

Chapter 10

Photosynthesis

Key Concepts

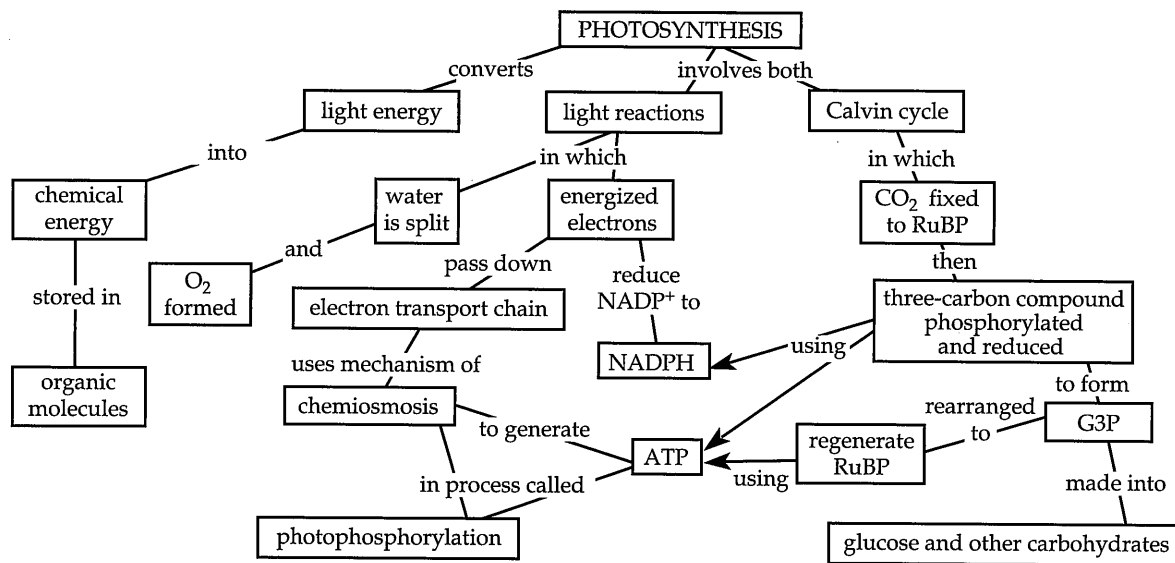
10.1 Photosynthesis converts light energy to the chemical energy of food

10.2 The light reactions convert solar energy to the chemical energy of ATP and NADPH

10.3 The Calvin cycle uses ATP and NADPH to convert CO₂ to sugar

10.4 Alternative mechanisms of carbon fixation have evolved in hot, arid climates

Framework



Chapter Review

In **photosynthesis**, the light energy of the sun is converted into chemical energy stored in organic molecules. Organisms obtain the organic molecules they require for energy and carbon skeletons by autotrophic or heterotrophic nutrition. **Autotrophs** “feed themselves” in the sense that they make their own organic molecules from inorganic raw materials. Plants, algae, some other protists, and some prokaryotes are photoautotrophs.

Heterotrophs are consumers. They may eat plants or animals or decompose organic litter, but almost all are ultimately dependent on photoautotrophs for food and oxygen.

10.1 Photosynthesis converts light energy to the chemical energy of food

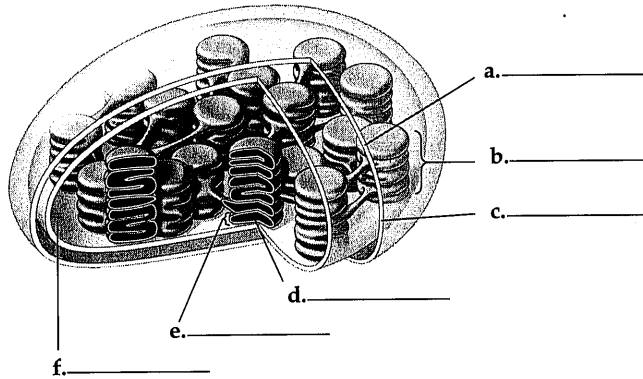
Chloroplasts: The Sites of Photosynthesis in Plants Chloroplasts, found mainly in the **mesophyll** tissue of the leaf, contain **chlorophyll**, the green pigment that absorbs the light energy that drives photosynthesis. CO₂ enters and O₂ exits the leaf through **stomata**. Veins carry water from the roots to leaves and distribute sugar to nonphotosynthetic tissue.

A chloroplast consists of a double membrane surrounding a dense fluid called the **stroma** and an elaborate membrane system called **thylakoids**, enclosing the

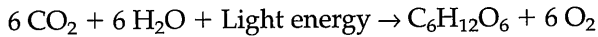
thylakoid space. Thylakoid sacs may be stacked to form grana. Chlorophyll is embedded in the thylakoid membrane.

INTERACTIVE QUESTION 10.1

Label the indicated parts in this diagram of a chloroplast.



Tracking Atoms through Photosynthesis: Scientific Inquiry If only the net consumption of water is considered, the equation for photosynthesis is the reverse of respiration:



Using evidence from bacteria that utilize hydrogen sulfide (H_2S) for photosynthesis, C. B. van Niel hypothesized that all photosynthetic organisms need a hydrogen source and that plants split water as a source of electrons from hydrogen, releasing oxygen. Scientists confirmed this hypothesis by using a heavy isotope of oxygen (^{18}O). Labeled O_2 was produced in photosynthesis only when water, rather than carbon dioxide, contained the labeled oxygen.

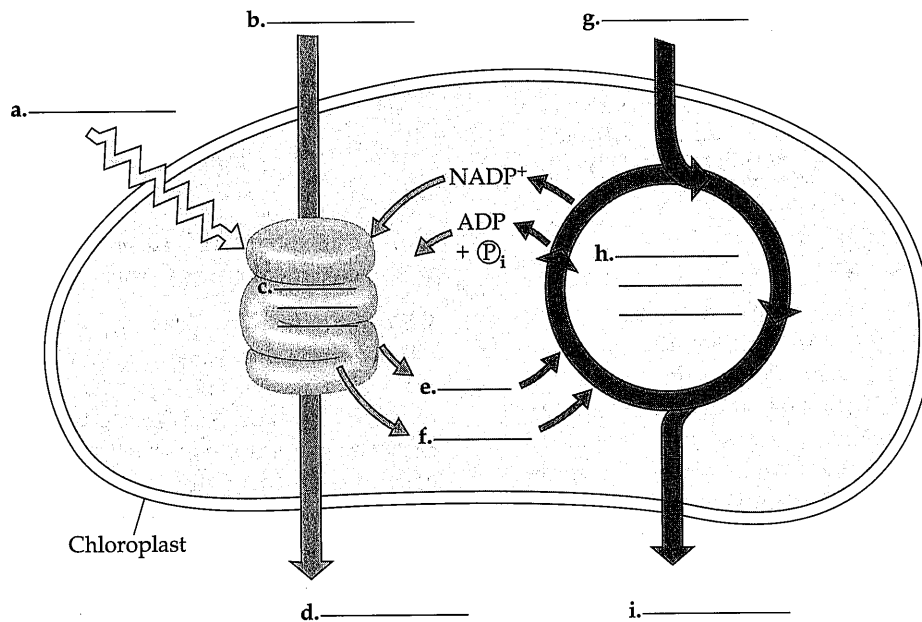
Photosynthesis is a redox process like respiration but differs in the direction of electron flow. The electrons increase their potential energy when they travel from water to reduce CO_2 into sugar, and light provides this energy.

The Two Stages of Photosynthesis: A Preview Solar energy is converted into chemical energy in the **light reactions**. Light energy absorbed by chlorophyll drives the transfer of electrons and hydrogen from water to the electron acceptor NADP^+ , which is reduced to NADPH and temporarily stores energized electrons. Oxygen is released when water is split. ATP is formed during the light reactions, using chemiosmosis in a process called **photophosphorylation**.

In the **Calvin cycle**, carbon dioxide is incorporated into existing organic compounds by **carbon fixation**, and these compounds are then reduced to form carbohydrate. NADPH and ATP from the light reactions supply the reducing power and chemical energy needed for the Calvin cycle.

INTERACTIVE QUESTION 10.2

Fill in the blanks in this overview of photosynthesis in a chloroplast. Indicate the locations of the processes c. and h.



10.2 The light reactions convert solar energy to the chemical energy of ATP and NADPH

The Nature of Sunlight Electromagnetic energy, also called electromagnetic radiation, travels as rhythmic wave disturbances of electrical and magnetic fields. The distance between the crests of the electromagnetic waves, their **wavelength**, ranges across the **electromagnetic spectrum**, from short gamma waves to long radio waves. The small band of radiation from about 380 to 750 nm is called **visible light**.

Light also behaves as if it consists of discrete particles called **photons**, which have a fixed quantity of energy. The amount of energy in a photon is inversely related to its wavelength.

■ INTERACTIVE QUESTION 10.3

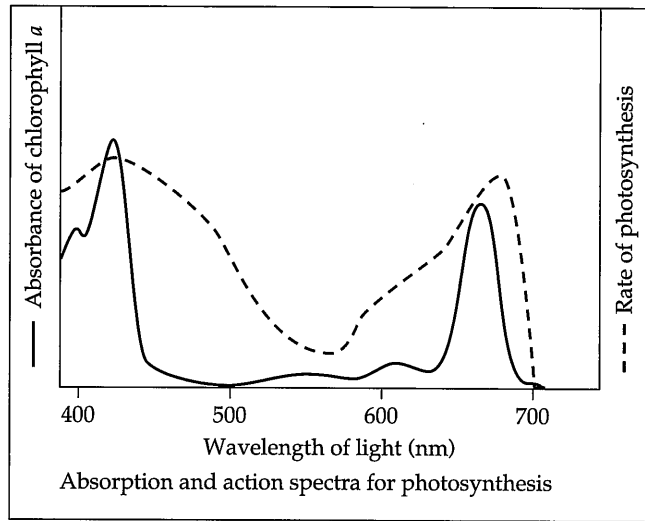
A photon of which color of light would contain more energy: orange (620 nm) or blue (480 nm)? Why?

Photosynthetic Pigments: The Light Receptors A **spectrophotometer** measures the amounts of light of different wavelengths absorbed by a pigment. The **absorption spectrum** of **chlorophyll a**, the pigment that participates directly in the light reactions, shows that it absorbs violet-blue and red light best. Accessory pigments such as **chlorophyll b** and some **carotenoids** absorb light of different wavelengths and broaden the spectrum of colors useful in photosynthesis. Some carotenoids function in photoprotection by absorbing excessive light energy that might damage chlorophyll or interact with oxygen to form reactive molecules. (These pigments act as antioxidants.)

■ INTERACTIVE QUESTION 10.4

An **action spectrum** shows the relative rates of photosynthesis under different wavelengths of light. Label the ab-

sorption and action spectra on this graph. Why are these lines different?



Excitation of Chlorophyll by Light When a pigment molecule absorbs energy from a photon, one of the molecule's electrons is elevated to an orbital where it has more potential energy. Only photons whose energy is equal to the difference between the ground state and the excited state for that molecule are absorbed.

The excited state is unstable. Energy is released as heat as the electron drops back to its ground-state orbital. Isolated chlorophyll molecules also emit photons of light, called fluorescence, as their electrons return to ground state.

A Photosystem: A Reaction Center Associated with Light-Harvesting Complexes Photosystems, located in the thylakoid membrane, contain a number of **light-harvesting complexes** and a **reaction-center**, a protein complex with two special chlorophyll *a* molecules and a **primary electron acceptor**. When a pigment molecule in a light-harvesting complex absorbs a photon, the energy is passed from pigment to pigment until it

reaches the reaction center. In a redox reaction, an excited electron of a reaction-center chlorophyll *a* is trapped by the primary electron acceptor before it can return to the ground state.

There are two types of photosystems in the thylakoid membrane. The chlorophyll *a* molecule at the reaction center of **photosystem II (PSII)** is called P680, after the wavelength of light (680 nm) it absorbs best. At the reaction center of **photosystem I (PSI)** is a chlorophyll *a* molecule called P700.

INTERACTIVE QUESTION 10.5

Describe the components of a photosystem.

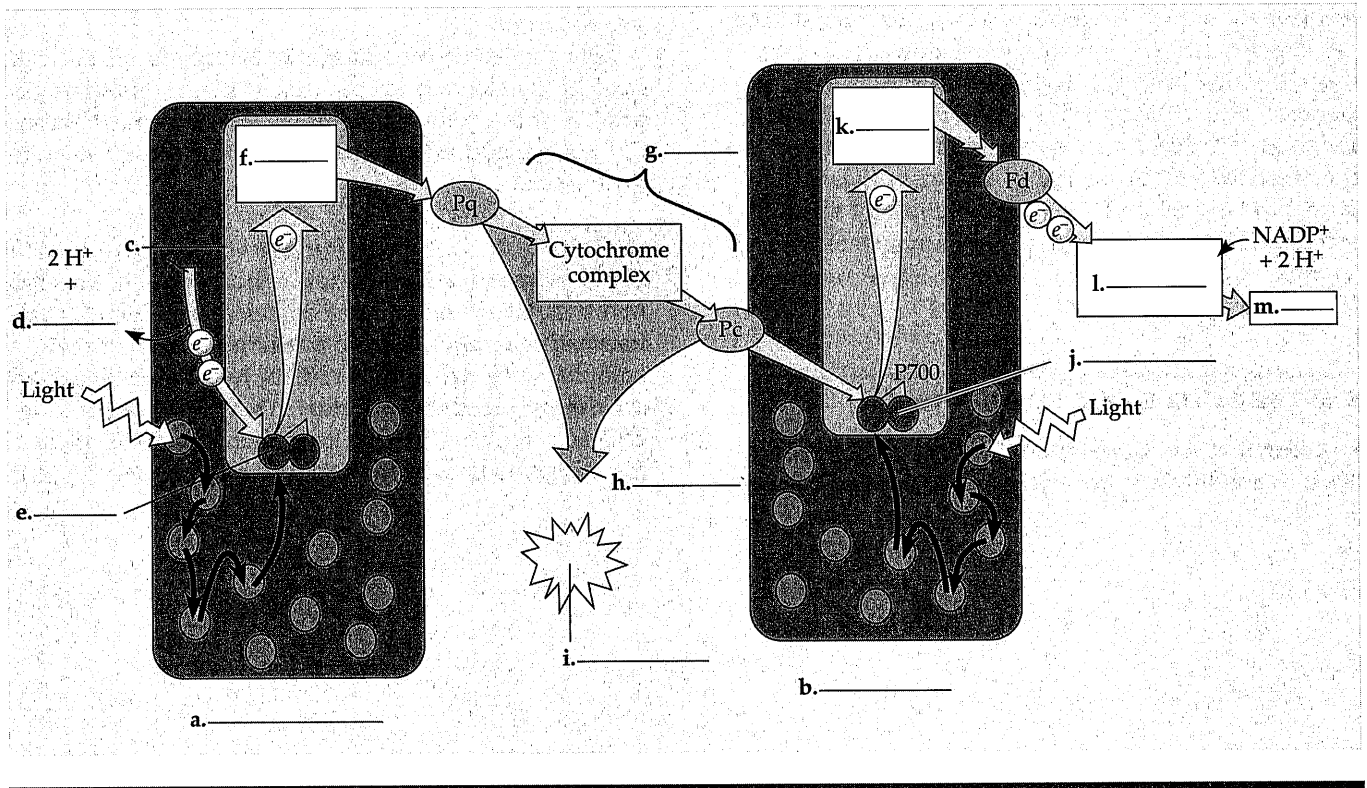
Noncyclic Electron Flow In **noncyclic electron flow**, electrons pass continuously from water to NADP^+ . An excited electron of P680 in photosystem II is trapped by the primary electron acceptor. P680 is a strong oxidizing agent, and its electron hole is filled when an enzyme removes electrons from water, splitting it into two electrons, two H^+ and an oxygen atom that immediately combines with another oxygen to form O_2 .

The primary electron acceptor passes the photoexcited electron to an electron transport chain made up of plastoquinone (Pq), a cytochrome complex, and plastocyanin (Pc). The energy released as electrons “fall” through the electron transport chain is used in the synthesis of ATP.

At the bottom of the electron transport chain, the electron passes to P700 in photosystem I to replace the photoexcited electron captured by its primary electron acceptor. This primary electron acceptor passes the electron down a second electron transport chain through ferredoxin (Fd), from which the enzyme NADP^+ reductase transfers electrons to NADP^+ . (Review this electron path by completing Interactive Question 10.6.)

INTERACTIVE QUESTION 10.6

Fill in the steps of noncyclic electron flow in the diagram below. Circle the important products that will be used to provide chemical energy and reducing power to the Calvin cycle.



Cyclic Electron Flow In cyclic electron flow, electrons excited from P700 in PSI are passed from Fd to the cytochrome complex and back to P700. Neither NADPH nor O₂ is generated. The Calvin cycle requires more ATP than NADPH, and the additional ATP may be supplied by the cyclic flow of electrons, perhaps in response to a buildup of NADPH.

■ INTERACTIVE QUESTION 10.7

- On the diagram in Interactive Question 10.6 sketch the path that electrons from P700 take during cyclic electron flow.
 - Why is neither oxygen nor NADPH generated by cyclic electron flow?
 - How, then, is ATP produced by cyclic electron flow?
-

A Comparison of Chemiosmosis in Chloroplasts and Mitochondria Chemiosmosis in mitochondria and in chloroplasts is very similar. The key difference is that in respiration, chemical energy from food is transferred to ATP, whereas in chloroplasts light energy is transformed to the chemical energy of ATP.

In chloroplasts, the electron transport chain pumps protons from the stroma into the thylakoid space. As H⁺ diffuses back through ATP synthase, ATP is formed on the stroma side, where it is available for the Calvin cycle.

■ INTERACTIVE QUESTION 10.8

- In the light, the proton gradient across the thylakoid membrane is as great as 3 pH units. On which side is the pH lowest?
 - What three factors contribute to the formation of this large difference in H⁺ concentration between the thylakoid space and the stroma?
-

10.3 The Calvin cycle uses ATP and NADPH to convert CO₂ to sugar

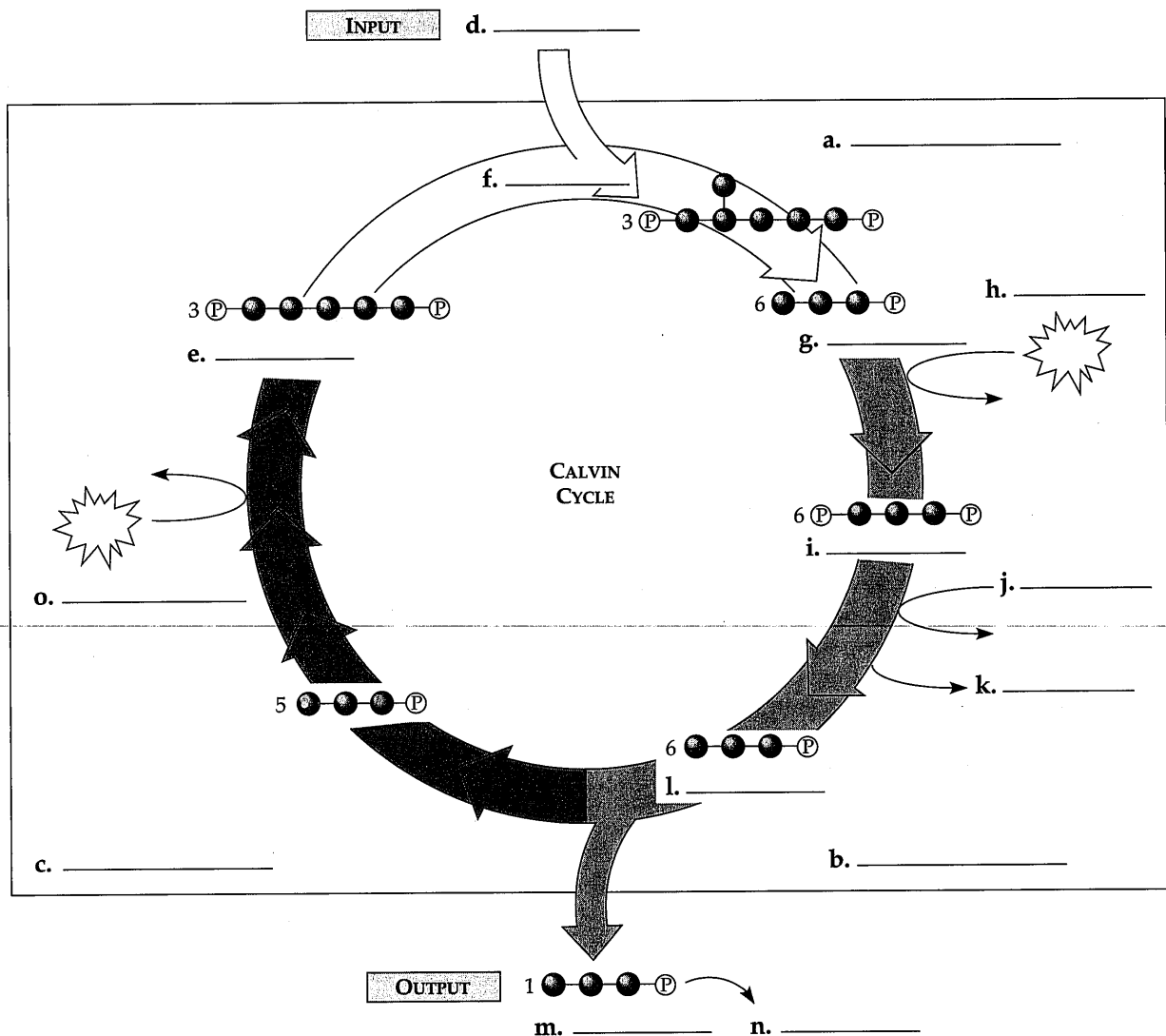
The Calvin cycle turns three times to fix three molecules of CO₂ and produce one molecule of the three-carbon sugar **glyceraldehyde-3-phosphate (G3P)**. The cycle can be divided into three phases:

- Carbon fixation:** CO₂ is added to a five-carbon sugar, ribulose biphosphate (RuBP), in a reaction catalyzed by the enzyme RuBP carboxylase (**rubisco**). The unstable six-carbon intermediate that is formed splits into two molecules of 3-phosphoglycerate.
- Reduction:** Each molecule of 3-phosphoglycerate is then phosphorylated by ATP to form 1,3-bisphosphoglycerate. Two electrons from NADPH reduce this compound to create G3P. The cycle must turn three times to create a net gain of one molecule of G3P.
- Regeneration of CO₂ acceptor (RuBP):** The rearrangement of five molecules of G3P into the three molecules of RuBP requires three more ATP.

Nine molecules of ATP and six of NADPH are required to synthesize one G3P. (To review this process, complete the summary diagram of the Calvin cycle in Interactive Question 10.9.)

INTERACTIVE QUESTION 10.9

Label the three phases (a through c) and key molecules (d through o) in this diagram of the Calvin cycle.



10.4 Alternative mechanisms of carbon fixation have evolved in hot, arid climates

Photorespiration: An Evolutionary Relic? In most plants, CO₂ enters the Calvin cycle and the first product of carbon fixation is 3-phosphoglycerate. When these C₃ plants close their stomata on hot, dry days to limit water loss, CO₂ concentration in the leaf air spaces falls, slowing the Calvin cycle. As more O₂ than CO₂ accumulates, rubisco adds O₂ in place of CO₂ to RuBP. The product splits and a two-carbon compound leaves the chloroplast and is broken down to release CO₂. This seemingly wasteful process is called **photorespiration**.

INTERACTIVE QUESTION 10.10

What possible explanation is there for photorespiration, a process that can result in the loss of as much as 50% of the carbon fixed in the Calvin cycle?

C₄ Plants In C₄ plants, CO₂ is first added to a 3-carbon compound, PEP, with the aid of an enzyme (**PEP carboxylase**) that has a high affinity for CO₂. The

resulting four-carbon compound formed in the **mesophyll cells** of the leaf is transported to **bundle-sheath cells** tightly packed around the veins of the leaf. The compound is broken down to release CO_2 , creating concentrations high enough that rubisco will accept CO_2 rather than O_2 and initiate the Calvin cycle.

■ INTERACTIVE QUESTION 10.11

- Where does the Calvin cycle take place in C_4 plants?
- How can C_4 plants successfully perform the Calvin cycle in hot, dry conditions when C_3 plants would be undergoing photorespiration?

CAM Plants Many succulent plants close their stomata during the day to prevent water loss, but open them at night to take up CO_2 and incorporate it into a variety of organic acids. **CAM plants** break these compounds down to release CO_2 during daylight so that the Calvin cycle can proceed. Unlike the C_4 pathway, the **crassulacean acid metabolism (CAM)** pathway does not structurally separate carbon fixation from the Calvin cycle; instead, the two processes are separated in time.

The Importance of Photosynthesis: A Review

About 50% of the organic material produced by photosynthesis is used as fuel for cellular respiration in the mitochondria of plant cells; the rest is used as carbon skeletons for synthesis of organic molecules (proteins, lipids, and a great deal of cellulose), stored as starch, or lost through photorespiration. About 160 billion metric tons of carbohydrate per year are produced by photosynthesis.

Word Roots

- auto-** = self; **-troph** = food (*autotroph*: an organism that obtains organic food molecules without eating other organisms)
- chloro-** = green; **-phyll** = leaf (*chlorophyll*: photosynthetic pigment in chloroplasts)
- electro-** = electricity; **magnet-** = magnetic (*electromagnetic spectrum*: the entire spectrum of radiation)
- hetero-** = other (*heterotroph*: an organism that obtains organic food molecules by eating other organisms or their by-products)

- meso-** = middle (*mesophyll*: the green tissue in the middle, inside of a leaf)
- photo-** = light (*photosystem*: cluster of pigment molecules)

Structure Your Knowledge

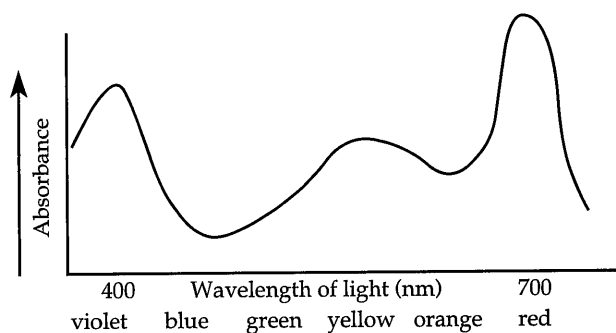
- You have already filled in the blanks in several diagrams of photosynthesis. To really understand this process, however, you should create your own representation. In a diagrammatic form, outline the key events of photosynthesis. Trace the flow of electrons through photosystem II and I, the production of ATP and NADPH by the light reactions and their transfer into the Calvin cycle, and the major steps in the production of G3P. Note where these reactions occur in the chloroplast. You can compare your creation to the sketch in the answer section. Then talk a friend through the steps in your diagram. Perhaps your study group can combine several representations into a clear, concise summary of this chapter.
- Create a concept map to confirm your understanding of the chemiosmotic synthesis of ATP in photophosphorylation.

Test Your Knowledge

MULTIPLE CHOICE: Choose the one best answer.

- Which of the following is mismatched with its location?
 - light reactions—grana
 - electron transport chain—thylakoid membrane
 - Calvin cycle—stroma
 - ATP synthase—double membrane surrounding chloroplast
 - splitting of water—thylakoid space
- Photosynthesis is a redox process in which
 - CO_2 is reduced and water is oxidized.
 - NADP^+ is reduced and RuBP is oxidized.
 - CO_2 , NADP^+ , and water are reduced.
 - O_2 acts as an oxidizing agent and water acts as a reducing agent.
 - G3P is reduced and the electron transport chain is oxidized.

3. Blue light has more energy than red light. Therefore, blue light
 - a. has a longer wavelength than red light.
 - b. has a shorter wavelength than red light.
 - c. contains more photons than red light.
 - d. has a broader electromagnetic spectrum than red light.
 - e. is absorbed faster by chlorophyll *a*.
4. A spectrophotometer can be used to measure
 - a. the absorption spectrum of a substance.
 - b. the action spectrum of a substance.
 - c. the amount of energy in a photon.
 - d. the wavelength of visible light.
 - e. the efficiency of photosynthesis.
5. Accessory pigments within chloroplasts are responsible for
 - a. driving the splitting of water molecules.
 - b. absorbing photons of different wavelengths of light and passing that energy to P680 or P700.
 - c. providing electrons to the reaction-center chlorophyll after photoexcited electrons pass to NADP⁺.
 - d. pumping H⁺ across the thylakoid membrane to create a proton-motive force.
 - e. anchoring chlorophyll *a* within the reaction center.
6. Below is an absorption spectrum for an unknown pigment molecule. What color would this pigment appear to you?



- a. violet
 - b. blue
 - c. green
 - d. yellow
 - e. red
7. Noncyclic electron flow along with chemiosmosis in the chloroplast results in the production of
 - a. ATP only.
 - b. ATP and NADPH.
 - c. ATP and G3P.
 - d. ATP and O₂.
 - e. ATP, NADPH, and O₂.
 8. The chlorophyll known as P680 has its electron "holes" filled by electrons from
 - a. photosystem I.
 - b. photosystem II.
 - c. water.
 - d. NADPH.
 - e. accessory pigments.
 9. CAM plants avoid photorespiration by
 - a. fixing CO₂ into organic acids during the night; these acids then release CO₂ during the day.
 - b. performing the Calvin cycle at night.
 - c. fixing CO₂ into four-carbon compounds in the mesophyll, which release CO₂ in the bundle-sheath cells.
 - d. using PEP carboxylate to fix CO₂ to ribulose bisphosphate (RuBP).
 - e. keeping their stomata closed during the day.
 10. Electrons that flow through the two photosystems have their highest potential energy in
 - a. water.
 - b. P680.
 - c. NADPH.
 - d. the electron transport chain.
 - e. photoexcited P700.
 11. Chloroplasts can make carbohydrate in the dark if provided with
 - a. ATP and NADPH and CO₂.
 - b. an artificially induced proton gradient.
 - c. organic acids or four-carbon compounds.
 - d. a source of hydrogen.
 - e. photons and CO₂.
 12. In the chemiosmotic synthesis of ATP in chloroplast, H⁺ diffuses through the ATP synthase
 - a. from the stroma into the thylakoid space.
 - b. from the thylakoid space into the stroma.
 - c. from the intermembrane space into the matrix.
 - d. from the cytoplasm into the intermembrane space.
 - e. from the matrix into the stroma.
 13. In C₄ plants, the Calvin cycle
 - a. takes place at night.
 - b. only occurs when the stomata are closed.
 - c. takes place in the mesophyll cells.
 - d. takes place in the bundle-sheath cells.
 - e. uses PEP carboxylase instead of rubisco because of its greater affinity for CO₂.

14. How many "turns" of the Calvin cycle are required to produce one molecule of glucose?
- 1
 - 2
 - 3
 - 6
 - 12
15. In green plants, most of the ATP for synthesis of proteins, cytoplasmic streaming, and other cellular activities comes directly from
- photosystem I.
 - photosystem II.
 - the Calvin cycle.
 - oxidative phosphorylation.
 - photophosphorylation.
16. Six molecules of G3P formed in the Calvin cycle are used to produce
- three molecules of glucose.
 - three molecules of RuBP and one G3P.
 - one molecule of glucose and four molecules of 3-phosphoglycerate.
 - one G3P and three four-carbon intermediates.
 - none of the above, since three molecules of G3P result from three turns of the Calvin cycle.
17. A difference between electron transport in photosynthesis and respiration is that in photosynthesis
- NADPH rather than NADH passes electrons to the electron transport chain.
 - ATP synthase releases ATP into the stroma rather than into the cytosol.
 - light provides the energy to push electrons to the top of the electron chain, rather than energy from the oxidation of food molecules.
 - an H^+ concentration gradient rather than a proton-motive force drives the phosphorylation of ATP.
 - both a and c are correct.
18. NADPH and ATP from the light reactions are both needed
- in the carbon fixation stage to provide energy and reducing power to rubisco.
 - to regenerate three RuBP from five G3P (glyceraldehyde-3-phosphate).
 - to combine two molecules of G3P to produce glucose.
 - to reduce 3-phosphoglycerate to G3P.
 - to reduce the H^+ concentration in the stroma and contribute to the proton-motive force.
19. What portion of an illuminated plant cell would you expect to have the lowest pH?
- nucleus
 - cytosol
 - chloroplast
 - stroma of chloroplast
 - thylakoid space
20. How does cyclic electron flow differ from non-cyclic electron flow?
- No NADPH is produced by cyclic electron flow.
 - No O_2 is produced by cyclic electron flow.
 - The cytochrome complex in the electron transport chain is not involved in cyclic electron flow.
 - Both a and b are correct.
 - a, b, and c are correct.
21. What does rubisco do?
- reduces CO_2 to G3P
 - regenerates RuBP with the aid of ATP
 - combines electrons and H^+ to reduce $NADP^+$ to NADPH
 - adds CO_2 to RuBP in the carbon fixation stage
 - transfers electrons from NADPH to 1,3-bisphosphoglycerate to produce G3P
22. What are the final electron acceptors for the electron transport chains in the light reactions of photosynthesis and in cellular respiration?
- O_2 in both
 - CO_2 in both
 - H_2O in the light reactions and O_2 in respiration
 - P700 and $NADP^+$ in the light reactions and NAD^+ or FAD in respiration
 - $NADP^+$ in the light reactions and O_2 in respiration
- Use the following for questions 23 through 28.
- Indicate if the following events occur during
- respiration
 - photosynthesis
 - both respiration and photosynthesis
 - neither respiration nor photosynthesis
- _____ 23. Chemiosmotic synthesis of ATP
- _____ 24. Reduction of oxygen
- _____ 25. Reduction of CO_2
- _____ 26. Reduction of NAD^+
- _____ 27. Oxidation of $NADP^+$
- _____ 28. Oxidative phosphorylation