5.1 Photosynthesis: An Introduction

photoautotroph an organism that makes its own food using energy from the Sun

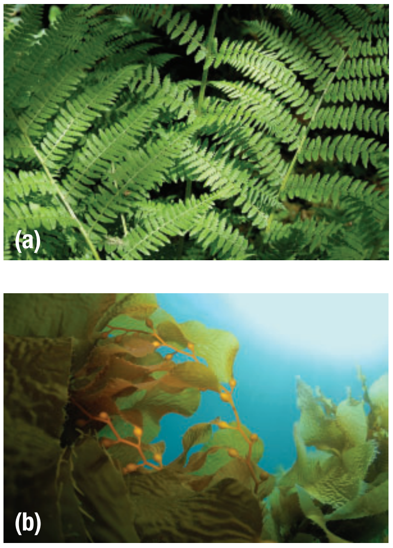


Figure 1 (a) Green plants and (b) kelp are examples of photoautotrophs.

Photosynthetic organisms make their own food using energy derived from the Sun. **Photoautotrophs** are the primary producers on Earth, converting light energy into chemical energy and using it to assemble complex organic molecules from simple inorganic raw materials (**Figure 1**). Producers use the organic molecules they create as energy sources for their own activities and as the organic building blocks of their own bodies. Producers also serve—directly or indirectly—as food sources for consumers, the organisms that live by eating other organisms. Consumers use some of the organic molecules obtained from producers to obtain energy, and some as building materials for their cells and body parts. This is analogous to a person using wood both as fuel for heating and cooking, and as a building material. Eventually, the bodies of both producers and consumers provide chemical energy and building materials for decomposers, which feed on dead and decaying organisms. Decomposers ultimately return simple inorganic molecules back into the soil, air, or water, making the inorganic molecules available once again to photosynthetic organisms.

It may seem that this cycling of matter through producers, consumers, and decomposers can continue indefinitely with no further input. However, recall the second law of thermodynamics: entropy increases with every energy transformation or chemical reaction. As a result, some useful free energy is lost at each stage of the cycle. Therefore, there must be a continual input of free energy from the Sun for life on Earth to continue. The pathway of photosynthesis is responsible for this vital task.

The Two Stages of Photosynthesis

Photosynthesis has two distinct stages. The light-dependent reactions are directly associated with the absorption of photons of light. The light-independent reactions (called the Calvin cycle) do not require light themselves, but they are dependent on products of the light-dependent reactions (**Figure 2**).

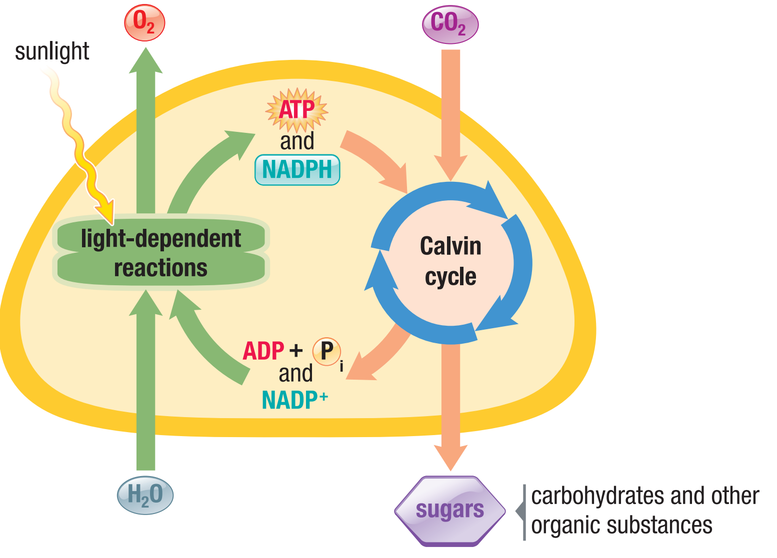


Figure 2 Both stages of photosynthesis occur in the chloroplasts of photosynthetic eukaryotes as well as in photosynthetic prokaryotes.

light-dependent reactions the first stage of photosynthesis, during which water molecules are split as light energy is absorbed and transformed into chemical energy in ATP and NADPH

During the **light-dependent reactions**, light energy is captured by pigment molecules and used to synthesize nicotinamide adenine dinucleotide phosphate (NADPH) and ATP. During this process, a water molecule is split and an electron transport chain transfers high-energy electrons to $NADP^+$ carrier molecules to establish a proton gradient across a membrane. Oxygen is generated when the water molecule is split and is released to the environment. Energy stored in the proton gradient is used to generate ATP.

In the **Calvin cycle**, the now high-energy electrons carried by NADPH and the energy stored in ATP molecules are used to convert CO_2 into high-energy organic compounds (Figure 2). This process is called CO_2 fixation. With the addition of electrons and protons (H^+), CO_2 is first converted to a simple 3-carbon carbohydrate. It is then used to synthesize larger molecules, such as glucose. Carbohydrates are the major end products of photosynthesis, but the reduced carbon produced by photosynthesis is also the source of the carbon backbone for a huge range of other molecules, including lipids and proteins. In fact, all the organic molecules of plants are assembled as direct or indirect products of photosynthesis.

Calvin cycle the second stage of the photosynthesis process that uses ATP and NADPH to convert CO_2 to sugars

The general chemical equation for photosynthesis is

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

This equation suggests that photosynthesis is simply the reverse reaction of aerobic cellular respiration. However, as you will soon learn, while there are important steps that mirror the respiration pathway, photosynthesis is not merely the citric acid cycle and glycolysis in reverse.

Research This

Experimenting with Jan Baptist van Helmont

Skills: Researching, Evaluating, Communicating

SKILLS HANDBOOK A4.1

Jan Baptist van Helmont (1579–1644) was a pioneer in chemistry and experimental methods. He was also one of the first scientists to study the processes that allow plants to grow. His famous willow tree experiment is the subject of this research activity.

1. Use the Internet and other sources to investigate van Helmont's famous willow tree experiment.

A. Describe the experiment that van Helmont performed. T/I
   - (i) How long did his experiment take?
   - (ii) Outline his experimental procedure, including the variables that he controlled and measured.
   - (iii) How did his conclusions differ from the expected results?
   - (iv) What source of mass did van Helmont not account for in his experiment?

B. Explain how van Helmont's experiments allowed scientists to gain information in a different manner, rather than simply making assumptions based on casual observations. T/I

C. (i) How do his conclusions illustrate the challenge of designing experiments and accounting for all variables?
   - (ii) How would you redesign van Helmont's experiment? T/I

D. Expand your Internet search to discover which scientist's experiments provided information on the role of CO_2 in photosynthesis. T/I

WEB LINK

Chloroplasts: Photosynthesis Machines

In photosynthetic eukaryotes, both the light-dependent reactions and the Calvin cycle take place within the chloroplast, an organelle formed from three membranes that define three distinct compartments (**Figure 3,** next page). An outer membrane covers the entire surface of the organelle, and a second, inner membrane lies just inside the outer membrane. The aqueous environment within the inner membrane is the stroma. The enzymes that catalyze the reactions of the Calvin cycle are found in the stroma of the chloroplast. Also within the stroma is the third membrane system, the thylakoid membranes, or thylakoids. The thylakoids form interconnected stacks of flattened discs called grana (singular: granum). The space enclosed by a thylakoid is called the thylakoid lumen. The thylakoid membrane is where the light-dependent reactions of photosynthesis occur. The thylakoid membrane also gives leaves their green colour, because the chlorophyll and other accessory pigments are embedded within it.

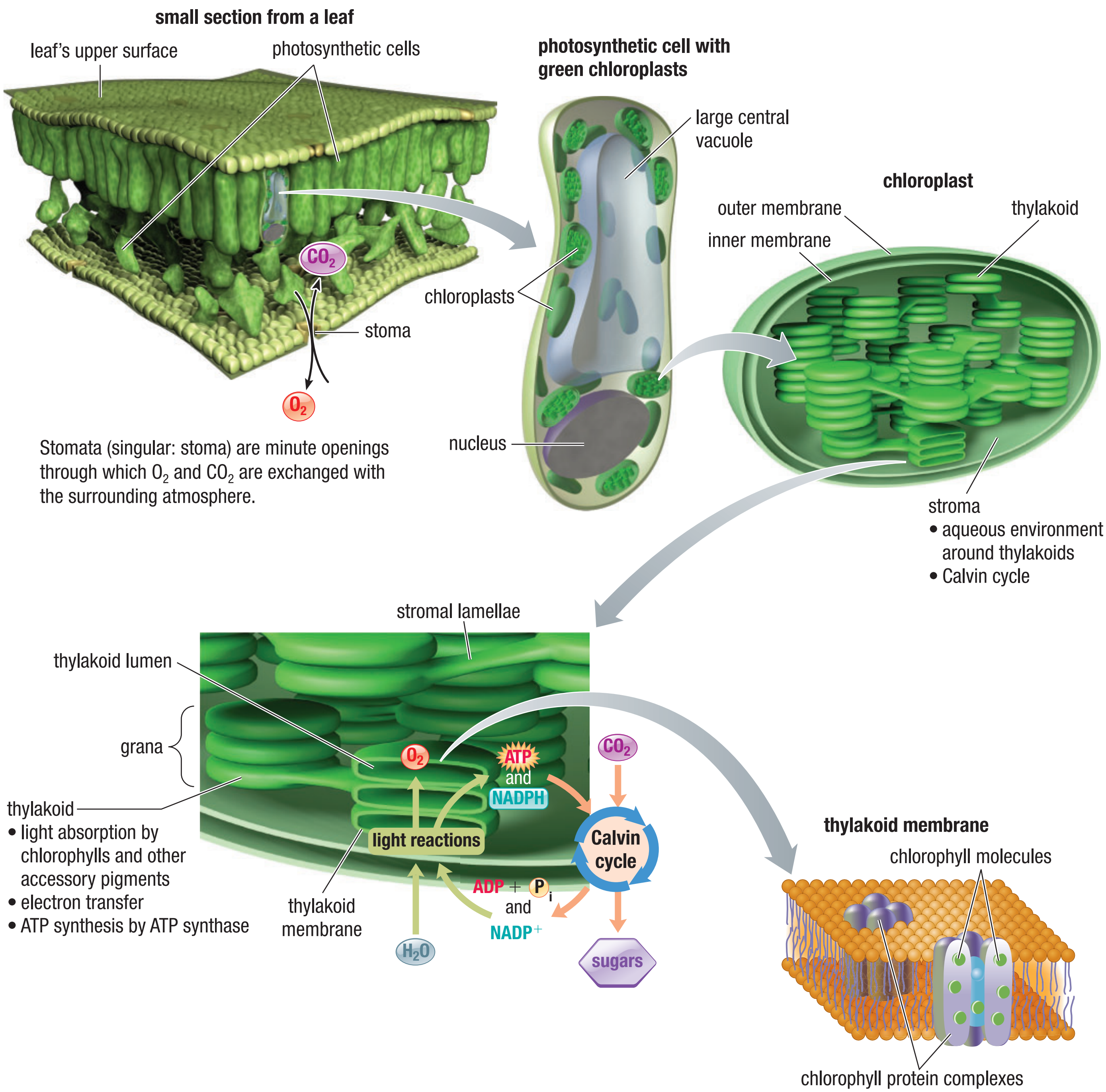


Figure 3 The membranes and compartments of chloroplasts

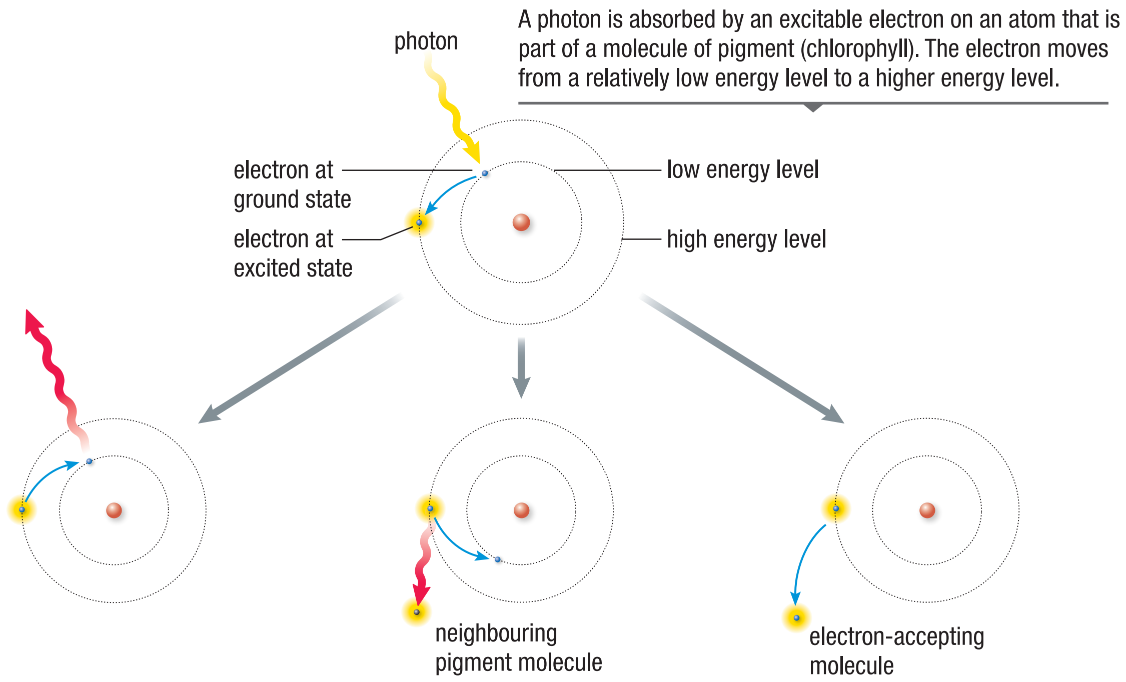
Capturing Light Energy

The ability to trap light energy and convert it into chemical energy requires a sophisticated photochemical apparatus that is unique in biology. This section describes the components of the light-dependent reactions that are located in the thylakoid membranes. There are two points about light and pigment molecules that are important in photosynthesis. First, the absorption of a photon by a pigment molecule excites a single electron, moving it from a low energy, or ground state, to a higher energy, or excited state. Second, the difference between the energy level of the ground state and the energy level of the excited state must be equivalent to the energy of the photon of light that was absorbed. If the energies are not equivalent, the photon cannot be absorbed by the pigment.

Following light absorption, there are three possible outcomes for the excited electron within a pigment molecule. The relative probability of each outcome that takes place depends on the environment surrounding the pigment molecules, including the presence of other molecules.

In the first possible outcome, the excited electron simply returns to its ground state (**Figure 4(a)**). Its energy is released as either thermal energy or fluorescence. Fluorescence is the emission of light of a longer wavelength (lower energy) than the absorbed light. Fluorescence emits lower energy because a small amount of the energy of the photon that was initially absorbed is always lost as thermal energy. Remember that energy transformations are never 100 % efficient. In the second possible outcome, the energy of the excited electron is transferred to an electron in a neighbouring pigment molecule (**Figure 4(b)**). This now high-energy electron in the second pigment molecule is excited, and the original electron returns to its ground state. This requires the two molecules to be very closely and precisely aligned with one another. In the third possible outcome, the excited-state electron may itself be transferred to a nearby electron-accepting molecule (**Figure 4(c)**). This last outcome is one of the most important steps in photosynthesis—the energizing and transferring of an electron. In photosynthesis, the key electron-accepting molecule is called a **primary electron acceptor**.

primary electron acceptor a molecule capable of accepting electrons and becoming reduced during photosynthesis



(a) The electron returns to its ground state by emitting a less energetic photon (fluorescence) or by releasing energy as thermal energy.

(b) The electron returns to its ground state, and the energy released is transferred to a different electron in a neighbouring pigment molecule.

(c) The high-energy electron is accepted by an electron-accepting molecule, the primary acceptor.

Figure 4 There are three possible fates of an excited-state electron.

How Chlorophylls and Carotenoids Cooperate in Light Absorption

Chlorophylls are the major photosynthetic pigments in plants, green algae, and cyanobacteria. The most dominant types of chlorophylls are chlorophyll *a* and chlorophyll *b*, which have slightly different structures (**Figure 5(a)**, next page). In photosynthetic prokaryotes other than cyanobacteria, closely related molecules called bacteriochlorophylls carry out the same functions. The second major group of photosynthetic pigments is the carotenoids (**Figure 5(b)**, next page).

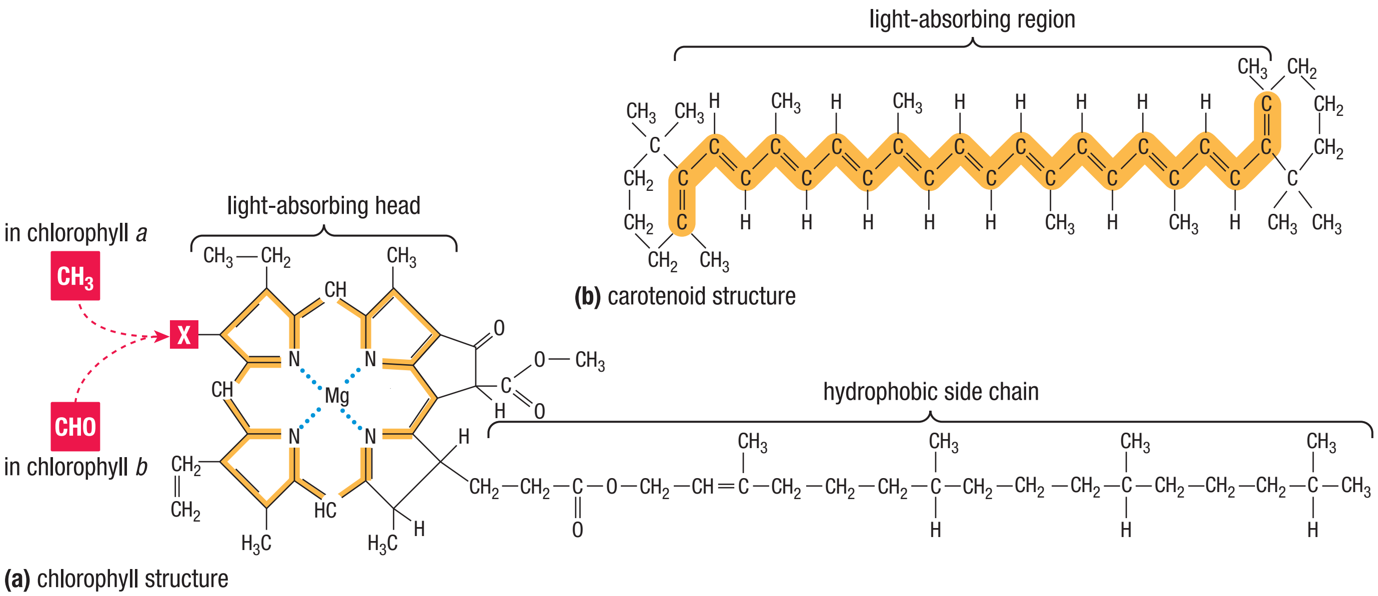


Figure 5 (a) Chlorophylls *a* and *b* differ only in the side group attached at the X. Light-absorbing electrons are distributed among the bonds shaded in orange. (b) In carotenoids, the electrons that absorb light are distributed in a series of alternating double and single bonds in the backbone of the pigment.

antenna complex a cluster of light-absorbing pigments embedded in the thylakoid membrane able to capture and transfer energy to special chlorophyll *a* molecules in the reaction centre

reaction centre a complex of proteins and pigments that contains the primary electron acceptor

During photosynthesis, chlorophyll *a* becomes oxidized and donates an electron to a primary electron acceptor. Carotenoids and chlorophyll *b* are referred to as accessory pigments because after light absorption, they transfer this excitation energy to molecules of chlorophyll *a*. This set of accessory pigments, referred to as an **antenna complex**, captures light energy and transfers it to a chlorophyll *a* molecule and the primary electron acceptor in the **reaction centre** (**Figure 6**).

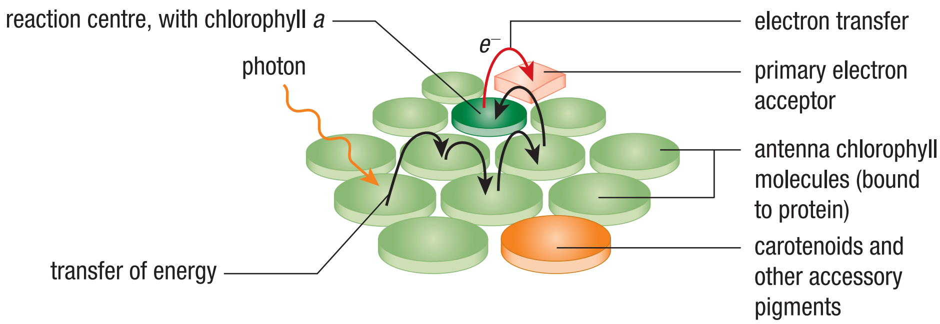


Figure 6 The antenna complex captures light energy and transfers it to the reaction centre.

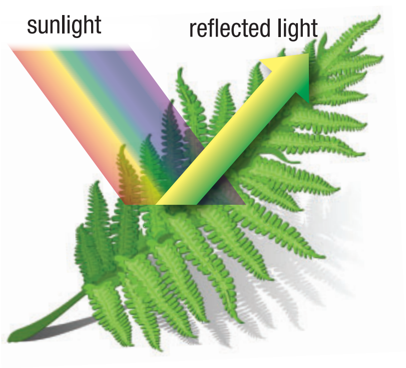


Figure 7 Leaves appear green because chlorophylls reflect green and some yellow light but absorb wavelengths in other parts of the spectrum.

A pigment molecule does not absorb all wavelengths of light. The wavelengths that are not absorbed are transmitted (pass through the object) or reflected. The green and yellow light is reflected, making the plant leaves containing chlorophyll *a* appear green (**Figure 7**). This reflected light is what gives the pigment its distinctive colour. You can determine which wavelengths of light a pigment absorbs by producing an **absorption spectrum**—a plot of the absorption of light as a function of wavelength. An absorption spectrum is produced using an instrument called a spectrophotometer, which analyzes a sample of the pigment. For example, chlorophyll *a* absorbs strongly blue and red light but does not absorb green or yellow light. Each pigment absorbs light over a different range of wavelengths (**Figure 8(a)**, next page). Note that carotenoids do not absorb light waves in the red and yellow range. These light waves are reflected back to your eyes as the colour orange. As you might guess from the name, carotenoids are found in carrots. There is a wide variety of other pigments, which give rise to the diversity of colours found in plant life around the world. The vivid colours of fall foliage appear when the dominant green chlorophyll degrades from the leaves and other pigments are revealed. These pigments reflect colours other than green.

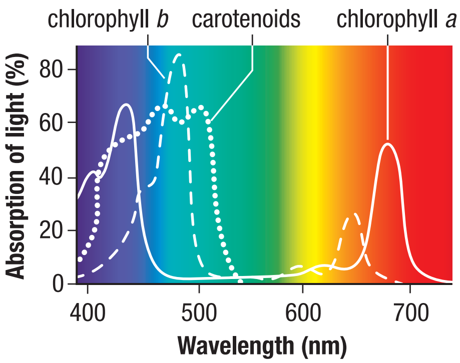
absorption spectrum a plot of the amount of light energy of various wavelengths that a substance absorbs

Photosynthesis depends on the absorption of light by chlorophylls and carotenoids acting in combination. The effectiveness of light of various wavelengths in driving photosynthesis is plotted as an **action spectrum** for photosynthesis (**Figure 8(b)**). The action spectrum is usually determined by using a suspension of chloroplasts or algal cells and measuring the amount of O_2 released by photosynthesis at different wavelengths of visible light. If an action spectrum for a physiological phenomenon matches the absorption spectrum of a pigment, it is very likely that the two are linked.

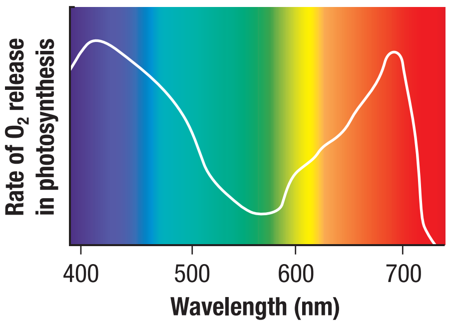
action spectrum a plot of the effectiveness of light energy of different wavelengths in driving a chemical process

UNIT TASK **BOOKMARK**

You can use what you have learned about the absorption spectrum and the action spectrum to design your Unit Task investigation on page 252.



(a) absorption spectra



(b) action spectrum

Figure 8 These graphs show (a) the absorption spectra of the photosynthetic pigments, chlorophylls *a* and *b* and carotenoids, and (b) the action spectrum in higher plants, representing the combined effects of chlorophylls and carotenoids. Notice how the spectra match.

Theodor Engelmann produced one of the first action spectra in 1882. He used only a light microscope and a glass prism to determine which wavelengths of light were most effective for photosynthesis. Engelmann placed a strand of a green alga, *Spirogyra*, on a glass microscope slide, along with water containing aerobic bacteria (bacteria that require oxygen to survive). He adjusted the prism so that it split a beam of light into its separate colours, which spread like a rainbow across the strand (**Figure 9**). After a short time, he noticed that the bacteria had begun to cluster around the algal strand in the regions where oxygen was being released in the greatest quantity—the regions in which photosynthesis was proceeding at the greatest rate. Those regions corresponded to the colours (wavelengths) of light that were being absorbed most effectively by the alga. The largest clusters were under the blue and violet light at one end of the strand and the red light at the other end. Very few bacteria were found under the green light. This provided compelling evidence of the influence of different colours of light on photosynthesis.

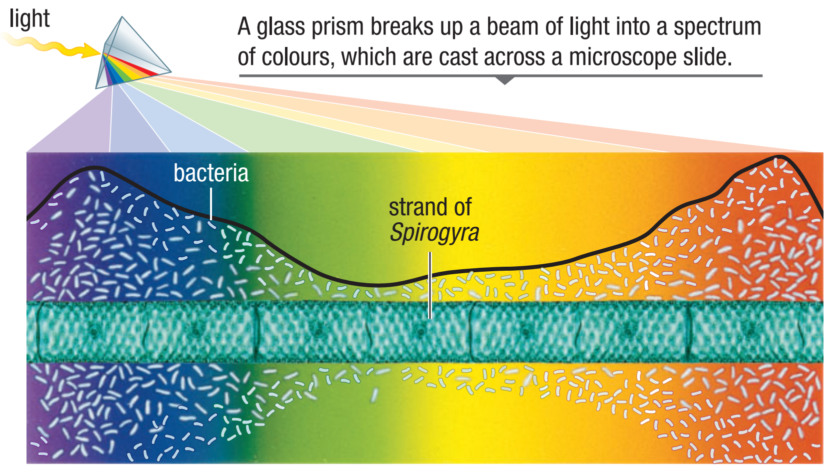


Figure 9 Engelmann's 1882 experiment revealed the action spectrum of light used in photosynthesis by *Spirogyra*, a green alga. The bacteria clustered in areas where the most oxygen was produced. Oxygen is a product of photosynthesis.

Pigments and Photosystems

Pigment molecules are bound very precisely to a number of different proteins. They do not float freely within the thylakoid membranes. These pigment proteins are organized into photosystems. Each photosystem is composed of the large antenna complex (also called a light-harvesting complex) of proteins and some 250 to 400 pigment molecules surrounding a central reaction centre. The reaction centre of a photosystem comprises a small number of proteins, each bound to a pair of specialized chlorophyll *a* molecules, as well as the primary electron acceptor (**Figure 10**). Light energy absorbed by the antenna complex is transferred to specialized chlorophyll molecules in the reaction centre. Light energy is converted to chemical energy when a reaction centre chlorophyll donates an electron to the primary electron acceptor. This electron, in turn, is passed along an electron transport chain.

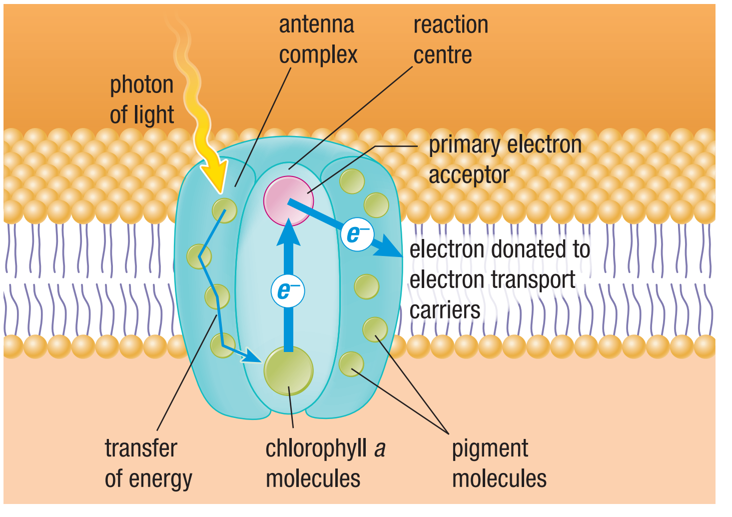


Figure 10 A photosystem composed of a light-harvesting antenna complex and a reaction centre

photosystem I a collection of pigment proteins that includes chlorophyll *a* and absorbs light at the 700 nm wavelength

photosystem II a collection of pigment proteins that includes chlorophyll *a* and absorbs light at the 680 nm wavelength

There are two kinds of photosystems: photosystem I and photosystem II (also called PSI and PSII). The reaction centre of **photosystem I** contains specialized chlorophyll *a* molecules, which are known as P700 molecules (P = pigment) because they absorb light optimally at a wavelength of 700 nm. The reaction centre of **photosystem II** contains P680 chlorophyll *a* molecules, which absorb light optimally at a wavelength of 680 nm. P700 and P680 are structurally identical to other chlorophyll *a* molecules. Their specific patterns of energy absorption result from interactions with proteins in the photosystem. The photosystems were numbered based on the order they were discovered. However, in photosynthesis, the actions of photosystem II occur before those of photosystem I.

Photosystems trap photons of light and use the energy to energize a chlorophyll *a* molecule in the reaction centre. The chlorophyll *a* molecule is then oxidized as it transfers a high-energy electron to the primary electron acceptor. High rates of oxidation-reduction can be achieved within the photosystem when the pigments in the large antennae complex absorb the light of a range of wavelengths and efficiently transfer the energy to the reaction centre. In the sections that follow, you will learn how the high-energy electrons generated by photosystems can be used to drive ATP synthesis and to assemble the high-energy organic molecules that plants and animals use as food. You will also learn how these processes might be used to develop new light-gathering and energy-producing technologies.

Investigation 5.1.1

Light and Photosynthesis (p. 241)
In Investigation 5.1.1, you will explore the products of photosynthesis and the importance of light in their creation.

5.1 Review

Summary

- Producers use photosynthesis to convert light energy into chemical energy, which is then stored and used to assemble energy-rich organic molecules that are used by producers and consumers.
- Photosynthesis has two stages—the light-dependent reactions and the light-independent reactions (the Calvin cycle).
- The light-dependent reactions take place in the thylakoid membranes of the chloroplasts. Energy captured during the light-dependent reactions is used to synthesize NADPH and ATP.
- The Calvin cycle takes place in the stroma of the chloroplasts. It uses NADPH and ATP to convert carbon dioxide into simple carbohydrates.
- Chlorophylls, carotenoids, and other pigments absorb light energy during photosynthesis. Different pigments absorb light of different wavelengths, as shown by their absorption spectra. Light that is not absorbed is reflected. This reflected light gives pigments their colour.
- The action spectrum of photosynthesis in green plants is highest in the red and blue regions of the spectrum.
- Pigments, including chlorophylls and carotenoids, are organized into two types of photosystems: photosystem I and photosystem II. Each photosystem contains a reaction centre surrounded by an antenna complex that helps capture photons of light energy and energize electrons.

Questions

1. Why are photoautotrophs considered to be primary producers? K/U
2. Draw a labelled diagram that illustrates the relationship between the two stages of photosynthesis. Refer to your diagram to explain why these stages are considered interdependent. K/U C
3. Use a diagram to explain the relationship between the absorption of light energy and electron energy levels within an atom. Describe the three possible fates of an electron after it has jumped to a higher energy state. K/U C
4. Certain marine algae are able to live in low light, at depths of more than 100 m. These algae appear almost black deep under water, but usually appear red when brought to the surface. T/I
   (a) Would you expect these species to contain more or less chlorophyll than green algae? Why?
   (b) Would you expect these species to perform photosynthesis more efficiently under a green light source or a red light source? Explain your reasoning.
   (c) Things tend to look bluish underwater because water absorbs red light more effectively than blue light. How might this fact help account for the characteristics of the deep-water species of algae?
5. What are the thylakoids? Why are they important for photosynthesis? K/U
6. Write a series of steps that could be used as an experimental procedure for Engelmann's famous investigation that revealed the action spectrum of a living alga. T/I C
7. Compare an absorption spectrum of a pigment with the action spectrum for photosynthesis. K/U
8. Sketch a graph that shows what you would expect to be the overall action spectrum of the main pigments in the leaves in **Figure 11**. Explain your reasoning. C A

Figure 11