Chapter 10

Photosynthesis

Lecture Outline

Overview

- Life on Earth is solar powered.
- The chloroplasts of plants use a process called photosynthesis to capture light energy from the sun and convert it to chemical energy stored in sugars and other organic molecules.

A. The Process That Feeds the Biosphere

1. Plants and other autotrophs are the producers of the biosphere.

- Photosynthesis nourishes almost all the living world directly or indirectly.
  - All organisms use organic compounds for energy and for carbon skeletons.
  - Organisms obtain organic compounds by one of two major modes: autotrophic nutrition or heterotrophic nutrition.
- **Autotrophs** produce their organic molecules from CO_2 and other inorganic raw materials obtained from the environment.
  - Autotrophs are the ultimate sources of organic compounds for all heterotrophic organisms.
  - Autotrophs are the *producers* of the biosphere.
- Autotrophs can be separated by the source of energy that drives their metabolism.
  - *Photo*autotrophs use light as a source of energy to synthesize organic compounds.
    - Photosynthesis occurs in plants, algae, some other protists, and some prokaryotes.
  - *Chemo*autotrophs harvest energy from oxidizing inorganic substances, such as sulfur and ammonia.
    - Chemoautotrophy is unique to prokaryotes.
- **Heterotrophs** live on organic compounds produced by other organisms.
  - These organisms are the *consumers* of the biosphere.
  - The most obvious type of heterotrophs feeds on other organisms.
    - Animals feed this way.
  - Other heterotrophs decompose and feed on dead organisms or on organic litter, like feces and fallen leaves.
    - Most fungi and many prokaryotes get their nourishment this way.
  - Almost all heterotrophs are completely dependent on photoautotrophs for food and for oxygen, a by-product of photosynthesis.

2. Photosynthesis converts light energy to the chemical energy of food.

- All green parts of a plant have chloroplasts.

- However, the leaves are the major site of photosynthesis for most plants.
  - There are about half a million chloroplasts per square millimeter of leaf surface.
- The color of a leaf comes from **chlorophyll,** the green pigment in the chloroplasts.
  - Chlorophyll plays an important role in the absorption of light energy during photosynthesis.
- Chloroplasts are found mainly in **mesophyll** cells forming the tissues in the interior of the leaf.
- O_2 exits and CO_2 enters the leaf through microscopic pores called **stomata** in the leaf.
- Veins deliver water from the roots and carry off sugar from mesophyll cells to nonphotosynthetic areas of the plant.
- A typical mesophyll cell has 30–40 chloroplasts, each about 2–4 microns by 4–7 microns long.
- Each chloroplast has two membranes around a central aqueous space, the **stroma.**
- In the stroma is an elaborate system of interconnected membranous sacs, the **thylakoids.**
  - The interior of the thylakoids forms another compartment, the *thylakoid space.*
  - Thylakoids may be stacked into columns called *grana.*
- Chlorophyll is located in the thylakoids.
  - Photosynthetic prokaryotes lack chloroplasts.
  - Their photosynthetic membranes arise from infolded regions of the plasma membranes, folded in a manner similar to the thylakoid membranes of chloroplasts.

B. The Pathways of Photosynthesis

1. Evidence that chloroplasts split water molecules enabled researchers to track atoms through photosynthesis.

- Powered by light, the green parts of plants produce organic compounds and O_2 from CO_2 and H_2O.
- The equation describing the process of photosynthesis is:
  - $6CO_2 + 12H_2O + \text{light energy} \rightarrow C_6H_{12}O_6 + 6O_2 + 6H_2O$
  - $C_6H_{12}O_6$ is glucose.
- Water appears on both sides of the equation because 12 molecules of water are consumed, and 6 molecules are newly formed during photosynthesis.
- We can simplify the equation by showing only the net consumption of water:
  - $6CO_2 + 6H_2O + \text{light energy} \rightarrow C_6H_{12}O_6 + 6O_2$
- The overall chemical change during photosynthesis is the reverse of cellular respiration.
- In its simplest possible form: $CO_2 + H_2O + \text{light energy} \rightarrow [CH_2O] + O_2$
  - $[CH_2O]$ represents the general formula for a sugar.
- One of the first clues to the mechanism of photosynthesis came from the discovery that the O_2 given off by plants comes from H_2O, not CO_2.
  - Before the 1930s, the prevailing hypothesis was that photosynthesis split carbon dioxide and then added water to the carbon:
    - Step 1: $CO_2 \rightarrow C + O_2$
    - Step 2: $C + H_2O \rightarrow CH_2O$

- C. B. van Niel challenged this hypothesis.
- In the bacteria that he was studying, hydrogen sulfide (H_2S), not water, is used in photosynthesis.
- These bacteria produce yellow globules of sulfur as a waste, rather than oxygen.
- Van Niel proposed this chemical equation for photosynthesis in sulfur bacteria:
  - $CO_2 + 2H_2S \rightarrow [CH_2O] + H_2O + 2S$

- He generalized this idea and applied it to plants, proposing this reaction for their photosynthesis:
  - $CO_2 + 2H_2O \rightarrow [CH_2O] + H_2O + O_2$
- Thus, van Niel hypothesized that plants split water as a source of electrons from hydrogen atoms, releasing oxygen as a byproduct.
- Other scientists confirmed van Niel's hypothesis twenty years later.
  - They used ^{18}O, a heavy isotope, as a tracer.
  - They could label either $C^{18}O_2$ or $H_2{}^{18}O$.
  - They found that the ^{18}O label only appeared in the oxygen produced in photosynthesis when water was the source of the tracer.
- Hydrogen extracted from water is incorporated into sugar, and oxygen is released to the atmosphere (where it can be used in respiration).
- Photosynthesis is a redox reaction.
  - It reverses the direction of electron flow in respiration.
- Water is split and electrons transferred with H^+ from water to CO_2, reducing it to sugar.
  - Because the electrons increase in potential energy as they move from water to sugar, the process requires energy.
  - The energy boost is provided by light.

2. Here is a preview of the two stages of photosynthesis.

- Photosynthesis is two processes, each with multiple stages.
- The **light reactions** *(photo)* convert solar energy to chemical energy.
- The **Calvin cycle** *(synthesis)* uses energy from the light reactions to incorporate CO_2 from the atmosphere into sugar.
- In the light reactions, light energy absorbed by chlorophyll in the thylakoids drives the transfer of electrons and hydrogen from water to **$NADP^+$** (nicotinamide adenine dinucleotide phosphate), forming NADPH.
  - NADPH, an electron acceptor, provides reducing power via energized electrons to the Calvin cycle.
  - Water is split in the process, and O_2 is released as a by-product.
- The light reaction also generates ATP using chemiosmosis, in a process called **photophosphorylation.**
- Thus light energy is initially converted to chemical energy in the form of two compounds: NADPH and ATP.
- The Calvin cycle is named for Melvin Calvin who, with his colleagues, worked out many of its steps in the 1940s.
- The cycle begins with the incorporation of CO_2 into organic molecules, a process known as **carbon fixation.**

- The fixed carbon is reduced with electrons provided by NADPH.
- ATP from the light reactions also powers parts of the Calvin cycle.
- Thus, it is the Calvin cycle that makes sugar, but only with the help of ATP and NADPH from the light reactions.
- The metabolic steps of the Calvin cycle are sometimes referred to as the light-independent reactions, because none of the steps requires light *directly.*
- Nevertheless, the Calvin cycle in most plants occurs during daylight, because that is when the light reactions can provide the NADPH and ATP the Calvin cycle requires.
- While the light reactions occur at the thylakoids, the Calvin cycle occurs in the stroma.

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

- The thylakoids convert light energy into the chemical energy of ATP and NADPH.
- Light is a form of electromagnetic radiation.
- Like other forms of electromagnetic energy, light travels in rhythmic waves.
- The distance between crests of electromagnetic waves is called the **wavelength.**
  - Wavelengths of electromagnetic radiation range from less than a nanometer (gamma rays) to more than a kilometer (radio waves).
- The entire range of electromagnetic radiation is the **electromagnetic spectrum.**
- The most important segment for life is a narrow band between 380 to 750 nm, the band of **visible light.**
- While light travels as a wave, many of its properties are those of a discrete particle, the **photon.**
  - Photons are not tangible objects, but they do have fixed quantities of energy.
- The amount of energy packaged in a photon is inversely related to its wavelength.
  - Photons with shorter wavelengths pack more energy.
- While the sun radiates a full electromagnetic spectrum, the atmosphere selectively screens out most wavelengths, permitting only visible light to pass in significant quantities.
  - Visible light is the radiation that drives photosynthesis.
- When light meets matter, it may be reflected, transmitted, or absorbed.
  - Different pigments absorb photons of different wavelengths, and the wavelengths that are absorbed disappear.
  - A leaf looks green because chlorophyll, the dominant pigment, absorbs red and blue light, while transmitting and reflecting green light.
- A **spectrophotometer** measures the ability of a pigment to absorb various wavelengths of light.
  - It beams narrow wavelengths of light through a solution containing the pigment and measures the fraction of light transmitted at each wavelength.
  - An **absorption spectrum** plots a pigment's light absorption versus wavelength.
- The light reaction can perform work with those wavelengths of light that are absorbed.
- There are several pigments in the thylakoid that differ in their absorption spectra.
  - **Chlorophyll *a*,** the dominant pigment, absorbs best in the red and violet-blue wavelengths and least in the green.

- Other pigments with different structures have different absorption spectra.

- Collectively, these photosynthetic pigments determine an overall **action spectrum** for photosynthesis.
  - An action spectrum measures changes in some measure of photosynthetic activity (for example, O_2 release) as the wavelength is varied.
- The action spectrum of photosynthesis was first demonstrated in 1883 in an elegant experiment performed by Thomas Engelmann.
  - In this experiment, different segments of a filamentous alga were exposed to different wavelengths of light.
  - Areas receiving wavelengths favorable to photosynthesis produced excess O_2.
  - Engelmann used the abundance of aerobic bacteria that clustered along the alga at different segments as a measure of O_2 production.
- The action spectrum of photosynthesis does not match exactly the absorption spectrum of any one photosynthetic pigment, including chlorophyll *a*.
- Only chlorophyll *a* participates directly in the light reaction, but accessory photosynthetic pigments absorb light and transfer energy to chlorophyll *a*.
  - **Chlorophyll *b*,** with a slightly different structure than chlorophyll *a*, has a slightly different absorption spectrum and funnels the energy from these wavelengths to chlorophyll *a*.
  - **Carotenoids** can funnel the energy from other wavelengths to chlorophyll *a* and also participate in *photoprotection* against excessive light.
  - These compounds absorb and dissipate excessive light energy that would otherwise damage chlorophyll.
  - They also interact with oxygen to form reactive oxidative molecules that could damage the cell.
- When a molecule absorbs a photon, one of that molecule's electrons is elevated to an orbital with more potential energy.
  - The electron moves from its ground state to an excited state.
  - The only photons that a molecule can absorb are those whose energy matches exactly the energy difference between the ground state and excited state of this electron.
  - Because this energy difference varies among atoms and molecules, a particular compound absorbs only photons corresponding to specific wavelengths.
  - Thus, each pigment has a unique absorption spectrum.
- Excited electrons are unstable.
- Generally, they drop to their ground state in a billionth of a second, releasing heat energy.
- Some pigments, including chlorophyll, can also release a photon of light in a process called fluorescence.
  - If a solution of chlorophyll isolated from chloroplasts is illuminated, it will fluoresce and give off heat.
- Chlorophyll excited by absorption of light energy produces very different results in an intact chloroplast than it does in isolation.
- In the thylakoid membrane, chlorophyll is organized along with proteins and smaller organic molecules into **photosystems.**
- A photosystem is composed of a reaction center surrounded by a light-harvesting complex.

- Each **light-harvesting complex** consists of pigment molecules (which may include chlorophyll *a*, chlorophyll *b*, and carotenoid molecules) bound to particular proteins.
- Together, these light-harvesting complexes act like light-gathering “antenna complexes” for the reaction center.
- When any antenna molecule absorbs a photon, it is transmitted from molecule to molecule until it reaches a particular chlorophyll *a* molecule, the **reaction center.**
- At the reaction center is a **primary electron acceptor,** which accepts an excited electron from the reaction center chlorophyll *a*.
    - The solar-powered transfer of an electron from a special chlorophyll *a* molecule to the primary electron acceptor is the first step of the light reactions.
- Each photosystem—reaction-center chlorophyll and primary electron acceptor surrounded by an antenna complex—functions in the chloroplast as a light-harvesting unit.
- There are two types of photosystems in the thylakoid membrane.
    - **Photosystem I (PS I)** has a reaction center chlorophyll *a* that has an absorption peak at 700 nm.
    - **Photosystem II (PS II)** has a reaction center chlorophyll *a* that has an absorption peak at 680 nm.
    - The differences between these reaction centers (and their absorption spectra) lie not in the chlorophyll molecules, but in the proteins associated with each reaction center.
    - These two photosystems work together to use light energy to generate ATP and NADPH.
- During the light reactions, there are two possible routes for electron flow: cyclic and noncyclic.
- **Noncyclic electron flow,** the predominant route, produces both ATP and NADPH.
    1. Photosystem II absorbs a photon of light. One of the electrons of P680 is excited to a higher energy state.
    2. This electron is captured by the primary electron acceptor, leaving the reaction center oxidized.
    3. An enzyme extracts electrons from water and supplies them to the oxidized reaction center. This reaction splits water into two hydrogen ions and an oxygen atom that combines with another oxygen atom to form O2.
    4. Photoexcited electrons pass along an electron transport chain before ending up at an oxidized photosystem I reaction center.
    5. As these electrons “fall” to a lower energy level, their energy is harnessed to produce ATP.
    6. Meanwhile, light energy has excited an electron of PS I’s P700 reaction center. The photoexcited electron was captured by PS I’s primary electron acceptor, creating an electron “hole” in P700. This hole is filled by an electron that reaches the bottom of the electron transport chain from PS II.
    7. Photoexcited electrons are passed from PS I’s primary electron acceptor down a second electron transport chain through the protein ferredoxin (Fd).
    8. The enzyme NADP+ reductase transfers electrons from Fd to NADP+. Two electrons are required for NADP+’s reduction to NADPH. NADPH will carry the reducing power of these high-energy electrons to the Calvin cycle.
- The light reactions use the solar power of photons absorbed by both photosystem I and photosystem II to provide chemical energy in the form of ATP and reducing power in the form of the electrons carried by NADPH.

- Under certain conditions, photoexcited electrons from photosystem I, but not photosystem II, can take an alternative pathway, **cyclic electron flow.**
  - Excited electrons cycle from their reaction center to a primary acceptor, along an electron transport chain, and return to the oxidized P700 chlorophyll.
  - As electrons flow along the electron transport chain, they generate ATP by **cyclic photophosphorylation.**
  - There is no production of NADPH and no release of oxygen.
- What is the function of cyclic electron flow?
- Noncyclic electron flow produces ATP and NADPH in roughly equal quantities.
- However, the Calvin cycle consumes more ATP than NADPH.
- Cyclic electron flow allows the chloroplast to generate enough surplus ATP to satisfy the higher demand for ATP in the Calvin cycle.
- Chloroplasts and mitochondria generate ATP by the same mechanism: chemiosmosis.
  - In both organelles, an electron transport chain pumps protons across a membrane as electrons are passed along a series of increasingly electronegative carriers.
  - This transforms redox energy to a proton-motive force in the form of an H^+ gradient across the membrane.
  - ATP synthase molecules harness the proton-motive force to generate ATP as H^+ diffuses back across the membrane.
- Some of the electron carriers, including the cytochromes, are very similar in chloroplasts and mitochondria.
- The ATP synthase complexes of the two organelles are also very similar.
- There are differences between oxidative phosphorylation in mitochondria and photophosphorylation in chloroplasts.
- Mitochondria transfer chemical energy from food molecules to ATP; chloroplasts transform light energy into the chemical energy of ATP.
- The spatial organization of chemiosmosis also differs in the two organelles.
- The inner membrane of the mitochondrion pumps protons from the mitochondrial matrix out to the intermembrane space. The thylakoid membrane of the chloroplast pumps protons from the stroma into the thylakoid space inside the thylakoid.
- The thylakoid membrane makes ATP as the hydrogen ions diffuse down their concentration gradient from the thylakoid space back to the stroma through ATP synthase complexes, whose catalytic knobs are on the stroma side of the membrane.
- The proton gradient, or pH gradient, across the thylakoid membrane is substantial.
  - When chloroplasts are illuminated, the pH in the thylakoid space drops to about 5 and the pH in the stroma increases to about 8, a thousandfold different in H^+ concentration.
- The light-reaction "machinery" produces ATP and NADPH on the stroma side of the thylakoid.
- Noncyclic electron flow pushes electrons from water, where they have low potential energy, to NADPH, where they have high potential energy.
  - This process also produces ATP and oxygen as a by-product.

4. The Calvin cycle uses ATP and NADPH to convert CO_2 to sugar.

- The Calvin cycle regenerates its starting material after molecules enter and leave the cycle.

- The Calvin cycle is anabolic, using energy to build sugar from smaller molecules.
- Carbon enters the cycle as CO_2 and leaves as sugar.
- The cycle spends the energy of ATP and the reducing power of electrons carried by NADPH to make sugar.
- The actual sugar product of the Calvin cycle is not glucose, but a three-carbon sugar, **glyceraldehyde-3-phosphate (G3P).**
- Each turn of the Calvin cycle fixes one carbon.
- For the net synthesis of one G3P molecule, the cycle must take place three times, fixing three molecules of CO_2.
- To make one glucose molecule requires six cycles and the fixation of six CO_2 molecules.
- The Calvin cycle has three phases.

Phase 1: Carbon fixation

- In the **carbon fixation** phase, each CO_2 molecule is attached to a five-carbon sugar, ribulose bisphosphate (RuBP).
  - This is catalyzed by RuBP carboxylase or **rubisco.**
  - Rubisco is the most abundant protein in chloroplasts and probably the most abundant protein on Earth.
  - The six-carbon intermediate is unstable and splits in half to form two molecules of 3-phosphoglycerate for each CO_2.

Phase 2: Reduction

- During **reduction,** each 3-phosphoglycerate receives another phosphate group from ATP to form 1,3-bisphosphoglycerate.
- A pair of electrons from NADPH reduces each 1,3-bisphosphoglycerate to G3P.
  - The electrons reduce a carboxyl group to the aldehyde group of G3P, which stores more potential energy.
- If our goal was the net production of one G3P, we would start with $3CO_2$ (3C) and three RuBP (15C).
- After fixation and reduction, we would have six molecules of G3P (18C).
  - One of these six G3P (3C) is a net gain of carbohydrate.
    - This molecule can exit the cycle and be used by the plant cell.

Phase 3: Regeneration

- The other five G3P (15C) remain in the cycle to **regenerate** three RuBP. In a complex series of reactions, the carbon skeletons of five molecules of G3P are rearranged by the last steps of the Calvin cycle to regenerate three molecules of RuBP.
- For the net synthesis of one G3P molecule, the Calvin cycle consumes nine ATP and six NADPH.
- The light reactions regenerate ATP and NADPH.
- The G3P from the Calvin cycle is the starting material for metabolic pathways that synthesize other organic compounds, including glucose and other carbohydrates.

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

- One of the major problems facing terrestrial plants is dehydration.
- At times, solutions to this problem require tradeoffs with other metabolic processes, especially photosynthesis.
- The stomata are not only the major route for gas exchange (CO_2 in and O_2 out), but also for the evaporative loss of water.
- On hot, dry days, plants close their stomata to conserve water. This causes problems for photosynthesis.
- In most plants **(C_3 plants),** initial fixation of CO_2 occurs via rubisco, forming a three-carbon compound, 3-phosphoglycerate.
  - C_3 plants include rice, wheat, and soybeans.
- When their stomata partially close on a hot, dry day, CO_2 levels drop as CO_2 is consumed in the Calvin cycle.
- At the same time, O_2 levels rise as the light reaction converts light to chemical energy.
- While rubisco normally accepts CO_2, when the O_2:CO_2 ratio increases (on a hot, dry day with closed stomata), rubisco can add O_2 to RuBP.
- When rubisco adds O_2 to RuBP, RuBP splits into a three-carbon piece and a two-carbon piece in a process called **photorespiration.**
  - The two-carbon fragment is exported from the chloroplast and degraded to CO_2 by mitochondria and peroxisomes.
  - Unlike normal respiration, this process produces no ATP.
    - In fact, photorespiration *consumes* ATP.
  - Unlike photosynthesis, photorespiration does not produce organic molecules.
    - In fact, photorespiration *decreases* photosynthetic output by siphoning organic material from the Calvin cycle.
- A hypothesis for the existence of photorespiration is that it is evolutionary baggage.
- When rubisco first evolved, the atmosphere had far less O_2 and more CO_2 than it does today.
  - The inability of the active site of rubisco to exclude O_2 would have made little difference.
- Today it does make a difference.
  - Photorespiration can drain away as much as 50% of the carbon fixed by the Calvin cycle on a hot, dry day.
- Certain plant species have evolved alternate modes of carbon fixation to minimize photorespiration.
- **C_4 plants** first fix CO_2 in a four-carbon compound.
  - Several thousand plants, including sugarcane and corn, use this pathway.
- A unique leaf anatomy is correlated with the mechanism of C_4 photosynthesis.
- In C_4 plants, there are two distinct types of photosynthetic cells: bundle-sheath cells and mesophyll cells.
  - **Bundle-sheath cells** are arranged into tightly packed sheaths around the veins of the leaf.
  - **Mesophyll cells** are more loosely arranged cells located between the bundle sheath and the leaf surface.
- The Calvin cycle is confined to the chloroplasts of the bundle-sheath cells.

- However, the cycle is preceded by the incorporation of CO_2 into organic molecules in the mesophyll.
- The key enzyme, phosphoenolpyruvate carboxylase, adds CO_2 to phosphoenolpyruvate (PEP) to form oxaloacetate.
    - **PEP carboxylase** has a very high affinity for CO_2 and can fix CO_2 efficiently when rubisco cannot (i.e., on hot, dry days when the stomata are closed).
- The mesophyll cells pump these four-carbon compounds into bundle-sheath cells.
    - The bundle-sheath cells strip a carbon from the four-carbon compound as CO_2, and return the three-carbon remainder to the mesophyll cells.
    - The bundle-sheath cells then use rubisco to start the Calvin cycle with an abundant supply of CO_2.
- In effect, the mesophyll cells pump CO_2 into the bundle-sheath cells, keeping CO_2 levels high enough for rubisco to accept CO_2 and not O_2.
- C_4 photosynthesis minimizes photorespiration and enhances sugar production.
- C_4 plants thrive in hot regions with intense sunlight.
- A second strategy to minimize photorespiration is found in succulent plants, cacti, pineapples, and several other plant families.
    - These plants are known as CAM plants for crassulacean acid metabolism.
    - They open their stomata during the night and close them during the day.
        - Temperatures are typically lower at night, and humidity is higher.
    - During the night, these plants fix CO_2 into a variety of organic acids in mesophyll cells.
    - During the day, the light reactions supply ATP and NADPH to the Calvin cycle, and CO_2 is released from the organic acids.
- Both C_4 and CAM plants add CO_2 into organic intermediates before it enters the Calvin cycle.
    - In C_4 plants, carbon fixation and the Calvin cycle are spatially separated.
    - In CAM plants, carbon fixation and the Calvin cycle are temporally separated.
- Both eventually use the Calvin cycle to make sugar from carbon dioxide.

6. Here is a review of the importance of photosynthesis.

- In photosynthesis, the energy that enters the chloroplasts as sunlight becomes stored as chemical energy in organic compounds.
- Sugar made in the chloroplasts supplies the entire plant with chemical energy and carbon skeletons to synthesize all the major organic molecules of cells.
    - About 50% of the organic material is consumed as fuel for cellular respiration in plant mitochondria.
    - Carbohydrate in the form of the disaccharide sucrose travels via the veins to nonphotosynthetic cells.
        - There, it provides fuel for respiration and the raw materials for anabolic pathways, including synthesis of proteins and lipids and formation of the extracellular polysaccharide cellulose.
        - Cellulose, the main ingredient of cell walls, is the most abundant organic molecule in the plant, and probably on the surface of the planet.
- Plants also store excess sugar by synthesis of starch.
    - Starch is stored in chloroplasts and in storage cells in roots, tubers, seeds, and fruits.

- Heterotrophs, including humans, may completely or partially consume plants for fuel and raw materials.
- On a global scale, photosynthesis is the most important process on Earth.
    - It is responsible for the presence of oxygen in our atmosphere.
    - Each year, photosynthesis synthesizes 160 billion metric tons of carbohydrate.