CHAPTER 10 - PHOTOSYNTHESIS

Life on Earth is solar powered
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 or heterotrophic

AUTOTROPHS (=producers)
  - produce organic molecules from CO₂ and other inorganic raw materials obtained from the environment
  - ultimate source of organic compounds for heterotrophs
  - Photoautotrophs use light as a source of energy to synthesize organic compounds.
    - Photosynthesis occurs in plants, algae, some other protists, and some prokaryotes.
  - Chemoautotrophs harvest energy from oxidizing inorganic substances, such as sulfur and ammonia
    - unique to prokaryotes

HETEROTROPHS (=consumers)
  - live on organic compounds produced by other organisms
  - dependent on photoautotrophs for food and for oxygen (by-product of photosynthesis)

PHOTOSYNTHESIS:
  - converts light energy to the chemical energy of food
    \[ 6\text{CO}_2 + 6\text{H}_2\text{O} + \text{light energy} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2 \]
  - Happens in all green parts of plants but leaves are the major site
    - about half a million chloroplasts/mm² of leaf surface
  - Color of leaf due to green pigment chlorophyll

Chloroplasts found mainly in mesophyll cells in the interior of the leaf
  - 30-40 chloroplasts/typical mesophyll cell
  - CO₂ and water vapor exits and CO₂ enters leaf through microscopic pores on underside of leaf = stoma (pl. stomata)

GUARD CELLS control openings - OPEN if TURGID; CLOSED if FLACCID
VEINS bring water from the roots and carry off sugar from mesophyll cells to nonphotosynthetic areas of plant
  - XYLEM - carries water
  - PHLOEM - carries sugar/nutrients

CHLOROPLAST:
  - Surrounded by DOUBLE membrane
  - Central fluid filled space = STROMA
  - System of interconnected membranous sacs = THYLAKOIDS
  - Stack of thylakoids = GRANUM (pl. GRANAE)
  - Fluid filled compartment inside thylakoid = THYLAKOID SPACE (lumen)
  - Chlorophyll is located in membranes of thylakoid sacs

Photosynthetic prokaryotes lack chloroplasts
  - photosynthetic membranes = infolded regions of the plasma membrane

LIGHT
  - form of electromagnetic radiation
  - Energy = inversely related to its wavelength (ie, shorter wavelengths pack more energy)
  - Visible light = 380-750 nm
SPECTROPHOTOMETER
- measures the ability of pigment to absorb various wavelengths of light
- beams narrow wavelengths of light through a solution containing the pigment
- measures the fraction of light transmitted at each wavelength
- Absorption spectrum plots a pigment's light absorption versus wavelength.

PIGMENTS = light absorbing molecules
- Only chlorophyll a participates directly in the light reactions;
- Other pigments have different absorption spectra;
  - funnel energy to chlorophyll a

Chlorophyll a (the dominant pigment)
- ABSORBS best in the red & violet-blue wavelengths;
- REFLECTS green wavelengths = reason plants "look" green

Chlorophyll b - slightly different structure
- funnels energy to chlorophyll a

CAROTENOIDS = accessory pigments (red, yellow, orange);
- Include: CAROTENES (orange) and XANTHOPHYLLS (yellow)
  - funnel the energy to chlorophyll a
  - photoprotection - protect chlorophyll from excessive light

CHLOROPHYLL
Porphin ring with MAGNESIUM cofactor in center
Plants have a and b forms - slight difference in functional groups
Chlorophyll a is universal
Other forms found in algae and cyanobacteria

EXCITING ELECTRONS:
When a molecule absorbs a photon of light an electron is elevated to an orbital with more potential energy
  - Electron moves from ground state → excited state
  - Excited electrons are unstable
    - 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 when excited (= FLUORESCENCE)
  - Outside of chloroplasts, if chlorophyll is illuminated, it will fluoresce and give off heat

PHOTOSYSTEMS in thylakoid membranes
- reaction center containing chlorophyll a and "primary electron acceptor"
- surrounded by a light-harvesting complex of other pigments and proteins (chlorophyll b, carotenoids)
- act as "antenna" to collect light energy → chlorophyll a → "primary electron acceptor"

Photosystem II (PS II) reaction center absorption peak at 680 nm (P$_{680}$)
Photosystem I (PS I) reaction center absorption peak at 700 nm (P$_{700}$)

TWO STAGES OF PHOTOSYNTHESIS:
1) LIGHT REACTIONS (Light dependent reactions)
  - convert solar energy to the chemical energy of ATP and NADPH
2) CALVIN CYCLE (Light independent reactions)
  - uses energy from the light reactions to incorporate CO$_2$ from the atmosphere into sugar.
    Named for Melvin Calvin (Got Nobel in 1961 for figuring out pathway)
**LIGHT REACTIONS:**
- Use solar power to store chemical energy in ATP and reducing power in electron carrier NADPH
- REQUIRE sunlight
- Two possible routes

1) **NONCYCLIC (LINEAR) ELECTRON FLOW** (= predominant route) produces both ATP and NADPH
   - Photosystem II absorbs a photon of light
   - One of the electrons of $P_{680}$ reaction center is excited to a higher energy state
   - Electron is captured by the primary electron acceptor, leaving the reaction center oxidized
   - Electrons are replaced by splitting a water molecule in thylakoid space
   - Oxygen released from water splitting combines with another oxygen atom; released as O$_2$ to atmosphere
   - Hydrogen released from water splitting accumulates in thylakoid space
   - Photoexcited electrons pass along electron transport chain ending up at Photosystem I reaction center
     - Energy from electrons “falling down” ETC is used by CYTOCHROMES to pump H$^+$ ions into thylakoid space
       - When chloroplasts are illuminated, thylakoid space pH ~5; stroma pH ~ 8 (1000 fold difference)
   - Photosystem I absorbs a photon of light
   - One of the electrons of $P_{700}$ reaction center is excited to a higher energy state
   - Electron is captured by the primary electron acceptor, leaving the reaction center oxidized
   - Electrons are replaced by electrons passed from PS II down ETC
   - Photoexcited electrons pass down a second electron transport chain through the protein FERRIDOXIN (Fd)
   - Enzyme transfers 2 electrons to NADP$^+$ (nicotinamide adenine dinucleotide phosphate) to produce NADPH
   - H$^+$ ions in thylakoid space provide energy to produce ATP as they diffuse down their gradient (ELECTROMOTIVE FORCE) back into the stroma through ATP SYNTHASE

2) **CYCLIC ELECTRON FLOW**
   - alternative pathway for photoexcited electrons from photosystem I = CYCLIC PHOTOPHOSPHORYLATION
   - Photoexcited electrons return to CYTOCHROMES instead of passing to Ferridoxin
   - So produces only ATP; NO NADPH; no OXYGEN
   - Used because NON CYCLIC FLOW makes equal amounts of ATP and NADPH
     - Calvin cycle requires more ATP than NADPH
     - Way to regulate amounts of ATP and NADPH needed for Calvin cycle
CHEMIOSMOSIS IN CHLOROPLASTS AND MITOCHONDRIA

SIMILARITIES

• Used by chloroplasts and mitochondria to generate ATP
• Energy from ELECTRON TRANSPORT CHAIN used to pump protons across a membrane
• Creates a H⁺ gradient across membrane
• ATP SYNTHASE uses energy from diffusion of H⁺ ions back across membrane to generate ATP
• Some electron carriers (cytochromes) are similar in both chloroplasts/mitochondria

DIFFERENCES:

OXIDATIVE PHOSPHORYLATION in MITOCHONDRIA

• Mitochondria transfer chemical energy from food molecules to ATP
• Mitochondrial INNER MEMBRANE pumps protons from MATRIX out to the INTERMEMBRANE SPACE
• ATP made as H⁺ ions diffuse back to stroma

PHOTOPHOSPHORYLATION in CHLOROPLASTS

• Chloroplasts transform light energy into the chemical energy of ATP
• Chloroplast THYLAKOID membrane pumps protons from the stroma into the thylakoid space

CALVIN CYCLE (= LIGHT INDEPENDENT PHASE)

• Originally called “Dark reactions” but don’t just happen at night
• Happens in stroma
• Uses ATP and NADPH (made in Light Reactions) to convert CO₂ to sugar
• regenerates its starting material after molecules enter and leave the cycle
• anabolic - uses energy to build sugar from smaller molecules
• Carbon enters the cycle as CO₂ and leaves as sugar
• Actual sugar product = three-carbon sugar, glyceraldehyde-3-phosphate (G3P)
• Each turn of the Calvin cycle fixes carbon from 1 CO₂; 3 turns to make 1 G3P; 6 turns to make 1 glucose
• Uses 18 ATP’s and 12 NADPH’s to make 1 glucose
**CALVIN CYCLE**

**Phase 1: Carbon fixation**

Each CO$_2$ molecule is attached to a five-carbon sugar, RIBULOSE BISPHOSPHATE (RuBP)
- This is catalyzed by RuBP carboxylase (=RUBISCO)
- Rubisco = most abundant protein in chloroplasts; probably the most abundant protein on Earth
- Unstable six-carbon intermediate splits in half to form two three carbon 3-phosphoglycerate for each CO$_2$

**Phase 2: Reduction**

ATP provides energy; NADPH provides reducing power to reduce intermediates
Three carbon GLYCERALDEHYDE-3-PHOSPHATE (G3P) is produced
G3P exits the cycle; = starting material for metabolic pathways that synthesize other organic compounds, including glucose and other carbohydrates

**Phase 3: Regeneration**

Rest of molecules rearrange to regenerate the starting RuBP molecules
For the net synthesis of one G3P molecule, the Calvin cycle consumes nine ATP and six NADPH (X 2 for glucose)
Light reactions regenerate ATP and NADPH

WHERE DOES THE OXYGEN IN SUGAR COME FROM: H$_2$O or CO$_2$?

CO$_2$ + H$_2$O + light energy $\rightarrow$ [CH$_2$O] + O$_2$

[CH$_2$O] represents the general formula for a sugar
Before 1930's thought splitting H$_2$O provided oxygen for sugar
Experiments with radio-labeled oxygen isotopes in H$_2$O and CO$_2$ showed oxygen in carbo's comes from CO$_2$

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$_2$O

Photosynthesis is a REDOX REACTION
- It reverses the direction of electron flow in cellular respiration
- H$_2$O is OXIDIZED (loses electrons)
- CO$_2$ is REDUCED (gains electrons) to make sugar
- Process requires energy (provided by light)

C$_3$ PLANTS = Most plants (EX: rice, wheat, and soybeans)
Rubisco fixes CO$_2$ into three carbon compound (3PGA)
Calvin cycle happens during day when ATP and NADPH are available from light reactions

PROBLEM: Closing stomata on hot dry days to conserve water, reduces CO$_2$ needed for photosynthesis
When CO$_2$ is low Rubisco adds O$_2$ to RuBP instead of CO$_2$
= PHOTORESPIRATION
Rubisco adds O$_2$ to RuBP, RuBP splits into a three-carbon piece and a two-carbon piece
Two-carbon fragment is exported from chloroplast and degraded to CO$_2$ by mitochondria and peroxisomes.
- Unlike normal respiration, consumes ATP instead of making it
- Unlike photosynthesis, siphons organic material from the Calvin cycle instead of making sugar
- Photorespiration can drain away as much as 50% of the carbon fixed by the Calvin cycle on a hot, dry day.

PHOTORESPIRATION may be evolutionary baggage
When rubisco first evolved, the atmosphere had far less O$_2$ and more CO$_2$ than it does today
Inability of the active site of rubisco to exclude O$_2$ would have made little difference then,
BUT makes a difference today when O$_2$ in atmosphere is higher
Alternative mechanisms of carbon fixation
Certain plant species have evolved alternate modes of carbon fixation to minimize photorespiration

C₄ PLANTS - EX: sugarcane and corn
Minimizes photorespiration and allows plant to efficiently fix CO₂ at low concentrations
Allows plants to thrive in hot regions with intense sunlight
Unique leaf anatomy; spatial separation of CO₂ fixation from air/into sugar
BUNDLE SHEATH cells arranged into tightly packed sheaths around leaf veins
MESOPHYLL cells more loosely arranged cells located between bundle sheath cells and leaf surface

PEP CARBOXYLASE in mesophyll cells has very high affinity for CO₂:
Can fix CO₂ efficiently at low levels when rubisco can’t
CO₂ fixed into a FOUR CARBON compound/ pumped into BUNDLE SHEATH cells
CO₂ is released in Bundle sheath cells, keeping CO₂ levels high enough for rubisco to work in Calvin cycle

PEP Carboxylase also found in some bacteria, but not animals or fungi.

CRASSULACEAN ACID METABOLISM (CAM) PLANTS - EX: Succulents, cacti, pineapples
Evolved in hot, dry environments
TEMPORAL separation of CO₂ fixation from air/into sugar
Open stomata during night when temps are lower and humidity higher
Close them during the day to save water
AT NIGHT: Fix CO₂ in mesophyll cells
Use PEP carboxylase, like C₄ plants, to fix CO₂ forming four carbon compounds
Stored in vacuoles
DURING DAY:
Light reactions supply ATP & NADPH;
CO₂ is released from organic acids to complete Calvin cycle

IMPORTANCE OF PHOTOSYNTHESIS:
Energy from sunlight = stored as chemical energy in organic compounds
Sugar made in the chloroplasts supplies the entire plant with chemical energy
AND with carbon skeletons to synthesize all the major organic molecules of cells
- Carbohydrate (as disaccharide sucrose) travels via the veins to nonphotosynthetic cells
- About 50% = consumed as fuel for cellular respiration in plant mitochondria
Also provides raw materials for anabolic pathways, including synthesis of proteins and lipids and formation of the extracellular polysaccharide cellulose
Cellulose = main ingredient of cell walls; = most abundant organic molecule in the plant, maybe on Earth
Plants also store excess sugar by synthesis of starch
in chloroplasts and in storage cells in roots, tubers, seeds, and fruits.

On a global scale, photosynthesis is the most important process on Earth
° Provides food energy for heterotrophs, including humans
° It is responsible for the presence of oxygen in our atmosphere.
° Each year, photosynthesis synthesizes 160 billion metric tons of carbohydrate