Chapter 10
Photosynthesis

AP Biology
Overview: The Process That Feeds the Biosphere

• **PHOTOSYNTHESIS** converts solar energy from the sun to chemical energy stored in sugar and other organic molecules.

  – Photosynthesis nourishes almost the entire living world directly or indirectly.

• Organisms get the organic compounds they use for energy and carbon skeletons by one of 2 major modes:

  – 1) Autotrophic nutrition
  – 2) Heterotrophic nutrition
**Autotrophs**

- **Autotrophs** are self-feeders
  - They sustain themselves without eating anything that comes from other living beings
  - They get their organic molecules from CO$_2$ and other inorganic raw materials from the environment
  - Autotrophs are the *PRODUCERS* of the biosphere
    - They are the ultimate source of organic compounds for all non-autotrophic organisms
  - Almost all plants are autotrophs
    - They only nutrients they require are water and minerals from soil and CO$_2$ from the air
    - More specifically, plants are *PHOTOAUTOTROPHS* (organisms that use light as a source of energy to make organic substances)
  - Photosynthesis also occurs in algae, certain other protists, and some prokaryotes
Heterotrophs

- **Heterotrophs** obtain organic material by consuming compounds produced by other organisms
  - The most obvious form of “other-feeding” occurs when animals eat plants or other animals
    - Heterotrophic nutrition can also be more subtle:
      - Decomposers consume the remains of dead organisms by breaking down and feeding on organic litter such as carcasses, feces, and fallen leaves
        - Most fungi and many types of prokaryotes get their nourishment this way
    - Heterotrophs are the **CONSUMERS** of the biosphere
  - Almost all heterotrophs, including humans, are completely dependent (directly or indirectly) on photoautotrophs for food and oxygen (the byproduct of photosynthesis)
Concept 10.1: Photosynthesis converts light energy to the chemical energy of food.
Evolution of Photosynthesis

- Chloroplasts are structurally similar to and likely evolved from photosynthetic bacteria
  - The process of photosynthesis most likely originated in a group of bacteria that had infolded regions of plasma membrane
    - These infolded regions likely contained clusters of photosynthetic enzymes and other molecules
  - In existing photosynthetic bacteria, infolded photosynthetic membranes function in a similar way to the internal membranes of the chloroplast
    - The original chloroplast, in fact, is thought to have been a photosynthetic prokaryote that lived inside a eukaryotic cell
  - Photosynthetic organisms are able to harness light energy to make organic compounds due to the structural organization of the cell
Chloroplasts: The Sites of Photosynthesis in Plants

- All green parts of a plant have chloroplasts but the leaves are the major sites of photosynthesis in most plants
  - There are ~ ½ a million chloroplasts/mm² of leaf surface
    - The color of a leaf comes from **CHLOROPHYLL** – the green pigment located in chloroplasts
  - Light energy absorbed by chlorophyll drives the production of organic molecules in the chloroplast
    - CO₂ enters the leaf and O₂ exits by way of **STOMATA** – microscopic pores in the leaf
    - Water absorbed by roots is delivered to the leaf in veins
      - Leaves also use these veins to export sugar to roots and other nonphotosynthetic parts of the plant
Chloroplasts are found mainly in the cells of the **MESOPHYLL** – tissue in the interior of the leaf.

- A typical mesophyll cell has 30-40 chloroplasts, each of which measures 2-4 µm by 4-7 µm
  - A double-membrane envelope encloses the **STROMA** – the dense fluid in a chloroplast

- A system of interconnected membranous sacs called **THYLAKOIDS** separate the stroma from another compartment in the interior of the thylakoids called the **THYLAKOID SPACE**
  - Chlorophyll is found in the thylakoid membranes
  - Thylakoid sacs are stacked in columns called **GRANA**
Although some of the steps of photosynthesis are not completely understood, the overall equation has been known since the 1800s:

- In the presence of light, green parts of the plant produce organic compounds and oxygen from CO$_2$ and water:

  $$6 \text{ CO}_2 + 12 \text{ H}_2\text{O} + \text{Light energy} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6 \text{ O}_2 + 6 \text{ H}_2\text{O}$$

- The direct product of photosynthesis is actually a 3-carbon sugar that can be used to make glucose.

- Water appears on both sides of the equation because 12 molecules are consumed and 6 molecules are formed.
The Splitting of Water

- The oxygen given off by plants comes from water, NOT CO₂
  - Chloroplasts split water into hydrogen and oxygen
    - We used to think that the oxygen came from splitting CO₂
  - Experiments showed that oxygen from plants was radioactively labeled with the heavy isotope 18O only if water was the source of the tracer
  - If the tracer (18O) was introduced to the plant in the form of CO₂, the label did NOT show up in the released CO₂

Reactants:
- 6 CO₂
- 12 H₂O

Products:
- C₆H₁₂O₆
- 6 N₂
- 6 O₂
Photosynthesis as a Redox Process

• Both photosynthesis and cellular respiration involve redox reactions

  • Photosynthesis reverses the direction of electron flow seen in cellular respiration

    – Water is split and electrons are transferred along with H+ ions from water to CO₂, reducing it to a sugar (H₂O is oxidized, CO₂ reduced)

  • Because electrons INCREASE in potential energy as they move from water to sugar, photosynthesis REQUIRES energy (endergonic)

    – This energy boost is provided by light
The Two Stages of Photosynthesis: *The Light Reactions*

- Photosynthesis is NOT a single process but 2 processes, each with multiple steps
  - 1) Light reactions (the “photo” part of photosynthesis)
  - 2) Calvin cycle (the “synthesis” part)

- Light reactions occur in the thylakoids and convert solar energy to chemical energy
  - Water is split, providing a source of electrons and H+ ions
    - This gives off oxygen as a byproduct
  - Light absorbed by chlorophyll drives the transfer of electrons and H+ ions from water to an acceptor called NADP+ (nicotinamide adenine dinucleotide phosphate), reducing it to NADPH
  - ATP is generated using chemiosmosis to power the addition of a phosphate group to ADP—called *PHOTOPHOSPHORYLATION*

- ***Light energy is therefore converted to chemical energy in the form of NADPH (a source of electrons with reducing power) and ATP***

- ***Light reactions produce NO sugar***
The Two Stages of Photosynthesis: The Calvin Cycle

- The Calvin cycle occurs in the STROMA
  - It begins by incorporating CO₂ from the air into organic molecules already present in the chloroplast – known as CARBON FIXATION
    - Calvin cycle then reduces this fixed carbon by the addition of electrons
      - Reducing power is provided by NADPH from the light reactions
    - Calvin cycle also uses the power of ATP generated in the light reactions to convert CO₂ into a carbohydrate
  - Calvin cycle is sometimes referred to as the DARK REACTIONS or light-independent reactions because none of the steps require light DIRECTLY
    - Calvin cycle still normally occurs in daylight in most plants, however, because ATP and NADPH from the light reactions is needed
Summary of The Two Stages of Photosynthesis

Thus, in summary, the light reactions (in the thylakoids):

- Split $\text{H}_2\text{O}$
- Release $\text{O}_2$
- Reduce $\text{NADP}^+$ to NADPH
- Generate ATP from ADP by photophosphorylation

The Calvin cycle (in the stroma):

- Forms sugar from $\text{CO}_2$, using ATP and NADPH
Concept Check 10.1

1) How do the reactant molecules of photosynthesis reach the chloroplasts in leaves?

2) How did the use of an oxygen isotope help elucidate the chemistry of photosynthesis?

3) The Calvin cycle clearly requires the products of the light reactions. ATP and NADPH. Suppose a classmate asserts that the converse is not true – that the light reactions don’t depend on the Calvin cycle and, without continual light, could just keep on producing ATP and NADPH. Do you agree or disagree? Explain.
Concept 10.2: The light reactions convert solar energy to the chemical energy of ATP and NADPH
Understanding Photosynthesis: Properties of Light

- Chloroplasts are chemical factories powered by the sun
  - Thylakoids transform light energy into the chemical energy of ATP and NADPH
  - To understand this conversion better, we need to understand some important properties of light
The Nature of Sunlight

- Light is a form of energy known as **ELECTROMAGNETIC ENERGY** or electromagnetic radiation
  - It travels in waves (similar to those created by dropping a pebble into a pond)
    - The distance between crests of electromagnetic waves is called a **WAVELENGTH**
  - Wavelengths can range from less than a nanometer (gamma rays) to more than a kilometer (radio waves)
The Electromagnetic Spectrum

- The entire range of radiation is called the **ELECTROMAGNETIC SPECTRUM**
  - The radiation known as **VISIBLE LIGHT** is a narrow band on the spectrum from about 380-750 nm in wavelength
    - This is the radiation that drives photosynthesis
  - The model of light as waves explains many of light’s properties, but in certain respects, light behaves as though it consists of discrete particles called **PHOTONS**
    - Photons are not tangible objects (something you can see) but **ACT** like objects in that each of them has a fixed amount of energy
      - Amount of energy is inversely related to the wavelength of light (shorter wavelength = greater energy)
Photosynthetic Pigments: The Light Receptors

- When light meets matter, it can do one of 3 things:
  - 1) Be reflected
  - 2) Transmitted
  - 3) Be absorbed

- Substances that absorb visible light are called **PIGMENTS**

- Different pigments absorb light of different wavelengths
  - Wavelengths that are absorbed disappear
  - The color that we see is the color that is most reflected or transmitted by the pigment
    - Leaves look green because chlorophyll absorbs violet-blue and red light but transmits and reflects green light
    - Pigments that absorb ALL wavelengths appear black

Animation: Light and Pigments
Spectrophotometers

- An instrument called a SPECTROPHOTOMETER can measure the ability of a pigment to absorb different wavelengths of light
  - This machine directs beams of light of different wavelengths through a solution of pigment
  - The fraction of light transmitted at each wavelength is then measured
Spectrophotometers

1) White light is separated into colors (wavelengths) by a prism

2) One by one, the different colors of light are passed through the sample (chlorophyll in this example)
   - Green light and blue light are shown here

3) Transmitted light strikes a photoelectric tube which converts the light energy into electricity

4) Electrical current is measured by a galvanometer
   - Indicates the fraction of light transmitted through the sample
   - From this, we can determine the amount of light absorbed

- ***High transmittance = Low absorption***
There are 3 types of pigments found in chloroplasts:

1) Chlorophyll a – participates directly in light reactions
2) Chlorophyll b
3) A group of accessory pigments called **CAROTENOIDS**

**Absorption spectra**

(a) Absorption spectra

- Chlorophyll a
- Chlorophyll b
- Carotenoids

**Wavelength of light (nm)**

400 500 600 700

**Action spectrum**

Rate of photosynthesis (measured by O₂ release)
Absorption and Action Spectra

- A graph plotting a pigment’s light absorption versus wavelength is called an **ABSORPTION SPECTRUM**
  - The spectrum of chlorophyll a suggests that violet-blue and red light work best for photosynthesis (since they are absorbed)
  - Green is least effective
  - This is confirmed by an **ACTION SPECTRUM** for photosynthesis
    - An action spectrum profiles the relative effectiveness of different wavelengths of radiation in driving the process of photosynthesis
    - It is prepared by illuminating chloroplasts with different colors of light and then plotting the wavelengths against some measure photosynthetic rate (like CO$_2$ consumption or O$_2$ release)
The action spectrum for photosynthesis was first demonstrated by a German botanist in 1883 named Theodor W. Engelmann.

- He used bacteria that was filament-shaped to measure the rates of photosynthesis in algae.
- Engelmann illuminated alga with light that had been passed through a prism.
- This exposed different segments of the alga to different wavelengths.
- He then used aerobic bacteria, which tend to cluster near an oxygen source, to determine which segments of the alga were releasing the most oxygen (and thus photosynthesizing the most).
- Bacteria congregated in greatest numbers around the parts of the alga illuminated with violet-blue or red light.
Functions of Accessory Pigments: Chlorophyll b

- Although chlorophyll a is the main photosynthetic pigment, accessory pigments like chlorophyll b and carotenoids are also useful in photosynthesis
  - Chlorophyll b has a slightly different absorption spectra than chlorophyll a
    - Chlorophyll b is more olive green
      - This broadens the spectrum of colors for photosynthesis
Functions of Accessory Pigments: Carotenoids

- Carotenoids are hydrocarbons that are various shades of yellow and orange
  - They absorb violet and blue-green light
  - This may also broaden the spectrum of colors used to drive photosynthesis
  - A more important function seems to be **PHOTOPROTECTION**:
    - Carotenoids absorb and dissipate excessive light energy that would otherwise damage chlorophyll or interact with oxygen to form reactive oxidative molecules that are dangerous to the cell
    - Similar carotenoids are found in the human eye
Excitation of Chlorophyll by Light

- When a molecule absorbs a photon of light, one of the molecule’s electrons is elevated to an orbital where it has more potential energy.
  - When an electron is in its normal orbital, the pigment molecule is said to be in its **GROUND STATE**.
- When absorption of a photon boosts an electron to an orbital of higher energy, the molecule is said to be in an **EXCITED STATE**.
Excitation of Chlorophyll by Light

- The only photons absorbed are those whose energy is exactly equal to the energy difference between the ground state and the excited state
  - This energy difference is different for different molecules
- It also means that pigments absorb only photons corresponding to a specific wavelength, explaining why each pigment has a unique absorption spectrum
Excitation of Chlorophyll by Light: Fluorescence

- Electrons cannot remain in their excited state for long because it is unstable
  - Excited electrons usually drop back down to their ground-state orbital in a billionth of a second
    - Excess energy is released as heat
      - Ex) Conversion of light energy to heat is what makes top of cars so hot on sunny day
  - Some pigments (including chlorophyll) give off light as well as heat after absorbing photons
    - As excited electrons fall back to their ground state, photons are given off
      - This afterglow is called **FLUORESCENCE**
A Photosystem: A Reaction-Center Complex Associated with Light-Harvesting Complexes

- Chlorophyll molecules do not exist in isolation, but are organized with other small organic molecules and proteins into **PHOTOSYSTEMS**

- Photosystem is composed of a protein complex called a **REACTION-CENTER COMPLEX (RCC)** surrounded by many **LIGHT-HARVESTING COMPLEXES**

- Light-harvesting complexes are made up of different pigment molecules (which may include chlorophylls a and b, as well as carotenoids) bound to proteins

- A number and variety of pigment molecules allow a photosystem to gather light over a larger surface and portion of the spectrum than any single pigment molecule could otherwise

- Light-harvesting complexes act like an antenna for the RCC

  - Energy is transferred from one pigment molecule to another in the complex (like a human “wave”) until it is passed to the RCC
Light Reactions: Primary Electron Acceptors

- The RCC has a molecule that can accept electrons, becoming reduced
  - This molecule is called the **PRIMARY ELECTRON ACCEPTOR**
- A pair of chlorophyll a molecules in the RCC are special because they can transfer their excited electrons to the primary electron acceptor
  - This ability is due to their environment (location and association with other molecules)
    - The transfer of excited electrons to the primary electron acceptor is a REDOX reaction
  - Isolated chlorophyll fluoresces because there is no electron acceptor, so the potential energy of the excited electron is lost as light and heat
  - The solar-powered transfer of an electron from the reaction-center chlorophyll a to the primary electron acceptor is the 1st step of the light reactions
Photosystems I and II

- There are 2 types of photosystems involved in the light reactions of photosynthesis: Photosystems I and II (PSI and PSII)
  - These photosystems are named in order of their discovery (photosystem II functions 1\textsuperscript{st} in the light reactions)
    - Each photosystem has a different reaction-center complex:
      - It includes a specific kind of primary electron acceptor next to a pair of special chlorophyll a molecules associated with specific proteins
        - The reaction-center chlorophyll a molecules of PS II is known as $P680$
          - It absorbs light at a wavelength of 680 nm best (red part of spectrum)
        - Chlorophyll a at reaction-center complex of PS I is called $P700$
          - It most effectively absorbs light at wavelengths of 700 nm (far-red part of spectrum)
    - P680 and P700 have nearly identical chlorophyll a molecules
      - Their association with different proteins in the thylakoid membrane affects their electron distribution and accounts for the slight difference in light-absorbing properties
Linear Electron Flow

• The flow of electrons during the light reactions of photosynthesis can either be cyclic or linear
  
  – Linear electron flow, however, is the primary pathway

• It involves both photosystems

• It produces ATP and NADPH using light energy
1) A photon of light strikes a pigment molecule in the light-harvesting complex

- This boosts one of its electrons to a higher energy level

  • As this electron falls back to ground state, an electron in a nearby pigment molecule is raised to its excited state

  • The process continues and this relayed energy reaches the P680 pair of chlorophyll a molecules in the PS II reaction-center complex

    - An electron in this pair of chlorophylls is then excited to a higher energy state

2) This excited electron in the special chlorophyll a molecules is transferred from P680 to the primary electron acceptor

   - Because the resulting form of P680 is missing an electron, we can refer to it as P680+
3) An enzyme catalyzes the splitting of a water molecule into 2 electrons, 2 H+ ions, and an oxygen atom

- The electrons are supplied one by one to the P680+ pair of pigment molecules
  - Each electron replaces one that was transferred to the primary electron acceptor
  - P680+ is the strongest biological oxidizing agent known – its electron “hole” must be filled
    - This helps the transfer of electrons from the split water molecule
  - The oxygen atom immediately combines with another oxygen atom (from the splitting of a second water molecule), forming O₂
    - This O₂ is released as the byproduct of photosynthesis
Light Reactions: Steps 4 and 5

4) Each photo-excited electron passes from primary electron acceptor of PS II to PS I using an ETC
   - The components of this ETC are similar to those of the ETC of cellular respiration

5) The “fall” of electrons to a lower energy level is exergonic
   - This energy is used to build up a proton gradient across the thylakoid membrane
     - Diffusion of these H+ ions back across the membrane drives ATP synthesis
Light Reactions: Step 6

6) Electrons travel down the ETC to the PS I reaction-center complex

- Here, an electron of the P700 pair of chlorophyll a molecules has been excited by another photon of light

- This photoexcited electron is then transferred to PS I’s primary electron acceptor, creating an electron “hole” in P700, creating P700+

  - P700+ can then accept an electron from PS II once it reaches the end of the ETC
Light Reactions: Steps 7 and 8

• 7) Photoexcited electrons are passed from the primary electron acceptor of PS I down a second ETC through a protein called ferredoxin (Fd)
  
  – This occurs in a series of redox reaction
  
  – No proton gradient is created, so no ATP is produced

• 8) An enzyme called NADP+ reductase catalyzes the transfer of pair of electrons from ferredoxin to NADP+, creating NADPH
  
  – Electrons are now available for the reactions of the Calvin cycle
An Analogy For the Light Reactions

- A mechanical analogy for the light reactions
  - People = primary electron acceptors of PS II and I
  - P680 and P700 = see-saws
Cyclic Electron Flow

- In some cases, photoexcited electrons can take an alternative path called **CYCLIC ELECTRON FLOW**
  - This uses PS I but NOT PS II
  - No NADPH is produced
  - No release of oxygen
  - Surplus ATP is generated

- During cyclic electron flow, photoexcited electrons from PS I are shunted back from ferredoxin (Fd) to chlorophyll via the cytochrome complex and the protein plastocyanin (Pc) of the 1<sup>st</sup> ETC
  - ATP synthesis is supplemented but no NADPH is produced
  - The ferredoxin molecules shown are actually the same Fd molecules
  - Parts shaded in gray do not occur
Several groups of photosynthetic bacteria are known to have PS I but not PS II

- Ex) Purple sulfur bacteria
  - We believe that these bacterial groups are descendents of bacteria in which photosynthesis first evolved

Cyclic electron flow can also occur in photosynthetic species that have both photosystems

- Ex) Cyanobacteria
  - Though this process is probably an “evolutionary left-over,” there is at least one benefit
    - Mutant plants that can’t carry out cyclic electron flow do not grow well under intense light
      - This is evidence that cyclic electron flow may be photoprotective
A Comparison of Chemiosmosis in Chloroplasts and Mitochondria

- Chloroplasts and mitochondria make ATP in the same basic way, using chemiosmosis (generation of H+ gradient as electrons are passed along the ETC)
  - Mitochondria use chemiosmosis to transfer energy from food to ATP

- Chloroplasts transform light energy into the chemical energy of ATP
  - The spatial organization of chemiosmosis differs slightly between chloroplasts and mitochondria but also shows similarities
Chemiosmosis in Mitochondria vs. Chloroplasts

- The inner membrane of the mitochondria pumps H+ ions from the mitochondrial matrix out to the intermembrane space

- The thylakoid membrane of chloroplasts pumps H+ ions from the stroma into the thylakoid space (inside the thylakoid)

  - The intermembrane space and thylakoid space are thus comparable spaces in these 2 organelles, as are the mitochondrial matrix and the stroma

  - ATP synthesis occurs in both organelles as H+ ions diffuse back into the mitochondrial matrix in mitochondria or the stroma in chloroplasts
Summary of the Light Reactions

- Summary of light reactions:
  - Electron flow pushes electrons from water (low potential energy) to NADPH (high potential energy)
    - This light-driven electron current also makes ATP
  - Oxygen is generated as a by-product from the splitting of water
- NADPH and ATP are produced on the side of the chloroplast membrane facing the stroma
  - Both NADPH and ATP are necessary for the next part of photosynthesis – the Calvin cycle
    - The Calvin cycle takes place in the stroma
Summary of the Light Reactions

1) Water is split by PS II on side of membrane facing thylakoid space

2) A mobile carrier called Plastoquinone (Pq) transfers electrons to the cytochrome complex
   - 4 protons are translocated across the membrane into the thylakoid space

3) H+ ion is removed from stroma and taken up by NADP+, along with 2 electrons, forming NADPH
   - Diffusion of H+ from thylakoid space back to stroma powers ATP synthase
1) What color of light is least effective in driving photosynthesis? Explain.

2) Compared to a solution of isolated chlorophyll, why do intact chloroplasts release less heat and fluorescence when illuminated?

3) In the light reactions, what is the initial electron donor? Where do the electrons end up?

4) In an experiment, isolated chloroplasts placed in a solution with the appropriate components can carry out ATP synthesis. Predict what would happen to the rate of synthesis if a compound is added to the solution that makes membranes freely permeable to hydrogen ions.
Concept 10.3: The Calvin cycle uses ATP and NADPH to convert CO$_2$ to sugar
The Calvin Cycle vs. the Citric Acid Cycle

- The Calvin cycle is similar to the citric acid cycle in that a starting material is regenerated after molecules enter and leave the cycle
  - TCA cycle is catabolic (Breaks glucose down)
    - This releases energy
  - The Calvin cycle is anabolic (builds sugar from smaller molecules)
    - This consumes energy
Overview of the Calvin Cycle

• The carbohydrate produced directly from the Calvin cycle is not actually glucose, but a 3-carbon sugar called glyceraldehyde-3-phosphate (G3P)
  
  To make one G3P, the Calvin cycle must take place 3 times, using 3 molecules of CO$_2$

• The Calvin cycle can be divided into 3 phases:
  
  1) Carbon fixation

  2) Reduction

  3) Regeneration of the CO2 acceptor
The Calvin Cycle: Step 1

- Step 1) Carbon fixation
  - The Calvin cycle incorporates each CO$_2$ molecule (one at a time) by attaching it to a 5-C sugar called ribulose bisphosphate (RuBP)
    - This reaction is catalyzed by an enzyme called **RUBISCO**
    - The resulting product is a very unstable 6-C intermediate that immediately splits in half, forming 2 molecules of 3-phosphoglycerate (for each CO$_2$ fixed)
The Calvin Cycle: Step 2

- **Step 2) Reduction**
  - Each 3-phosphoglycerate receives another phosphate from ATP, forming 2 molecules of 1,3-bisphosphoglycerate

- 1,3-bisphosphoglycerate is reduced by NADPH (gains 2 electrons) and also loses a phosphate group, forming 2 molecules of glyceraldehyde-3-phosphate (G3P)

- For every 6 G3P generated, only 1 can be used to make glucose; the other 5 must be recycled to regenerate RuBP
The Calvin Cycle: Step 3

- Step 3) Regeneration of the CO₂ acceptor
  - The carbon skeletons of the 5 recycled G3P molecules are rearranged into 3 molecules of RuBP
    - This requires 3 more ATP
  - RuBP is now prepared to receive CO₂ again and the cycle continues

- Net synthesis of 1 G3P requires 9 ATP and 6 NADPH
  - G3P spun off from Calvin cycle becomes the starting material for metabolic pathways that make other organic compounds, including glucose
Concept Check 10.3

1) To synthesize one glucose molecule, the Calvin cycle uses ______ molecules of CO$_2$, ______ molecules of ATP, and ______ molecules of NADPH.

2) Explain why the large numbers of ATP and NADPH molecules used during the Calvin cycle are consistent with the high value of glucose as an energy source.

3) Explain why a poison that inhibits an enzyme in the Calvin cycle will also inhibit the light reactions.
Concept 10.4:
Alternative mechanisms of carbon fixation have evolved in hot, arid climates
Photosynthesis and Adaptation to Terrestrial Life

• Plants have been adapting to problems with terrestrial life since they evolved 475 mya

  • One of these major problems is water loss (dehydration)

  – Solutions to this problem often involve tradeoffs, such as the compromise between photosynthesis and preventing too much water loss

• CO₂ needed for photosynthesis enters leaves through pores called stomata

  – Stomata are also the same way plants lose water through evaporation (transpiration)

• On hot days, dry days most plants close their stomata to help conserve water

  – This response also reduces the rate of photosynthesis, since access to CO2 is limited and oxygen builds up

• These conditions favor a process called photorespiration
C₃ Plants

- In most plants, carbon is initially fixed using the enzyme rubisco during the Calvin cycle
  - This produces a 3-carbon compound (3-phosphoglycerate)

- These plants are therefore called C₃ plants
  - Examples of C₃ plants are rice, wheat, and soybeans
Photorespiration: An Evolutionary Relic?

- When stomata of C₃ plants close on hot days, the plants produce less sugar because of the limited amount of CO₂ available to run the Calvin cycle
  - As CO₂ becomes scarce, rubisco begins to add oxygen to the Calvin cycle instead of CO₂
  - The resulting compound is split and rearranged to form CO₂
- This process is called **PHOTORESPIRATION** because it occurs in the light (photo) and consumes oxygen while producing CO₂ (respiration)
  - Photorespiration generates no ATP (unlike cellular respiration)
    - It actually **CONSUMES** ATP
  - Photorespiration makes no sugars
    - It decreases photosynthetic output because organic molecules needed for Calvin cycle to make sugar are instead used to make CO₂ that is released and not fixed
Scientists believe that photorespiration may be a metabolic relic from a much earlier time when the atmosphere had less oxygen and more CO₂.

- In this ancient atmosphere, the inability of rubisco’s active site to exclude oxygen would not have made much difference (not much oxygen around)
  - Modern rubisco probably retained some of this chance affinity for oxygen

Recently, we have discovered that photorespiration plays a protective role in plants.

- Plants that have defects preventing photorespiration are more susceptible to damage caused by too much light
  - This is evidence for the hypothesis that photorespiration neutralizes the otherwise damaging products of the light reactions that build up in the absence of the Calvin cycle

Despite its photoprotective role, photorespiration is problematic on hot, dry days.

- In many plants, including crop plants, photorespiration drains away as much as 50% of the carbon fixed in the Calvin cycle
C₄ Plant Anatomy

- Some plants are called *C₄ plants* because they use an alternate mode of carbon fixation prior to the Calvin cycle that forms a 4-carbon compound as its first product.
  - C₄ plants include corn, sugarcane, and members of the grass family.
  - C₄ plants leaf anatomy is also different:
    - C₄ plant leaves have 2 types of cells:
      1. **Bundle-sheath cells** – arranged in tightly packed sheaths around veins of leaf.
      2. **Mesophyll cells** – found between the bundle sheath cells and are more loosely arranged.
The C₄ Pathway

The Calvin cycle occurs in the chloroplasts of the bundle sheath cells

- Carbon fixation (prior to Calvin cycle) occurs in mesophyll cells:

  1) An enzyme called PEP carboxylase adds CO₂ to phosphoenolpyruvate (PEP), forming oxaloacetate
    - This enzyme has a much higher affinity for CO₂ than rubisco and no affinity for oxygen
    - It thus fixes carbon much more efficiently than in C₃ plants (especially on hot, dry days)
  2) Mesophyll cells export their 4-carbon product to bundle sheath cells through plasmodesmata
  3) Once inside bundle sheath cells, this 4-carbon compound releases CO₂ so that it can enter the carbon cycle

- C₄ plants thus minimize the cost of photorespiration by incorporating CO₂ into four-carbon compounds in mesophyll cells
CAM Plants

- Another photosynthetic adaptation to hot, dry conditions has evolved in many water-storing plants (cacti, pineapples)
  - These plants open stomata during the night and close them during the day (the reverse of other plants)
    - This helps conserve water, but also prevents CO$_2$ from entering leaves
    - CO$_2$ is instead taken in at night and incorporated into a variety of organic acids
  - This mode of carbon fixation is called \textit{crassulacean acid metabolism} (CAM); named for the family of plants in which this process was first discovered
    - The mesophyll cells of CAM plants store these organic acids in their vacuoles until morning
    - Then during the day, CO$_2$ is released from these organic acids to be used in the Calvin cycle
In both C₄ and CAM plants, CO₂ is incorporated into organic acids and then transferred to the Calvin cycle.

- In C₄ plants, carbon fixation and the Calvin cycle occur in 2 different types of cells.
- In CAM plants, they occur in the same cells but at different times (mesophyll cells).
The energy entering chloroplasts as sunlight gets stored as chemical energy in organic compounds.

- Sugar made in the chloroplasts supplies chemical energy and carbon skeletons to synthesize the organic molecules of cells.

- Plants store excess sugar as starch in structures such as roots, tubers, seeds, and fruits.

- In addition to food production, photosynthesis produces the $O_2$ in our atmosphere.
A Review of Photosynthesis

- **Light Reactions:**
  - Carried out in thylakoid membrane
  - Convert light energy to the chemical energy of ATP and NADPH
  - Split water and release CO$_2$ into the atmosphere

- **Calvin Cycle:**
  - Takes place in stroma
  - Uses ATP and NADPH to convert CO$_2$ to the sugar G3P
  - Returns ADP, inorganic phosphate, and NADP+ to the light reactions
• 1) Explain why photorespiration lowers photosynthetic output for plants.

• 2) The presence of only PS I, not PS II, in the bundle-sheath cells of C\textsubscript{4} plants has an effect on oxygen concentration. What is that effect, and how might that benefit the plant?

• 3) How would you expect the relative abundance of C\textsubscript{3} versus C\textsubscript{4} and CAM species to change in a geographic region whose climate becomes much hotter and drier?
You should now be able to:

1. Describe the structure of a chloroplast
2. Describe the relationship between an action spectrum and an absorption spectrum
3. Trace the movement of electrons in linear electron flow
4. Trace the movement of electrons in cyclic electron flow
5. Describe the similarities and differences between oxidative phosphorylation in mitochondria and photophosphorylation in chloroplasts

6. Describe the role of ATP and NADPH in the Calvin cycle

7. Describe the major consequences of photorespiration

8. Describe two important photosynthetic adaptations that minimize photorespiration