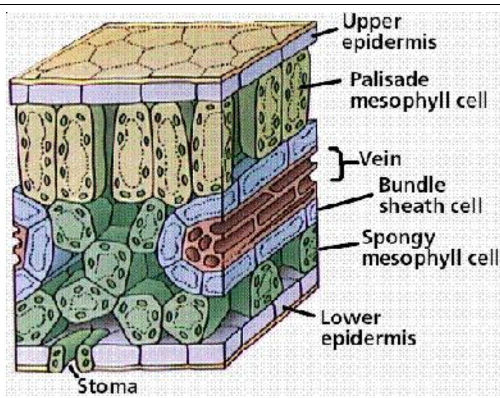
CHAPTER 10 PHOTOSYNTHESIS

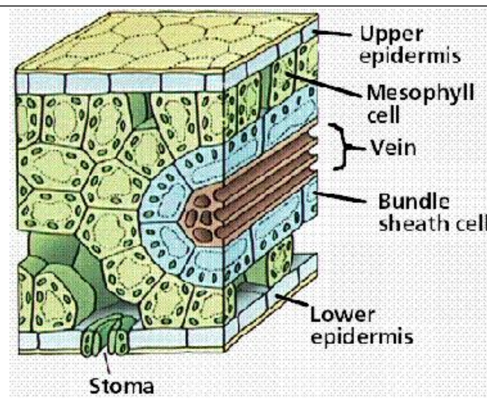
A. Photosynthesis in Nature

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

- **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 nonautotrophic organisms.
  - Autotrophs are the producers of the biosphere.
- **Heterotrophs** live on organic compounds produced by other organisms.
  - These organisms are the consumers of the biosphere.

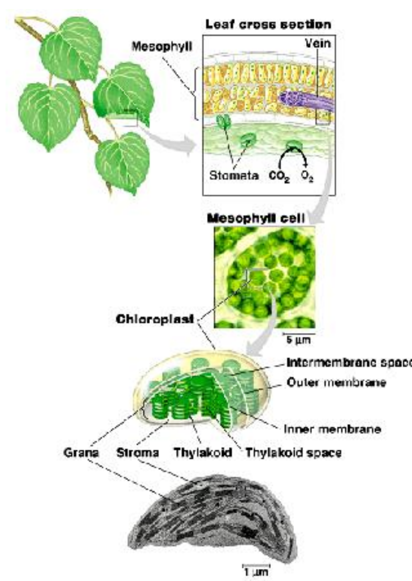
2. Chloroplasts are the sites of photosynthesis in plants

- Any green part of a plant has chloroplasts.
- However, the leaves are the major site of photosynthesis for most plants.
- 



C3 Plant Leaf C4 Plant Leaf

  - There are about half a million chloroplasts per square millimeter of leaf surface.
- 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, **stomata**, in the leaf. Veins deliver water.
- A typical mesophyll cell has 30-40 chloroplasts, each about 2-4 microns by 4-7 microns long.

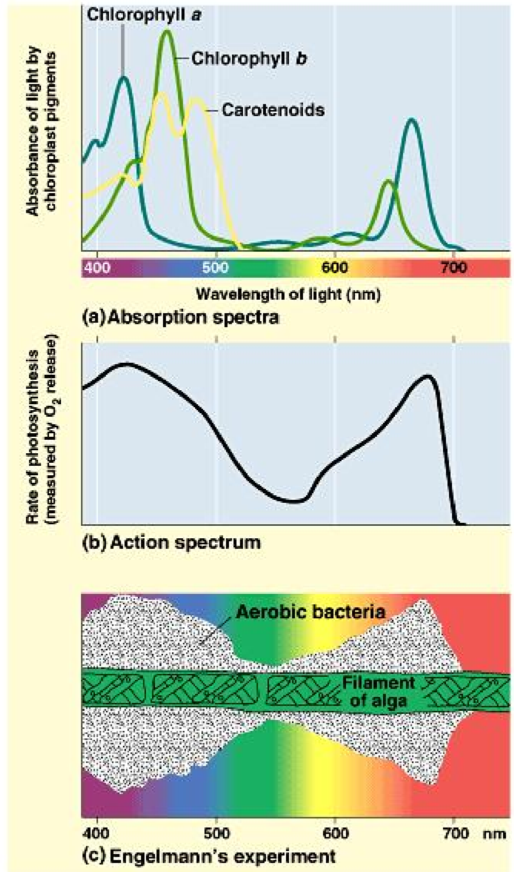


B. The Pathways of Photosynthesis

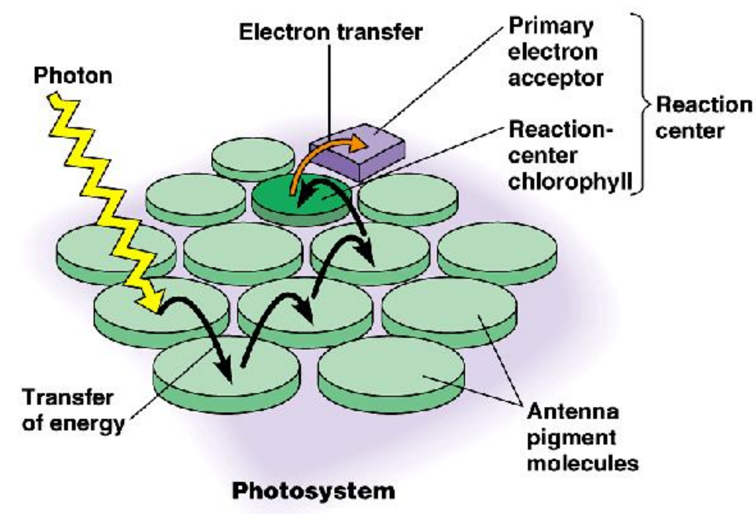
1. The light reactions convert solar energy to the chemical energy of ATP and NADPH: *a closer look*

In the thylakoid are several pigments that differ in their absorption spectrum.

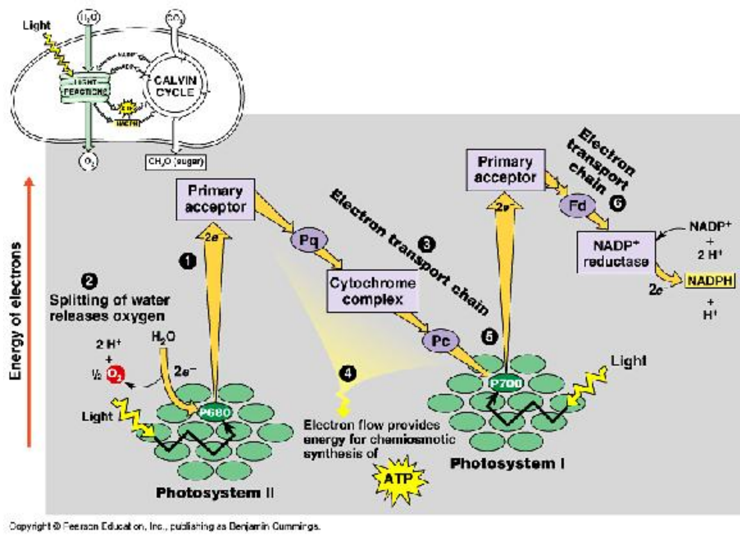
- **Chlorophyll *a***, the dominant pigment, absorbs best in the red and blue wavelengths, and least in the green.
- Other pigments with different structures have different absorption spectra.



- 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 by an elegant experiment by Thomas Engelmann.
- Only chlorophyll *a* participates directly in the light reactions but accessory photosynthetic pigments absorb light and transfer energy to chlorophyll *a*.
  - **Chlorophyll *b***, **Carotenoids** -funnels the energy from these wavelengths to chlorophyll *a*.
- In the thylakoid membrane, chlorophyll is organized along with proteins and smaller organic molecules into **photosystems**.
- 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 removes an excited electron from the reaction center chlorophyll *a*.
  - This starts the light reactions.

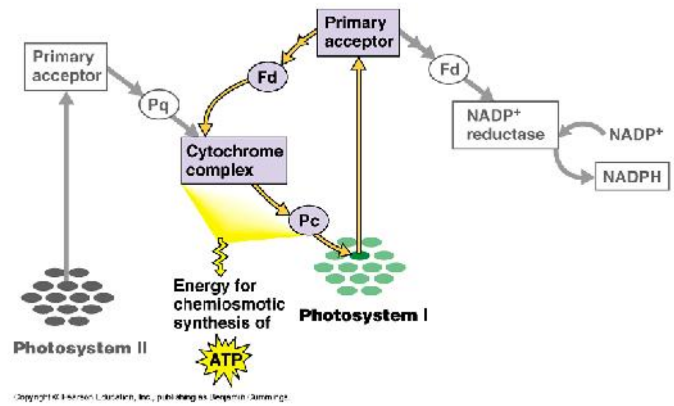


- There are two types of photosystems.
  - **Photosystem I** has a reaction center chlorophyll, the P700 center, that has an absorption peak at 700nm.
  - **Photosystem II** has a reaction center with a peak at 680nm.
  - The differences between these reaction centers (and their absorption spectra) lie 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.

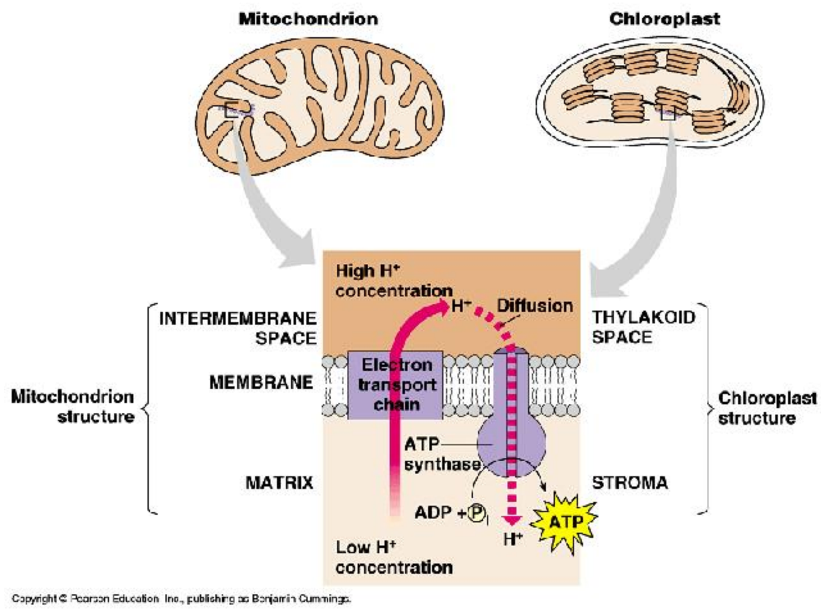


- 1) When photosystem II absorbs light, an excited electron is captured by the primary electron acceptor, leaving the reaction center oxidized.
- 2) An enzyme extracts electrons from water and supplies them to the oxidized reaction center.
  - This reaction splits water into two hydrogen ions and an oxygen atom, which combines with another to form O_2.
- 3) Photoexcited electrons pass along an electron transport chain before ending up at an oxidized photosystem I reaction center.
- 4) As these electrons pass along the transport chain, their energy is harnessed to produce ATP.
  - The mechanism of **noncyclic photophosphorylation** is similar to the process on oxidative phosphorylation in Respiration
- 5) At the bottom of this electron transport chain, the electrons fill an electron "hole" in an oxidized P700 center.
- 6) This hole is created when photons excite electrons on the photosystem I complex.
  - The excited electrons are captured by a second primary electron acceptor, which transmits them to a second electron transport chain.
  - Ultimately, these electrons are passed from the transport chain to $NADP^+$, creating 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.

- **cyclic electron flow.**Under certain conditions, photoexcited electrons from photosystem I, but not photosystem II, can take an alternative pathway,
    - 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**.
- Noncyclic electron flow produces ATP and NADPH in roughly equal quantities.
- However, the Calvin cycle consumes more ATP than NADPH.

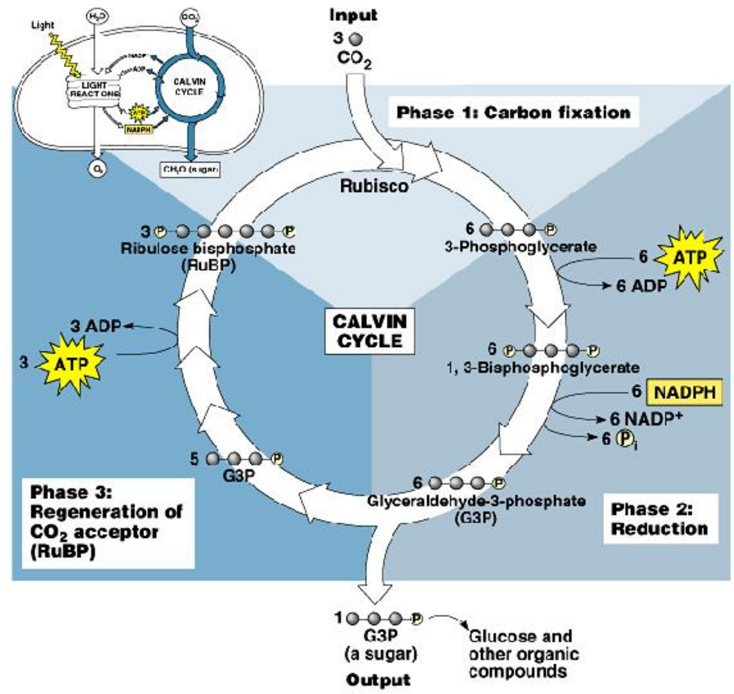


- Cyclic electron flow allows the chloroplast to generate enough surplus ATP to satisfy the higher demand for ATP in the Calvin cycle.
- Chloroplasts and mitochondria generate ATP by the same mechanism: chemiosmosis.



4. The Calvin cycle uses ATP and NADPH to convert CO_2 to sugar: *a closer look*

- The Calvin cycle regenerates its starting material after molecules enter and leave the cycle.
- CO_2 enters the cycle and leaves as sugar.
- The cycle spends the energy of ATP and the reducing power of electrons carried by NADPH to make the 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 would require six cycles and the fixation of six CO_2 molecules.
- The Calvin cycle has three phases.

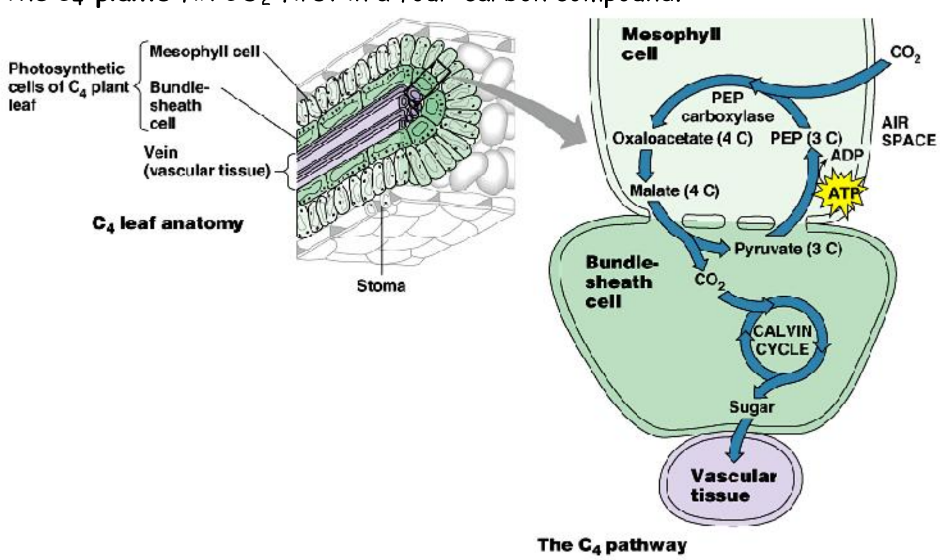


- In the **carbon fixation** phase, each CO_2 molecule is attached to a five-carbon sugar, ribulose bisphosphate (RuBP).
  - This is catalyzed by RuBP carboxylase or **rubisco**.
  - The six-carbon intermediate splits in half to form two molecules of 3-phosphoglycerate per CO_2.
- During **reduction**, each 3-phosphoglycerate receives another phosphate group from ATP to form 1,3-bisphosphoglycerate.
- If our goal was to produce one G3P net, 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 to be used by the plant cell.
  - The other **five** (15C) must remain in the cycle to regenerate three RuBP.
- For the net synthesis of one G3P molecule, the Calvin recycle consumes nine ATP and six NAPDH.
  - It "costs" three ATP and two NADPH per CO_2.

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

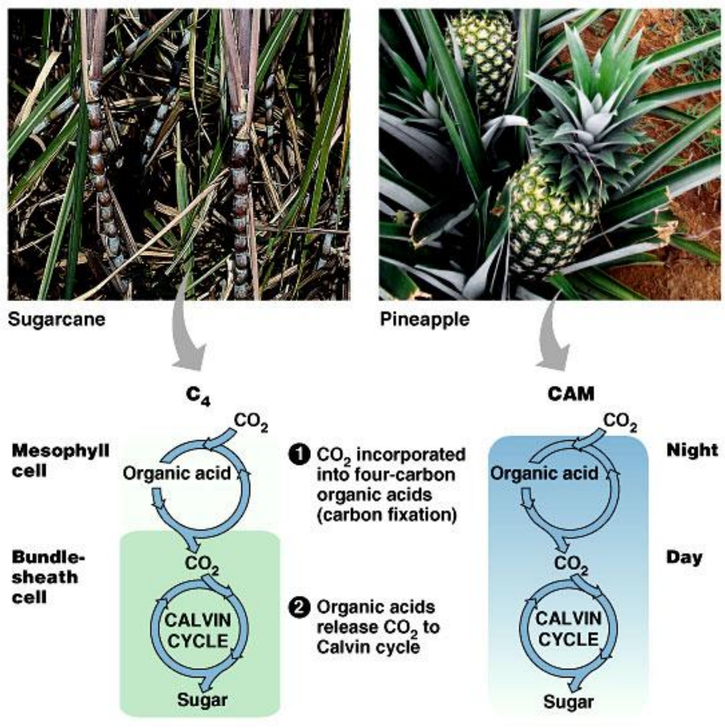
- One of the major problems facing terrestrial plants is dehydration.
- At times, solutions to this problem conflict with other metabolic processes, especially photosynthesis.

- 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 the stomata to conserve water, but this causes problems for photosynthesis.
- In most plants (**C_3 plants**) initial fixation of CO_2 occurs via rubisco and results in a three-carbon compound, 3-phosphoglycerate.
  - These plants include rice, wheat, and soybeans.
- When their stomata are closed 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, nor additional organic molecules.
- Photorespiration *decreases* photosynthetic output by siphoning organic material from the Calvin cycle.
- A hypothesis for the existence of photorespiraton (a inexact requirement for CO_2 versus O_2 by rubisco) 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.
- The **C_4 plants** fix CO_2 first in a four-carbon compound.



  - Several thousand plants, including sugercane and corn, use this pathway.
- In C_4 plants, **mesophyll cells** incorporate CO_2 into organic molecules.

    - The key enzyme, phosphoenolpyruvate carboxylase, adds CO_2 to phosphoenolpyruvate (PEP) to form oxaloacetetate.
    - **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, as CO_2, from the four-carbon compound 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, known as **CAM plants** for **crassulacean acid metabolism (CAM),** open stomata during the night and close them during the day.



(a) Spatial separation of steps (b) Temporal separation of steps

        - 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 incorporate light energy into the production of sugar.

6. Photosynthesis is the biosphere's metabolic foundation: *a review*

- 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 building the extracellular polysaccharide cellulose.
- Plants also store excess sugar by synthesizing starch.
  - Some is stored as starch in chloroplasts or 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 to the welfare of life on Earth.
  - Each year, photosynthesis synthesizes 160 billion metric tons of carbohydrate per year.