Chapter 10

Photosynthesis

Key Concepts

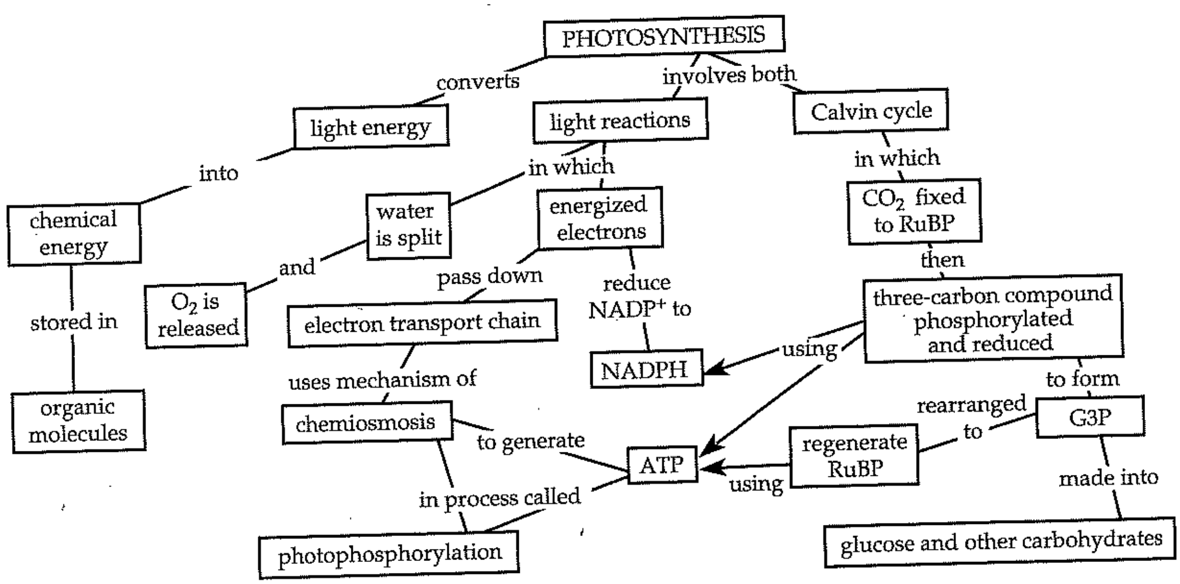
10.1 Photosynthesis converts light energy to the chemical energy of food

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

10.3 The Calvin cycle uses the chemical energy of ATP and NADPH to reduce CO_2 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. **Autotrophs** "feed themselves" in the sense that they make their own organic molecules from inorganic raw materials. Autotrophs are the *producers* of the biosphere. Plants, algae, some other unicellular eukaryotes, and some prokaryotes are photoautotrophs.

Heterotrophs are *consumers.* They may eat plants or animals or decompose organic litter, but almost all ultimately depend on photoautotrophs for food and O_2.

10.1 Photosynthesis converts light energy to the chemical energy of food

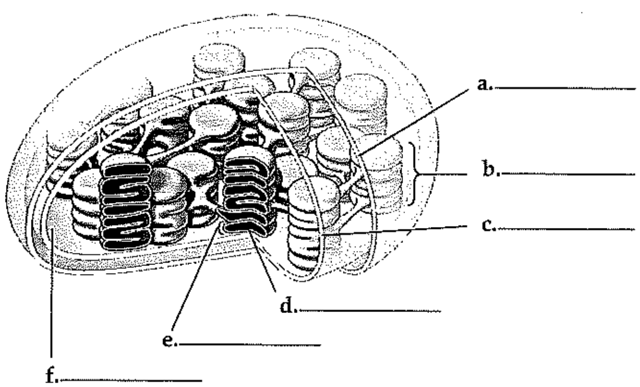
The first photosynthetic organisms were likely bacteria with clusters of photosynthetic enzymes and other molecules embedded in infoldings of the plasma membrane.

Chloroplasts: The Sites of Photosynthesis in Plants Chloroplasts are located mainly in the **mesophyll** tissue of the leaf. CO_2 enters and O_2 exits the leaf through **stomata.** Veins carry water from the roots to the leaves and distribute sugar to nonphotosynthetic tissue.

A chloroplast consists of a double membrane surrounding a dense fluid called the **stroma** and a membrane system of sacs called **thylakoids,** which encloses the *thylakoid space.* Thylakoid sacs may be stacked to form *grana.* **Chlorophyll,** the green pigment that absorbs the light energy that drives photosynthesis, is embedded in the thylakoid membrane.

INTERACTIVE QUESTION 10.1

Label the indicated parts in the following diagram of a chloroplast.



Tracking Atoms Through Photosynthesis: Scientific Inquiry Taking into account only the net consumption of water and considering glucose as the product (even though the direct product is a three-carbon sugar), the equation for photosynthesis is the reverse of respiration:

$$6\ CO_2 + 6\ H_2O + \text{Light energy} \rightarrow C_6H_{12}O_6 + 6\ O_2$$

The simplest equation is $CO_2 + H_2O \rightarrow [CH_2O] + O_2$.

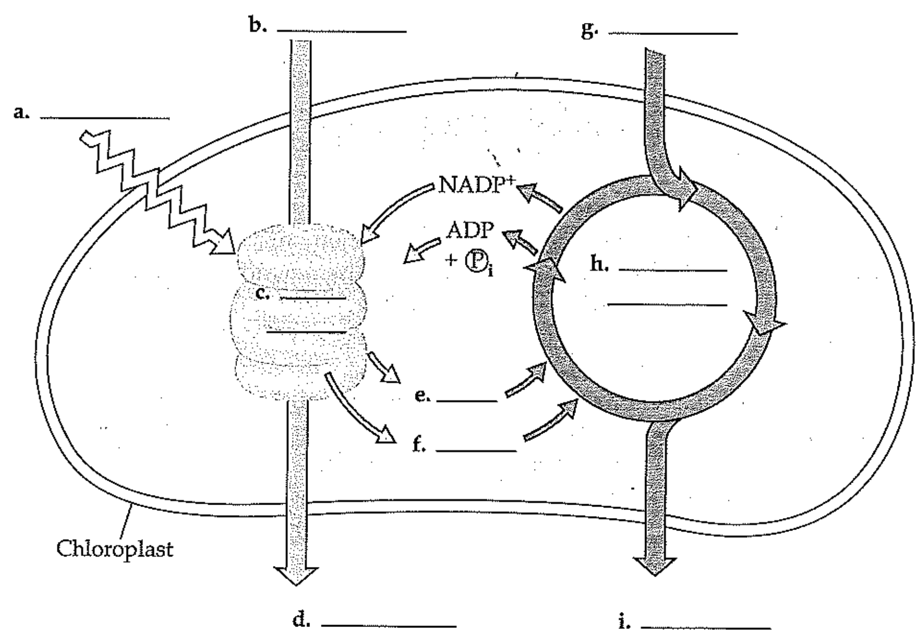
Using evidence from bacteria that utilize hydrogen sulfide (H_2S) for photosynthesis, C. B. van Niel hypothesized that photosynthetic organisms need a hydrogen source and that plants use H_2O as their hydrogen source and release O_2. This hypothesis was later confirmed by experiments that used a heavy isotope of oxygen (^{18}O). Labeled O_2 was produced only when water, but not carbon dioxide, contained ^{18}O.

Photosynthesis, like respiration, is a redox process, but it 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 the energy for this endergonic process.

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 ions from water to the electron acceptor **$NADP^+$**, which is reduced to NADPH and temporarily stores electrons. Oxygen is released when water is split. ATP is formed

INTERACTIVE QUESTION 10.2

Fill in the blanks in the following overview of photosynthesis in a chloroplast. Indicate the locations of the stages c and h.



during the light reactions, using chemiosmosis in a process called **photophosphorylation.**

In the **Calvin cycle,** CO_2 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.

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 electric and magnetic fields. The distance between the crests of electromagnetic waves, called their **wavelength,** ranges across the **electromagnetic spectrum,** from short gamma waves to long radio waves. The small band of radiation from about 380 nm to 750 nm is called **visible light** and is the radiation that drives photosynthesis.

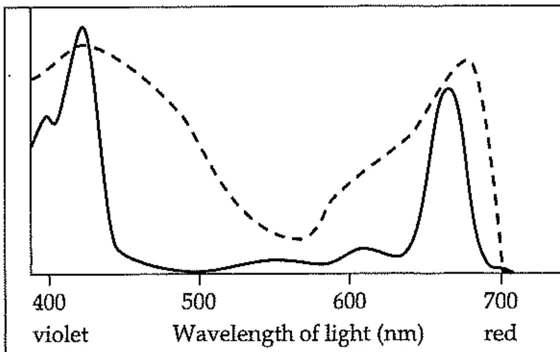
Light also behaves as if it consists of discrete particles called **photons,** which have a fixed quantity of energy. The amount of energy in a photon is inversely related to its wavelength.

Photosynthetic Pigments: The Light Receptors *Pigments* are substances that absorb light. A **spectrophotometer** measures the amount 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 accessory pigments called **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.)

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 the ground state.

INTERACTIVE QUESTION 10.3

An **action spectrum** shows the relative rates of photosynthesis under different wavelengths of light. The following graph includes both an absorption spectrum and an action spectrum. Label the left *y*-axis for the absorption spectrum and the right *y*-axis for the action spectrum. Then indicate the line that represents the absorption spectrum for chlorophyll *a* and the line for the action spectrum for photosynthesis. Why are these lines different?



Absorption and action spectra for photosynthesis

A Photosystem: A Reaction-Center Complex Associated with Light-Harvesting Complexes Embedded in thylakoid membranes are numerous **photosystems,** each composed of several **light-harvesting complexes** and a **reaction-center complex.** A reaction-center complex contains 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. What happens then? In a redox reaction, an excited electron from the reaction-center chlorophyll *a* pair is captured 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* molecules of the reaction center of **photosystem II (PSII)** are called P680, after the wavelength of light (680 nm) they absorb best. At the reaction center of **photosystem I (PSI)** are chlorophyll *a* molecules called P700.

INTERACTIVE QUESTION 10.4

Describe the components of a photosystem.

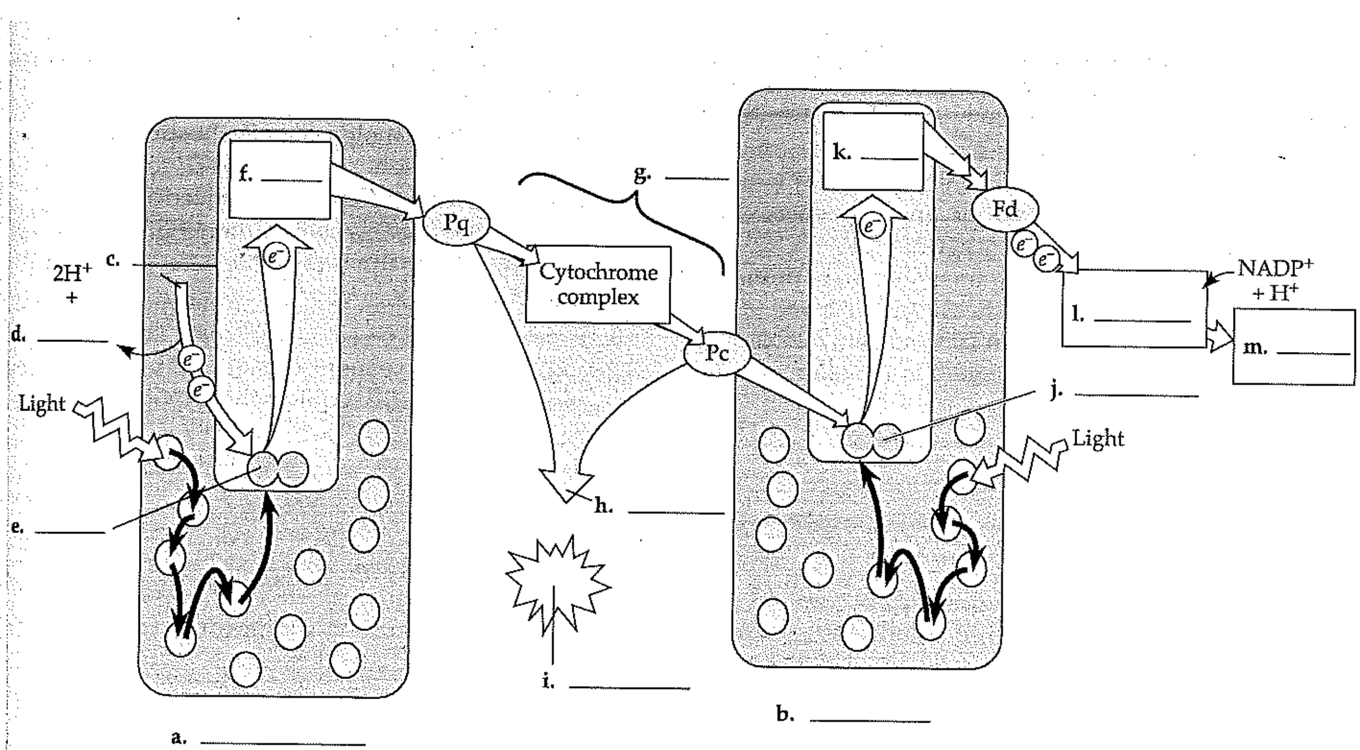
Linear Electron Flow Through a sequence called **linear electron flow,** electrons pass from water to $NADP^+$ through the two photosystems. A pigment molecule absorbs a photon of light, and the energy is relayed through other pigment molecules of the light-harvesting complex to the P680 pair of chlorophyll *a* molecules in the PS II reaction-center complex. An excited electron of P680 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 atom 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 to pump protons into the thylakoid space, contributing to the proton gradient used for the synthesis of ATP.

At the bottom of the electron transport chain, the electron passes to $P700^+$ in photosystem I. It replaces the photoexcited electron that was captured by its primary electron acceptor when PSI absorbed a photon. This primary electron acceptor passes the electron down a second electron transport chain through ferredoxin (Fd), from which the enzyme $NADP^+$ reductase transfers two electrons to reduce $NADP^+$ to NADPH.

INTERACTIVE QUESTION 10.5

Identify the components of linear electron flow in the following diagram. Circle the important products that will 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. Several groups of photosynthetic bacteria have only a single photosystem and generate ATP by cyclic electron flow. Photosynthesis may have evolved in a form similar to cyclic electron flow. Cyclic electron flow may be photoprotective in eukaryotic photosynthesizers.

INTERACTIVE QUESTION 10.6

a. On the diagram in Interactive Question 10.5, sketch the path that electrons from P700 take during cyclic electron flow.

b. Why is neither O_2 nor NADPH generated by cyclic electron flow?

c. 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. Electron transport chains built into a membrane pump protons across the membrane as electrons are passed down the chain in a series of redox reactions. In respiration, however, organic molecules provide the electrons, and chemical energy is transferred to ATP; in chloroplasts, by contrast, water provides the electrons, and 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 to the Calvin cycle.

INTERACTIVE QUESTION 10.7

a. In the light, the proton gradient across the thylakoid membrane is as great as 3 pH units. On which side is the pH lowest?

b. What three factors contribute to the formation of this large difference in H^+ concentration between the thylakoid space and the stroma?

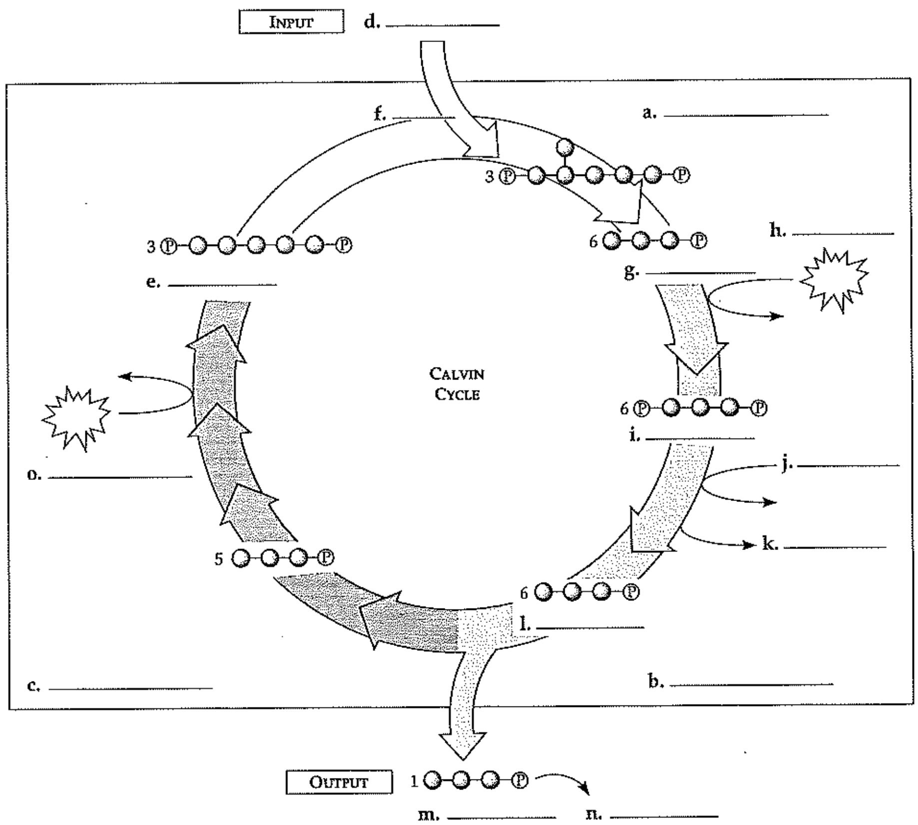
10.3 The Calvin cycle uses the chemical energy of ATP and NADPH to reduce CO_2 to sugar

It takes three turns of the Calvin cycle to fix three molecules of CO_2 and produce one molecule of the three-carbon sugar **glyceraldehyde-3-phosphate (G3P).** The cycle can be divided into three phases:

1. *Carbon fixation:* CO_2 is added to a five-carbon sugar, ribulose bisphosphate (RuBP), in a reaction catalyzed by the enzyme RuBP carboxylase-oxygenase (**rubisco**). The resulting unstable six-carbon intermediate splits into two molecules of 3-phosphoglycerate.
2. *Reduction:* Each molecule of 3-phosphoglycerate is then phosphorylated by ATP to form 1,3-bisphosphoglycerate. Two electrons from NADPH reduce this compound to G3P. The cycle must turn three times to create a net gain of one molecule of G3P.
3. *Regeneration of CO_2 acceptor (RuBP):* The rearrangement of five molecules of G3P into three molecules of RuBP requires three more ATP.

INTERACTIVE QUESTION 10.8

Label the three phases (a, b, and c) and key molecules in the following diagram of the Calvin cycle. How many ATP and NADPH are needed to synthesize one G3P molecule?



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

Photorespiration: An Evolutionary Relic? In most plants, the first product of carbon fixation is a three-carbon compound, 3-phosphoglycerate, formed in the Calvin cycle. When these C_3 **plants** close their stomata on hot, dry days to limit water loss, CO_2 concentration in the leaf air spaces falls, slowing the Calvin cycle. As more O_2 than CO_2 accumulates, rubisco adds O_2 to RuBP in place of CO_2. The product splits, and a two-carbon compound exits the chloroplast and is broken down to release CO_2. This seemingly wasteful process is called **photorespiration.**

INTERACTIVE QUESTION 10.9

What are two possible explanations for the existence of photorespiration, a process that can result in the loss of as much as 50% of the carbon fixed in the Calvin cycle?

C_4 Plants In C_4 **plants,** CO_2 is first added to the three-carbon compound PEP, with the aid of an enzyme (**PEP carboxylase**) that has a high affinity for CO_2. 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, which rubisco then fixes in the Calvin cycle.

Increasing atmospheric CO_2 concentrations and the resulting global climate change with an increase in temperature may affect the distribution of C_3 and C_4 plants and change the structure of various plant communities.

INTERACTIVE QUESTION 10.10

a. Where does the Calvin cycle take place in C_4 plants?

b. How can C_4 plants successfully utilize the Calvin cycle in hot, dry conditions when C_3 plants would be undergoing photorespiration?

c. Why does C_4 photosynthesis requires more ATP than does C_3 photosynthesis?

CAM Plants Many desert succulent plants close their stomata during the day, helping to prevent water loss. At night, they open their stomata and take up CO_2, incorporating it into a variety of organic acids in a mode of carbon fixation called **crassulacean acid metabolism (CAM).** During daylight, **CAM plants** break these compounds down and release CO_2, allowing the Calvin cycle to proceed. Unlike the C_4 pathway, the 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 the synthesis of organic molecules (proteins, lipids, and a great deal of cellulose), stored as starch, or lost through photorespiration. Each year about 160 billion metric tons of carbohydrate are produced by photosynthesis.

Word Roots

auto- = self; **-troph** = food (*autotroph:* an organism that obtains organic food molecules without eating other organisms, but by using energy from the sun or from the oxidation of inorganic substances to make organic molecules from inorganic ones)

chloro- = green; **-phyll** = leaf (*chlorophyll:* a green, photosynthetic pigment located in membranes within the chloroplasts of plants and algae and in the membranes of certain prokaryotes)

electro- = electricity; **magnet-** = magnetic (*electromagnetic spectrum:* the entire spectrum of electromagnetic radiation, ranging in wavelength from less than a nanometer to more than a kilometer)

hetero- = other (*heterotroph:* an organism that obtains organic food molecules by eating other organisms or substances derived from them)

meso- = middle (*mesophyll:* leaf cells specialized for photosynthesis, located in C_3 and CAM plants between the upper and lower epidermis; in C_4 plants, they are located between the bundle-sheath cells and the epidermis)

photo- = light (*photosystem:* a light-capturing unit located in the thylakoid membrane, consisting of a reaction-center complex surrounded by numerous light-harvesting complexes)

Structure Your Knowledge

1. You have already filled in the blanks in several diagrams of photosynthesis. To really understand this process, however, try to create your own representation. In a diagrammatic form, trace the flow of electrons and the production of ATP and NADPH in the light reactions. Then outline the three major stages in the production of G3P. Indicate where these reactions occur in the chloroplast. You can compare your diagram to the sketch in the answers section. Perhaps your study group can collaboratively create a clear, concise summary of this chapter.

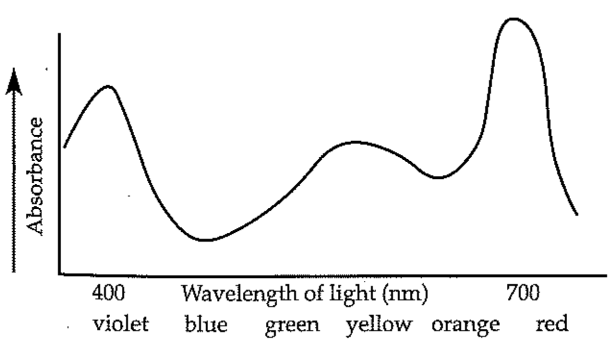
2. Create a concept map to confirm your understanding of the chemiosmotic synthesis of ATP in photophosphorylation.

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Which of the following processes or structures is mismatched with its location?
   a. electron transport chain—thylakoid membrane
   b. Calvin cycle—stroma
   c. ATP synthase—double membrane surrounding chloroplast
   d. splitting of water—thylakoid space

2. Photosynthesis is a redox process in which
   a. CO_2 is reduced and water is oxidized.
   b. $NADP^+$ is reduced and G3P is oxidized.
   c. CO_2, $NADP^+$, and water are reduced.
   d. O_2 acts as an oxidizing agent and water acts as a reducing agent.
3. Which of the following statements is *false*?
   a. When isolated chlorophyll molecules absorb photons, their electrons fall back to ground state, giving off heat and light.
   b. Accessory pigments, cyclic electron flow, and photorespiration may all contribute to photoprotection, protecting plants from the detrimental effects of intense light.
   c. In both photosynthetic prokaryotes and eukaryotes, ATP synthases catalyze the production of ATP within the cytosol of the cell.
   d. In sulfur bacteria, H_2S is the hydrogen (and thus electron) source for photosynthesis.
4. A spectrophotometer can be used to measure the
   a. absorption spectrum of a pigment.
   b. action spectrum of a reaction.
   c. amount of energy in a photon.
   d. wavelength of visible light.
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 *a* molecules.
   d. pumping H^+ across the thylakoid membrane to create a proton-motive force.
6. The following diagram is an absorption spectrum for an unknown pigment molecule. What color would this pigment appear to you?



   a. violet
   b. blue
   c. green
   d. red
7. Linear electron flow along with chemiosmosis in the chloroplast results in the formation of
   a. ATP only.
   b. ATP and NADPH.
   c. ATP and O_2.
   d. ATP, NADPH, and O_2.
8. The chlorophyll known as $P680^+$ has its electron "holes" filled by electrons from
   a. photosystem I.
   b. photosystem II.
   c. water.
   d. accessory pigments.
9. Which of the following substances is/are the final electron acceptor(s) for the electron transport chains in the light reactions of photosynthesis and in cellular respiration?
   a. O_2 in both
   b. H_2O in the light reactions, and O_2 in respiration
   c. P700 and $NADP^+$ in the light reactions, and NAD^+ or FAD in respiration
   d. $NADP^+$ in the light reactions, and O_2 in respiration
10. In photosynthesis, the splitting of water
    a. releases oxygen, which will be used in the Calvin cycle.
    b. provides electrons that reduce $NADP^+$ to NADPH.
    c. provides electrons that produce the electron gradient used in the chemiosmotic synthesis of ATP.
    d. occurs in photosystem II on the stroma side of the thylakoid membrane.
11. Which of the following parts of an illuminated plant cell would you expect to have the lowest pH?
    a. cytosol
    b. chloroplast
    c. stroma of chloroplast
    d. thylakoid space
12. A difference between electron transport in photosynthesis and respiration is that in photosynthesis,
    a. NADPH rather than NADH passes electrons to the electron transport chain.
    b. ATP synthase releases ATP into the stroma rather than into the cytosol.
    c. light provides the energy to push electrons to the top of the electron chain, rather than energy from the oxidation of food molecules.
    d. an H^+ concentration gradient rather than a proton-motive force drives the phosphorylation of ATP.

13. How does cyclic electron flow differ from linear electron flow?
   a. No NADPH is produced by cyclic electron flow.
   b. No O_2 is produced by cyclic electron flow.
   c. The cytochrome complex in the electron transport chain is not involved in cyclic electron flow.
   d. Both **a** and **b** are correct.

14. Chloroplasts could make carbohydrate in the dark if provided with
   a. ATP, NADPH, and CO_2.
   b. an artificially induced proton gradient.
   c. organic acids or four-carbon compounds.
   d. photons and CO_2.

15. The disaccharide sucrose is the form of carbohydrate transported throughout a plant body. How many turns of the Calvin cycle does it take to produce one molecule of sucrose?
   a. 2   c. 11
   b. 6   d. 12

16. Both NADPH and ATP from the light reactions are needed
   a. in the carbon fixation stage to provide energy and reducing power to rubisco.
   b. to regenerate three RuBP from five G3P.
   c. to combine two molecules of G3P to produce glucose.
   d. to reduce 3-phosphoglycerate to G3P.

17. RuBP carboxylase-oxygenase is the enzyme that
   a. can add O_2 to RuBP when CO_2 levels are low and O_2 levels are high.
   b. regenerates RuBP with the aid of ATP.
   c. adds CO_2 to RuBP in the carbon fixation stage.
   d. Both **a** and **c** are correct.

18. In C_4 plants,
   a. initial carbon fixation takes place in the mesophyll cells.
   b. photorespiration requires more energy than it does in C_3 plants.
   c. the Calvin cycle, which takes place in the bundle-sheath cells, uses PEP carboxylase instead of rubisco because of its greater affinity for CO_2.
   d. All of the above are correct.

19. CAM plants avoid photorespiration by
   a. keeping their stomata closed during the day.
   b. performing the Calvin cycle at night.
   c. fixing CO_2 into four-carbon compounds in the mesophyll, which then release CO_2 in the bundle-sheath cells.
   d. fixing CO_2 into organic acids during the night, which then provide CO_2 during the day.

20. In green plants, most of the ATP for synthesis of proteins, cytoplasmic streaming, and other cellular activities comes directly from
   a. photosystem II.
   b. cyclic electron flow.
   c. oxidative phosphorylation.
   d. photophosphorylation.

For each of the events listed in questions 21 through 26, indicate whether the event occurs during
   a. respiration
   b. photosynthesis
   c. both respiration and photosynthesis
   d. neither respiration nor photosynthesis

21. Chemiosmotic synthesis of ATP
22. Reduction of oxygen
23. Oxidative phosphorylation
24. Reduction of CO_2
25. Oxidation of NAD^+
26. Reduction of $NADP^+$