CHAPTER 10: PHOTOSYNTHESIS

CHAPTER SYNOPSIS

Eukaryotic chloroplasts are composed of stacks of thylakoid disks called grana located within the stroma, a fluid matrix. The photosynthetic pigments are bound to the thylakoid membrane which pumps protons from the stroma to the interior. ATP molecules are generated as the protons diffuse back out to the stroma. The enzymes of the Calvin cycle are in the stroma.

Photosynthesis is composed of two very different processes: the light reactions and the Calvin cycle. The light reactions occur in eukaryotic chloroplasts on specific photosynthetic membranes of bacteria. The pigment captures a photon of light and excites one of its electrons. The excited electron shuttles through various carrier molecules to a final acceptor and chemiosmotically generates ATP and NADPH. The Calvin cycle fixes carbon by using the products of the light reactions to chemically reduce carbon dioxide into organic molecules.

Early research in plant physiology showed that plants did not derive major nutrients from the soil to support their growth, but that the sun's energy and carbon dioxide were required. Light energy exists in the form of packets called photons. Photons of short wavelength light are more energetic than photons of long wavelength light. The energy in these photons is captured by carotenoid or chlorophyll pigments. The former absorb photons with a broad range of energy and are not highly efficient while the latter absorb a narrow range of photons very efficiently. Most photosynthetic organisms use chlorophylls as their light gathering pigment.

Early photosynthetic bacteria exhibited cyclic photophosphorylation, a process that only produces ATP and does not provide for biosynthesis. The bacterial reaction center channels its light energy to P_{870} which then passes to a primary electron acceptor. The electron returns to the pigment through an electron transport chain. This drives a proton pump and produces ATP through chemiosmosis. Other bacteria improved on this photosystem, utilizing chlorophyll *a* to absorb the more energetic photons associated with shorter wavelengths of light. The P_{680} pigment of photosystem II became the first stage of a two stage photosystem while P_{700} remained as the pigment of photosystem I. The excited electron of photosystem II drives a proton pump and chemiosmotically generates ATP. The electron then passes on to photosystem I where it absorbs another photon of energy. This electron is channeled to the primary electron acceptor where it generates reducing power by reducing $NADP^+$ to NADPH. The electron removed from photosystem II is replaced by an electron obtained from the splitting of a molecule of water. Oxygen is a byproduct of this reaction, called noncyclic photophosphorylation.

Carbon fixation is similar to glycolysis, but run in reverse. The Calvin cycle uses ATP energy and NADPH reducing power to make organic molecules from carbon dioxide. Carbon dioxide attaches to the five-carbon molecule ribulose bisphosphate (RuBP) and is then split into two molecules of three-carbon phosphoglycerate (PGA) by an enzyme called rubisco. Some of these molecules are used to reconstitute RuBP; others are assembled into sugars via glyceraldehyde-3-phosphate (G3P). Six turns of the cycle are needed to form glucose.

Plants that exhibit C_3 photosynthesis lose much of their fixed carbon when RuBP carboxylase interferes with the Calvin cycle, a process called photorespiration. C_4 plants expend ATP to concentrate carbon dioxide in the cells that carry out the Calvin cycle. This high concentration of carbon dioxide prevents RuBP carboxylase from binding oxygen and thus reduces photorespiration. The loss of ATP greatly outweighs the potential loss of fixed carbon. Many succulent plants reduce photorespiration by closing their stomata and thus decrease the amount of carbon dioxide present during the day. These plants are called CAM plants; they use both C_3 and C_4 pathways within the same cells. C_4 plants use both pathways, but do each in a different cell.

CHAPTER OBJECTIVES

- State the overall equation for photosynthesis and explain why water is included on both sides.
- Identify the locations for the light reactions and the Calvin cycle within a plant chloroplast.
- Understand the discovery of the photosynthetic processes from an historical perspective.
- Understand how light energy is packaged and how its absorption is related to wavelength.
- Explain how electrons are captured by and transferred through the various molecules of a plant's photocenter.
- Describe cyclic photosynthesis in terms of the organisms in which it occurs, its energy capture molecules, and its energy yield in ATPs.
- Understand how photosystem I and photosystem II in plants produce ATP and NADH.
- Describe the Calvin cycle in plants. Include the significance of ATP and NADH and the ultimate product(s) of the reaction.
- Understand how photorespiration affects C_3 photosynthesis.
- Compare C_4 and CAM photosynthesis and how they combat photorespiration.

KEY TERMS

absorption spectrum
accessory pigment
action spectrum
C_3 photosynthesis
C_4 photosynthesis
Calvin cycle
carbon fixation
carotenoid
chlorophyll
crassulacean acid metabolism (CAM)
cyclic photophosphorylation
light reactions
noncyclic photophosphorylation
photorespiration
photosystem
photosystem I
photosystem II
pigment
reaction center

CHAPTER OUTLINE

10.0 Introduction

I. PHOTOSYNTHESIS ENABLES LIFE TO EXIST ON EARTH

A. Certain Organisms Capture Energy from Sunlight fig 10.1

B. Use Energy to Build Energy-Rich Food Molecules

10.1 What is photosynthesis?

I. THE CHLOROPLAST AS A PHOTOSYNTHETIC MACHINE

A. Life Is Powered by Sunshine
   1. Most living cells used energy captured from the sun by plants
   2. Radiant energy from the sun is equal to 1 million atomic bombs
   3. Photosynthesis captures only 1% of that energy to sustain all life

B. The Photosynthetic Process: A Summary
   1. Photosynthesis occurs in bacteria, algae, green plants fig 10.2
   2. In plant leaves, photosynthesis occurs in the chloroplasts

3. Three stages of photosynthesis
    a. Capture energy from the sun
    b. Use energy to make ATP and NADPH
    c. Use ATP and NADPH to make carbon molecules from CO_2 (carbon fixation)
4. First two stages occur in presence of light: Light reactions
5. Third stage occurs with or without light: Calvin cycle
6. Carbon dioxide + water + light → glucose + water + oxygen

C. Inside the Chloroplast
1. Internal membranes organized into flattened sacs called thylakoids
2. Numerous thylakoids stacked in arrangements called grana
3. Surrounding thylakoids is semiliquid stroma
4. Photosystem: Network of photosynthetic pigments bound to membranes in thylakoids
    a. Each pigment molecule capable of capturing photons
    b. Protein lattice holds pigments in close contact
    c. Light strikes pigment molecule, energy passes from molecule to molecule
    d. Energy reaches key molecule in reaction center, touching membrane-bound protein
    e. Energy transferred to protein, passed to series of other proteins
    f. Makes ATP, NADPH, and builds organic molecules
5. Photosystem is antenna, gather light from multiple pigment molecules

10.2 Learning about photosynthesis: An experimental journey

I. THE ROLE OF SOIL AND WATER

A. van Helmont's Plant Growth Experiments
1. Weighed tree and soil in pot
2. Plant grew five years, only water added
3. Plant weight gain greater than weight loss of soil
4. Thus determined that plant substance not derived from soil
5. Incorrectly concluded weight gain due to water

B. Further Studies Examine the Importance of Air
1. Experiments by Priestly to determine nature of air
    a. Sprig of mint restored air in jar that a burning candle had depleted
    b. Mouse could breathe in jar after plant but not before
    c. Living vegetation added something to the air
2. Ingenhousz reproduced and expanded Priestley's experiments
    a. Air restored only in presence of sunlight
    b. Occurred only with green plant leaves, not roots
    c. Proposed that plants split CO_2 into carbon and oxygen
    d. Oxygen released as gas into air
    e. Carbon and water combined to form carbohydrates
3. In 1804, Swiss botanist discovered water was necessary reactant
4. Overall reaction: $CO_2 + H_2O + \text{light energy} \rightarrow (CH_2O) + O_2$

II. DISCOVERY OF THE LIGHT-INDEPENDENT REACTIONS

A. Blackman's Experiments in 1905
1. Questioned role of light in photosynthesis
    a. Discovered photosynthesis was a two-step process
    b. Only one step used light directly

2. Measured several parameters
   a. Light intensity
   b. CO_2 concentration
   c. Temperature
3. Experimental results
   a. Light intensity low
      1) Photosynthesis accelerated by increasing light intensity
      2) Increasing temperature, CO_2 had no effect
   b. Light intensity high
      1) Increase in CO_2 accelerated photosynthesis
      2) Increase in temperature accelerated photosynthesis

B. Blackman's Conclusions
1. Initial "light" reactions independent of temperature
2. Second "dark" reactions independent of light, limited by CO_2
   a. "Dark" reactions occur in light
   b. Light not directly involved in reactions
3. Temperature increase effects only work up to 35°C
   a. At this temperature, plant enzymes begin to be denatured
   b. Concluded that enzymes carry out dark reactions

III. THE ROLE OF LIGHT

A. van Niel's Experiments in 1930s
1. van Niel examined photosynthesis in bacteria
   a. Purple sulfur bacteria convert H_2S into sulfur, do not release oxygen
   b. $CO_2 + 2H_2S + \text{light energy} \rightarrow (CH_2O) + H_2O + 2S$
2. Recognized parallel to Ingenhouz's equation
   a. $CO_2 + 2H_2A + \text{light energy} \rightarrow (CH_2O) + H_2O + 2A$
   b. Proposed H_2A is an electron donor, product A comes from splitting H_2A
   c. Thus O_2 from photosynthesis comes from H_2O not CO_2

B. Experiments Reproduced Using Radioactive Oxygen in 1950s
1. Green plants supplied with ^{18}O water
   a. As predicted, ^{18}O found in oxygen gas not carbohydrate
   b. $CO_2 + H_2{}^{18}O + \text{light energy} \rightarrow (CH_2O) + H_2O + {}^{18}O_2$
2. Carbohydrate typically produced by plants and algae is glucose
   a. Glucose is a six carbon sugar
   b. Balanced equation: $6CO_2 + 12H_2O + \text{light energy} \rightarrow C_6H_{12}O_6 + 6\,O_2$

C. Present Knowledge
1. First stage requires light
   a. Reduces electron carrier NADP to NADPH
   b. Makes ATP
2. Second stage is Calvin cycle
   a. NADPH and ATP reduce carbon in CO_2 and makes glucose
   b. Glucose used to synthesis other organic molecules

IV. THE ROLE OF REDUCING POWER

A. Convert CO_2 into Organic Matter Via Carbon Fixation
1. First proposed by van Neil
2. Powered by reducing power (H^+) made by splitting water molecule

B. Further Experiments in 1950s
  1. Hill's experiments
    a. Light energy used to generate reducing power
    b. Isolated chloroplasts reduce dye
    c. Release oxygen in response to light
  2. Later experiments showed electrons from water transferred to $NADP^+$
  3. Arnon experiments
    a. Illuminated chloroplasts without CO_2 accumulate ATP
    b. CO_2 added, ATP and NADPH used up, organic molecules made
  4. Importance of these experiments
    a. Photosynthesis occurs only in chloroplasts
    b. Light-dependent reactions use light to reduce $NADP^+$ and make ATP
    c. Light-independent reactions reduce CO_2 to form simple sugars

10.3 Pigments capture energy from sunlight

I. THE BIOPHYSICS OF LIGHT

A. The Photoelectric Effect
  1. Intensity of a generated spark was increased in the presence of light
  2. Photoelectric effect discovered by Heinrich Hertz
    a. Investigated spark generation and electromagnetic (radio) waves
    b. Strength intensified by the brightness and wavelength of light
  3. Planck proposed concept of energy units in 1901
    a. Predicted black body radiation curve
    b. Assumed that light behaved as units of photon energy
  4. Photoelectric effect explained by Einstein
    a. Ultraviolet light blasted electrons from the wire hoop
    b. Create positive ions and facilitate passage of current across gap
    c. Visible light did not have enough energy to cause this reaction

B. The Energy in Photons
  1. Photons possess different amounts of energy
  2. Energy content inversely proportional to the wavelength fig 10.4
    a. Highest energy wavelengths are short wavelength gamma rays
    b. Least energetic wavelengths are long wavelength radio waves
    c. Energy in visible light
      1) Violet has short wavelength and high energy photons
      2) Red has long wavelength and low energy photons

C. Ultraviolet Light
  1. Sunlight contains short, energetic ultraviolet light
  2. Was a probable source of energy in the primitive earth
  3. Current earth shielded by the ozone layer
  4. Ultraviolet light causes sunburns
  5. Holes have appeared in ozone layer, threaten to increase incidence of skin cancers

D. Absorption Spectra and Pigments
  1. Absorption of light energy dependent on its energy and kind of molecule it hits
  2. Electrons occupy discrete energy levels while orbiting in their atoms
  3. Specific atoms can absorb only certain photons of light
    a. Any given molecule has a characteristic absorption spectrum
    b. Can only absorb photons of certain energy level
  4. Pigments are molecules that absorb light, include carotenoids and chlorophylls

5. Chlorophylls absorb light within narrow ranges
    a. Chlorophyll *a* and *b* absorb violet-blue and red light fig 10.5
    b. Neither absorbs light between 500 and 600 nanometers, green light
    c. Wavelength not absorbed by chlorophylls reflected to eyes as green
    d. Chlorophyll *a* is primary photosynthetic pigment
        1) Directly converts light energy to chemical energy
        2) Cannot capture all wavelengths of light
    e. Chlorophyll *b* is an accessory pigment
        1) Has an absorption spectrum shifted toward green light
        2) Can absorb wavelengths that chlorophyll *a* cannot
    f. Carotenoids are also accessory pigments that expand energy capture

II. CHLOROPHYLLS AND CAROTENOIDS

A. Characteristics of Chlorophylls
1. Absorb photons by excitation like the photoelectric effect
2. Complex ring structure called a porphyrin ring
3. Magnesium ion within a network of alternating single and double bonds
4. Side groups of the molecule alter absorption properties fig 10.6
5. Spectrum influenced by local microenvironment of chlorophyll-protein associations

B. Englemann Experiments
1. Attempted to characterize chlorophyll's absorption spectrum fig 10.7
    a. Arranged algal filament across a miniature spectrum on a microscope slide
    b. Used aerotactic bacteria to assess rate of oxygen production
    c. Most bacteria accumulated in red and violet-blue regions
2. Chlorophyll *a* users include plants, algae, and most photosynthetic bacteria
3. Do not use retinal pigment because of its low photoefficiency
4. Chlorophyll absorbs in two narrow bands, but with great efficiency

C. Carotenoids fig 10.8, *10.5
1. Carbon ring linked to chains with alternating double, single bonds
2. Absorb photons over a broad range, not highly efficient
3. Include β-carotene
    a. Two carbon rings connected by 18 carbon chain, alternating single and double bonds
    b. If split in half, two molecules of vitamin A produced
    c. Oxidation of vitamin A makes retinal, involved in vertebrate vision
    d. Connection between carotene (carrots) and enhanced vision

III. ORGANIZING PIGMENTS INTO PHOTOSYSTEMS

A. Absorbing Light Energy
1. Light reactions occur on photosynthetic membranes
    a. Photosynthesis occurs on cell membranes in bacteria
    b. In plants and algae, photosynthesis occurs in chloroplasts
        1) Evolutionary descendants of photosynthetic bacteria
        2) Photosynthetic membranes located within the chloroplasts
2. Light reactions occur in four stages
    a. Primary photoevent
        1) Photon of light captured by a pigment
        2) Electron within the pigment is excited
    b. Charge separation
        1) Excitation energy transferred to chlorophyll pigment called reaction center
        2) Transfers energetic electron to acceptor molecule

- c. Electron transport
    - 1) Excited electron shuttled along electron-carrier molecules
    - 2) Carrier molecules embedded within photosynthetic membrane
    - 3) Transports proton across membrane, generates proton concentration gradient
    - 4) Electron induces transport of proton across membrane
    - 5) Electron is passed to an acceptor
- d. Chemiosmosis
    - 1) Protons accumulate on one side of membrane
    - 2) Flow back through specific protein complexes
    - 3) Flow of protons drives chemiosmotic synthesis of ATP
    - 4) Just like aerobic respiration

B. Discovery of Photosystems

- 1. Measure how much light produces how much photosynthesis fig 10.9
    - a. Output increases linearly at low intensities
    - b. Output lessens at high intensities
    - c. Saturation occurs at high-intensity light
        - 1) At saturation all light-absorbing capacity is in use
        - 2) Adding more light does no good
- 2. Emerson-Arnold experiments
    - a. Test if, at saturation, all pigment molecules are in use
    - b. Measure oxygen yield of *Chlorella* with microbursts of light
    - c. If intensity of flashes increased, yield per flash increased to saturation
    - d. Saturation achieved at one molecule of O_2 per 2,500 chlorophyll molecules
    - e. Conclusion that photons absorbed by groups of molecules not individual molecules
    - f. Clusters of chlorophyll and accessory pigments called photosystems
    - g. Reaction center of photosystem acts as energy sink, traps excitation energy
    - h. Emerson and Arnold observed individual reaction centers

C. Architecture of a Photosystem

- 1. Light captured by network of pigments called the photosystem
    - a. Network of chlorophyll *a*, accessory pigments, and associated proteins
    - b. Held in protein matrix on surface of photosynthetic membrane
    - c. Arrangement permits channeling of energy to a central point
    - d. Molecule then passes energy out of photosystem to make ATP
- 2. Consists of two closely linked components
    - a. Antenna complex: Hundreds of pigment molecules
    - b. Reaction center: One or more chlorophyll *a* molecules to pass energy out
- 3. The antenna complex fig 10.10
    - a. Captures photons from sunlight
    - b. Web of chlorophyll molecules held to thylakoid membrane by protein matrix
    - c. May contain a varying amount of carotenoids
    - d. Photosystem protein matrix holds pigment in optimal orientation
        - 1) Excitation energy passes from one molecule to another
        - 2) After energy passes, excited electron returns to lower energy state
        - 3) Excited electrons do not physically pass from pigment to pigment, only energy
        - 4) Funnels energy from many electrons to reaction center
- 4. The reaction center
    - a. Transmembrane protein-pigment complex
    - b. Model: Purple photosynthetic bacteria
        - 1) Two chlorophyll *a* molecules act as trap for photon energy
        - 2) Pass excited electron to an electron acceptor positioned as neighbor
        - 3) Whole electron transferred, not just its energy
        - 4) Photon excitation moves away from chlorophylls

        5) Key conversion of light to chemical energy
    c. Energy transfers from reaction center to primary electron acceptor fig 10.11
        1) Two chlorophyll *a* molecules act as trap for photon energy
        2) Pass excited electron to a primary electron acceptor (quinone)
        3) Reduces quinone and makes it a strong electron donor
        4) Weak donor then donates a low-energy electron to chlorophyll
        5) Restores original condition of chlorophyll
    d. Weak donor is water in plant chloroplasts

IV. HOW PHOTOSYSTEMS CONVERT LIGHT TO CHEMICAL ENERGY

A. Bacteria Use a Single Photosystem

1. Sulfur bacteria evolved photosynthetic units three billion years ago
2. Electron joined with a proton to make hydrogen
    a. In these bacteria, absorption peak is at 870 nanometers (near infrared, not visible)
    b. Transmission of energetic electron along electron transport chain
    c. Combine with proton to form hydrogen atom
    d. Sulfur bacteria extract proton from H_2S, sulfur by-product
    e. Other organisms extract proton from H_2O, oxygen by-product
3. Electron is recycled to chlorophyll
    a. Ejection of electron from bacterial reaction center (P_{870}) leaves it one electron short
    b. Electron must be returned before it can function again
    c. Bacteria channel electron back via electron-transport system
    d. Passage drives proton pump, chemiosmotically generates an ATP per three electrons
4. Overall process called cyclic photophosphorylation fig 10.12
    a. Process is not a true circle
    b. Electron leaving P_{870} reaction center is high-energy
    c. Electron returned to reaction center has “normal” energy level
    d. Difference in energy is what drives proton pump
5. Limitations of cyclic photophosphorylation
    a. Geared only towards energy production
    b. Does not provide for biosynthesis
    c. Ultimate point of photosynthesis is to generate carbon compounds
        1) Sugars are more reduced than CO_2, have more hydrogen atoms
        2) Bacteria inefficiently scavenge hydrogens from other sources

B. Why Plants Use Two Photosystems

1. Other bacteria evolved an improved version of the photosystem
2. Solved the reducing power problem
    a. Improved original photosynthetic process
    b. New process used chlorophyll *a*
3. Second system called photosystem II
    a. Molecules of chlorophyll *a* are arranged with a different geometry
    b. More of shorter wavelengths are absorbed than in earlier process
    c. In plants, the earlier process is called photosystem I
4. Photosystems have different absorption peaks
    a. Photosystem II pigment is 680 nanometers, called P_{680}
    b. Photosystem I pigment is 700 nanometers, called P_{700}
5. Photosystems work together to carry out noncyclic electron transfer
6. Measure rate of photosynthesis using different wavelength light
    a. Wavelengths used were red and far-red light
    b. Photosynthesis rate greater with both together than combination of two separate
    c. Called enhancement effect fig 10.13
        1) Two photosystems act in series, after one another

        2) One absorbs in red, other absorbs in far-red
    7. Advantage of two photosystems
        a. Solves problem of obtaining reducing power
        b. Z diagram of photosystems I and II fig 10.14
        c. Electrons originate from water, end up in NADPH
        d. Difference in redox potential +820mV for water, –320mV for NADPH

V. HOW THE TWO PHOTOSYSTEMS OF PLANTS WORK TOGETHER

A. The Two Stage System Is Called Noncyclic Photophosphorylation
- 1. Path of electrons is not circular
  - a. Electron does not return to origin, but goes to NADPH
  - b. Electrons replenished by splitting water
- 2. Photosystem II acts first
  - a. Excited electron used to make ATP
  - b. Passes electron on to photosystem I, drives production of NADPH
  - c. Two electrons from water makes one NADPH and slightly more than one ATP

B. Photosystem II
- 1. Reaction center resembles that of purple bacteria
  - a. More than ten transmembrane protein subunits
  - b. Antenna complex is over 250 molecules of chlorophyll *a* and accessory pigments
- 2. Oxygen atoms of two water molecules bind to manganese atoms in enzyme labeled Z
- 3. Enzyme splits water, removes electrons one at a time
- 4. Electrons fill void left in reaction center
- 5. When four electrons removed from 2 water molecules, O_2 is released

C. The Path to Photosystem I
- 1. Quinone is primary electron acceptor for electrons leaving photosystem II
- 2. Reduced quinone, called plastoquinone (Q) is a strong electron donor
- 3. Passes excited electron to proton pump called b_6-f complex
- 4. Complex located in thylakoid membrane fig 10.15
- 5. Resembles bc_1 complex in mitochondria respiratory electron transport chain
- 6. With arrival of electron, complex pumps proton into thylakoid space
- 7. Plastocyanin (PC) carries electron to photosystem I

D. Making ATP: Chemiosmosis fig 10.16
- 1. Thalakoid is closed compartment
  - a. Protons pumped from stroma by b_6-f complex
  - b. Splitting water produces more protons that add to gradient
- 2. Thylakoid membrane is impermeable to most molecules and protons
  - a. Proton transit occurs at ATP-synthetase proton channels
  - b. Channels are knobs on external surface of thylakoid membrane
  - c. ATP released into surrounding fluid within chloroplast, the stroma
- 3. Stroma contains enzymes that catalyze reactions of carbon fixation

E. Photosystem I
- 1. Reaction center called P_{700}
  - a. Transmembrane complex of at least 13 protein subunits
  - b. Antenna complex of 130 chlorophyll *a* and accessory pigment molecules
- 2. Accepts electron from plastocyanin to fill hole from exit of light-excited electron
- 3. Boosts energy of exiting electron to very high level
- 4. Passes electron to ferredoxin (Fd), an iron-sulfur protein

F. Making NADPH
   1. Ferredoxin on outside (stromal side) of thylakoid membrane
   2. Reduced ferredoxin carries very high-potential electrons
   3. Two such electrons donated to $NADP^+$ to make NADPH
   4. Reaction catalyzed by NADP reductase bound to the membrane
   5. Contributes further to proton gradient

G. Making More ATP
   1. Above events make slightly more than 1 ATP
   2. One-and-one-half ATP per NADPH required to fix carbon
   3. Extra ATP made when plant switches to cyclic photophosphorylation mode
      a. Light-excited electron leaving photosystem I makes ATP instead of NADPH
      b. Energetic electron passed back to b_6-f complex
      c. Complex pumps out proton, adding to proton gradient, driving chemiosmosis
   4. Proportions of cyclic and noncyclic photophosphorylation determine ATP and NADPH production

10.4 Cells use the energy and reducing power captured by the light reactions to make organic molecules

I. THE CALVIN CYCLE

A. Products of the Light-Dependent Reactions Used to Build Organic Molecules
   1. Energy: Photosystem II ATP drives endergonic reactions
   2. Reducing power: Photosystem I NADPH provides hydrogens and energetic electrons

B. Carbon Fixation
   1. CO_2 must be attached to an organic molecule
   2. Atmospheric CO_2 is reduced during carbon fixation
   3. Two intermediates of glycolysis reassembled
      a. Fructose 6-phosphate (F6P) + glyceraldehyde 3-phosphate (G3P)
      b. Reassembled to form five-carbon molecule ribulose 1,5 bisphosphate (RuBP)
   4. CO_2 binds to RuBP during carbon fixation fig 10.17
   5. Forms two molecules of 3-C phosphoglycerate (PGA)
   6. Catalyzed by RuBP carboxylase (rubisco)
      a. Enzyme is comparatively slow, 3 molecules per second
      b. Many copies are needed
      c. May be most abundant protein on earth

C. Discovering The Calvin Cycle
   1. Blackman concluded that photosynthetic reactions were enzyme-catalyzed
      a. Based on temperature dependence
      b. Cyclical series of reaction similar to Krebs cycle
      c. Cycle called Calvin cycle after its discoverer
   2. Cycle begins when CO_2 binds RuBP to form 3-carbon PGA
   3. Process called C_3 photosynthesis

D. The Energy Cycle
   1. Photosynthesis and energy-capturing metabolisms are related fig 10.18
      a. Photosynthesis uses respiration products as starting substrates
      b. Respiration uses photosynthesis products as starting substrates
      c. Calvin cycle uses part of the glycolytic process in reverse
      d. Electron transport proteins in plants and mitochondria are related
   2. Photosynthesis is one important aspect of plant biology

II. REACTIONS OF THE CALVIN CYCLE

- A. A Complex Series of Reactions fig 10.19
  - 1. Three CO_2 (3 Cs) fixed to RuBP (15 Cs) by rubisco to form 6 PGA (18 Cs)
  - 2. Complex cycle of rearrangements result in
    - a. Reforming RuBP
    - b. Producing glyceraldehyde 3-phosphate (G3P)
  - 3. Three turns of cycle use three CO_2, make 3 G3P, reform 3 RuBP fig 10.20
  - 4. Light required indirectly for some of the CO_2 reduction reactions
    - a. Five Calvin cycle enzymes are light activated, include rubisco
    - b. Become functional or operate better in light
    - c. Light promotes transport of 3-C intermediates across chloroplast membranes
    - d. Light promotes influx of Mg^{++} into stroma, further activates rubisco

- B. Output of the Calvin Cycle
  - 1. G3P is intermediate in glycolysis
  - 2. If exported from cell, converted to fructose 6-phosphate, glucose 1-phosphate
  - 3. F6P and G1P further converted to sucrose
  - 4. If G3P levels very high
    - a. Some G3P converted into G1P by reversing reactions similar to ones of glycolysis
    - b. G1P combined into insoluble polymer of long chains of starch
    - c. Stored as starch grains in chloroplast

III. PHOTORESPIRATION

- A. Evolution Favors Workable, Not Always Optimal Solutions
  - 1. Rubisco (RuBP carboxylase) secondarily interferes with Calvin cycle
    - a. Initiates oxidation (not carboxylation) of RuBP, O_2 incorporated
    - b. CO_2 is released without the production of ATP or NADPH
    - c. Process called photorespiration, acts to undo photosynthesis
  - 2. Both reactions occur at the same active site
    - a. At 25°C, 20% of photosynthetically fixed carbon lost to photorespiration
    - b. Loss increases as temperature increases
    - c. Oxidation rate increases more with temperature increase than carboxylation
  - 3. In $C_{3,}$ photosynthesis RuBP carboxylated by rubisco to form 3-C compound
  - 4. C_4 photosynthesis uses different system
    - a. Uses phosphoenolpyruvate (PEP) not RuBP
    - b. PEP carboxylated to form 4-C compound
    - c. Uses PEP carboxylase which has no oxidation activity
    - d. Photorespiration does not occur
  - 5. PEP carboxylase has greater affinity for CO_2 than rubisco
    - a. 4-C compound modified and decarboxylated, releases CO_2
    - b. CO_2 captured by rubisco and shunted to Calvin cycle
    - c. Concentration of CO_2 to O_2 increased, photorespiration minimized
  - 6. C_3 plants lose one fourth to one half of their fixed carbon in this way
    - a. Loss is related to increased temperature
    - b. Major impact on tropical agriculture

- B. The C_4 Pathway
  - 1. Reactions occur in two different kinds of cells
    - a. C_4 photosynthesis occurs in mesophyll cells
    - b. Calvin cycle occurs in bundle-sheath cells
  - 2. Concentrate CO_2 by carboxylating phosphoenolpyruvate (PEP) fig 10.21
    - a. Resulting four-carbon oxaloacetate converted to malate

  - b. Malate (4-C) conveyed to bundle-sheath cells, impermeable to CO_2
  - c. Malate decarboxylated to pyruvate (3-C), releasing CO_2 in the cell
  - d. CO_2 concentration builds up in bundle-sheath cells
  - e. Pyruvate returns to mesophyll cell, changed back to PEP
  - f. Requires two high energy bonds, ATP becomes AMP
- 3. Increased concentration of CO_2 in bundle-sheath cell, limits photorespiration
  - a. High cost (2ATP) of transporting CO_2 into bundle-sheath cells
  - b. Costs total of 12 ATP to form 1 glucose molecule
  - c. C_4 photosynthesis uses 30 ATP, C_3 photosynthesis uses 18 ATP
  - d. Cost worth it in hot climates, saves loss of fixed carbon via photorespiration

C. The Crassulacean Acid Pathway
- 1. Crassulacean acid metabolism (CAM) also used by plants in hot climates fig 10.22
- 2. Succulents open their stomata at night and close them during the day
  - a. Stomal pattern opposite that of other plants
  - b. CO_2 fixed at night via C_4 pathway
  - c. Decarboxylated during day to produce high levels of CO_2
  - d. High CO_2 drives Calvin cycle, minimizes photorespiration
- 3. CAM plants use both C_3 and C_4 pathways
  - a. Use C_4 at night, C_3 during day
  - b. Both pathways occur in same cells
  - c. C_4 plants do both pathways, but in two different cells

INSTRUCTIONAL STRATEGY

PRESENTATION ASSISTANCE:

Many texts simply present photosynthesis straight through. Here it is presented from an evolutionary as well as biochemical viewpoint. PS I with P_{700} was "invented" first and makes enough ATP for growth and reproduction, but doesn't produce NADPH or fix carbon. PS II with P_{680} was "invented" next and added to the front of PS I. In cyanobacteria, algae, and plants, PS II occurs first and is followed by PS I. (This evolution is different from cellular respiration where the new process was added to the end of the original one.) PS II produces ATP while PS I now generates NADPH, reducing power used to fix carbon in the Calvin cycle. You may want to ask why it wouldn't be simpler to just add PS II to the end of PS I so that PS I could still make ATP with PS II generating NADPH. (ANSWER: The electron from P_{700} isn't energetic enough to split water, the one from P_{680} has more energy. Remember that photon energy is inversely proportional to the wavelength.)

Stress why water is split, why oxygen is produced, and that two photons of different energy are needed for PS I/PS II photosynthesis. It is important that the students also remember that the Calvin cycle (aka the dark reaction) does not ONLY occur in the dark. It also occurs in the light, but does not require light to occur as do the light reactions.

Many students may confuse photorespiration with cellular respiration, but they are two entirely different processes. Although they both produce CO_2, photorespiration is a damaging reaction because it does not produce ATP.

VISUAL RESOURCES:

Chloroplasts reradiate light with a longer wavelength than the light that they are initially illuminated. A beaker of chloroplasts illuminated with normal light will reradiate at invisible infrared wavelengths. One that is illuminated with higher energy ultraviolet light will reradiate in the visible red range.