Chapter 2

Photosynthesis and Carbon Metabolism

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Additional information is available at the end of the chapter

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Abstract

Photosynthesis takes place in chloroplasts of green plants and algae and results in the conversion of radiant energy into chemical energy. Water and carbon dioxide are the raw materials; plants can produce sugars by using chlorophyll and light energy. During the first reaction of photosynthesis, ATP and NADPH are produced from light energy. Oxygen and hydrogen are released from water broken during the light reaction. In the dark reaction, CO_2 is converted into glucose by consuming energy that comes from first step of photosynthesis.

Keywords: ATP, NADPH, CO_2, light reactions, dark reactions

1. Light energy

The organism's life on the world depends on photosynthesis process, so it is considered as the essential process. Photosynthesis is defined as the reduction of carbon dioxide into carbohydrate by the green plants utilizing light energy. Diverse types of biological molecules are created directly or indirectly from the photosynthesis products. During respiration process, the organic materials release energy to be used for metabolic processes. The only natural process that can provide oxygen for living organisms is the photosynthesis process [1].

In higher plants, leaves are the organs in which photosynthesis process occurs. Biologists concentrate on organ structure and their biochemical and physiological function. A good example of organ function is plants leaves. Some of the plant leaves alter their shape for distinct purposes, but still their main function is food synthesis. Leaves trend to maximize their area and change their angles to insure to receive enough light. Leaf observed as photosynthetic engine implements photosynthesis efficiently in stress condition [2].

Photosynthesis occurs not only in eukaryotic organisms such as green plants and green algae but also in prokaryotic organisms such as cyanobacteria and certain groups of bacteria. In higher plants and green algae, photosynthesis reactions occur in the chloroplast, which acts as a thermodynamic machine. The chloroplast tricks the radiant energy of sunlight and saves some of it in a stable chemical energy. The reactions that accomplish these energy transformations are identified as the light-dependent reactions or the first stage of photosynthesis. Energy generated by the light-dependent reactions is subsequently used to reduce inorganic CO_2 to organic carbon in the form of sugars. Both the carbon and the energy conserved in these sugars are then used to build the order and structure that distinguishes living organisms from their inorganic surroundings (Duysens et al., 1961).

1.1. Leaf structure

In higher plant, leaf structure especially the upper site, is more suitable to receive much sunlight. However, the lower site reflects and scatters light. Cell arrangement in side leaf is also more important beside leaf morphology. Leaves in dicotyledonous plants have two epidermises: upper and lower covered by cuticle. Mesophyll tissues, which contain the photosynthetic tissues, are found between the two epidermal layers. Generally, there are 1–3 palisade mesophyll cells in upper photosynthetic tissue. Palisade cells are special cells in shape. In lower site, there are spongy mesophyll cells, which have isodiametric shape. Leaf in monocotyledonous is similar to leaf in dicotyledonous, but there are no special mesophyll cells.

Generally, there is more number of chloroplasts in palisade cells, which have high concentration of chlorophyll than spongy mesophyll cells. The presence of more chloroplast does not mean having higher photosynthesis rate, which occurs in the upper part of the leaf. Dicotyledonous leaves have more chloroplasts in their palisade; however, a little cell volume can have more chloroplasts. Much light will pass through the first cell layer without being absorbed because the pigments get combined to the chloroplast.

Light absorption efficiency may be affected by factors that change the light direction. The surface of leaf cell may reflect off the light. If a pigment absorbs light energy, one of three things will occur: first, energy is dissipated as heat. Second, the energy may be emitted immediately as a longer wavelength, a phenomenon known as fluorescence. Third, energy may trigger a chemical reaction, as in photosynthesis. Grana and mitochondria structure in chloroplasts have dimensions parallel to active wavelength in photosynthesis. Light is scattered by grana and mitochondria. Deflection, reflection and scattering increase the effect of light on leaf. Longer light wave increases the number of photons absorbed by leaves [3].

The light absorbed by palisade cell is not much as projected as it is thought and has lower light reduction efficiency. This may be due to the palisade that acts as a light guide. Some of the incident light goes through the intercellular spaces between the palisade cells in much the same way as the light is transmitted by an optical fiber. It is likely that photosynthesis in the highest layer of palisade is light saturated. Any excess of light would be wasteful and lead to photoinhibition. Thus, the increased diffusion of light to the lower cell layers resulting in both scattering light and the light-guide impact would no doubt be advantageous by contributing

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to a more efficient allocation of photosynthetic energy throughout the leaf. Different plants have different leaves. Due to environmental situations, leaves may make some changes for adaptation. Light interception capacity has been compromised in favor of a reduced surface-to-volume ratio, a modification that helps to combat dehydration when exposed to dry air. Leaves become more thicker to store more water in desert land area. In extreme cases, such as the cacti, the leaves have been reduced to spikes and the stem has taken over the double functions of water storage and photosynthesis. Within the leaf mesophyll cells of plants, the chloroplast is the organelle that transforms light energy into ATP and NADPH to convert CO_2 to sugars. ATP is synthesized by chemiosmosis, whereas NADPH is the product of coupled electron transfer reactions in the chloroplast thylakoid membranes. The enzymatic reaction involved in the conversion of CO_2 to sugars takes place in the chloroplast stroma [4].

1.2. Light reactions stage

There are two photosystems in light reactions, photosystems I and II, in the thylakoid membranes. Each photosystem has a complex of numerous chlorophyll and carotenoid molecules (known as light-harvesting antennae), which is associated with membrane proteins. Innumerable units of these photosystems are arranged on the thylakoid membranes in the chloroplast. When light attacks a pigment molecule in each photosystem, the energy is channeled into a reaction center, which consists of chlorophyll, a molecule bound to a membrane protein. In photosystem I, the reaction center is called P700, in the red region of the spectrum, which indicates the wavelength of maximum absorption of light; the center of reaction for photosystem II is P680, again indicating the peak absorbance. Some enzymes and coenzymes, which are associated with photosystem, act as electron carries in thylakoid membranes. Energy is formed in P700 when one photon of light attacks one molecule of pigment in photosystem I. An electron is excited and ejected when P700 absorbs energy leaving P700 in an oxidized state. The emitted electron will be picked by a primary electron acceptor, and then electron will be moved to ferredoxin and finally to NADP+ reducing it to NADPH +H, which are the first products of the light reactions. In photosystem II, another photon of light will be absorbed by a chlorophyll molecule that will transfer its energy to the reaction center P680 (Beardsley and Tim [5]). When P680 absorbs this energy, an excited electron is ejected and passed on to another primary electron acceptor, leaving P680 in an oxidized state. Electron from water will compensate the electron, which is lost by P680, and this reaction is still not clear and is catalyzed by an enzyme on the thylakoid membrane that requires manganese atoms, and water molecules in this reaction will split into H and O_2; the source of both electrons and protons is hydrogen. The electron from primary electron acceptor will push through the other electron carriers that include plastoquinone (Pq), cytochrome complex, and plastocyanin (Pc). The electron is finally passed in photosystem I to oxidize P700. ATP is created during the transfer of electrons, from the thylakoid lumen into the stroma by an ATP synthase in the membrane. The mechanism of ATP production through protons passage remains unclear. The whole process is drives by sunlight energy as showing in Photosystem II to Photosystem I. Water is continually replenished from the electrons that are lost from P680. In noncyclic photophosphorylation, the reduction of NADP is the final step from one-way electron transfers. Cyclic way of electron transfer occurs just in photosystem I. The electrons, instead of being passed to NADP from ferredoxin, may be passed to the cytochrome complex and then back to P700. Through this process, ATP may be generated, which is known as cyclic photophosphorylation, and electrons' flow begins and ends with P700. The only constant supply of oxygen gas in atmosphere is photosynthesis through diffuses out of the leaves into the atmosphere. The current 20% oxygen content in the atmosphere is the result of 3.5 billion years of photosynthesis. Cyanobacteria are the first photosynthetic organisms that began to accumulate oxygen, in ancient time, when there was no oxygen. Now most of the living organisms depend on oxygen for cellular respiration, and therefore, it is the energy that maintains life. The flow of electrons and moves from water to NADPH is powered by sunlight energy. The result of the light reactions is ATP and NADPH that are needed to drive the biochemical reactions or dark reaction in the Calvin cycle [6].

2. The Calvin cycle (dark reactions)

The atmosphere considers carbon dioxide as the main source, which produces sugar through photosynthesis process. Carbon dioxide occupies approximately 0.035% of earth's atmosphere, which enters the leaf by diffusing through the stomata. Carbon fixation reactions, which reduces CO_2 to the sugar, are sometimes known as Calvin cycle or C3 pathway. These reactions do not use light directly but utilize the ATP and NADPH produced through the light reactions sometimes referred as light-independent reactions or dark reactions. The dark reactions take place in stroma of chloroplast where many reactions were catalyzed by enzymes. This pathway was worked out by Melvin Calvin, in association with Andrew Benson and James Bassham, during the late 1940s and early 1950s. The pathway is named in honor of Calvin, who received a Nobel Prize for his work in 1961. The following discussion will be limited to the main events of the Calvin cycle. The end product of this pathway is the synthesis of a six-carbon sugar, which requires the input of carbon dioxide. To produce single molecule of a six-carbon sugar, it needs to join six molecules of CO_2 by six turns of the cycle. The first process is the cooperation of CO_2 with ribulose-1, 5-bisphosphate (RUBP), a five-carbon sugar with two phosphate groups. The enzyme ribulose bisphosphate carboxylase (RUBISCO) catalyzes carboxylation reaction. The most abundant protein on the Earth is RUBISCO (12.5–25% of total leaf protein). Carboxylation produces an unstable six-carbon transitional that immediately splits into two molecules of a three-carbon compound, with one phosphate group known as phosphoglyceric acid (PGA), or phosphoglycerate. In total, 12 molecules of PGA is yielded from six turns of the cycle, and these molecules of phosphoglyceraldehyde (PGAL) come from the conversion of about 12 PGA molecules. 12 NADPH and 12 ATP are required for this step, which supply the energy for this reaction. Six molecules of RUBP were regenerated from 10 of the 12 glyceraldehyde phosphate molecules in a complex series of interconversions that require six more ATP and allow the cycle to continue. Two molecules of glyceraldehyde phosphate are the net gain from six turns of the Calvin cycle; these are converted into one molecule of fructose-1, 6-bisphosphate, which is converted to glucose. The glucose produced is converted into starch, sucrose, or a variety of other products, thus completing the conversion of solar energy into chemical energy. All steps of photosynthesis process can be concluded in simple

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equation, which reflects raw materials and end products of the process. Many plants utilize various carbon fixation cycles that consist of a prefixation of CO_2 before the Calvin cycle. Prefixation occurs in two pathways, C4 and the CAM pathways. Many tropical and subtropical plants, such as maize, sorghum and sugarcane, have the C4 pathway. This pathway takes place in mesophyll cells to fix carbon dioxide into organic acids with a four-carbon compound, so-called C4 pathway; then, this compound is broken down to release carbon dioxide in cells surrounding the vascular bundle. More efficient transfer of CO_2 in C4 pathway and greater photosynthetic rates under conditions of high light intensity, low CO_2 concentrations and high temperature. Crassulacean acid metabolism (CAM) pathway has the same step that functions in a number of plants of desert environments, cacti and succulents. This pathway was initially described among members of the plant family Crassulaceae. CAM plants are unusual in that their stomata are closed during the daytime but open at night. Thus, they fix CO_2 during the nighttime hours, incorporating it into four-carbon organic acids. During the daylight hours, these compounds are broken down to release CO_2 to continue on into the Calvin cycle. This different pathway allows carbon fixation to occur at night when transpiration rates are very low, an obvious advantage in hot, dry desert environments [7].

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