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UNIT 1: METABOLIC PROCESSES

D. Alternative Pathways of Carbon Fixation

C_3 Plants in Hot, Arid Climates

C_3 plants use rubisco to add CO_2 to RuBp. The resulting compound is a 3-carbon molecule called **PGA**. Rice, wheat, soybeans, and Kentucky blue grass are examples of C_3 plants. On hot, dry days most plants close their stomata to conserve water but at the same time reduce CO_2 intake, which reduces photosynthesis rates. If stomata are closed, O_2 builds up & CO_2 can't enter. This results in **photorespiration** – a process where rubisco accepts O_2 in the place of CO_2, since oxygen levels increase, and carbon dioxide levels decrease. Figure 1, p. 168, demonstrates how photorespiration rates increase as photosynthesis rates decrease, with increasing temperature, and stomatal closure. Rubisco adds O_2 to the Calvin cycle, instead of CO_2. The product splits, and the two-carbon compound piece is exported from the chloroplast, to the mitochondria, where peroxisomes break it down and CO_2 is released. Unlike respiration, photorespiration makes no ATP. Unlike photosynthesis, photorespiration makes no food. Photorespiration appears to be a feeble attempt, by the plant, to produce CO_2 when levels are low. The problem is that important, valuable Calvin acids are "siphoned" out of the photosynthetic pathway, and the photorespiratory-produced CO_2 is not fixed since the organic acid that is involved in the "fixing" (namely RuBp) was consumed to make the CO_2 in the first place. Photorespiration does not benefit C_3 plants at all, which would lead you to ask the question: why does it happen? One of the proposed explanations as to why C_3 plants photorespire, is that this mechanism is in fact a remnant trait that was once adaptive when plants grew in low O_2 atmospheric concentrations, but is now maladaptive since the environment has changed. Modern rubisco retains some of its ancestral affinity for O_2, which makes photorespiration inevitable.

Some plants undergo an alternate carbon fixation pathway, which minimizes photorespiration, especially in hot, arid conditions. These strategies have evolved as both modifications in biochemistry and in plant physiology. The following two pathways represent solutions to the problem of maintaining photosynthesis when stomata close on sunny, hot, dry days.

C_4 Plants in Hot, Arid Climates

C_4 plants are plants that undergo a different carbon fixation process than C_3 plants. Sugar cane, corn, and crab grass are examples of C_4 plants. Figure 2, p. 169, shows a C_4 leaf cross-section. The differences between C_3 leaf anatomy and C_4 leaf anatomy is notable. Click on http://www.emc.maricopa.edu/faculty/farabee/BIOBK/BioBookPS.html#C-4 for an illustration of both leaf types. C_4 plants have two types of photosynthetic cells in their leaf tissue. Bundle sheath cells surround veins, and mesophyll cells surround the bundle sheath cells. All three cells are connected via plasmodesmata (cell-cell connections – kind of like underground tunnels connecting two buildings) This anatomical arrangement of photosynthetic cells, together with the biochemical modifications within these cells, establishes the difference between C_3 carbon fixing and C_4 carbon fixing. In the C_4 pathway the Calvin cycle is preceded by the incorporation of CO_2 into an organic acid in the mesophyll cell first. The CO_2 is added to **phosphoenolpyruvate (PEP)** to make **oxaloacetate** with the help of special C_4 fixing enzyme called **phosphoenolpyruvate carboxylase (PEPc)**. Oxaloacetate is a 4-carbon organic acid, which is the reason why this is called the C_4 pathway. PEPc has a much higher "grab" or affinity for CO_2 than rubisco does, especially when levels of CO_2 are low. Basically, PEPc can "fix" CO_2 efficiently when rubisco cannot. The oxaloacetate becomes **malate**, which then enters the bundle sheath cells via the plasmodesmata. The malate loses a CO_2 and becomes a 3-carbon **pyruvate**. The pyruvate moves into the mesophyll cell and is greeted by an ATP. The ATP phosphorylates the pyruvate to recreate the PEP so that the cycle is complete. This "pre-Calvin" cycle ensures a continuous "pumping" of CO_2 molecules into the bundle sheath cells, thereby maintaining a high concentration of CO_2 rubisco in the Calvin cycle. Effectively, the C_4 pathway minimizes photorespiration (during low CO_2 levels), and maximizes sugar production. Figure 2, p. 169 illustrates the C_4 pathway in detail. The C_4 pathway uses almost twice as much ATP as the C_3 pathway to produce glucose. However, without this pathway, photorespiration would stress the plant out so much that it would not survive!

CAM Plants in Hot, Arid Climates

Unlike most plants, some plants, such as cacti and pineapple plants, open their stomata at night and close them during the day to prevent water loss, since they live in very hot and dry environments. Closing stomates during the day prevents water loss, however limits the amount of CO_2 in the leaves. To compensate for these low CO_2 levels, the stomates open at night to let in CO_2 when temperatures are relatively lower. CAM plants incorporate CO_2 into an acid called crassulacean acid, within the mesophyll cells, and store it in vacuoles overnight. During the day, when ATP and NADPH are made by light reactions, the CO_2 is released from the organic acids so it can be incorporated into sugar in the Calvin cycle. CAM stands for "Crassulacean acid metabolism", since all the plants in the Crassulacean family, commonly known as succulent plants, undergo this CO_2 fixing process.

Comparing C_3, C_4, and CAM Photosynthesis

Figure 4, p. 171, illustrates C_3, C_4, and CAM CO_2 fixation. In C_3 plants, low levels of CO_2 cause rubisco to go “schizo” – it no longer binds to CO_2. Instead, it bonds to oxygen. The result is a decrease in CO_2 uptake, a siphoning off of Calvin acids, and an increase in photorespiration rates. C_3 plants do not have a mechanism to help them fix CO_2 when it occurs in low levels. In C_4 plants, the first part of carbon fixation and the Calvin cycle occur in separate compartments of the leaf. In CAM plants, the two steps occur in the same compartment, but at different times of the day. Figure 3, p. 170, illustrates a comparison of C_4 and CAM plants. Both methods initially produce organic acids that eventually transfer CO_2 to the C_3 Calvin cycle. In C_4 plants, these two processes occur in two different types of cells at the same time, connected by plasmodesmata (spatial separation). In CAM plants, the two processes occur in the same compartment cell, but at different times (temporal separation): carbon fixation into organic acids during the night and the Calvin cycle during the day.

Homework: 1-9, p. 172