ENERGY

An Introduction to Metabolism
(Chapter 8)

YOU MUST KNOW…

- Examples of endergonic and exergonic reactions.
- The key role of ATP in energy coupling.

An organism's metabolism transforms matter and energy, subject to the laws of thermodynamics (8.1)

- **Metabolism** is the totality of an organism's chemical reactions. Metabolism as a whole manages the material and energy resources of the cell.
- A **catabolic pathway** leads to the release of energy by the breakdown of complex molecules to simpler compounds. *Example*: Catabolic pathways occur when your digestive enzymes break down food and release energy.
- **Anabolic pathways** consume energy to build complicated molecules from simpler ones. *Example*: Anabolic pathways occur when your body links together amino acids to form muscle protein in response to physical exercise.
- **Energy** is defined as the capacity to do work. Anything that is moving is said to possess **kinetic energy**. An object at rest can possess **potential energy** if it has stored energy as a result of its position or structure. **Chemical energy**, a form of potential energy, is stored in molecules, and the amount of chemical energy a molecule possesses depends on its chemical bonds.
- **Thermodynamics** is the study of energy transformations that occur in matter.
    - The **first law of thermodynamics** states that the energy of the universe is constant and that energy *can* be transferred and transformed, but it *cannot* be created or destroyed.
    - The **second law of thermodynamics** states that every energy transfer or transformation increases the entropy, or the amount of disorder or randomness, in the universe.

The free-energy change of a reaction tells us whether or not the reaction occurs spontaneously (8.2)

- **Free energy** is defined as the part of a system's energy that is able to perform work when the temperature of a system is uniform.
- **ΔG** is a symbol for a change in free energy.
    - An **exergonic reaction** is one in which energy is released. Exergonic reactions occur spontaneously (that does not necessarily mean quickly) and release free energy to the system. $\Delta G < 0$.

- An **endergonic reaction** is one that requires energy in order to proceed. Endergonic reactions absorb free energy; that is, they require free energy from the system. $\Delta G > 0$.
- Is the breakdown of glucose in cellular respiration exergonic or endergonic? (ΔG is -686 kcal/mol.)

ATP powers cellular work by coupling exergonic reactions to endergonic reactions (8.3)

- A key feature in the way cells manage their energy resources to do cell work is **energy coupling**, the use of an exergonic process to drive an endergonic one.
- The primary source of energy for cells in energy coupling is **ATP (adenosine triphosphate)**. Study Figure 8.9 and note that ATP is made up of the nitrogenous base adenine, bonded to ribose and a chain of three phosphate groups. When a phosphate group is hydrolyzed, energy is released in an exergonic reaction.
- Work in the cell is done by the release of a phosphate group from ATP. The exergonic release of the phosphate group is used to do the endergonic work of the cell. When ATP transfers one phosphate group through hydrolysis, it becomes **ADP (adenosine diphosphate)**.

CONNECT TO THE CURRICULUM FRAMEWORK

Essential Knowledge 2.A.1 is about the constant input of free energy required by all living systems. The preceding section about entropy, ATP/ADP, and endergonic/exergonic reactions is an important part of your study. Take your time to understand this material well!

Cellular Respiration and Fermentation
(Chapter 9)

YOU MUST KNOW…

- The summary equation of cellular respiration including the source and fate of the reactants and products.
- The difference between fermentation and cellular respiration.
- The role of glycolysis in oxidizing glucose to two molecules of pyruvate.
- How pyruvate is moved from the cytosol into the mitochondria and introduced into the citric acid cycle.
- How electrons from NADH and $FADH_2$ are passed to a series of electron acceptors to produce ATP by chemiosmosis.
- The roles of the mitochondrial membrane, proton (H^+) gradient, and ATP synthase in generating ATP.

TIP FROM THE READERS

Oxidation-reduction reactions, fermentation, cellular respiration, and photosynthesis are among the most technically challenging sections of the course. Here, we focus on the major steps of each of the processes as well as the results. Questions on the AP Biology Exam are likely to focus on the energy transfers of photosynthesis and respiration – not on the exact reactions that create the products, nor are you expected to know the names of the enzymes involved in the process. As you work through these chapters, compare and contrast the two fundamental cell processes.

Catabolic pathways yield energy by oxidizing organic fuels (9.1)

- **Catabolic pathways** occur when molecules are broken down and their energy is released. You should know these two catabolic pathways:
  - **Fermentation** is the partial degradation of sugars that occurs without the use of oxygen.
  - **Aerobic respiration** is the most prevalent and efficient catabolic pathway in which oxygen is consumed as a reactant along with the organic fuel.
- Carbohydrates, fats, and proteins canal be broken down to release energy in cellular respiration. However, glucose is the primary molecule that is used in cellular respiration. The standard way of representing the process of cellular respiration shows glucose being broken down in the following reaction:

$$C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O + \text{Energy (686 kcal/mol of glucose)}$$

- The exergonic release of energy from glucose is used to phosphorylate ADP to ATP. Life processes constantly consume ATP; cellular respiration burns fuels and uses the energy to regenerate ATP.
- The reactions of cellular respiration are of a type termed **oxidation-reduction** (**redox**) reactions. In redox reactions electrons are transferred from one reactant to another.
    - The loss of one or more electrons from a reactant is called **oxidation**. When a reactant is *oxidized*, it loses electrons and, consequently, energy.
    - The gain of one or more electrons is **reduction**. When a reactant is *reduced*, it gains electrons and, therefore, energy.
- At key steps in cellular respiration, electrons are stripped from glucose. Each electron travels with a proton, thereby forming a hydrogen atom. The hydrogen atoms are not transferred directly to oxygen, as the formula might suggest, but instead are usually passed to an electron carrier, the coenzyme **NAD^+** (a derivative of the B vitamin niacin). Within the cell **NAD^+** accepts two electrons, plus the stabilizing hydrogen ion, to form **NADH**. Note that NADH has been reduced and therefore has gained energy.
- Figure 9.6 shows the three stages of cellular respiration. Each stage is separately featured in the next three concepts. Use this figure to begin to develop an overall concept of the process of cellular respiration.

Glycolysis harvests chemical energy by oxidizing glucose to pyruvate (9.2)

- In **glycolysis** (which occurs in the cytosol), the degradation of glucose begins as it is broken down into two pyruvate molecules. The six-carbon glucose molecule is split into two three-carbon sugars through a long series of steps.
- In the course of glycolysis, there is an ATP-consuming phase and an ATP-producing phase. In the ATP-consuming phase, two ATP molecules are consumed, which helps destabilize glucose and make it more reactive. Later in glycolysis, four ATP molecules are produced; thus, glycolysis results in a net gain of two ATP. Two NADH are also produced, which will be utilized in the electron transport system (which requires oxygen) to produce ATP (see Figure 9.6).
- Notice the *net* energy gain in glycolysis as indicated in Figure 9.8 – two ATP molecules and two NADH molecules. Most of the potential energy of the glucose molecule still resides in the two remaining pyruvates, which will now feed into the citric acid cycle, as discussed in the next concept.

After pyruvate is oxidized, the citric acid cycle completes the energy-yielding oxidation of organic molecules (9.3)

- After glycolysis, **pyruvate is oxidized to acetyl CoA**. This junction between glycolysis and the citric acid cycle is shown in Figure 9.11. Note the following steps in this figure:
    - A transport protein moves pyruvate from the cytosol into the matrix of the mitochondria.

- In the matrix an enzyme complex catalyzes three reactions: a CO_2 **is removed**, electrons are stripped from pyruvate to convert NAD^+ to NADH, and coenzyme A joins with the remaining two-carbon fragment to form acetyl CoA.
- Two acetyl CoA molecules are produced per glucose. Acetyl CoA now enters the enzymatic pathway termed the citric acid cycle.

- In the **citric acid cycle** (which occurs in the mitochondrial matrix), the job of breaking down glucose is completed with CO_2 released as a waste product. Each turn of the citric acid cycle requires the input of one acetyl CoA. The citric acid cycle must make two turns before the glucose is completely oxidized.
- Study Figure 9.11 and note that the citric acid cycle results in the following:
    - Each turn of the citric acid cycle produces **2 CO_2**, **3 NADH**, **1 $FADH_2$**, and **1 ATP**.
    - Because each glucose yields *two* pyruvates, the *total* products of the citric acid cycle are usually listed as the result of two cycles:

      4 CO_2, **6 NADH**, **2 $FADH_2$**, and **2 ATP**
- Note that at the end of the citric acid cycle the six original carbons in glucose have been released as CO_2. (You are exhaling this gas as you study.) Only two ATP molecules, however, have been produced. Where is all the energy? The energy is held in the electrons in the electron carriers, NADH and $FADH_2$. These electrons will be utilized by the electron transport system, explained in the next concept.

During oxidative phosphorylation, chemiosmosis couples electron transport to ATP synthesis (9.4)

- Use Figure 9.15 as a map to understand the process of electron transport.
    1. The electron transport chain is embedded in the inner membrane of the mitochondria. Notice that it is composed of three transmembrane proteins that work as hydrogen pumps and two carrier molecules that transport electrons between hydrogen pumps. There are thousands of such electron transport chains in the inner mitochondrial membrane.
    2. The electron transport chain is powered by electrons from the electron carrier molecules NADH and $FADH_2$ ($FADH_2$ is also a B vitamin coenzyme that functions as an electron acceptor in the citric acid cycle). As the electrons flow through the electron chain, the loss of energy by the electrons is used to power the pumping of protons across the inner membrane. At the end of the electron chain, the electrons combine with two hydrogen ions and oxygen to form water. Notice that O_2 is the final electron acceptor, and when it is not available, the transport of electrons comes to a screeching halt! No hydrogen ions are pumped and no ATP is produced.
    3. The hydrogen ions flow back down their gradient through a channel in the transmembrane protein known as ATP synthase. **ATP synthase** harnesses the **proton-motive force** – the gradient of hydrogen ions – to phosphorylate ADP, forming ATP. The proton-motive force is in place because the inner membrane of the mitochondria is impermeable to hydrogen ions. Like water behind a dam with its only exit being a

spillway, electrons are held behind the inner membrane with their only exit, ATP synthase.

4. This process is referred to as chemiosmosis. **Chemiosmosis** is an energy-coupling mechanism that uses energy stored in the form of an H^+ gradient across a membrane to drive cellular work (ATP synthesis in our example). The electron transport chain and chemiosmosis compose **oxidative phosphorylation**. This specific term is used because ADP is phosphorylated and oxygen is necessary to keep the electrons flowing.
5. The ATP yield per molecule ofglucose is 30 to 32 ATP. Oxidative phosphorylation produces 26 to 28 of the total. (You may notice that this number is less than you might have learned in an earlier text, but it more accurately reflects the current biochemical analysis.)

Fermentation and anaerobic respiration enable cells to produce ATP without the use of oxygen (9.5)

- **Anaerobic respiration** by certain prokaryotes generates ATP without oxygen using an electron transport chain.
- **Fermentation** is an expansion of glycolysis in which ATP is generated by substrate-level phosphorylation.
- Fermentation consists of glycolysis (recall that glycolysis produces two net ATP molecules) and reactions that regenerate NAD^+. In glycolysis oxygen is not needed to accept electrons; NAD^+ is the electron acceptor. Therefore, the pathways of fermentation must regenerate NAD^+.
- In **alcohol fermentation**, pyruvate is converted to ethanol, releasing CO_2 and oxidizing NADH in the process to create more NAD^+.
- In **lactic acid fermentation**, pyruvate is reduced by NADH (NAD^+ is formed in the process), and lactate is formed as a waste product.
- **Facultative anaerobes** can make ATP by aerobic respiration if oxygen is present but can switch to fermentation under anaerobic conditions. On a cellular level, your muscle cells operate as facultative anaerobes. **Obligate anaerobes** cannot survive in the presence of oxygen.

Glycolysis and the citric acid cycle connect to many other metabolic pathways (9.6)

- In addition to glucose and other sugars, proteins and fats are often used to generate ATP through cellular respiration. Because the equation for aerobic respiration is always based on glucose, it is important for you to know that there are other molecules that enter the pathway.
- **Phosphofructokinase** (PFK) is an allosteric enzyme that functions early in the pathway of glycolysis and acts as a regulator of respiration. It is inhibited by high levels of ATP, which stops the catalytic pathway of glycolysis. Adequate ATP? Breakdown of glucose → pyruvate is not required.
- By controlling the rate of the entire process of cellular respiration, phosphofructokinase is considered the pacemaker of respiration. Consider this as an excellent example of regulation of a process by negative feedback.

Photosynthesis
(Chapter 10)

YOU MUST KNOW…

- The summary equation of photosynthesis including the source and fate of the reactants and products.
- How leaf and chloroplast anatomy relate to photosynthesis.
- How photosystems convert solar energy to chemical energy.
- How linear electron flow in the light reactions results in the formation of ATP, NADPH, and O_2.
- How the formation of a proton gradient in the light reactions is used to form ATP from ADP + inorganic phosphate by ATP synthase.
- How the Calvin cycle uses the energy molecules of the light reactions (ATP and NADPH) to produce carbohydrates (G3P) from CO_2.

Photosynthesis converts light energy to the chemical energy of food (10.1)

- Before you look at the molecular details of photosynthesis, it is important to think of photosynthesis in an ecological context.
  - Life on Earth is solar powered by autotrophs. **Autotrophs** are "self-feeders"; they sustain themselves without eating anything derived from other organisms. Autotrophs are the ultimate source of organic compounds and are therefore known as *producers*.
  - **Heterotrophs** live on compounds produced by other organisms and are thus known as *consumers*. Animals immediately come to mind as heterotrophs, but also remember that decomposers like fungi and many prokaryotes are heterotrophs. Heterotrophs are dependent on the process of photosynthesis for both food and oxygen.
- **Chloroplasts** are the specific sites of photosynthesis in plants cells.
  - Use Figure 10.4 to become familiar with the structure of chloroplasts. An envelope of two membranes encloses the **stroma**, which is a dense fluid-filled area. Within the stroma is a vast network of interconnected membranous sacs called **thylakoids**. The thylakoids segregate the stroma from another compartment, the **thylakoid space**.
  - Note that the thylakoids set up compartments separate from the stroma. This will allow a proton gradient to be established.
  - **Chlorophyll** is located in the thylakoid membranes and is the light-absorbing pigment that drives photosynthesis and gives plants their green color.
- The exterior of the lower epidermis of a leaf contains many tiny pores called stomata, through which carbon dioxide enters and oxygen and water vapor exit the leaf. The loss of water through open stomata is *transpiration*.

STUDY TIP: Practice drawing a chloroplast. Label its parts and know what major events occur in each region.

- The overall reaction of photosynthesis looks like this:

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

  - Notice that the overall chemical change during photosynthesis is the reverse of the one that occurs during cellular respiration.
  - All the oxygen you breathe was formed in the process of photosynthesis when a water molecule was split! Water is split for its electrons, which are transferred along with hydrogen ions from water to carbon dioxide, reducing it to sugar. This process requires energy (an endergonic process), which is provided by the sun.
- Photosynthesis is a chemical process that requires two stages to complete.
  - The **light reactions** occur in the thylakoid membranes where solar energy is converted to chemical energy. The net products of the light reactions are **NADPH** (which store electrons), **ATP**, and **oxygen**. Here are the primary events.
    1. Light energy is absorbed by chlorophyll, which drives the transfer of electrons from water to $NADP^+$, forming **NADPH**.
    2. Water is split during these reactions, and O_2 is released.
    3. **ATP** is generated, using chemiosmosis to power the addition of a phosphate group to ADP, a process called **photophosphorylation**.
  - The **Calvin cycle** occurs in the stroma, where CO_2 from the air is incorporated into organic molecules in **carbon fixation**. The Calvin cycle uses the fixed carbon plus NADPH and ATP from the light reactions in the formation of new sugars.
- Use Figure 10.6 to help in understanding where reactions occur and the overall purpose of the two stages of photosynthesis. If you understand the big picture, the details will be easier to comprehend.

The light reactions convert solar energy to the chemical energy of ATP and NADPH (10.2)

- Not surprisingly, light is an important concept in photosynthesis. It is the primary energy source for life on Earth.
  - Light is electromagnetic energy, and it behaves as though it is made up of discrete particles, called **photons** – each of which has a fixed quantity of energy.
  - Substances that absorb light are called **pigments**, and different pigments absorb light of different wavelengths. Chlorophyll is a pigment that absorbs violet-blue and red light while transmitting and reflecting green light. This is why we see summer leaves as green.
  - A graph plotting a pigment's light absorption versus wavelength is called an **absorption spectrum**. The absorption spectrum of chlorophyll provides clues to the effectiveness of different wavelengths for driving photosynthesis. This is confirmed by an action spectrum.

- An **action spectrum** for photosynthesis graphs the effectiveness of different wavelengths of light in driving the process of photosynthesis. Note examples of both of these graphs in your text, Figure 10.10.
- The action spectrum confirms that plants use energy from red and blue light (which is absorbed) and very little energy from green light (which is reflected).

- Photons of light are absorbed by certain groups of pigment molecules in the thylakoid membrane of chloroplasts. These groups are called **photosystems** and consist of two parts: a light-harvesting complex and a reaction center.
  - The **light-harvesting complex** is made up of many chlorophyll and carotenoid molecules (accessory pigments in the thylakoid membrane); this allows the complex to gather light effectively. When chlorophyll absorbs light energy in the form of photons, one of the molecule's electrons is raised to an orbital of higher potential energy. The chlorophyll is then said to be in an "excited" state.
  - Like a human "wave" at a sports arena, the energy is transferred to the **reaction center** of the photosystem. The reaction center consists of two chlorophyll *a* molecules, which donate the electrons to the second member of the reaction center, the **primary electron acceptor**. The solar-powered transfer of an electron from the reaction-center chlorophyll *a* pair to the primary electron acceptor is the first step of the light reactions. This is the conversion of light energy to chemical energy and what makes photoautotrophs the producers of the natural world.
- Thylakoid membranes contain two photosystems that are important to photosynthesis – **photosystem I (PS I)** and **photosystem II (PS II)**. PS I is sometimes designated P700 because the chlorophyll *a* in the reaction center of this photosystem absorbs red light of this wavelength the best; PS II is sometimes referred to as P680 for the same reason. Don't let switches in designation be confusing.
- Following are the major steps of the light reactions of photosynthesis. The key to the light reactions is a flow of electrons through the photosystems in the thylakoid membrane, a process called **linear (noncyclic) electron flow**. Find each step in Figure 10.14 as you read the following summary:
  - Photosystem II absorbs light energy, allowing the P680 reaction center of two chlorophyll *a* molecules to donate an electron to the primary electron acceptor. The reaction-center chlorophyll is oxidized and now requires an electron.
  - An enzyme splits a water molecule into two hydrogen ions, two electrons, and an oxygen atom. The electrons are supplied to the P680 chlorophyll *a* molecules. The oxygen combines with another oxygen atom, forming the O_2 that will be released into the atmosphere.
  - The original excited electron passes from the primary electron acceptor of photosystem II to photosystem I through an electron transport chain (similar to the electron chain in cellular respiration).

- The energy from the transfer of electrons down the electron transport chain is used to pump protons, creating a gradient that is used in chemiosmosis to phosphorylate ADP to ATP. ATP will be used as energy in the formation of carbohydrates in the Calvin cycle.
- Meanwhile, light energy has also activated PS I, resulting in the donation of an electron to its primary electron acceptor. The electrons just donated to PS I are replaced by the electrons from PS II. (Keep in mind that the ultimate source of electrons is water.)
- The primary electron acceptor of photosystem I passes the excited electrons along to another electron transport chain, which transmits them to $NADP^+$, which is reduced to NADPH – the second of the two important light-reaction products. The high-energy electrons of NADPH are now available for use in the Calvin cycle.

- Chloroplasts and mitochondria generate ATP by the same basic mechanism: chemiosmosis. Examining Figure 10.18 will quickly demonstrate the same basic chemiosmotic plan as cellular respiration. Use Figure 10.18 to illustrate the following:
  - An electron transport chain uses the flow of electrons to pump protons across the thylakoid membrane from the stroma into the thylakoid space.
  - A proton-motive force is created within the thylakoid space that can be utilized by ATP synthase to phosphorylate ADP to ATP. This occurs when protons (H^+) flow out of the thylakoid space, down their electrochemical gradient, through ATP synthase and into the stroma. Notice that the proton-motive force is generated in three places: (1) hydrogen ions from water; (2) hydrogen ions pumped across the membrane by the cytochrome complex; (3) the removal of a hydrogen ion from the stroma when $NADP^+$ is reduced to NADPH.
  - Although similar, chemiosmosis in cellular respiration and photosynthesis are not identical. In addition to some spatial differences, the key conceptual difference is that mitochondria use chemiosmosis to transfer chemical energy from food molecules to ATP, whereas chloroplasts transform light energy into chemical energy in ATP. This is the essence of the difference between a consumer and a producer.

The Calvin cycle uses the chemical energy of ATP and NADPH to convert CO2 to sugar (10.3)

- In the course of the **Calvin cycle**, carbon enters in the form of CO_2 and leaves in the form of a sugar. The cycle spends ATP as an energy source and consumes NADPH as reducing power for adding high-energy electrons to make the sugar. Use Figure 10.19 to chart each step summarized in the outline that follows. You must note that in order to net one molecule of G3P, the cycle must go through three rotations and fix three molecules of CO_2.
- These are the major steps of the Calvin cycle. It is not important that you memorize the intermediate organic molecules, but it is important to understand the conceptual scheme of reducing CO_2 to a sugar.
  - Three CO_2 molecules are attached to three molecules of the five-carbon sugar **ribulose bisphosphate (RuBP)**. These reactions are catalyzed by the enzyme **rubisco** (probably the most common protein in the biosphere) and produce an unstable product that

immediately splits into two 3-carbon compounds called 3-phosphoglycerate. At this point carbon has been fixed – the incorporation of CO_2 into an organic compound.
    - The 3-phosphoglycerate molecules are phosphorylated (using ATP from the light reactions) to become 1,3-bisphosphoglycerate.
    - Next, six NADPH (from the light reactions) reduce the six 1,3-bisphosphoglycerate molecules to six **glyceraldehyde 3-phosphate (G3P)**.
    - *One* G3P leaves the cycle to be used by the plant cell. (Two G3P molecules can combine to form glucose, which is generally listed as the final product of photosynthesis.)
    - Finally, the three beginning RuBPs are generated as the *five* G3Ps remaining are reworked into three of the starting molecules, with the expenditure of three ATP molecules. Notice that the 5G3P molecules have 15 carbons, which are rearranged to 3 RuBPs with 15 carbons. With the generation of new RuBPs the Calvin cycle begins again.
- In the Calvin cycle, the formation of one net G3P requires the following energy molecules:
    - *Nine molecules of ATP* are consumed (to be replenished by the light reactions) along with *six molecules of NADPH* (also to be replenished by the light reactions).
    - One of the six G3P molecules produced in the Calvin cycle is a net gain and will be used for biosynthesis or the energy needs of the cell.

WHAT'S IMPORTANT TO KNOW

Knowledge of C_4/CAM photosynthesis is not required for the AP exam, but you may use the information here as a nice example of evolutionary adaptations to arid conditions.

Alternative mechanisms of carbon fixation have evolved in hot, arid climates (10.4)

- Because CO_2 enters the leaf through stomata, the same pores through which water exits the leaf in transpiration, having open stomata quickly lead to dehydration in arid habitats.
- The specific problem for C_3 plants is as follows:
    - On hot, dry days C_3 plants must keep their stomata closed to conserve water – thus, no CO_2 uptake. Therefore, they produce less sugar because the declining levels of CO_2 in the leaf starve the Calvin cycle.
    - Additionally, the enzyme rubisco can bind O_2 in place of CO_2. This causes the oxidation or breakdown of RuBP, resulting in a loss of energy and carbon for the plant – a metabolic process called **photorespiration**. Photorespiration can drain away as much as 50% of the carbon fixed by the Calvin cycle!
- How can hot, arid regions have any plants? They have metabolic and structural adaptations that reduce photorespiration. The two most important of these adaptations are C_4 and CAM plants.
- C_4 plants have two strategies for reducing photorespiration.
    - **Structural strategy**. In C_3 photosynthesis the light reactions and the Calvin cycle occur in the same cell. This puts the production of O_2 in close proximity to rubisco, leading to

photorespiration. In C_4 plants the two stages of photosynthesis are separated spatially into different cells. One cell specializes in the light reactions, while the other type of cell specializes in the Calvin cycle. This spatially separates the two phases of photosynthesis, thus reducing photorespiration.

  - **Biochemical strategy**. C_4 plants have an extra enzyme PEP carboxylase, to fix carbon. PEP carboxylase does not combine with O_2, so it helps to further reduce photorespiration. PEP carboxylase acts as a CO_2 pump, helping to keep the concentration of CO_2 higher in the cells specializing in the Calvin cycle, again reducing photorespiration. Notice that C_4 plants still do the Calvin cycle and still use rubisco but have structural and biochemical adaptations that allow photosynthesis to occur even on hot, dry days.
- **CAM photosynthesis** is another adaptation to hot, dry climates.
  - CAM stands for *crassulacean acid metabolism*, referring to the family Crassulaceae in which the process was first discovered. (This is a group with succulent plants like the jade plant.)
  - CAM plants keep their stomata closed during the day to prevent excessive water loss. Of course, this also prevents gas exchange. At night, the stomata open and CO_2 is fixed in organic acids and stored in vacuoles. In the morning when the stomata close, the plant cells release the stored CO_2 from the acids and proceed with photosynthesis.
  - In CAM plants the two stages of photosynthesis are separated temporarily.
- In both C_4 and CAM photosynthesis, CO_2 is first transformed into an organic intermediate before it enters the Calvin cycle. All of the processes – C_3, C_4, and CAM photosynthesis – use the Calvin cycle; they just have different methods for getting there.

From Resource Acquisition and Transport in Vascular Plants (Chapter 36)

Sugars are transported from sources to sinks via the phloem (36.5)

- Phloem transports organic products of photosynthesis from the leaves throughout the plant, a process called **translocation**. The mechanism for translocation is **pressure flow**.
- Phloem always carry sugars from a sugar source to a sugar sink. A **sugar source** is an organ that is a net producer of sugar, such as the leaves. A **sugar sink** is an organ that is a net consumer or storer of sugar, such as a fruit, or roots during the summer. Follow Figure 36.16 while noting the key steps.
  - Sucrose is loaded into the sieve tubes at the sugar source. Proton pumps are used to create an electrochemical gradient that is utilized to load sucrose. This decreases water potential and causes the uptake of water, creating positive pressure.
  - The pressure is relieved at the sugar sink by the unloading of sucrose followed by the loss of water. In leaf-to-root translocation, xylem recycles the water back to the sugar source. Translocation via pressure flow is a second example of bulk flow.