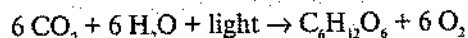


Photosynthesis

Review

Like cellular respiration, photosynthesis requires that you apply your knowledge of chemistry. Again, you will need to know the names of important molecules, describe their sequence in metabolic processes, and describe how the processes accomplish their metabolic objectives.

Photosynthesis is the process of capturing free energy in sunlight and storing that energy in chemical bonds, especially glucose. The general chemical equation describing photosynthesis is



Note that this equation for photosynthesis is the reverse of the equation for cellular respiration, except that the energy required by photosynthesis comes from light. The processes are interconnected: Energy stored in chemical bonds by photosynthesis is extracted from those bonds by respiration to make adenosine triphosphate (ATP). The energy in ATP is then used to do cellular work through metabolic processes.

The process of photosynthesis begins with light-absorbing pigments in chloroplasts of plant cells. A pigment molecule is able to absorb the energy from light only within a narrow range of wavelengths. The dominant light-absorbing pigment is the green chlorophyll *a*, while other accessory pigments include other chlorophylls and various red, orange, and yellow carotenoids. Together, these pigments complement each other to maximize energy absorption across the sunlight spectrum. When light is absorbed by one of these pigments, the energy from the light is incorporated into electrons within the atoms that make up the molecule. These energized electrons (or "excited" electrons) are unstable and almost immediately re-emit the absorbed energy. The energy is then reabsorbed by electrons of a nearby pigment molecule. The process of energy absorption, followed by energy re-emission, continues, with the energy bouncing from one pigment molecule to another. The process ends when the energy is absorbed by one of two special chlorophyll *a* molecules, P_{680} or P_{700} . These two chlorophyll molecules, named with numbers that represent the wavelengths at which they absorb their maximum amounts of light (680 and 700 nanometers, respectively), are different from other chlorophyll molecules because of their association with various nearby pigments. Together with these other pigments, chlorophyll P_{700} forms a pigment cluster called photosystem I (PS I). Chlorophyll P_{680} forms photosystem II (PS II).

Photosynthesis includes the following processes:

1. **Noncyclic photophosphorylation** and **cyclic photophosphorylation** use H_2O and the energy in sunlight to generate ATP, NADPH, and O_2 .
2. The **Calvin cycle** uses CO_2 and the energy in ATP and NADPH to make glucose.

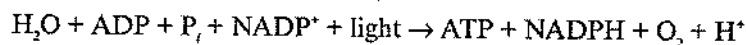
The chemical reactions for photosynthesis are illustrated in Figure 5-1. Refer to the figure as you read the following descriptions of the metabolic processes.

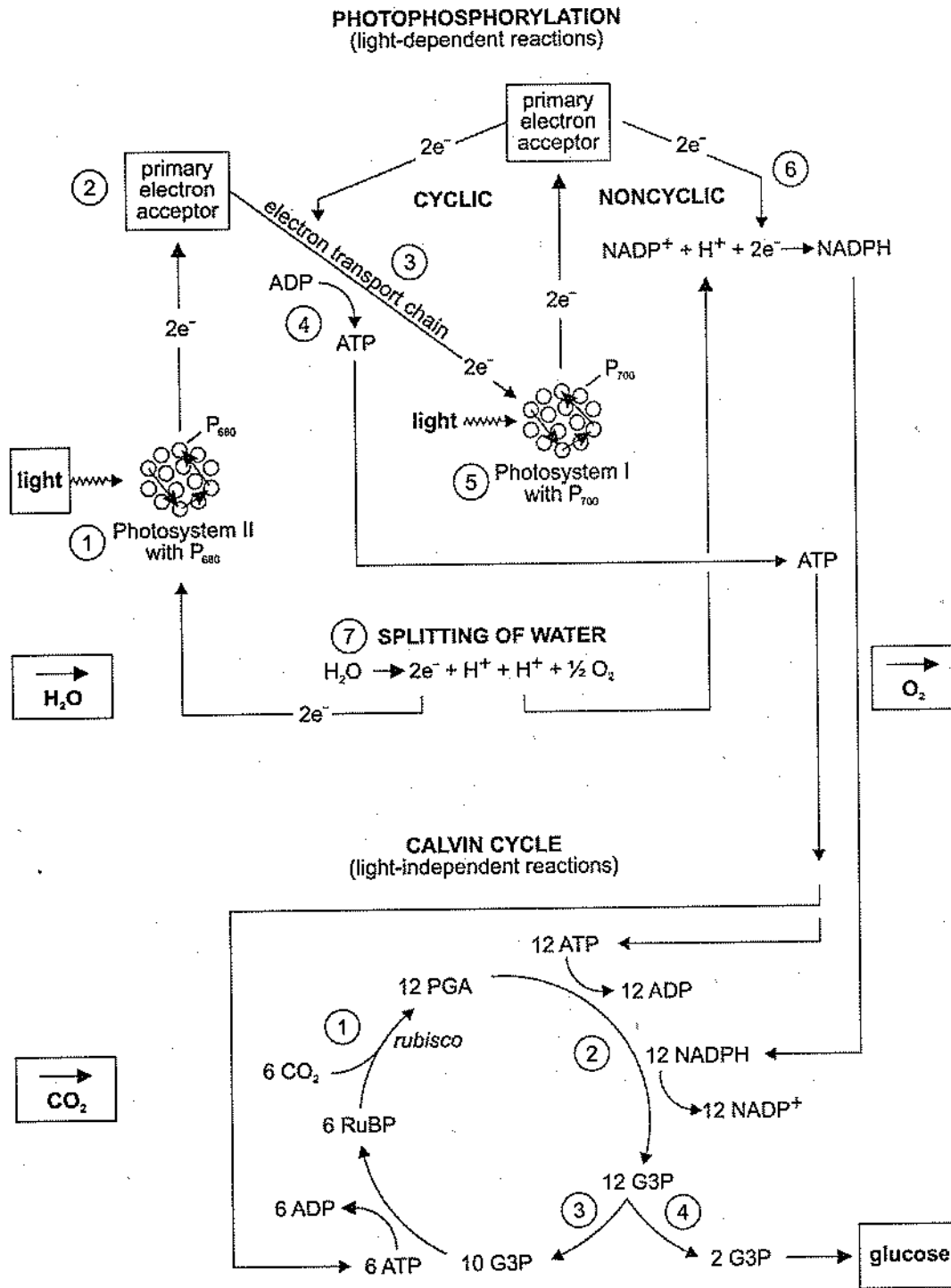
Noncyclic Photophosphorylation

Photophosphorylation is the process of using energy derived from light (photo) to generate ATP from adenosine diphosphate (ADP) and P_i (phosphorylation). Noncyclic photophosphorylation begins with PS II and follows these seven steps:

1. **Photosystem II.** Electrons trapped by P₆₈₀ in photosystem II are energized by light. In Figure 5-1, two electrons are shown moving “up,” signifying an increase in their energy.
2. **Primary electron acceptor.** Two energized electrons are passed to a molecule called the primary electron acceptor. This electron acceptor is called “primary” because it is the first in a chain of electron acceptors.
3. **Electron transport chain.** Electrons pass through an electron transport chain (ETC). This chain consists of proteins in the thylakoid membrane of the chloroplast that pass electrons from one carrier protein to the next. Some carrier proteins, such as the **cytochromes**, include nonprotein parts containing iron. The electron transport chains in photosynthesis are analogous to those in the inner mitochondrial membrane in oxidative phosphorylation.
4. **Phosphorylation.** As the two electrons move “down” the electron transport chain, they lose energy. The energy lost by the electrons as they pass along the electron transport chain is used to phosphorylate, on average, about 1.5 ATP molecules.
5. **Photosystem I.** The electron transport chain terminates with PS I (with P₇₀₀). Here the electrons are again energized by sunlight and passed to a primary electron acceptor (different from the one associated with PS II).
6. **NADPH.** The two electrons pass through a short electron transport chain. At the end of the chain, the two electrons combine with the coenzyme NADP⁺ and H⁺ to form NADPH. Like NADH in respiration, NADP⁺ is an electron acceptor that becomes energy-rich when it accepts these electrons. (You can keep the two coenzymes NADH and NADPH associated with the correct processes by using the P in NADPH as a reminder of the P in photosynthesis. The P in NADPH, however, actually represents phosphorus.)
7. **Splitting of water.** The two electrons that originated in PS II are now incorporated into NADPH. The loss of these two electrons from PS II is replaced when H₂O is split into two electrons, 2 H⁺ and ½ O₂. The two electrons from H₂O replace the lost electrons from PS II, one of the H⁺ provides the H in NADPH and the H in NADPH, and the ½ O₂ contributes to the oxygen gas that is released.

In summary, photophosphorylation takes the energy in light and the electrons in H₂O to make the energy-rich molecules ATP and NADPH. Because the reactions require light, they are often called **light-dependent reactions** or, simply, **light reactions**. The following equation informally summarizes the process:





Photosynthesis
Figure 5-1

Cyclic Photophosphorylation

A second photophosphorylation sequence (shown in Figure 5-1) occurs when the electrons energized in PS I are "recycled." In this sequence, energized electrons from PS I join with protein carriers and generate ATP as they pass along the electron transport chain. In contrast to noncyclic photophosphorylation, where electrons become incorporated into NADPH, electrons in cyclic photophosphorylation return to PS I. Here they can be energized again to participate in cyclic or noncyclic photophosphorylation. Cyclic photophosphorylation occurs simultaneously with noncyclic photophosphorylation to generate additional ATP. Two electrons passing through cyclic photophosphorylation generate, on average, about 1 ATP.

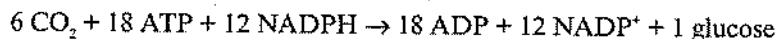
Calvin Cycle

The Calvin cycle "fixes" CO_2 . That is, it takes chemically unreactive, inorganic CO_2 and incorporates it into an organic molecule that can be used in biological systems. The biosynthetic pathway produces a single molecule of glucose ($\text{C}_6\text{H}_{12}\text{O}_6$). In order to accomplish this, the Calvin cycle must repeat six times, and use 6 CO_2 molecules. Thus, in Figure 5-1 and the discussion that follows, all the molecules involved have been multiplied by 6. Only the most important molecules are discussed:

1. **Carbon fixation:** 6 CO_2 combine with 6 RuBP to produce 12 PGA. The enzyme rubisco catalyzes the merging of CO_2 and RuBP. The Calvin cycle is referred to as C_3 photosynthesis because the first product formed, PGA, contains three carbon atoms.
2. **Reduction:** 12 ATP and 12 NADPH are used to convert 12 PGA to 12 G3P. The energy in the ATP and NADPH molecules is incorporated into G3P, making G3P a very energy-rich molecule. ADP, P_i , and NADP^+ are released and then re-energized in noncyclic photophosphorylation.
3. **Regeneration:** 6 ATP are used to convert 10 G3P to 6 RuBP. Regenerating the 6 RuBP originally used to combine with 6 CO_2 allows the cycle to repeat.
4. **Carbohydrate synthesis.** Note that 12 G3P were created in step 2, but only 10 were used in step 3. What happened to the remaining two? These two remaining G3P are used to build glucose. Other monosaccharides, like fructose and maltose, can also be formed. In addition, glucose molecules can be combined to form disaccharides, like sucrose, and polysaccharides, like starch and cellulose.

You should recognize that no light is directly used in the Calvin cycle. Thus, these reactions are often called **light-independent reactions** or even **dark reactions**. But be careful—the Calvin cycle occurs in the presence of light. This is because it is dependent upon the energy from ATP and NADPH, and these two energy-rich molecules can be created only during photophosphorylation, which can occur only in light.

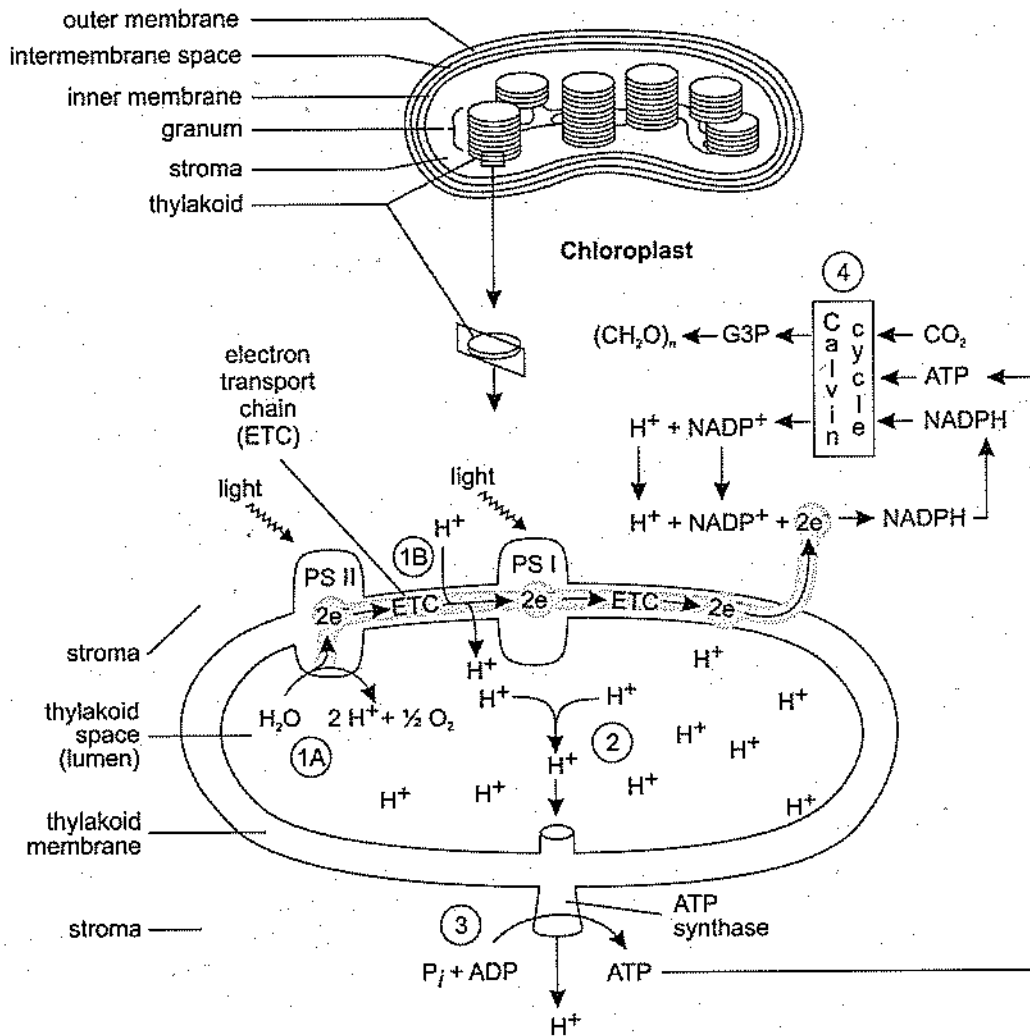
In summary, the Calvin cycle takes CO_2 from the atmosphere and the energy in ATP and NADPH to create a glucose molecule. Of course, the energy in ATP and NADPH represents energy from the sun captured during photophosphorylation. The Calvin cycle can be informally summarized as follows:



Chloroplasts

Chloroplasts are the sites where both the light-dependent and light-independent reactions of photosynthesis occur. Chloroplasts consist of the following areas (Figure 5-2):

1. **Outer membrane.** This membrane, like the plasma membrane, consists of a double layer of phospholipids.
2. **Intermembrane space.** This is the narrow area between the inner and outer membranes.
3. **Inner membrane.** This second membrane is also a double phospholipid bilayer.



Chemiosmosis in Chloroplasts

Figure 5-2

4. **Stroma.** The stroma is the fluid material that fills the area inside the inner membrane. The Calvin cycle occurs here, fixing carbon from CO₂ to generate G3P, the precursor to glucose.
5. **Thylakoids.** Suspended within the stroma are stacks of pancake-like membranes. Individual membrane layers (the “pancakes”) are **thylakoids**; an entire stack of thylakoids is a **granum** (plural, **grana**). The membranes of the thylakoids contain the protein complexes (including the photosystems PS I and PS II), cytochromes, and other electron carriers of the light-dependent reactions.
6. **Thylakoid lumen.** This is the inside, or lumen, of the thylakoid; H⁺ ions (protons) accumulate here.

Note how the spatial arrangement of the photosynthetic processes in chloroplasts is similar to that for the respiratory processes in mitochondria. In both cases, carrier proteins for electron transport chains are *embedded in membranes*. Also, enzymes for CO₂ processing occur in *fluids* adjacent to the membranes. Specifically, the enzymes for CO₂ utilization in the Calvin cycle occur in the stroma (*outside* the thylakoid membranes), while the enzymes for CO₂ generation in the Krebs cycle occur in the matrix (*inside* the cristae membranes).

Chemiosmosis in Chloroplasts

Chemiosmosis is the mechanism of ATP generation that occurs when energy is stored in the form of a *proton concentration gradient* across a membrane. The process in chloroplasts is analogous to ATP generation in mitochondria. The following four steps outline the process of photophosphorylation in chloroplasts (Figure 5-2):

1. **H⁺ ions (protons) accumulate inside thylakoids.** H⁺ are released into the inside space (lumen) of the thylakoid when water is split by PS II (see Figure 5-2, 1A). Also, H⁺ are carried from the stroma into the lumen by a cytochrome in the electron transport chain (ETC) between PS II and PS I (1B).
2. **A pH and electrical gradient across the thylakoid membrane is created.** As H⁺ accumulate inside the thylakoid, the pH *decreases*. Since some of these H⁺ come from outside the thylakoids (from the stroma), the H⁺ concentration decreases in the stroma and its pH *increases*. This creates a pH gradient consisting of differences in the concentration of H⁺ across the thylakoid membrane from a stroma pH 8 to a thylakoid pH 5 (a factor of 1,000). Since H⁺ ions are positively charged, their accumulation on the inside of the thylakoid creates an electric gradient (or voltage) as well.
3. **ATP synthase generates ATP.** The pH and electrical gradient represent potential energy, like water behind a dam. The channel protein ATP synthase allows the H⁺ to flow through the thylakoid membrane and out to the stroma. The energy generated by the passage of the H⁺ (like the water through turbines in a dam) provides the energy for the ATP synthase to phosphorylate ADP to ATP. The passage of about 3 H⁺ is required to generate 1 ATP.
4. **The Calvin cycle produces G3P using NADPH, CO₂, and ATP.** At the end of the electron transport chain following PS I, electrons combine with NADP⁺ and H⁺ to produce NADPH. With NADPH, ATP, and CO₂, 2 G3P are generated and subsequently used to make glucose or other carbohydrates, (CH₂O)_n.

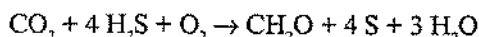
Photorespiration

Because of its critical function in catalyzing the fixation of CO₂ in all photosynthesizing plants, rubisco is the most common protein on Earth. However, it is not a particularly efficient molecule. In addition to its CO₂-fixing capabilities, it is also able to fix oxygen. The fixation of oxygen, a process called **photorespiration**, leads to two problems. The first is that the CO₂-fixing efficiency is reduced because, instead of fixing only CO₂, rubisco fixes some O₂ as well. The second problem is that the products formed when O₂ is combined with RuBP do not lead to the production of useful, energy-rich molecules like glucose. Instead, energy must be spent to break down the products of photorespiration inside specialized cellular organelles. Thus, considerable effort is made by plants to rid the cell of the products of photorespiration. Since the early atmosphere in which primitive plants originated contained very little oxygen, it is hypothesized that the early evolution of rubisco was not influenced by its O₂-fixing handicap.

Capturing Free Energy Without Light

Organisms that use *sunlight* as a source of free energy to drive photosynthesis and to produce carbohydrates are called **photoautotrophs**. Some prokaryotes, called **chemoautotrophs**, are able to use *inorganic substances* as a source of energy to generate organic molecules. This process, generally referred to as **chemosynthesis**, uses H₂S (hydrogen sulfide), NH₃ (ammonia), or NO₂⁻ (nitrite) as a source of energy.

One example of chemosynthesis occurs among symbiotic bacteria found growing in giant tube worms at deep ocean depths near hydrothermal vents. The bacteria use energy from H₂S to produce carbohydrates (shown here as CH₂O):



Review Questions

Multiple-Choice Questions

The questions that follow provide a review of the material presented in this chapter. Use them to evaluate how well you understand the terms, concepts, and processes presented. Actual AP multiple-choice questions are often more general, covering a broad range of concepts, and often more lengthy. For these types of questions, you should take the two practice exams in this book.

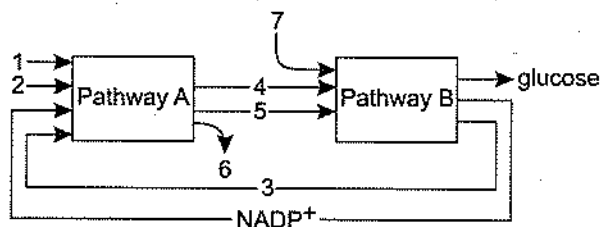
Directions: Each of the following questions or statements is followed by four possible answers or sentence completions. Choose the one best answer or sentence completion.

- Which of the following statements about photosynthetic pigments is true?
 - There is only one kind of chlorophyll.
 - Chlorophyll absorbs mostly green light.
 - Chlorophyll is found in the membranes of thylakoids.
 - P_{700} is a carotenoid pigment.
- When deciduous trees drop their leaves in the fall, the leaves turn to various shades of red, orange, and yellow. The source of these colors is
 - chlorophyll
 - carotenoids
 - fungal growth
 - natural decay of cell walls
- A product of noncyclic photophosphorylation is
 - NADPH
 - H_2O
 - CO_2
 - ADP
- Which of the following molecules contains the most stored energy?
 - ATP
 - NADPH
 - glucose
 - starch
- All of the following occur in cyclic photophosphorylation EXCEPT:
 - Electrons move along an electron transport chain.
 - Electrons in chlorophyll become excited.
 - ATP is produced.
 - NADPH is produced.

Questions 6–10 refer to the following lettered answer choices. Each answer may be used once, more than once, or not at all.

- A. cyclic photophosphorylation
 - B. noncyclic photophosphorylation
 - C. photorespiration
 - D. Calvin cycle
6. Combines O_2 with RuBP
 7. Stores energy obtained from light into NADPH
 8. Produces ATP without the need for H_2O and CO_2
 9. Occurs in the stroma of a chloroplast
 10. Requires electrons that are obtained by splitting water

Questions 11–14 refer to the following diagram. The two boxes represent the two major biosynthetic pathways in C_3 photosynthesis. Arrows represent reactants or products.

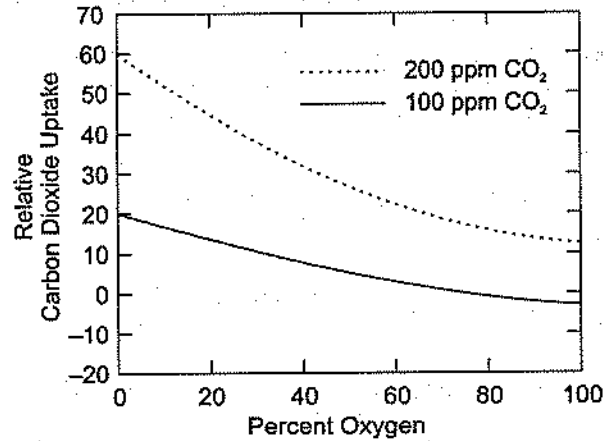


11. Arrow 1 could represent
 - A. ATP
 - B. H_2O
 - C. O_2
 - D. CO_2
12. Arrow 3 could represent
 - A. NADPH
 - B. ADP
 - C. O_2
 - D. electrons
13. Arrow 4 could represent
 - A. NADPH
 - B. ADP
 - C. glucose
 - D. electrons
14. Arrow 7 represents
 - A. ATP
 - B. NADPH
 - C. light
 - D. CO_2

15. All of the following are true about photosynthesis EXCEPT:

- A. The Calvin cycle usually occurs in the dark.
- B. The majority of the light reactions occurs on the thylakoid membranes in the chloroplast.
- C. Light energy is stored in ATP.
- D. A proton gradient drives the formation of ATP from ADP + P_i.

Questions 16–17 refer to the following graph that shows the relationship between CO₂ uptake by leaves and the concentrations of O₂ (percent of atmosphere in growth chambers) and CO₂ (ppm in growth chambers).



16. The relative CO₂ uptake is a measure of

- A. photosynthetic rate
- B. light intensity
- C. leaf size
- D. leaf temperature

17. According to the graph, the relative CO₂ uptake is best under which of the following conditions?

- A. 100 ppm CO₂, 20% O₂
- B. 100 ppm CO₂, 80% O₂
- C. 200 ppm CO₂, 20% O₂
- D. 200 ppm CO₂, 80% O₂

Free-Response Questions

The AP exam has long and short free-response questions. The long questions have considerable descriptive information that may include tables, graphs, or figures. The short questions are brief but may also include figures. Both kinds of questions have four parts and generally require that you bring together concepts from multiple areas of biology.

The questions that follow are designed to further your understanding of the concepts presented in this chapter. Unlike the free-response questions on the exam, they are narrowly focused on the material in this chapter. For free-response questions typical of the exam, take the two practice exams in this book.

Directions: The best way to prepare for the AP exam is to write out your answers as if you were taking the exam. Use complete sentences for all your answers and do *not* use outline form or bullets. You may use diagrams to supplement your answers, but be sure to describe the importance or relevance of your diagrams.

1. There are a variety of light-absorbing pigments in chloroplasts. Explain the purpose of having a variety of light-absorbing pigments.
2. During noncyclic photophosphorylation, electrons from the splitting of water populate photosystem II. Explain where these electrons from H_2O eventually end up.
3. Protons concentrate inside the thylakoids. Explain the purpose of this proton buildup.
4. Describe the biochemical pathways of the light-independent and light-dependent reactions in C_3 photosynthesis. Begin with a molecule of H_2O and CO_2 and end with a molecule of glucose.

Answers and Explanations

Multiple-Choice Questions

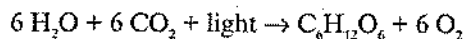
1. C. All of the light-absorbing pigments and most of the enzymes for the light reactions are found in the thylakoid membranes. There are several kinds of chlorophyll, including chlorophyll *a* and *b* (and *c* and *d* in certain algae). P_{700} and P_{680} are special chlorophyll *a* molecules, differing from other chlorophyll *a* molecules because of their special arrangement among nearby proteins and thylakoid membrane constituents. Chlorophyll is green because it *reflects* green light, not absorbs it. It looks green because the green light it reflects is the light we see. Similarly, carotenoids look orange or yellow because they reflect those colors.
2. B. The leaves turn to these colors because, as the leaves age, the tree begins to break down the chlorophyll (to extract its valuable components, like magnesium). In the absence of chlorophyll, the carotenoids are visible. As the various carotenoids break down, other colors become visible from carotenoids that still remain intact.
3. A. NADPH, ATP, and O_2 are the products of noncyclic photophosphorylation.
4. D. The molecules referenced in the question, in order of decreasing potential energy, are starch, glucose, NADPH, and ATP. Starch is a polymer of glucose. A single glucose molecule can provide about 30 ATP molecules, and a single NADPH can provide about 3 ATP molecules.
5. D. NADPH is produced only by noncyclic photophosphorylation.

6. C. The first step of carbon fixation occurs during the Calvin cycle when CO_2 combines with RuBP. Photorespiration, in contrast, occurs when O_2 , instead of CO_2 , combines with RuBP. The product of this reaction is transported to a peroxisome, where H_2O_2 is generated and subsequently broken down.
7. B. The energy-rich products of noncyclic photophosphorylation are ATP and NADPH.
8. A. During cyclic photophosphorylation, electrons energized by sunlight pass along an electron transport chain. About 1 ATP is generated from ADP and P_i with the energy from 2 electrons. This process can repeat as long as sunlight is available. H_2O (necessary for noncyclic photophosphorylation) and CO_2 (necessary for the Calvin cycle) are not needed for cyclic photophosphorylation.
9. D. Rubisco and the other enzymes that catalyze reactions in the Calvin cycle occur in the stroma. Most of the pigments and enzymes for photophosphorylation are embedded in the thylakoid membranes. The manganese-containing protein complex that catalyzes the splitting of water is embedded on the inner side of the thylakoid membrane, so the splitting of water occurs there.
10. B. The splitting of H_2O provides the electrons for noncyclic photophosphorylation. These electrons are incorporated in NADPH and ultimately find their way into glucose during the Calvin cycle.
11. B. It could also be light, but that is not an answer choice. You should test yourself on all aspects of this diagram: Pathway A is noncyclic photophosphorylation, and Pathway B is the Calvin cycle. Arrows 1 and 2: H_2O and light; arrow 3: ADP; arrows 4 and 5: ATP and NADPH; arrow 6: O_2 ; and arrow 7: CO_2 .
12. B. ADP is recycled. ADP is used in photophosphorylation to produce ATP. In the Calvin cycle (Pathway B), the energy in ATP is used, releasing ADP and P_i . The answer could also be NADP^+ , but that choice is not given (and, besides, NADP^+ is already shown in the figure).
13. A. It could also be ATP, but that is not an answer choice.
14. D. Arrow 7 represents CO_2 , which is necessary for Pathway B, the Calvin cycle. The Calvin cycle "fixes" CO_2 and produces G3P, the precursor to glucose.
15. A. Although the Calvin cycle is light-independent, it requires ATP and NADPH from photophosphorylation, which occurs only in light.
16. A. CO_2 uptake is a measure of Calvin cycle activity. The Calvin cycle generates glucose, the end product of photosynthesis. Many factors, including those provided in the other answer choices, influence photosynthetic rate. However, CO_2 uptake alone only indicates the amount of photosynthetic activity, not why that photosynthetic activity is occurring at some measured rate.
17. C. According to this graph, CO_2 uptake is greater when there is more CO_2 in the growth chamber (the 200 ppm curve), and when O_2 is minimum (the left side of the graph). Lower concentrations of O_2 minimize photorespiration.

Free-Response Questions

1. Each kind of light-absorbing pigment absorbs light energy over a different range of wavelengths. This allows the cell to absorb a greater amount of the incident light energy than if there were only one light-absorbing pigment.
2. After becoming energized in photosystem I, the electrons contribute to the formation of NADPH. Then, NADPH passes those electrons to the Calvin cycle, where they contribute partly to the regeneration of RuBP (so the Calvin cycle can repeat) and partly to the formation of carbohydrates.
3. The accumulation of protons in the thylakoid lumen creates a pH and electrical gradient across the thylakoid membrane. The gradient drives the movement of protons through ATP synthase, which, in turn, drives the phosphorylation of ADP to ATP.

4. Photosynthesis is the process by which water and light energy are used to fix inorganic carbon dioxide into glucose. The complete equation is



Various pigments exist in the photosynthetic membranes of plants. These include chlorophyll *a* and *b* and various carotenoids. The purpose of a variety of pigments is to absorb light energy (photons) of different wavelengths. The absorption spectrums of the pigments overlap so that they maximize the energy absorbed. When light energy is absorbed, the pigment becomes energized. The energy is then bounced around among pigments until it is absorbed by either of two special kinds of chlorophyll *a*, P₇₀₀ or P₆₈₀.

P₇₀₀ and P₆₈₀ are organized into separate photosystems (pigment systems), I and II. Cyclic photophosphorylation involves photosystem I. In cyclic photophosphorylation, the energy absorbed by the pigment system is captured by the P₇₀₀. As a result, two electrons are excited to a higher energy level, where they are absorbed by a primary electron acceptor. From here, the electrons are passed through an electron transport chain from electron acceptor to electron acceptor (some of which are cytochromes). During this transit, the energy loss of the electrons is used to bond a phosphate group to ADP, making it ATP (adenosine triphosphate). The process is called phosphorylation, and the result is that energy (originally from light) from the two electrons is trapped in an ATP molecule. The cycle is completed when the two electrons return to the photosystem pigments.

Noncyclic photophosphorylation is a more advanced system involving both photosystems I and II. It begins when chlorophyll P₆₈₀ in photosystem II traps photon energy and energizes two electrons. These two electrons are passed to a primary electron acceptor, then through an electron transport chain, producing, on average, 1.5 ATP and are then finally returned to photosystem I. Here the electrons are energized again (by light) and are received by another primary electron acceptor. These two electrons then combine with 2 H⁺ to form NADPH.

Meanwhile, a water molecule is split producing 2 electrons, 2 H⁺, and ½ O₂. The 2 electrons replace the electrons energized from photosystem II. The oxygen is released. One of the H⁺ combines with NADP⁺ and the 2 electrons from noncyclic photophosphorylation to produce NADPH. NADPH is then used to supply energy to the Calvin cycle.

The light-independent reactions (Calvin cycle) combine CO₂, NADPH, and ATP to form G3P and RuBP. It takes 6 CO₂ to create 2 G3P, so the cycle repeats six times to produce 2 G3P. The 2 G3P form glucose. Glucose can then be used to make various other carbohydrates, such as sucrose and starch, or it can be broken down to release its store of energy in the form of ATP to drive metabolic activities.

This is a thorough answer. Another way to answer this question would be to describe these processes as they occur in the chloroplast. In other words, focus on the activities of chemiosmosis. Illustrations such as those in this chapter would also get you points.