Chapter 10

Photosynthesis

Lecture Outline

Overview: The Process That Feeds the Biosphere

- 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.
- 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 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.
    - Almost all plants are autotrophs; the only nutrients they require are water and minerals from the soil and carbon dioxide from the air.
    - Plants are *photo*autotrophs, using light as a source of energy to synthesize organic compounds.
    - Photosynthesis also occurs in algae, some other protists, and some prokaryotes.
- **Heterotrophs** live on organic compounds produced by other organisms.
- Heterotrophs 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. These are decomposers.
    - 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.

Concept 10.1 Photosynthesis converts light energy to the chemical energy of food.

- Photosynthetic enzymes and other molecules of photoautotrophs are grouped together in a biological membrane, allowing the necessary series of chemical reactions to be carried out efficiently.
- The process of photosynthesis likely originated in a group of bacteria with infolded regions of the plasma membrane containing clusters of such molecules.

  - In existing photosynthetic bacteria, infolded photosynthetic membranes function similarly to the internal membranes of the chloroplast.
  - In fact, the original chloroplast is believed to have been a photosynthetic prokaryote that lived inside a eukaryotic cell.

Chloroplasts are the sites of photosynthesis in plants.

- 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 measuring about 2–4 μm by 4–7 μm.
- 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 in columns called *grana.*
- Chlorophyll is located in the thylakoids.
- Photosynthetic prokaryotes lack chloroplasts. Their photosynthetic membranes arise from infolded regions of the plasma membranes, also called thylakoid membranes.

Powered by light, photosynthesis produces 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, although the direct product of photosynthesis is actually a three-carbon sugar that can be used to make 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:

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

- Written this way, the overall chemical change during photosynthesis is the reverse of cellular respiration.
  - Both of these metabolic processes occur in plant cells. However, chloroplasts do not synthesize sugars by simply reversing the steps of respiration.
- In its simplest possible form, $CO_2 + H_2O + \text{light energy} \rightarrow [CH_2O] + O_2$, where $[CH_2O]$ represents the general formula for a carbohydrate.

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

- 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: $C + H_2O \rightarrow CH_2O$
- Cornelis B. van Niel challenged this hypothesis.
  - In the bacteria that he was studying, hydrogen sulfide (H_2S), rather than 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:

  $$CO_2 + 2H_2S \rightarrow [CH_2O] + H_2O + 2S$$
- Van Niel 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 by-product.
  - Sulfur bacteria: $CO_2 + 2H_2S \rightarrow [CH_2O] + H_2O + 2S$
  - Plants: $CO_2 + 2H_2O \rightarrow [CH_2O] + H_2O + O_2$
  - General: $CO_2 + 2H_2X \rightarrow [CH_2O] + H_2O + X_2$
- Twenty years later, scientists confirmed van Niel's hypothesis.
  - Researchers used ^{18}O, a heavy isotope, as a tracer to follow the fate of oxygen atoms during photosynthesis.
  - They labeled either $C^{18}O_2$ or $H_2{}^{18}O$.
  - They found that the ^{18}O label appeared in the oxygen produced in photosynthesis only when water was the source of the tracer.
- Hydrogen extracted from water is incorporated into sugar, and oxygen is released to the atmosphere.

Photosynthesis is a redox reaction.

- Both photosynthesis and aerobic respiration involve redox reactions.
- During cellular respiration, energy is released from sugar when electrons associated with hydrogen are transported by carriers to oxygen, forming water as a by-product.
- The electrons lose potential energy as they "fall" down the electron transport chain toward electronegative oxygen, and the mitochondrion harnesses that energy to synthesize ATP.
- Photosynthesis reverses the direction of electron flow.
- Water is split and electrons are 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.

A preview of the two stages of photosynthesis.

- Photosynthesis is two processes, each with multiple steps: light reactions and the Calvin cycle.
- 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.

- Water is split, providing a source of electrons and protons (H^+ ions) and giving off O_2 as a by-product.
- Light absorbed by chlorophyll drives the transfer of electrons and hydrogen ions from water to **$NADP^+$** (nicotinamide adenine dinucleotide phosphate), forming NADPH.
- 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, a source of electrons as reducing power that can be passed along to an electron acceptor, and ATP, the energy currency of cells.
- The light reactions produce no sugar; that happens in the second stage of photosynthesis, the Calvin cycle.
    - 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.
- In essence, the chloroplast uses light energy to make sugar by coordinating the two stages of photosynthesis.
- Whereas the light reactions occur at the thylakoids, the Calvin cycle occurs in the stroma.
    - In the thylakoids, molecules of $NADP^+$ and ADP pick up electrons and phosphate, respectively, and NADPH and ATP are then released to the stroma, where they play crucial roles in the Calvin cycle.

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

- Light is a form of electromagnetic energy or 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 shorter than a nanometer (gamma rays) to longer than a kilometer (radio waves).
- The entire range of electromagnetic radiation is the **electromagnetic spectrum.**
- The most important segment of the electromagnetic spectrum for life is a narrow band between 380 and 750 nm, the band of visible light detected as various colors by the human eye.
- Although light travels as a wave, many of its properties are those of a discrete particle, a **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.
- Although 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.

Photosynthetic pigments are light receptors.

- When light meets matter, the light 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 violet-blue light while transmitting and reflecting green light.
- A **spectrophotometer** measures the ability of a pigment to absorb various wavelengths of light.
  - A spectrophotometer beams narrow wavelengths of light through a solution containing the pigment and then measures the fraction of light transmitted at each wavelength.
  - An **absorption spectrum** plots a pigment's light absorption versus wavelength.
- The light reactions can perform work with those wavelengths of light that are absorbed.
- Several pigments in the thylakoid differ in their absorption spectra.
  - **Chlorophyll *a***, which participates directly in the light reactions, absorbs best in the red and violet-blue wavelengths and worst in the green.
  - Accessory pigments include *chlorophyll b* and a group of molecules called carotenoids.
- An overall **action spectrum** for photosynthesis profiles the relative effectiveness of different wavelengths of radiation in driving the process.
  - 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 a clever experiment performed by Thomas Engelmann.
  - 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.
  - His results are a striking match to the modern action spectrum.
- 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 reactions, 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 or interact with oxygen to form reactive oxidative molecules that could damage the cell.

When chlorophyll and other pigments absorb light, an electron is boosted to an excited state.

- When a molecule absorbs a photon, one of the 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 the excited state of this electron.
- Because this energy difference varies among atoms and molecules, a particular compound absorbs only photons corresponding to specific wavelengths.
- This is the reason 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.
- In isolation, some pigments emit light after absorbing photons, in a process called fluorescence.
    - If a solution of chlorophyll isolated from chloroplasts is illuminated, it fluoresces in the red-orange part of the spectrum and gives 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 protein complex called a **reaction-center complex**, which includes two special chlorophyll *a* molecules, surrounded by a number of light-harvesting complexes.
- Each **light-harvesting complex** consists of pigment molecules (which may include chlorophyll *a*, chlorophyll *b*, and carotenoids) bound to particular proteins.
    - The number and variety of pigment molecules enable a photosystem to harvest light over a larger surface and a larger portion of the spectrum than any single pigment molecule can.
- Together, the light-harvesting complexes act as an antenna for the reaction-center complex.
- When a pigment molecule absorbs a photon, the energy is transferred from pigment molecule to pigment molecule until it is funneled into the reaction-center complex.
- 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.
- As soon as the chlorophyll electron is excited to a higher energy level, the primary electron acceptor captures it in a redox reaction.
- Isolated chlorophyll fluoresces because there is no electron acceptor, so electrons of photoexcited chlorophyll drop right back to the ground state.
    - In a chloroplast, the potential energy represented by the excited electron is not lost.
- Each photosystem—a reaction-center complex surrounded by light-harvesting complexes—functions in the chloroplast as a unit.

There are two types of photosystems in the thylakoid membrane.

- **Photosystem II (PS II)** and **photosystem I (PS I)** each have a characteristic reaction-center complex—a particular kind of primary electron acceptor next to a pair of special chlorophyll *a* molecules associated with specific proteins.
    - The two photosystems were named in order of their discovery, but they function sequentially, with photosystem II functioning first.

- Photosystem II has a reaction-center chlorophyll *a* known as P680, with an absorption peak at 680 nm.
- Photosystem I has a reaction-center chlorophyll *a* known as P700, with an absorption peak at 700 nm.
- These two pigments, P680 and P700, are nearly identical chlorophyll *a* molecules.
- Their association with different proteins in the thylakoid membrane affects the electron distribution in the chlorophyll molecules and accounts for the slight differences in light-absorbing properties.
- These two photosystems work together in using light energy to generate ATP and NADPH.

During the light reactions, there are two possible routes for electron flow: linear and cyclic.

- **Linear electron flow** drives the synthesis of ATP and NADPH by energizing the two photosystems embedded in the thylakoid membranes of chloroplasts.
- During the light reactions, electrons flow through the photosystems and other molecular components built into the thylakoid membrane.
  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 P680 oxidized ($P680^+$).
  3. An enzyme extracts electrons from water and supplies them to the oxidized $P680^+$ pair. This reaction splits water into two hydrogen ions and an oxygen atom that combines with another oxygen atom to form O_2.
  4. Each photoexcited electron passes from the primary electron acceptor of PS II to PS I via an electron transport chain. The electron transport chain between PS II and PS I is made up of the electron carrier plastoquinone (Pq), a cytochrome complex, and a protein called plastocyanin (Pc).
  5. As these electrons "fall" to a lower energy level, their energy is harnessed to produce ATP. As electrons pass through the cytochrome complex, the pumping of protons builds a proton gradient that is subsequently used in chemiosmosis.
  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 (to produce $P700^+$). This hole is filled by an electron that reaches the bottom of the electron transport chain from PS II.
  7. Photoexcited electrons are passed in a series of redox reactions from PS I's primary electron acceptor down a second electron transport chain through the protein ferredoxin (Fd).
  8. The enzyme $NADP^+$ reductase catalyzes the 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 PS II and PS I to provide chemical energy in the form of ATP and reducing power in the form of the electrons carried by NADPH to the carbohydrate-synthesizing reactions of the Calvin cycle.
- Under certain conditions, photoexcited electrons from photosystem I, but not photosystem II, can take an alternative pathway, a short circuit called **cyclic electron flow**.
  - The electrons cycle back from ferredoxin (Fd) to the cytochrome complex and from there continue on to a P700 chlorophyll in the PS I reaction-center complex.
  - There is no production of NADPH and no release of oxygen.
  - Cyclic flow does, however, generate ATP.
- Several living groups of photosynthetic bacteria have photosystem I but not photosystem II.

- In these species, which include the purple sulfur bacteria, cyclic electron flow is the sole means of generating ATP in photosynthesis.
  - Evolutionary biologists believe that these bacterial groups are descendants of the bacteria in which photosynthesis first evolved, in a form similar to cyclic electron flow.
- Cyclic electron flow occurs in photosynthetic species that possess both photosystems, including cyanobacteria and plants. What is the function of cyclic electron flow in these autotrophs?
  - Mutant plants that are not able to carry out cyclic electron flow are capable of growing well in low light, but they do not grow well where light is intense.
  - This evidence supports the idea that cyclic electron flow may be *photoprotective,* protecting cells from light-induced damage.

Chloroplasts and mitochondria generate ATP by the same mechanism: chemiosmosis.

- In both chloroplasts and mitochondria, an electron transport chain pumps protons across a membrane as electrons are passed along a series of increasingly electronegative carriers.
- This process 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 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.
  - In mitochondria, the high-energy electrons dropped down the transport chain are extracted from organic molecules (which are thus oxidized), whereas in chloroplasts, the source of electrons is water.
  - Mitochondria use chemiosmosis to transfer chemical energy from food molecules to ATP; chloroplasts transform light energy into the chemical energy of ATP.
- The spatial organization of chemiosmosis differs slightly between chloroplasts and mitochondria, but similarities are also evident.
- 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.
- In the mitochondrion, protons diffuse down their concentration gradient from the intermembrane space through ATP synthase to the matrix, driving ATP synthesis.
  - In the chloroplast, ATP is synthesized as the hydrogen ions diffuse from the thylakoid space back to the stroma through ATP synthase complexes, whose catalytic knobs are on the stroma side of the membrane.
  - Thus, ATP forms in the stroma, where it is used to help drive sugar synthesis during the Calvin cycle.
- The proton (H^+) 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.
  - This gradient represents a thousandfold different in H^+ concentration.
- To summarize the light reactions:

  - Electron flow pushes electrons from water, where they have low potential energy, to NADPH, where they have high potential energy.
  - The light-driven electron current also generates ATP.
  - Thus, the equipment of the thylakoid membrane converts light energy to chemical energy stored in ATP and NADPH.
  - This process also produces oxygen as a by-product.

Concept 10.3 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: carbon fixation, reduction, and regeneration of the CO_2 acceptor.

Phase 1: Carbon fixation

- In the **carbon fixation** phase, each CO_2 molecule is attached to a five-carbon sugar, ribulose bisphosphate (RuBP).
  - This reaction 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.
- For every *three* molecules of CO_2, there are *six* molecules of G3P.
- One of these six G3P is a net gain of carbohydrate.
- This molecule exits the cycle to be used by the plant cell, while the other five molecules are recycled to regenerate the three molecules of RuBP.

Phase 3: Regeneration of the CO_2 acceptor (RuBP)

- The other five G3P 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.
- To accomplish this, the cycle spends three more molecules of ATP.
- The RuBP is now prepared to receive CO_2 again, and the cycle continues.
- 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.
- Neither the light reactions nor the Calvin cycle alone can make sugar from CO_2. Photosynthesis is an emergent property of the intact chloroplast that integrates the two stages of photosynthesis.

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

- One of the major problems facing terrestrial plants is dehydration.
- Metabolic adaptations to reduce dehydration often require trade-offs with other metabolic processes, especially photosynthesis.
- The stomata are both the major route for gas exchange (CO_2 in and O_2 out) and the main site of the evaporative loss of water.
    - On hot, dry days, plants close their stomata to conserve water.
    - With stomata closed, CO_2 concentrations in the air space within the leaf decrease and the concentration of O_2 released from the light reactions increases.
    - These conditions within the leaf favor an apparently wasteful process called photorespiration.

Photorespiration may be an evolutionary relic.

- 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 the stomata of C_3 plants 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 reactions convert light to chemical energy.
- Although rubisco normally accepts CO_2, as CO_2 becomes scarce, 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 and releasing CO_2 that would otherwise be fixed.
- One 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, however.
  - In many plants—including crop plants—photorespiration drains away as much as 50% of the carbon fixed by the Calvin cycle.
- At least in some cases, photorespiration plays a protective role in plants.
- Plants that are genetically defective in their ability to carry out photorespiration are more susceptible to damage induced by excess light.
- This is clear evidence that photorespiration acts to neutralize otherwise damaging products of the light reactions, which build up when a low CO_2 concentration limits the progress of the Calvin cycle.
- Whether there are other benefits of photorespiration is still unknown.
- As heterotrophs dependent on carbon fixation in chloroplasts for food, humans naturally view photorespiration as wasteful.
- If photorespiration could be reduced in certain plant species without otherwise affecting photosynthetic productivity, crop yields and food supplies might increase.

Certain plant species have evolved alternative modes of carbon fixation to minimize photorespiration.

- In one strategy, **C_4 plants** first fix CO_2 in a four-carbon compound.
  - Several thousand plants in 19 plant families, 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 in tightly packed sheaths around the veins of the leaf.
  - **Mesophyll cells** are more loosely arranged 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 the four-carbon product oxaloacetate.
  - **PEP carboxylase** has a very high affinity for CO_2 and no affinity for CO_2.
  - Therefore, PEP carboxylase can fix CO_2 efficiently when rubisco cannot (that is, on hot, dry days when the stomata are closed).
- The mesophyll cells pump these four-carbon compounds into bundle-sheath cells through plasmodesmata.
- The bundle-sheath cells strip a carbon from the four-carbon compound as CO_2, regenerating pyruvate, which is transported to the mesophyll cells.
- ATP is used to convert pyruvate to PEP, enabling the reaction cycle to continue.
- To generate the additional ATP, bundle-sheath cells carry out cyclic electron flow.
  - In fact, these cells contain PS I but no PS II, so cyclic electron flow is their only photosynthetic mode of generating ATP.

- 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.
    - ○ The cyclic series of reactions involving PEP carboxylase and the regeneration of PEP can be thought of as a CO_2-concentrating pump that is powered by ATP.
- 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 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.
- This mode of carbon fixation is called **crassulacean acid metabolism,** or **CAM**.
- The mesophyll cells of **CAM plants** store the organic acids they make during the night in their vacuoles until morning, when the stomata close.
- During the day, the light reactions supply ATP and NADPH to the Calvin cycle, and CO_2 is released from the organic acids to become incorporated into sugar.
- Both C_4 and CAM plants add CO_2 to organic intermediates before it enters the Calvin cycle.
    - ○ In C_4 plants, carbon fixation and the Calvin cycle are structurally separated.
    - ○ In CAM plants, carbon fixation and the Calvin cycle are temporally separated.
- Both types of plants eventually use the Calvin cycle to make sugar from carbon dioxide.

A review of the importance of photosynthesis.

- The light reactions capture solar energy and use it to make ATP and transfer electrons from water to $NADP^+$.
- The Calvin cycle uses the ATP and NADPH to produce sugar from carbon dioxide.
- 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 for the synthesis of all the major organic molecules of cells.
    - ○ About 50% of the organic material is consumed as fuel for cellular respiration in plant mitochondria. Some photosynthetic products are lost to photorespiration.
- Carbohydrate in the form of the disaccharide sucrose travels via the veins to nonphotosynthetic cells in the plant body.
- There, sucrose provides fuel for respiration and the raw materials for anabolic pathways, including synthesis of proteins and lipids and formation of the polysaccharide cellulose.
    - ○ Cellulose, the main ingredient of cell walls, is the most abundant organic molecule in the plant and probably on the surface of Earth.
- Plants also store excess sugar by the synthesis of starch.
    - ○ Starch is stored in chloroplasts and in storage cells of roots, tubers, seeds, and fruits.
- Heterotrophs, including humans, 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.
- No process is more important than photosynthesis to the welfare of life on Earth.