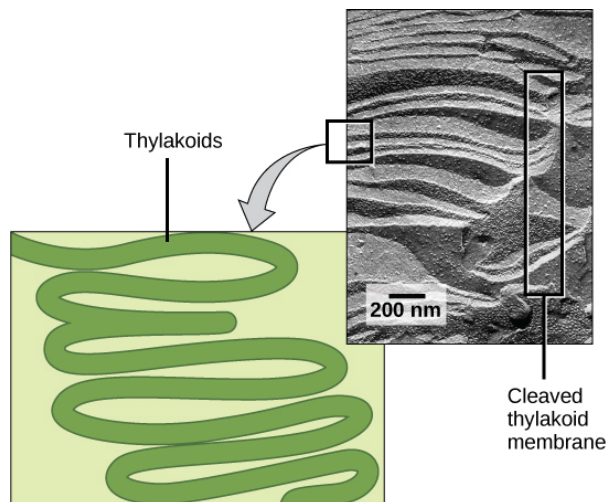


Figure 18. A photosynthetic prokaryote has infolded regions of the plasma membrane that function like thylakoids. Although these are not contained in an organelle, such as a chloroplast, all of the necessary components are present to carry out photosynthesis. (credit: scale-bar data from Matt Russell)

## Learning Objectives

Using the energy carriers formed in the first stage of photosynthesis, the Calvin cycle reactions fix  $\text{CO}_2$  from the environment to build carbohydrate molecules. An enzyme, RuBisCO, catalyzes the fixation reaction, by combining  $\text{CO}_2$  with RuBP. The resulting six-carbon compound is broken down into two three-carbon compounds, and the energy in ATP and NADPH is used to convert these molecules into G3P. One of the three-carbon molecules of G3P leaves the cycle to become a part of a carbohydrate molecule. The remaining G3P molecules stay in the cycle to be formed back into RuBP, which is ready to react with more  $\text{CO}_2$ . Photosynthesis forms a balanced energy cycle with the process of cellular respiration. Plants are capable of both photosynthesis and cellular respiration, since they contain both chloroplasts and mitochondria.

## ? Practice Question

Which part of the Calvin cycle would be affected if a cell could not produce the enzyme RuBisCO?

### Show Answer

None of the cycle could take place, because RuBisCO is essential in fixing carbon dioxide. Specifically, RuBisCO catalyzes the reaction between carbon dioxide and RuBP at the start of the cycle.

## Summary

Now that we've learned about the different pieces of photosynthesis, let's put it all together. This video walks you through the process of photosynthesis as a whole:



## Check Your Understanding

Answer the question(s) below to see how well you understand the topics covered in the previous section. This short quiz does **not** count toward your grade in the class, and you can retake it an unlimited number of times.

Use this quiz to check your understanding and decide whether to (1) study the previous section further or (2) move on to the next section.

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### 3.3: Cellular Respiration

What you'll learn to do: Identify the reactants and products of cellular respiration and where these reactions occur in a cell



Figure 1. A hummingbird needs energy to maintain prolonged flight. The bird obtains its energy from taking in food and transforming the energy contained in food molecules into forms of energy to power its flight through a series of biochemical reactions. (credit: modification of work by Cory Zanker)

Virtually every task performed by living organisms requires energy. Energy is needed to perform heavy labor and exercise, but humans also use energy while thinking, and even during sleep. In fact, the living cells of every organism constantly use energy.

Nutrients and other molecules are imported into the cell, metabolized (broken down) and possibly synthesized into new molecules, modified if needed, transported around the cell, and possibly distributed to the entire organism. For example, the large proteins that make up muscles are built from smaller molecules imported from dietary amino acids. Complex carbohydrates are broken down into simple sugars that the cell uses for energy.

Just as energy is required to both build and demolish a building, energy is required for the synthesis and breakdown of molecules as well as the transport of molecules into and out of cells. In addition, processes such as ingesting and breaking down pathogenic bacteria and viruses, exporting wastes and toxins, and movement of the cell require energy. From where, and in what form, does this energy come? How do living cells obtain energy, and how do they use it? This chapter will discuss different forms of energy and the physical laws that govern energy transfer. This chapter will also describe how cells use energy and replenish it, and how chemical reactions in the cell are performed with great efficiency.

In the process of photosynthesis, plants and other photosynthetic producers create glucose, which stores energy in its chemical bonds. You will actually study photosynthesis in more detail a bit later. But once photosynthesis has created glucose to store energy, both plants and consumers, such as animals, undergo a series of metabolic pathways, collectively called cellular respiration, to use that energy. Cellular respiration extracts the energy from the bonds in glucose and converts it into a form that all living things can use. Now let's take a more detailed look at how all eukaryotes—which includes humans!—make use of this stored energy.

#### Learning Objectives

- Describe the process of glycolysis and identify its reactants and products
- Describe the process of the citric acid cycle (Krebs cycle) and identify its reactants and products
- Describe the overall outcome of the citric acid cycle and oxidative phosphorylation in terms of the products of each
- Describe the location of the citric acid cycle and oxidative phosphorylation in the cell

#### Glycolysis

Even exergonic, energy-releasing reactions require a small amount of activation energy to proceed. However, consider endergonic reactions, which require much more energy input because their products have more free energy than their reactants. Within the cell, where does energy to power such reactions come from? The answer lies with an energy-supplying molecule called adenosine triphosphate, or **ATP**. ATP is a small, relatively simple molecule, but within its bonds contains the potential for a quick burst of energy that can be harnessed to perform cellular work. This molecule can be thought of as the primary energy currency of cells in the same way that money is the currency that people exchange for things they need. ATP is used to power the majority of energy-requiring cellular reactions.

## ATP in Living Systems

A living cell cannot store significant amounts of free energy. Excess free energy would result in an increase of heat in the cell, which would denature enzymes and other proteins, and thus destroy the cell. Rather, a cell must be able to store energy safely and release it for use only as needed. Living cells accomplish this using ATP, which can be used to fill any energy need of the cell. How? It functions as a rechargeable battery.

When ATP is broken down, usually by the removal of its terminal phosphate group, energy is released. This energy is used to do work by the cell, usually by the binding of the released phosphate to another molecule, thus activating it. For example, in the mechanical work of muscle contraction, ATP supplies energy to move the contractile muscle proteins.

### ATP Structure and Function

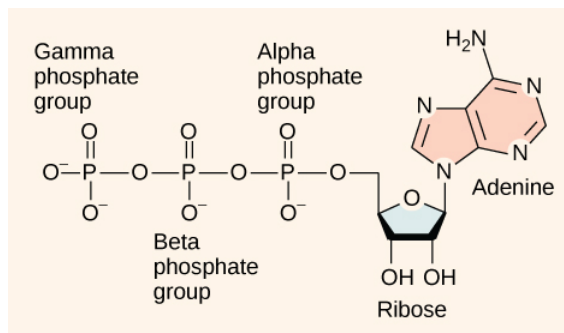


Figure 2. The structure of ATP shows the basic components of a two-ring adenine, five-carbon ribose, and three phosphate groups.

At the heart of ATP is a molecule of adenosine monophosphate (AMP), which is composed of an adenine molecule bonded to both a ribose molecule and a single phosphate group (Figure 2). Ribose is a five-carbon sugar found in RNA and AMP is one of the nucleotides in RNA. The addition of a second phosphate group to this core molecule results in adenosine diphosphate (ADP); the addition of a third phosphate group forms adenosine triphosphate (ATP).

The addition of a phosphate group to a molecule requires a high amount of energy and results in a high-energy bond. Phosphate groups are negatively charged and thus repel one another when they are arranged in series, as they are in ADP and ATP. This repulsion makes the ADP and ATP molecules inherently unstable. The release of one or two phosphate groups from ATP, a process called hydrolysis, releases energy.

### Glycolysis

You have read that nearly all of the energy used by living things comes to them in the bonds of the sugar, glucose. **Glycolysis** is the first step in the breakdown of glucose to extract energy for cell metabolism. Many living organisms carry out glycolysis as part of their metabolism. Glycolysis takes place in the cytoplasm of most prokaryotic and all eukaryotic cells.

Glycolysis begins with the six-carbon, ring-shaped structure of a single glucose molecule and ends with two molecules of a three-carbon sugar called pyruvate. Glycolysis consists of two distinct phases. In the first part of the glycolysis pathway, energy is used to make adjustments so that the six-carbon sugar molecule can be split evenly into two three-carbon pyruvate molecules. In the second part of glycolysis, ATP and nicotinamide-adenine dinucleotide (NADH) are produced (Figure 3).

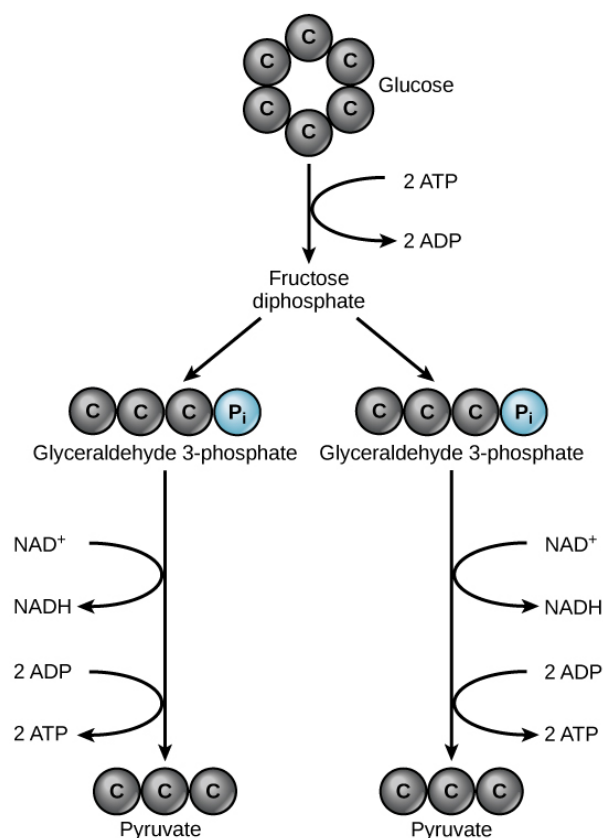


Figure 3. In glycolysis, a glucose molecule is converted into two pyruvate molecules.

If the cell cannot catabolize the pyruvate molecules further, it will harvest only two ATP molecules from one molecule of glucose. For example, mature mammalian red blood cells are only capable of glycolysis, which is their sole source of ATP. If glycolysis is interrupted, these cells would eventually die.

### Learning Objectives

ATP functions as the energy currency for cells. It allows cells to store energy briefly and transport it within itself to support endergonic chemical reactions. The structure of ATP is that of an RNA nucleotide with three phosphate groups attached. As ATP is used for energy, a phosphate group is detached, and ADP is produced. Energy derived from glucose catabolism is used to recharge ADP into ATP.

Glycolysis is the first pathway used in the breakdown of glucose to extract energy. Because it is used by nearly all organisms on earth, it must have evolved early in the history of life. Glycolysis consists of two parts: The first part prepares the six-carbon ring of glucose for separation into two three-carbon sugars. Energy from ATP is invested into the molecule during this step to energize the separation. The second half of glycolysis extracts ATP and high-energy electrons from hydrogen atoms and attaches them to NAD<sup>+</sup>. Two ATP molecules are invested in the first half and four ATP molecules are formed during the second half. This produces a net gain of two ATP molecules per molecule of glucose for the cell.

### Practice Question

Both prokaryotic and eukaryotic organisms carry out some form of glycolysis. How does that fact support or not support the assertion that glycolysis is one of the oldest metabolic pathways?

#### Show Answer

If glycolysis evolved relatively late, it likely would not be as universal in organisms as it is. It probably evolved in very primitive organisms and persisted, with the addition of other pathways of carbohydrate metabolism that evolved later.

## Citric Acid Cycle and Oxidative Phosphorylation

### The Citric Acid Cycle

In eukaryotic cells, the pyruvate molecules produced at the end of glycolysis are transported into mitochondria, which are sites of cellular respiration. If oxygen is available, aerobic respiration will go forward. In mitochondria, pyruvate will be transformed into a two-carbon acetyl group (by removing a molecule of carbon dioxide) that will be picked up by a carrier compound called coenzyme A (CoA), which is made from vitamin B<sub>5</sub>. The resulting compound is called acetyl CoA. (Figure 4). Acetyl CoA can be used in a variety of ways by the cell, but its major function is to deliver the acetyl group derived from pyruvate to the next pathway in glucose catabolism.

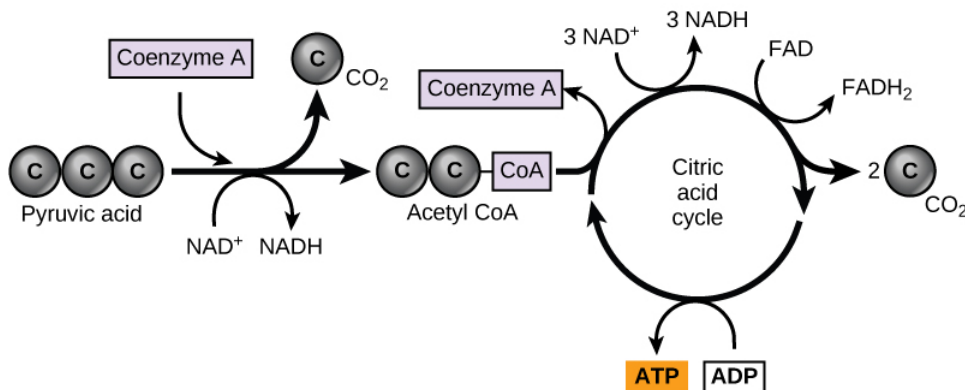


Figure 4. Pyruvate is converted into acetyl-CoA before entering the citric acid cycle.

Like the conversion of pyruvate to acetyl CoA, the citric acid cycle in eukaryotic cells takes place in the matrix of the mitochondria. Unlike glycolysis, the citric acid cycle is a closed loop: The last part of the pathway regenerates the compound used in the first step. The eight steps of the cycle are a series of chemical reactions that produces two carbon dioxide molecules, one ATP molecule (or an equivalent), and reduced forms (NADH and FADH<sub>2</sub>) of NAD<sup>+</sup> and FAD<sup>+</sup>, important coenzymes in the cell. Part of this is considered an aerobic pathway (oxygen-requiring) because the NADH and FADH<sub>2</sub> produced must transfer their electrons to the next pathway in the system, which will use oxygen. If oxygen is not present, this transfer does not occur.

Two carbon atoms come into the citric acid cycle from each acetyl group. Two carbon dioxide molecules are released on each turn of the cycle; however, these do not contain the same carbon atoms contributed by the acetyl group on that turn of the pathway. The two acetyl-carbon atoms will eventually be released on later turns of the cycle; in this way, all six carbon atoms from the original glucose molecule will be eventually released as carbon dioxide. It takes two turns of the cycle to process the equivalent of one glucose molecule. Each turn of the cycle forms three high-energy NADH molecules and one high-energy FADH<sub>2</sub> molecule. These high-energy carriers will connect with the last portion of aerobic respiration to produce ATP molecules. One ATP (or an equivalent) is also made in each cycle. Several of the intermediate compounds in the citric acid cycle can be used in synthesizing non-essential amino acids; therefore, the cycle is both anabolic and catabolic.

### Oxidative Phosphorylation

You have just read about two pathways in glucose catabolism—glycolysis and the citric acid cycle—that generate ATP. Most of the ATP generated during the aerobic catabolism of glucose, however, is not generated directly from these pathways. Rather, it derives from a process that begins with passing electrons through a series of chemical reactions to a final electron acceptor, oxygen. These reactions take place in specialized protein complexes located in the inner membrane of the mitochondria of eukaryotic organisms and on the inner part of the cell membrane of prokaryotic organisms. The energy of the electrons is harvested and used to generate an electrochemical gradient across the inner mitochondrial membrane. The potential energy of this gradient is used to generate ATP. The entirety of this process is called oxidative phosphorylation.

The electron transport chain (Figure 5a) is the last component of aerobic respiration and is the only part of metabolism that uses atmospheric oxygen. Oxygen continuously diffuses into plants for this purpose. In animals, oxygen enters the body through the respiratory system. Electron transport is a series of chemical reactions that resembles a bucket brigade in that electrons are passed rapidly from one component to the next, to the endpoint of the chain where oxygen is the final electron acceptor and water is produced. There are four complexes composed of proteins, labeled I through IV in Figure 5c, and the aggregation of these four complexes, together with associated mobile, accessory electron carriers, is called the electron transport chain. The electron

transport chain is present in multiple copies in the inner mitochondrial membrane of eukaryotes and in the plasma membrane of prokaryotes. In each transfer of an electron through the electron transport chain, the electron loses energy, but with some transfers, the energy is stored as potential energy by using it to pump hydrogen ions across the inner mitochondrial membrane into the intermembrane space, creating an electrochemical gradient.

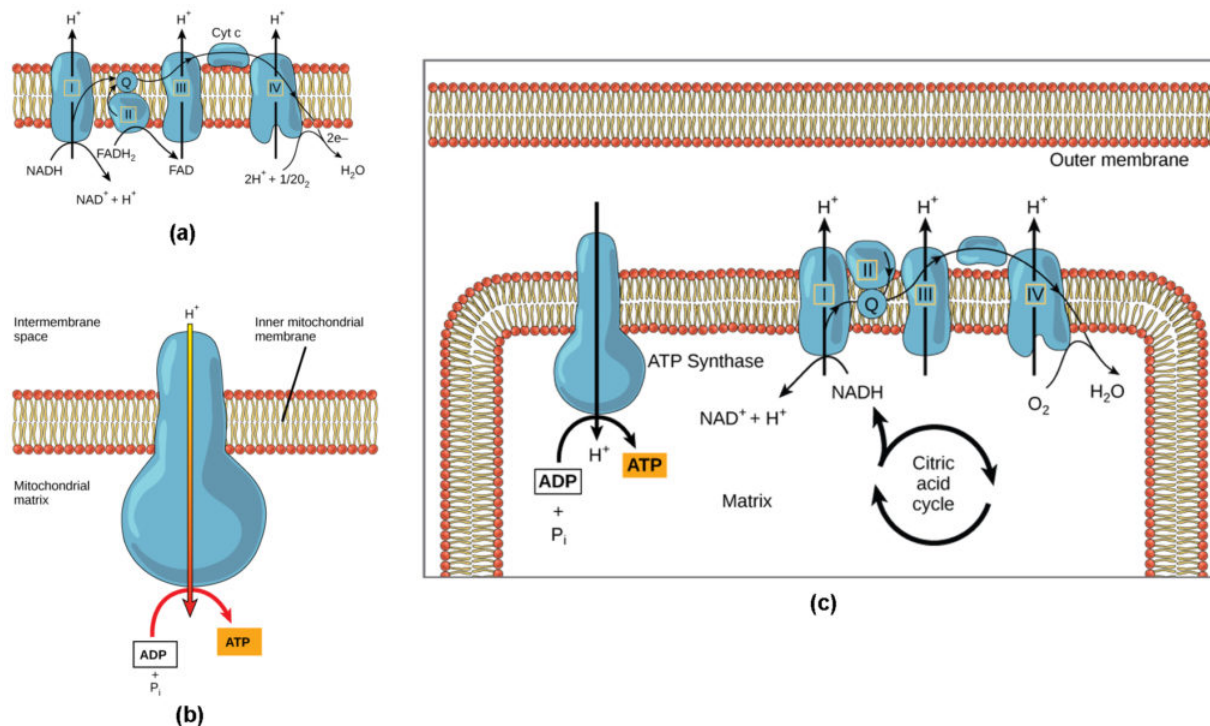


Figure 5. (a) The electron transport chain is a set of molecules that supports a series of oxidation-reduction reactions. (b) ATP synthase is a complex, molecular machine that uses an  $H^+$  gradient to regenerate ATP from ADP. (c) Chemiosmosis relies on the potential energy provided by the  $H^+$  gradient across the membrane.

### ? Practice Question

Cyanide inhibits cytochrome c oxidase, a component of the electron transport chain. If cyanide poisoning occurs, would you expect the pH of the intermembrane space to increase or decrease? What affect would cyanide have on ATP synthesis?

#### Show Answer

After cyanide poisoning, the electron transport chain can no longer pump electrons into the intermembrane space. The pH of the intermembrane space would increase, and ATP synthesis would stop.

Electrons from NADH and FADH<sub>2</sub> are passed to protein complexes in the electron transport chain. As they are passed from one complex to another (there are a total of four), the electrons lose energy, and some of that energy is used to pump hydrogen ions from the mitochondrial matrix into the intermembrane space. In the fourth protein complex, the electrons are accepted by oxygen, the terminal acceptor. The oxygen with its extra electrons then combines with two hydrogen ions, further enhancing the electrochemical gradient, to form water. If there were no oxygen present in the mitochondrion, the electrons could not be removed from the system, and the entire electron transport chain would back up and stop. The mitochondria would be unable to generate new ATP in this way, and the cell would ultimately die from lack of energy. This is the reason we must breathe to draw in new oxygen.

In the electron transport chain, the free energy from the series of reactions just described is used to pump hydrogen ions across the membrane. The uneven distribution of  $H^+$  ions across the membrane establishes an electrochemical gradient, owing to the  $H^+$  ions' positive charge and their higher concentration on one side of the membrane.

Hydrogen ions diffuse through the inner membrane through an integral membrane protein called ATP synthase (Figure 5b). This complex protein acts as a tiny generator, turned by the force of the hydrogen ions diffusing through it, down their electrochemical



gradient from the intermembrane space, where there are many mutually repelling hydrogen ions to the matrix, where there are few. The turning of the parts of this molecular machine regenerate ATP from ADP. This flow of hydrogen ions across the membrane through ATP synthase is called chemiosmosis.

Chemiosmosis (Figure 5c) is used to generate 90 percent of the ATP made during aerobic glucose catabolism. The result of the reactions is the production of ATP from the energy of the electrons removed from hydrogen atoms. These atoms were originally part of a glucose molecule. At the end of the electron transport system, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen ions attract hydrogen ions (protons) from the surrounding medium, and water is formed. The electron transport chain and the production of ATP through chemiosmosis are collectively called oxidative phosphorylation.

### ATP Yield

The number of ATP molecules generated from the catabolism of glucose varies. For example, the number of hydrogen ions that the electron transport chain complexes can pump through the membrane varies between species. Another source of variance stems from the shuttle of electrons across the mitochondrial membrane. The NADH generated from glycolysis cannot easily enter mitochondria. Thus, electrons are picked up on the inside of the mitochondria by either  $\text{NAD}^+$  or  $\text{FAD}^+$ . Fewer ATP molecules are generated when  $\text{FAD}^+$  acts as a carrier.  $\text{NAD}^+$  is used as the electron transporter in the liver and  $\text{FAD}^+$  in the brain, so ATP yield depends on the tissue being considered.

Another factor that affects the yield of ATP molecules generated from glucose is that intermediate compounds in these pathways are used for other purposes. Glucose catabolism connects with the pathways that build or break down all other biochemical compounds in cells, and the result is somewhat messier than the ideal situations described thus far. For example, sugars other than glucose are fed into the glycolytic pathway for energy extraction. Other molecules that would otherwise be used to harvest energy in glycolysis or the citric acid cycle may be removed to form nucleic acids, amino acids, lipids, or other compounds. Overall, in living systems, these pathways of glucose catabolism extract about 34 percent of the energy contained in glucose.

### Learning Objectives

The citric acid cycle is a series of chemical reactions that removes high-energy electrons and uses them in the electron transport chain to generate ATP. One molecule of ATP (or an equivalent) is produced per each turn of the cycle.

The electron transport chain is the portion of aerobic respiration that uses free oxygen as the final electron acceptor for electrons removed from the intermediate compounds in glucose catabolism. The electrons are passed through a series of chemical reactions, with a small amount of free energy used at three points to transport hydrogen ions across the membrane. This contributes to the gradient used in chemiosmosis. As the electrons are passed from NADH or  $\text{FADH}_2$  down the electron transport chain, they lose energy. The products of the electron transport chain are water and ATP. A number of intermediate compounds can be diverted into the anabolism of other biochemical molecules, such as nucleic acids, non-essential amino acids, sugars, and lipids. These same molecules, except nucleic acids, can serve as energy sources for the glucose pathway.

### Practice Questions

We inhale oxygen when we breathe and exhale carbon dioxide. What is the oxygen used for and where does the carbon dioxide come from?

#### Show Answer

The oxygen we inhale is the final electron acceptor in the electron transport chain and allows aerobic respiration to proceed, which is the most efficient pathway for harvesting energy in the form of ATP from food molecules. The carbon dioxide we breathe out is formed during the citric acid cycle when the bonds in carbon compounds are broken.

### Summary

Cellular respiration is a process that all living things use to convert glucose into energy. Autotrophs (like plants) produce glucose during photosynthesis. Heterotrophs (like humans) ingest other living things to obtain glucose. While the process can seem complex, this page takes you through the key elements of each part of cellular respiration.

## Let's Review

Cellular respiration is a collection of three unique metabolic pathways: glycolysis, the citric acid cycle, and the electron transport chain. Glycolysis is an anaerobic process, while the other two pathways are aerobic. In order to move from glycolysis to the citric acid cycle, pyruvate molecules (the output of glycolysis) must be oxidized in a process called pyruvate oxidation.

### Glycolysis

Glycolysis is the first pathway in cellular respiration. This pathway is anaerobic and takes place in the cytoplasm of the cell. This pathway breaks down 1 glucose molecule and produces 2 pyruvate molecules. There are two halves of glycolysis, with five steps in each half. The first half is known as the “energy requiring” steps. This half splits glucose, and uses up 2 ATP. If the concentration of pyruvate kinase is high enough, the second half of glycolysis can proceed. In the second half, the “energy releasing” steps, 4 molecules of ATP and 2 NADH are released. Glycolysis has a **net gain** of 2 ATP molecules and 2 NADH.

Some cells (e.g., mature mammalian red blood cells) cannot undergo aerobic respiration, so glycolysis is their **only** source of ATP. However, most cells undergo pyruvate oxidation and continue to the other pathways of cellular respiration.

### Pyruvate Oxidation

In eukaryotes, pyruvate oxidation takes place in the mitochondria. Pyruvate oxidation can only happen if oxygen is available. In this process, the pyruvate created by glycolysis is oxidized. In this oxidation process, a carboxyl group is removed from pyruvate, creating acetyl groups, which compound with coenzyme A (CoA) to form acetyl CoA. This process also releases CO<sub>2</sub>.

### Citric Acid Cycle

The citric acid cycle (also known as the Krebs cycle) is the second pathway in cellular respiration, and it also takes place in the mitochondria. The rate of the cycle is controlled by ATP concentration. When there is more ATP available, the rate slows down; when there is less ATP the rate increases. This pathway is a closed loop: the final step produces the compound needed for the first step.

The citric acid cycle is considered an aerobic pathway because the NADH and FADH<sub>2</sub> it produces act as temporary electron storage compounds, transferring their electrons to the next pathway (electron transport chain), which uses atmospheric oxygen. Each turn of the citric acid cycle provides a **net gain** of CO<sub>2</sub>, 1 GTP or ATP, and 3 NADH and 1 FADH<sub>2</sub>.

### Electron Transport Chain

Most ATP from glucose is generated in the electron transport chain. It is the only part of cellular respiration that directly consumes oxygen; however, in some prokaryotes, this is an anaerobic pathway. In eukaryotes, this pathway takes place in the inner mitochondrial membrane. In prokaryotes it occurs in the plasma membrane.

The electron transport chain is made up of 4 proteins along the membrane and a proton pump. A cofactor shuttles electrons between proteins I–III. If NAD is depleted, skip I: FADH<sub>2</sub> starts on II. In chemiosmosis, a proton pump takes hydrogens from inside mitochondria to the outside; this spins the “motor” and the phosphate groups attach to that. The movement changes from ADP to ATP, creating 90% of ATP obtained from aerobic glucose catabolism.

## Let's Practice

Now that you've reviewed cellular respiration, this practice activity will help you see how well you know cellular respiration:

A link to an interactive elements can be found at the bottom of this page.

Click here for a text-only version of the activity.

## Check Your Understanding

Answer the question(s) below to see how well you understand the topics covered in the previous section. This short quiz does **not** count toward your grade in the class, and you can retake it an unlimited number of times.

Use this quiz to check your understanding and decide whether to (1) study the previous section further or (2) move on to the next section.

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