Memories of Photosynthesis

By Michael Semler

The snow has finally returned to Wisconsin, and we can sit back, relax and enjoy some type of normality in our work schedules. If I might be so rude as to try and bring back memories of warm days and green vegetation, I would like to try and refresh our memories with one of the essential processes occurring in all plants. That process — photosynthesis — is the route by which virtually all energy enters our biosphere, and is no doubt the reason I will dwell on the systems and pathways involved.

Historically, plants were assumed to derive all their food from the soil. It was not until the 1600's that the Belgian physician Jan van Helmont conducted his famous experiment by planting a 5 pound willow tree in 200 pounds of soil. At the end of the 5 year experiment, during which only water was added, the willow weighed 169 pounds and the soil decreased in weight by 2 ounces. Van Helmont logically concluded, though incorrectly, that all the substance of the plant came from the water and none from the soil.

During 1771, Joseph Priestely, discovered a means of restoring air destroyed by burning a candle. Priestely put a living sprig of mint into air which a candle had burned out, another candle could be burned 10 days later in the same air. Dutch physicist Jan Ingenhaus confirmed Priestely's work and showed air was restored only in the presence of light and only by green plant parts. In 1796, Ingenhaus suggested that carbon dioxide was split in photosynthesis to yield oxygen. In the overall reaction for photosynthesis, it was assumed that the carbohydrates came from carbon and water and the released oxygen came from the carbon dioxide. This reasonable assumption was widely accepted, but quite wrong.

Ingenhaus' theory was accepted until 1930 when Stanfords' C.B. van Neil proposed that water, not carbon dioxide, was split in photosynthesis. Thus, the complete, balanced equation was determined to be:

$$6CO_2 + 12H_2O + LIGHT \longrightarrow C_6H_{12}O_6 + 6O_2 + 6H_2O$$

For about 200 years, light has been known to be essential for photosynthesis. In 1905, English plant physiologist, F. F. Blackman presented evidence of photosynthesis being a 2 stage process. The first stage being light dependent and known as the "Light Reactions" and the second stage being light independent and known as the "Dark Reactions." It is important to note that the dark reactions normally occur in the light because they require the products of the light reactions. The expression "dark reactions" merely indicates light is not directly involved.

In the first stage of photosynthesis, light energy is used to form adenosine tri phosphate (ATP) from adenosine di phosphate (ADP) and reduce the electron carrier molecule NADP to $NADPH_2$. In the second stage, the energy products from the first stage are used to reduce carbon, from carbon dioxide, to a simple sugar. This process converts chemical energy from carrier molecules to forms suitable for transport and storage in the plant.

Photosynthesis, in a basic reference, is the conversion of light energy to chemical energy. In order to start this process, light must first be absorbed. This energy absorption is done by compounds known as pigments, mainly found in the chloroplasts of cells. The relative importance of the pigments is based on the range of the light spectrum being absorbed. This range is known as its' absorption spectrum. Each pigment has a different absorption spectrum and thus, has a different action spectrum. The action spectrum defines the relative effectiveness of different wavelengths on the light requiring processes.

Of all the pigments in the plant, chlorophyll is the principle one involved in photosynthesis. There are several types of chlorophyll, which differ slighly in chemical structure. Chlorophyll A, the primary type of chlorophyll, occurs in all photosynthetic eukaryotes and prokaryotic cyanobacteria.

Chlorophyll B is present in vascular plants, bryophytes and certain other algae types. The absorption spectrum of chlorophyll B, an accessory pigment, is different from chlorophyll A and like all other pigments, serves to extend the usable light spectrum for photosynthesis. When a chlorophyll B molecule absorbs energy, it must transfer it to a chlorophyll A molecule, where it will then be converted to chemical energy.

Chlorophyll C, another accessory pigment, is present in the brown algae and the diatoms.

Two other classes of pigments are involved in light capture; the carotenoids and the phycobilins. These pigments must also transfer their energy to chlorophyll A and may not substitute for it. The carotenoids are red, orange and yellow, fat soluble pigments whose colors are normally masked by the more abundant chlorophyll. They are divided into 2 groups: the carotenes and xanthophylls, and like chlorophyll, are present in the thylakoid membranes of the chlorplasts.

The phycobilins, the third class of pigments, are water soluble and found in the cyanobacteria and the red algae.

These pigments are imbedded in the thylakoids in discrete units called photosystems. All pigments in the photosystem are capable of absorbing photons, but only one chlorophyll molecule in the system can use the energy. This special chlorophyll A molecule is called the reaction center. When the reaction center receives the absorbed energy, one of its' electrons is boosted to a higher energy level and transferred to an acceptor molecule to initiate energy flow.

In currently accepted models of the Light Reactions, two system exist. In Photosystem I, the reaction center has a wavelength absorption peak of 700 nanometers and is called P700. Photosystem II has a reaction center with an absorption peak of 680 nanometers and is called P680.

In the Light Reaction system, light energy trapped in the reaction center, P680, of Photosystem II boosts electron pairs to a higher energy level to a primary electron acceptor. The electrons are then passed along an electron transport chain to a somewhat lower energy level, the P700 reaction center. As they pass along this chain, some of the energy is stored in the form

of ATP. The "excited" electrons removed from the P680 reaction center are replaced by electrons from the splitting of water, releasing protons and oxygen.

Light energy absorbed by Photosystem I boosts the electrons accepted from Photosystem II to another primary electron acceptor. From this acceptor, they are passed via other electron carriers to the coenzyme NADP, resulting in the reduction of NADP to $NADPH_2$. The energy yield from the light ractions is stored in the form of $NADPH_2$ and ATP. Thus, in the presence of light, there is a continuous flow of electrons from water to Photosystem II to Photosystem I to NADP. The NADP is converted to $NADPH_2$, and along with the ATP, provides energy directly to the biosynthetic processes of the plant. The net harvest from the excitement of 12 electron pairs in the light reactions is 12 ATP molecules and 12 $NADPH_2$ molecules.

In the second stage of photosynthesis, the Dark Reactions, the energy from the first stage, $NADPH_2$ and ATP, are used to reduce carbon to sugars. This carbon, available from carbon dioxide, reaches the photosynthetic cells through the stomata of the leaf.

The reduction of carbon dioxide occurs in the stroma of the chloroplasts by means of the Calvin Cycle, also known as the three carbon pathway (C3) because of a three carbon intermediate molecule. The Calvin Cycle begins with the introduction of a single carbon dioxide molecule. It is then attached to the 5 carbon enzyme Ribulose 1,5 Bisphosphate (RuBP). The carbon dioxide is reduced in a series of reactions to give a single carbon atom. The RuBP is regenerated at the end of each cycle to start again and reduce another carbon dioxide molecule. Six turns of the cycle and 6 carbon dioxide molecules are required to produce a single six-carbon sugar.

The Calvin Cycle is not the only carbon fixing system. A second system, the 4-Carbon Pathway, or C4, has a 4-carbon compound oxaloacetate as the first detectable molecule. The C4 fixation system begins in the mesophyll cells. Here the oxaloacetate is formed when carbon dioxide is fixed to phosphoenylpyruvate (PEP), an enzyme which catalyzes the system. The oxaloacetate is quickly converted to malate, which then moves to the bundle sheath cells surrounding the vascular bundles of the leaf. It is then decarboxylated to carbon dioxide and pyruvate. The carbon dioxide enters the Calvin Cycle and is reduced as in the C3 system. The pyruvate returns to the mesophyll cells for regeneration to PEP to reenter the system and fix another carbon dioxide molecule.

One might ask why the C4 pathway evolved such a clumsy and energenically expensive method of providing carbon dioxide to the Calvin Cycle. The C4 pathway is better understood when we learn that the Calvin Cycle is always accompanied by photorespiration, a sequence which consumes oxygen and releases carbon dioxide. Photorespiration yields no energy and may consume up to 50% of the photosynthetically fixed carbon, under normal atmospheric conditions, converting it to carbon dioxide.

However, high carbon dioxide and low oxygen concentrations limit photorespiration. C4 plants have an advantage over C3 plants because of their ability to force carbon dioxide from the mesophyll to the bundle sheath cells, keeping a high carbon dioxide and a low oxygen concentration in the presence of the Calvin Cycle.

C4 plants also are superior utilizers of carbon dioxide because the PEP has a greater affinity for carbon dioxide at lower concentrations than the RuBP of the Calvin Cycle.

The C4 plants evolved in the tropics and are especially well adapted to high light intensities, high temperatures and dryness. The optimal temperature range for C4 plants is higher than for C3, and often C4 plants flourish at temperatures lethal for C3. Because of their more efficient use of carbon dioxide, C4 plants can obtain the same photosynthetic rate as C3, but with smaller stomatal openings and thus, with less water loss.

The difference between C3 and C4 plants can be found on golf courses. C3 grasses, such as Kentucky Bluegrass and Creeping Bentgrass, are often overwhelmed by the C4 plant, Crabgrass, which grows more rapidly in the heat of summer.

A third, and final carbon fixing pathway is the Crassulacean Acid Metabolism (CAM) system found in the succulents. In CAM plants, the carbon dioxide fixation by PEP into C4 compounds occurs at night and then stored. During the following day, the fixed carbon dioxide is transferred to the Calvin Cycle. Like the C3 plants, CAM photosynthesis occurs in the same cell.

CAM plants are largely dependent on carbon dioxide accumulation for photosynthesis at night because the stomata are closed during the day to retard water loss. Obviously, this is advantageous because of the high light intensities and high temperatures that succulents exist in.

No article could ever encompass an indepth look at photosynthesis, however, I hope I have brought back some of the important aspects involved. Our livelihood depends greatly on this process, and an understanding of it is far too important for us to ignore.