

mitochondria in the leaf to support oxidative phosphorylation. The remainder escapes to the atmosphere where it is used by aerobic organisms to support respiration.

As electrons move through the proteins that reside between PSII and PSI, they lose energy. This energy is used to move hydrogen atoms from the stromal side of the membrane to the thylakoid lumen. Those hydrogen atoms, plus the ones produced by splitting water, accumulate in the thylakoid lumen and will be used to synthesize ATP in a later step. Because the electrons have lost energy prior to their arrival at PSI, they must be re-energized by PSI, hence, another photon is absorbed by the PSI antenna. That energy is relayed to the PSI reaction center (called **P700**). P700 is oxidized and sends a high-energy electron to NADP^+ to form NADPH. Thus, PSII captures the energy to create proton gradients to make ATP, and PSI captures the energy to reduce NADP^+ into NADPH. The two photosystems work in concert, in part, to guarantee that the production of NADPH will roughly equal the production of ATP. Other mechanisms exist to fine-tune that ratio to exactly match the chloroplast's constantly changing energy needs.

Generating an Energy Carrier: ATP

As in the intermembrane space of the mitochondria during cellular respiration, the buildup of hydrogen ions inside the thylakoid lumen creates a *concentration gradient*. The passive diffusion of hydrogen ions from high concentration (in the thylakoid lumen) to low concentration (in the stroma) is harnessed to create ATP, just as in the electron transport chain of cellular respiration. The ions build up energy because of diffusion and because they all have the same electrical charge, repelling each other.

To release this energy, hydrogen ions will rush through any opening, similar to water jetting through a hole in a dam. In the thylakoid, that opening is a passage through a specialized protein channel called the ATP synthase. The energy released by the hydrogen ion stream allows ATP synthase to attach a third phosphate group to ADP, which forms a molecule of ATP (Figure 8.16). The flow of hydrogen ions through ATP synthase is called chemiosmosis because the ions move from an area of high to an area of low concentration through a semi-permeable structure of the thylakoid.

LINK TO LEARNING

Visit this [site \(http://openstax.org/l/light_reactions\)](http://openstax.org/l/light_reactions) and click through the animation to view the process of photosynthesis within a leaf.

8.3 Using Light Energy to Make Organic Molecules

By the end of this section, you will be able to do the following:

- Describe the Calvin cycle
- Define carbon fixation
- Explain how photosynthesis works in the energy cycle of all living organisms

After the energy from the sun is converted into chemical energy and temporarily stored in ATP and NADPH molecules, the cell has the fuel needed to build carbohydrate molecules for long-term energy storage. The products of the light-dependent reactions, ATP and NADPH, have lifespans in the range of millionths of seconds, whereas the products of the light-independent reactions (carbohydrates and other forms of reduced carbon) can survive almost indefinitely. The carbohydrate molecules made will have a backbone of carbon atoms. But where does the carbon come from? It comes from carbon dioxide—the gas that is a waste product of respiration in microbes, fungi, plants, and animals.

The Calvin Cycle

In plants, carbon dioxide (CO_2) enters the leaves through stomata, where it diffuses over short distances through intercellular spaces until it reaches the mesophyll cells. Once in the mesophyll cells, CO_2 diffuses into the stroma of the chloroplast—the site of light-independent reactions of photosynthesis. These reactions actually have several names associated with them. Another term, the **Calvin cycle**, is named for the man who discovered it, and because these reactions function as a cycle. Others call it the Calvin-Benson cycle to include the name of another scientist involved in its discovery. The most outdated name is “dark reaction,” because light is not directly required (Figure 8.17). However, the term dark reaction can be misleading because it implies incorrectly that the reaction only occurs at night or is independent of light, which is why most scientists and instructors no longer use it.

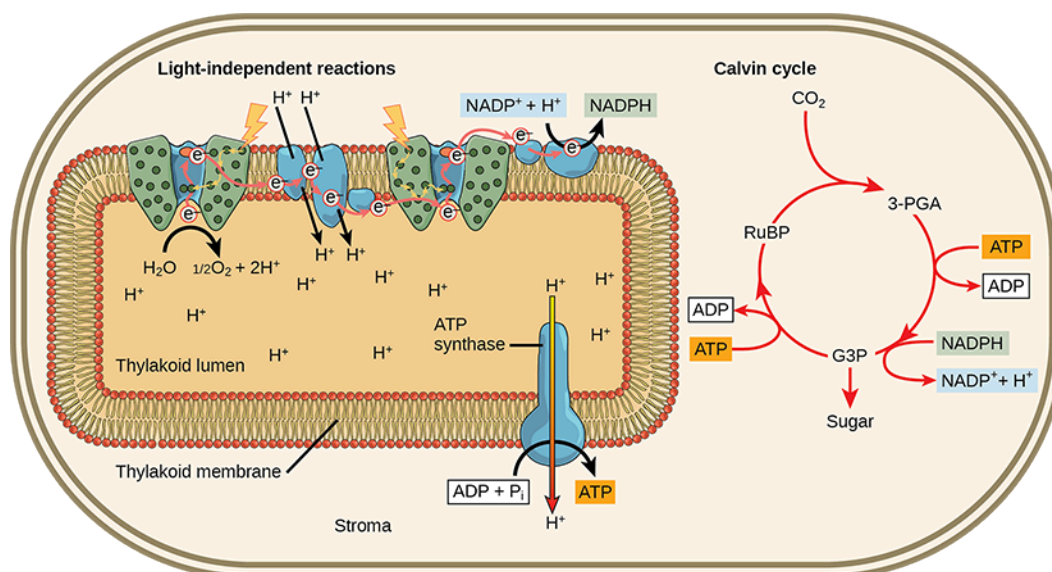


Figure 8.17 Light reactions harness energy from the sun to produce chemical bonds, ATP, and NADPH. These energy-carrying molecules are made in the stroma where carbon fixation takes place.

The light-independent reactions of the Calvin cycle can be organized into three basic stages: *fixation*, *reduction*, and *regeneration*.

Stage 1: Fixation

In the stroma, in addition to CO_2 , two other components are present to initiate the light-independent reactions: an enzyme called ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), and three molecules of ribulose biphosphate (RuBP), as shown in [Figure 8.18](#). RuBP has five atoms of carbon, flanked by two phosphates.



VISUAL CONNECTION

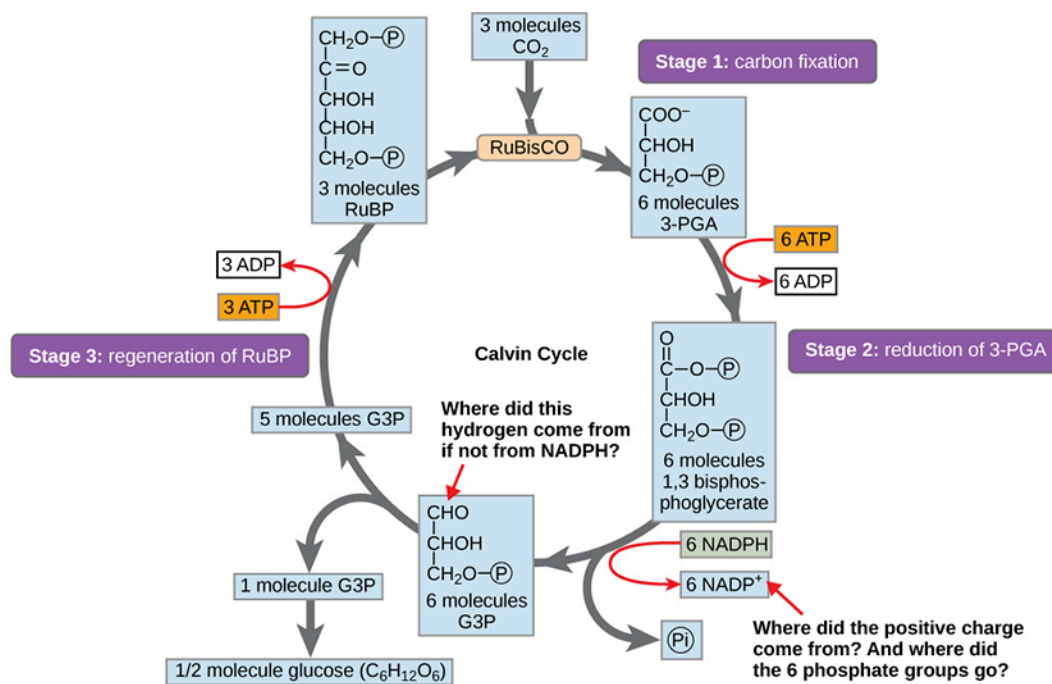


Figure 8.18 The Calvin cycle has three stages. In stage 1, the enzyme RuBisCO incorporates carbon dioxide into an organic molecule, 3-PGA. In stage 2, the organic molecule is reduced using electrons supplied by NADPH. In stage 3, RuBP, the molecule that starts the cycle,

is regenerated so that the cycle can continue. Only one carbon dioxide molecule is incorporated at a time, so the cycle must be completed three times to produce a single three-carbon G3P molecule, and six times to produce a six-carbon glucose molecule.

Which of the following statements is true?

- In photosynthesis, oxygen, carbon dioxide, ATP, and NADPH are reactants. G3P and water are products.
- In photosynthesis, chlorophyll, water, and carbon dioxide are reactants. G3P and oxygen are products.
- In photosynthesis, water, carbon dioxide, ATP, and NADPH are reactants. RuBP and oxygen are products.
- In photosynthesis, water and carbon dioxide are reactants. G3P and oxygen are products.

RuBisCO catalyzes a reaction between CO_2 and RuBP. For each CO_2 molecule that reacts with one RuBP, two molecules of another compound 3-phospho glyceric acid (3-PGA) form. PGA has three carbons and one phosphate. Each turn of the cycle involves only one RuBP and one carbon dioxide and forms two molecules of 3-PGA. The number of carbon atoms remains the same, as the atoms move to form new bonds during the reactions (3 C atoms from 3CO_2 + 15 C atoms from 3RuBP = 18 C atoms in 6 molecules of 3-PGA). This process is called **carbon fixation**, because CO_2 is “fixed” from an inorganic form into organic molecules.

Stage 2: Reduction

ATP and NADPH are used to convert the six molecules of 3-PGA into six molecules of a chemical called glyceraldehyde 3-phosphate (G3P). That is a reduction reaction because it involves the gain of electrons by 3-PGA. (Recall that a **reduction** is the gain of an electron by an atom or molecule.) Six molecules of both ATP and NADPH are used. For ATP, energy is released with the loss of the terminal phosphate atom, converting it into ADP; for NADPH, both energy and a hydrogen atom are lost, converting it into NADP^+ . Both of these molecules return to the nearby light-dependent reactions to be reused and re-energized.

Stage 3: Regeneration

Interestingly, at this point, only one of the G3P molecules leaves the Calvin cycle and is sent to the cytoplasm to contribute to the formation of other compounds needed by the plant. Because the G3P exported from the chloroplast has three carbon atoms, it takes three “turns” of the Calvin cycle to fix enough net carbon to export one G3P. But each turn makes two G3Ps, thus three turns make six G3Ps. One is exported while the remaining five G3P molecules remain in the cycle and are used to regenerate RuBP, which enables the system to prepare for more CO_2 to be fixed. Three more molecules of ATP are used in these regeneration reactions.

LINK TO LEARNING

This [link \(http://openstax.org/l/calvin_cycle\)](http://openstax.org/l/calvin_cycle) leads to an animation of photosynthesis and the Calvin cycle.



EVOLUTION CONNECTION

Photosynthesis

During the evolution of photosynthesis, a major shift occurred from the bacterial type of photosynthesis that involves only one photosystem and is typically anoxygenic (does not generate oxygen) into modern oxygenic (does generate oxygen) photosynthesis, employing two photosystems. This modern oxygenic photosynthesis is used by many organisms—from giant tropical leaves in the rainforest to tiny cyanobacterial cells—and the process and components of this photosynthesis remain largely the same. Photosystems absorb light and use electron transport chains to convert energy into the chemical energy of ATP and NADH. The subsequent light-independent reactions then assemble carbohydrate molecules with this energy.

In the harsh dry heat of the desert, plants must conserve every drop of water must be used to survive. Because stomata must open to allow for the uptake of CO_2 , water escapes from the leaf during active photosynthesis. Desert plants have evolved processes to conserve water and deal with harsh conditions. Mechanisms to capture and store CO_2 allows plants to adapt to living with less water. Some plants such as cacti ([Figure 8.19](#)) can prepare materials for photosynthesis during the night by a temporary carbon fixation/storage process, because opening the stomata at this time conserves water due to cooler temperatures. During the day cacti use the captured CO_2 for photosynthesis, and keep their stomata closed.



Figure 8.19 The harsh conditions of the desert have led plants like these cacti to evolve variations of the light-independent reactions of photosynthesis. These variations increase the efficiency of water usage, helping to conserve water and energy. (credit: Piotr Wojtkowski)

The Energy Cycle

Whether the organism is a bacterium, plant, or animal, all living things access energy by breaking down carbohydrate and other carbon-rich organic molecules. But if plants make carbohydrate molecules, why would they need to break them down, especially when it has been shown that the gas organisms release as a “waste product” (CO_2) acts as a substrate for the formation of more food in photosynthesis? Remember, living things need energy to perform life functions. In addition, an organism can either make its own food or eat another organism—either way, the food still needs to be broken down. Finally, in the process of breaking down food, called cellular respiration, heterotrophs release needed energy and produce “waste” in the form of CO_2 gas.

However, in nature, there is no such thing as “waste.” Every single atom of matter and energy is conserved, recycled over and over infinitely. Substances change form or move from one type of molecule to another, but their constituent atoms never disappear ([Figure 8.20](#)).

In reality, CO_2 is no more a form of waste than oxygen is wasteful to photosynthesis. Both are byproducts of reactions that move on to other reactions. Photosynthesis absorbs light energy to build carbohydrates in chloroplasts, and aerobic cellular respiration releases energy by using oxygen to metabolize carbohydrates in the cytoplasm and mitochondria. Both processes use electron transport chains to capture the energy necessary to drive other reactions. These two powerhouse processes, photosynthesis and cellular respiration, function in biological, cyclical harmony to allow organisms to access life-sustaining energy that originates millions of miles away in a burning star humans call the sun.

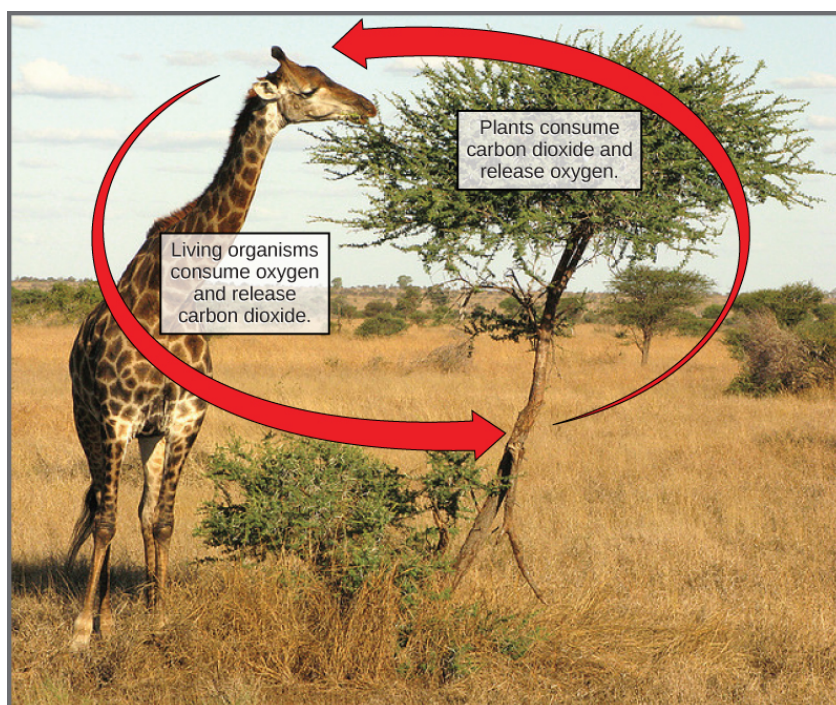


Figure 8.20 Photosynthesis consumes carbon dioxide and produces oxygen. Aerobic respiration consumes oxygen and produces carbon dioxide. These two processes play an important role in the carbon cycle. (credit: modification of work by Stuart Bassil)