Alternative Mechanisms of Carbon Fixation

5.4

In addition to light, plants need the raw materials for photosynthesis: carbon dioxide and water. Atmospheric carbon dioxide is available to every land plant and to aquatic plants whose leaves float on the surface of the water. For submerged aquatic plants, carbon dioxide is available in the form of dissolved carbonic acid. Carbon dioxide, however, makes up only 0.04 % of the atmosphere—a concentration $\frac{1}{500}$ that of the oxygen gas we breathe! This ratio has significant consequences for photosynthesis.

Preventing Water Loss

Water is the major component of the cytosol and is therefore always available for photosynthesis; however, all land plants have adaptations to limit water loss and respond to changes in water availability. These adaptations can reduce a plant's ability to exchange gases with its environment. Perhaps the most important adaptation for plants on land is the presence of a waxy cuticle. This thin waterproof layer covers the top and bottom surface of all terrestrial plant leaves. It seals off the interior of a leaf from the outside environment and prevents what would otherwise be a rapid loss of water by evaporation. To enable controlled gas exchange with the atmosphere, each leaf has many microscopic **stomata** (singular: stoma)—small pores on the leaf's surface that can be opened and closed by the surrounding pair of guard cells (**Figure 1**). The stomata open during the day, allowing carbon dioxide to enter and be used for photosynthesis. When the stomata are open, some water is lost through transpiration (loss of water vapour through stomata), but this water is replaced by water taken up by the plant's roots. At night, photosynthesis stops and the stomata close to conserve water. When a plant is at risk of losing too much water due to high temperatures or there is a shortage of water in the soil, the stomata remain closed even during the day.

stomata small pores in the surface of a leaf that can be opened and closed to control the exchange of gases between the atmosphere and the leaf interior

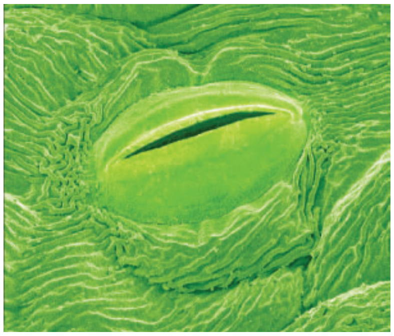


Figure 1 Gas exchange and water loss by a plant are controlled by the presence of stomata. Each stoma is formed from two guard cells.

Photorespiration: The Problem with Rubisco

All biological reactions are catalyzed by enzymes. As you have learned, the rate and efficiency with which enzymes function is influenced by many factors, including temperature, pH, and the presence of inhibitors. During photosynthesis, the functioning of the single most abundant enzyme on Earth can be problematic.

Rubisco is a very slow enzyme, catalyzing the fixation of only about three molecules of CO_2 per second. Its slow rate of catalysis is countered by its abundance within the cells. In addition to being slow, rubisco's active site occasionally binds with oxygen gas instead of carbon dioxide and catalyzes a reaction between a molecule of O_2 and RuBP. This ability to catalyze a reaction involving either CO_2 or O_2 is why rubisco is called ribulose-1,5-bisphosphate *carboxylase oxygenase*. One of the products of the reaction between O_2 and RuBP is a molecule that is not useful to the cell. This molecule must be converted back into a useful molecule to prevent too much RuBP from being wasted. The recovery pathway is long and involves reactions within the chloroplast, peroxisomes, and mitochondria. It consumes ATP and releases a molecule of CO_2. This means that, instead of fixing CO_2, the oxygenase activity of rubisco does the opposite. Since O_2 is a reactant in the recovery pathway and CO_2 is produced at later steps, the entire process is termed **photorespiration**.

photorespiration the catalysis of O_2 instead of CO_2 by rubisco into RuBP, which slows the Calvin cycle, consumes ATP, and results in a release of carbon

Under laboratory conditions, when concentrations of both O_2 and CO_2 are equal, the binding of CO_2 will happen more frequently because the active site of rubisco has a greater attraction for CO_2 than for O_2. In fact, the binding with CO_2 will occur about 80 times as fast as the binding with O_2. In nature, however, the atmosphere does not contain equal amounts of the two gases—it contains about 21 % O_2 and about 0.04 % CO_2. Since the amount of O_2 in the atmosphere is so much greater than the amount of CO_2, under normal atmospheric concentrations and at moderate temperatures rubisco

Figure 2 Plants living in hot, dry environments struggle to exchange gases with the atmosphere without suffering excessive water loss. These plants have evolved a variety of adaptations in response to the harsh conditions.

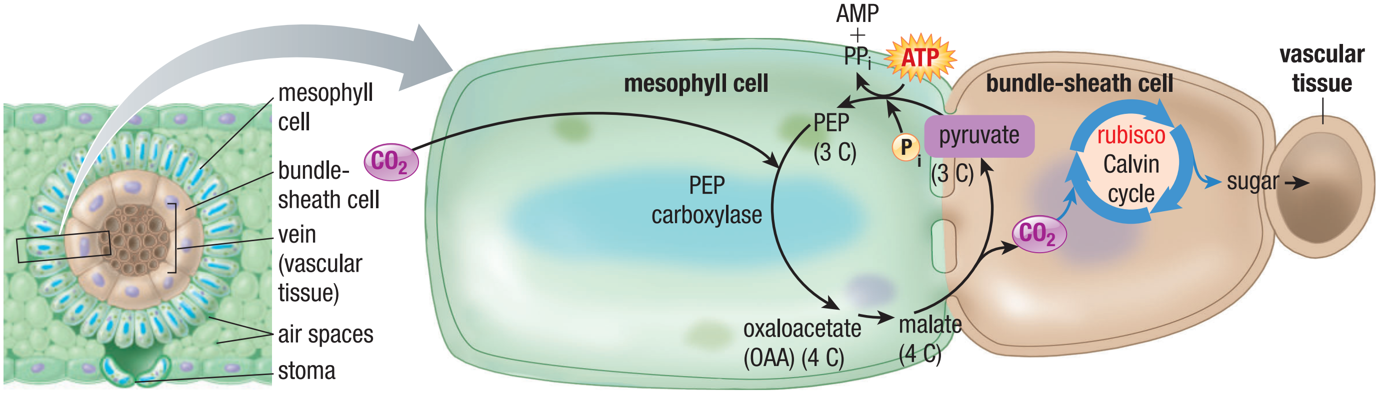
will bind with CO_2 about 75 % of the time. This means that 25 % of the time, rubisco binds with O_2 and releases rather than fixes a molecule of CO_2. This is a drain on cell resources, but the plant can still fix enough carbon to meet its normal demands for the production of energy-rich carbohydrates. However, if the supply of CO_2 in the cell is significantly reduced, photorespiration becomes a much more serious concern.

Many terrestrial plants, especially those living in hot, dry climates, face the problems of photorespiration and water loss (**Figure 2**). They need to open their stomata to let in CO_2 for the Calvin cycle, but they need to keep the stomata closed to conserve water. When stomata are closed, or even partly closed, less CO_2 can enter the leaf, and, as the CO_2 that is present is consumed in the Calvin cycle, its concentration drops and photorespiration increases. This dilemma is even worse in warm climates because the solubility of O_2 and CO_2 decreases as the temperature increases. (The stroma, where the Calvin cycle occurs, is an aqueous environment.) The solubility of CO_2 decreases more rapidly than that of O_2 as the temperature increases, resulting in a decrease in the $CO_2 : O_2$ ratio. As this ratio decreases, photorespiration increases. In high temperatures, as much as 50 % of the plant's energy could be wasted by photorespiration.

C_4 Plants

Some plant species found in hot, dry climates have an internal leaf structure and mode of carbon fixation that minimizes photorespiration. In these plants, the reactions of the Calvin cycle are performed by bundle-sheath cells, which surround the leaf veins (**Figure 3(a)**). Bundle-sheath cells are surrounded by mesophyll cells that separate them from the air spaces within the leaf. This separation reduces the exposure of the rubisco-containing bundle-sheath cells to oxygen gas and therefore reduces the rate of photorespiration. The mesophyll cells also reduce access to CO_2, but this is not a problem because they operate a second carbon fixation pathway called the **C_4 cycle.** In the C_4 cycle, CO_2 combines with a 3-carbon molecule, phosphoenolpyruvate (PEP), to produce the 4-carbon oxaloacetate. Oxaloacetate is then reduced to malate by electrons transferred from NADPH. The malate diffuses into the bundle-sheath cells, where it enters chloroplasts and is oxidized to pyruvate, releasing CO_2 (**Figure 3(b)**). The combined effect of the physical arrangement of cells and the C_4 pathway establishes a high concentration of CO_2 around the rubisco while reducing its exposure to oxygen.

C_4 cycle an alternative form of carbon fixation that some plants use, particularly in hot weather, to increase the concentration of CO_2 available for the Calvin cycle reactions



(a) C_4 leaf anatomy

(b) C_4 pathway

Figure 3 The C_4 cycle

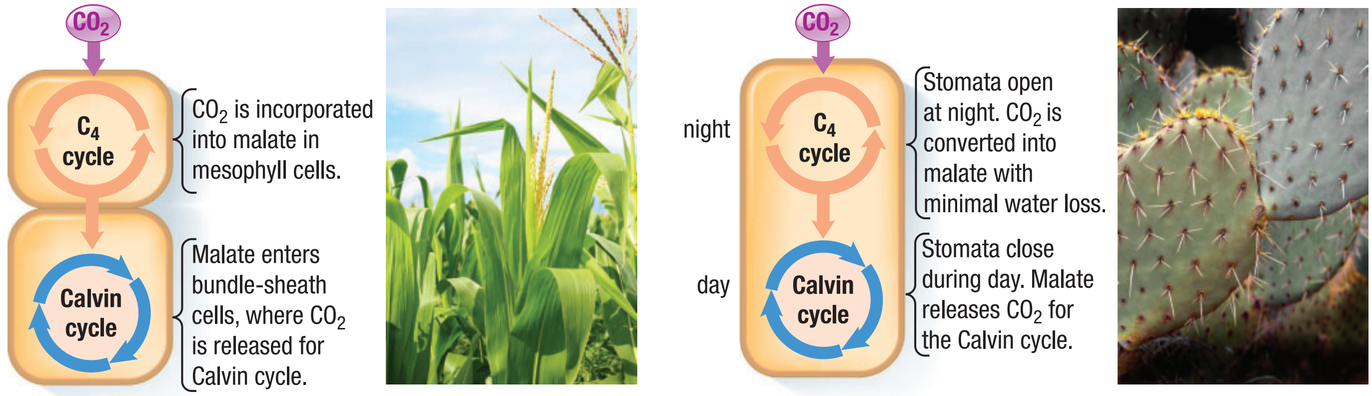
A key distinction between C_4 and C_3 metabolism is related to the binding of CO_2. In the C_4 cycle, the initial binding of CO_2, which incorporates CO_2 into phosphoenolpyruvate, is catalyzed by the enzyme PEP carboxylase. Unlike rubisco, PEP carboxylase has a much greater affinity for CO_2 than for O_2, so it can efficiently catalyze the binding of PEP regardless of the O_2 concentration near the enzyme. Many tropical plants and several temperate crop species, including corn and sugar cane, have C_4 metabolism. Remember that C_4 plants use the Calvin cycle as well.

Even though C_4 metabolism helps prevent photorespiration, it is not widespread among plants. For each turn of the C_4 cycle, the double hydrolysis of ATP to AMP (adenosine monophosphate) is required to regenerate PEP from pyruvate. This means that there is an additional energy requirement, equivalent to six ATP for each G3P produced by the Calvin cycle. However, in hot climates, photorespiration can decrease carbon fixation efficiency by over 50 %, so the C_4 pathway is worth the energy cost. Hot climates also tend to receive a lot of sunshine, so the additional ATP requirement is easily met by the cyclic light reactions. This enhanced efficiency has a number of implications. C_4 plants can open their stomata less than C_3 plants, enabling them to survive better in arid environments. C_4 plants also require one-third to one-sixth as much rubisco, and so have a much lower nitrogen demand. This enables them to survive in more nutrient-poor soil conditions. In temperate climates, the lower temperatures mean that photorespiration is less of a problem, and the additional ATP requirement is harder to meet with less sunshine. In Florida, for example, 70 % of native species are C_4 plants, but there are no C_4 species in Manitoba. CAREER LINK

CAM Plants

The C_4 plants run their Calvin and C_4 cycles simultaneously but in different locations (**Figure 4(a)**). Other plants run their Calvin cycle and C_4 cycle in the same cells, but do so at different times of the day (**Figure 4(b)**). These plants are known as **CAM** (**crassulacean acid metabolism**) plants. The name is derived from the Crassulaceae family in which the metabolic pathway was first observed, and from the plants' night-time accumulation of malic acid.

crassulacean acid metabolism (CAM) a metabolic pathway, used mostly by succulent plants, in which the Calvin cycle and the C_4 cycle are separated in time for better efficiency of CO_2 fixation



(a) plants controlling location of C_4 cycle

(b) plants controlling time of C_4 cycle (CAM)

Figure 4 (a) Some C_4 plants, such as corn, control the location of the C_4 and Calvin cycles. (b) CAM plants, such as beavertail cactus (*Opuntia basilaris*), also use a C_4 cycle, carrying out the two cycles in the same cells but at different times.

CAM plants typically live in regions that are hot and dry during the day and cool at night. These cacti and succulent species, with fleshy leaves or stems, have a low surface-to-volume ratio, and fewer stomata. Furthermore, their stomata open only at night, when they release the O_2 that accumulates from photosynthesis during the day and allow CO_2 to enter. The CO_2 that enters is fixed by a C_4 pathway into malate, which accumulates throughout the night and is stored in the form of malic acid in cell vacuoles. Daylight initiates the second phase of the CAM process. As the Sun rises and the temperature increases, the stomata close, reducing water loss and cutting off the exchange of gases with the atmosphere. Malic acid diffuses from cell vacuoles into the cytosol, where the malate is oxidized to pyruvate, and a high concentration of CO_2 is released. The high concentration of CO_2 favours the carboxylase activity of rubisco, allowing the Calvin cycle to proceed efficiently with little loss of CO_2 from photorespiration. The pyruvate produced by malate breakdown accumulates during the day, but is converted back to malate during the night. As in other C_4 plants, this step requires an expenditure of ATP. CAREER LINK

UNIT TASK **BOOKMARK**

You can use what you have learned about photosynthesis and climate to design your Unit Task investigation on page 252.

5.4 Review

Summary

- O_2 can compete with CO_2 for the active site of the enzyme rubisco, reducing the efficiency of photosynthesis. The resulting pathway is called photorespiration.
- Some plants have evolved a C_4 pathway as well as a physical arrangement and specialization of cells that bypass the problems of photorespiration. They do this by incorporating CO_2 into a 4-carbon compound in mesophyll cells and then transporting it to bundle-sheath cells.
- C_4 plants are significantly more efficient than C_3 plants at performing photosynthesis in hot and/or dry environments.
- Many cacti and succulent plants use crassulacean acid metabolism (CAM), which uses a C_4 cycle to fix carbon during the night and the Calvin cycle to produce carbohydrates during the day.

Questions

1. Explain why plants sometimes have difficulty getting all the CO_2 they need to photosynthesize efficiently. K/U
2. Wheat, corn, and rice are all grasses, and all are extremely important food crops for humans and livestock. Based on what you know about these plants, predict whether they are C_3, C_4, or CAM plants. Go online and conduct research to find out if your predictions were correct. T/I
3. Why does PEP carboxylase do a better job than rubisco at fixing CO_2 in plants that use the C_4 pathway? In what type of environment is PEP carboxylase more effective than rubisco? K/U
4. You and a friend are observing a field of lush green grass on a hot, sunny summer day. Your friend suggests that the grass must be growing quickly that day. Why might this not be the case? T/I
5. Which type of plant (C_3, C_4, or CAM) would you expect to grow most efficiently in each environment? Explain your reasoning. K/U T/I
   (a) a hot, wet tropical environment
   (b) an environment with extremely hot days but cool nights
   (c) a cool, damp environment
   (d) an environment with a moderate climate but nutrient-poor soil
6. Working with a partner, brainstorm a list of 10 different plant species. Do online research to determine, for as many of these plants as you can, what type of carbon fixation strategy they use. T/I
7. A student takes a variety of small houseplants and surrounds each plant with a clear plastic bag. After a few hours, the student observes that water vapour has condensed on the inside of some of the bags. T/I
   (a) Do you think such an experiment would provide any evidence of the type of carbon fixation strategy used by each plant? Explain your reasoning.
   (b) Would you expect different results if the student had conducted the experiment during the day versus during the night?
8. Suggest one or more reasons why scientists are interested in genetically modifying plants to change their carbon fixation pathways. T/I A
9. Which carbon fixation pathway would you expect an aloe vera plant (**Figure 5**) to use? Explain why. T/I

Figure 5 Aloe vera plant

WEB LINK