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Photosynthesis: How and Why?

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1. Introduction

The total solar energy absorbed by Earth is approximately 3,850,000 exajoules per year. This was more energy in one hour than the world used in one year! *Nature* uses very wonderful and interesting strategies to capture the energy in an interesting process: *Photosynthesis*.

To know more about photosynthesis, the first we should know about phototrophy. Phototrophy is the process by which organisms trap photons and store energy as chemical energy in the form of adenosine triphosphate (ATP). ATP transports chemical energy within cells for metabolism. There are three major types of phototrophy: Oxygenic and Anoxygenic photosynthesis, and Rhodopsin-based phototrophy. Photosynthesis is a chemical process that converts carbon dioxide into different organic compounds using solar energy. Oxygenic and anoxygenic photosynthesis undergo different reactions in the presence and absence of light (called light and dark reactions, respectively). In anoxygenic photosynthesis, light energy is captured and stored as ATP, without the production of oxygen. This means water is not used as primary electron donor. Phototrophic green bacteria, phototrophic purple bacteria, and heliobacteria are three groups of bacteria that use anoxygenic photosynthesis. Anoxygenic phototrophs have photosynthetic pigments called bacteriochlorophylls. Bacteriochlorophyll a and b have maxima wavelength absorption at 775 nm and 790 nm, respectively in ether. Unlike oxygenic phototrophs, anoxygenic photosynthesis only functions using a single photosystem. This restricts them to cyclic electron flow only, and they are therefore unable to produce O_2 from the oxidization of H_2O. In plants, algae and cyanobacteria, the photosynthetic processes results not only in the fixation of carbon dioxide (CO_2) from the atmosphere but also release of molecular oxygen to the atmosphere. This process is known as oxygenic photosynthesis.

Photosynthesis captures approximately 3,000 EJ per year in biomass and produces more than 100 billion tons of dry biomass annually (Barber, 2009). Photosynthesis is also necessary for maintaining the normal level of oxygen in the atmosphere.

It is believed that the first photosynthetic organisms evolved about 3,500 million years ago. In that condition, the atmosphere had much more carbon dioxide and organisms used hydrogen or hydrogen sulfide as sources of electron (Olson, 2006). Around 3,000 million years ago, Cyanobacteria appeared later and changed the Earth when they began to oxygenate the atmosphere, beginning about 2,400 million years ago. This new atmosphere was a revolution for complex life. The chloroplasts in modern plants are the descendants of

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these ancient symbiotic cyanobacteri (Gould et al., 2008). In plants and algae, photosynthesis takes place in chloroplasts. Each plant cell contains about 10 to 100 chloroplasts (Fig. 1).

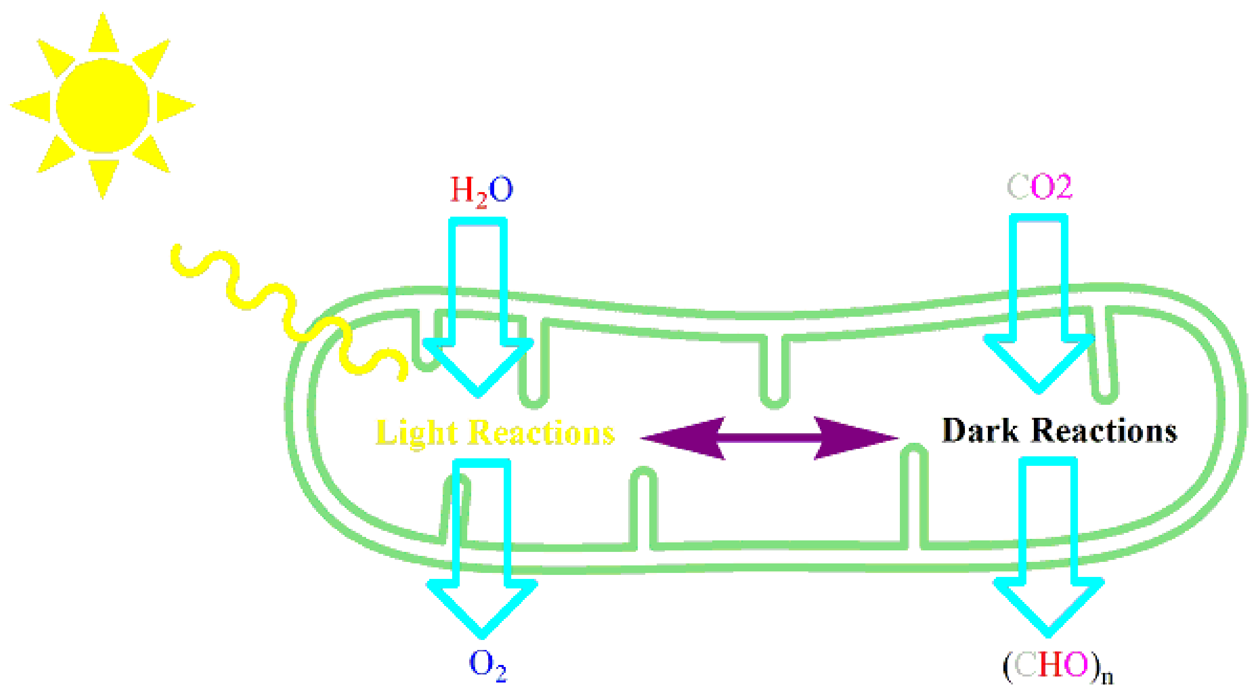

Fig. 1. In photosynthesis, organic synthesis and oxygen evolution reactions performs in two distinct enzymatic systems.

The chloroplast is composed of two membranes (phospholipid inner and outer membrane) and an intermembrane space between them. Within the membrane is an aqueous fluid called the stroma contains stacks (grana) of thylakoids, which are the site of photosynthesis. The thylakoids are flattened disks, bounded by a membrane with a lumen or thylakoid space within it. The site of photosynthesis is the thylakoid membrane, which contains integral and peripheral membrane protein complexes, including the pigments that absorb light energy, which form the photosystems. The first step in photosynthesis is the absorption of light by a pigment molecule of photosynthetic antenna resulting in conversion of the photon energy to an excited electronic state of pigment molecule. Plants absorb light primarily using the pigment chlorophyll. Besides chlorophyll, organisms also use pigments such as, phycocyanin, carotenes, xanthophylls, phycoerythrin and fucoxanthin (Fig. 2).
The most useful decay pathway is “energy transfer” to a photochemical reaction centers, and it is important to photosynthetic reactions. Excitons trapped by a reaction center provide the energy for the primary photochemical reactions. Subsequent electron transfer reactions occur in the dark which results in accumulation of chemical bound energy. In the other words, photosynthesis occurs in two stages. In the first stage, *light-dependent reactions* or *light reactions* capture the energy of light and use it to make the energy-storage molecules (ATP). During the second stage, the *light-independent reactions* use these products to capture and reduce carbon dioxide (Govindjee et al., 2010). The dark reaction doesn't directly need light, but it does need the products of the light reaction.
In the light reactions, a chlorophyll molecule of reaction center absorbs one photon and loses one electron. This electron is passed to a modified form of chlorophyll called pheophytin, which passes the electron to a quinone molecule, allowing the start of a flow

of electrons down an electron transport chain that leads to the ultimate reduction of NADP to NADPH.

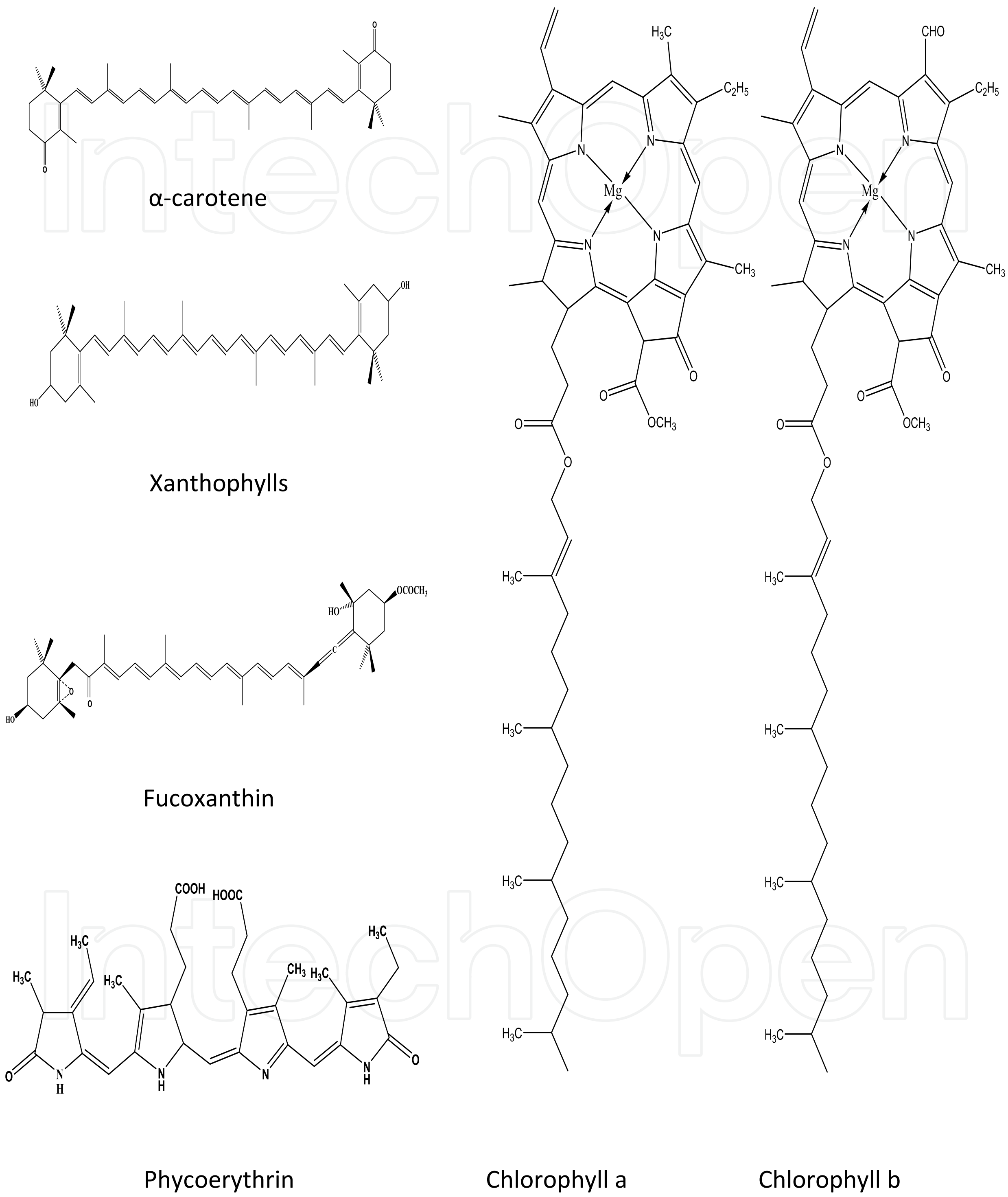

Fig. 2. Plants absorb light primarily using some pigments.

The proton gradient across the chloroplast membrane is used by ATP synthase for the concomitant synthesis of ATP. The chlorophyll molecule regains the lost electron from a water molecule and oxidizes it to dioxygen (O_2):

$$2H_2O + 2NADP^+ + 3ADP + 3P_i + light \rightarrow 2NADPH + 2H^+ + 3ATP + O_2$$

A good method to study of oxygen evolution in this process is to activate a photosynthetic system with short and intense light flashes and study of oxygen evolution reaction. Joliot's experiments in 1969 showed that flashes produced an oscillating pattern in the oxygen evolution and a maximum of water oxidation occurred on every fourth flash (Satoh et al., 2005). These patterns were very interesting because splitting of two water molecules to produce one oxygen molecule requires the removal of also four electrons. In 1970, Kok proposed an explanation for the observed oscillation of the oxygen evolution pattern (Kok et al., 1970). Kok's hypothesis (Kok et al., 1970) is that in a cycle of water oxidation succession of oxidizing equivalents is stored on each separate and independent water oxidizing complex, and when four oxidizing equivalents have been accumulated one by one an oxygen is spontaneously evolved (Kok et al., 1970). Each oxidation state of the water oxidizing complex is known as an "S-state" and S_0 being the most reduced state and S_4 the most oxidized state in the catalytic cycle (Fig. 3) (Kok et al., 1970). The S_1 state is dark-stable. The $S_4 \rightarrow S_0$ transition is light independent and in this state oxygen is evolved. Other S-state transitions are induced by the photochemical oxidation of oxidized chlorophyll (P_{680}^+) (Satoh et al., 2005).

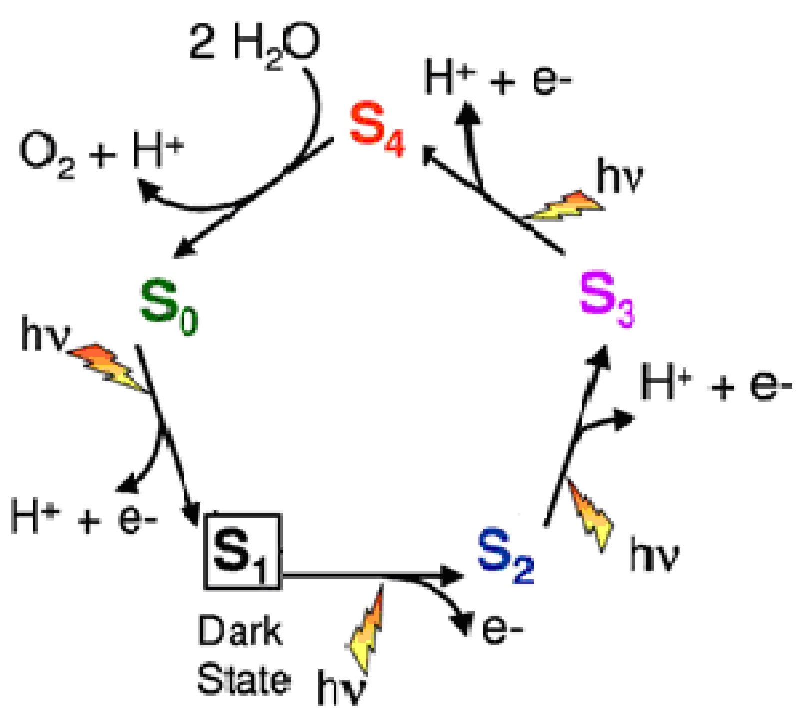

Fig. 3. Catalytic cycle proposed by Joliot and Kok for water oxidation, protons and electrons at photosystem II. The figure was reproduced from Sproviero et al., 2008.

Recently, Umena et al. (Umena et al., 2011) reported crystal structure of this calcium-manganese cluster of photosystem II at an atomic resolution. In this structure one calcium and four manganese ions are bridged by five oxygen atoms. Four water molecules were found also in this structure that two of them are suggested as the substrates for water oxidation (Fig. 4).

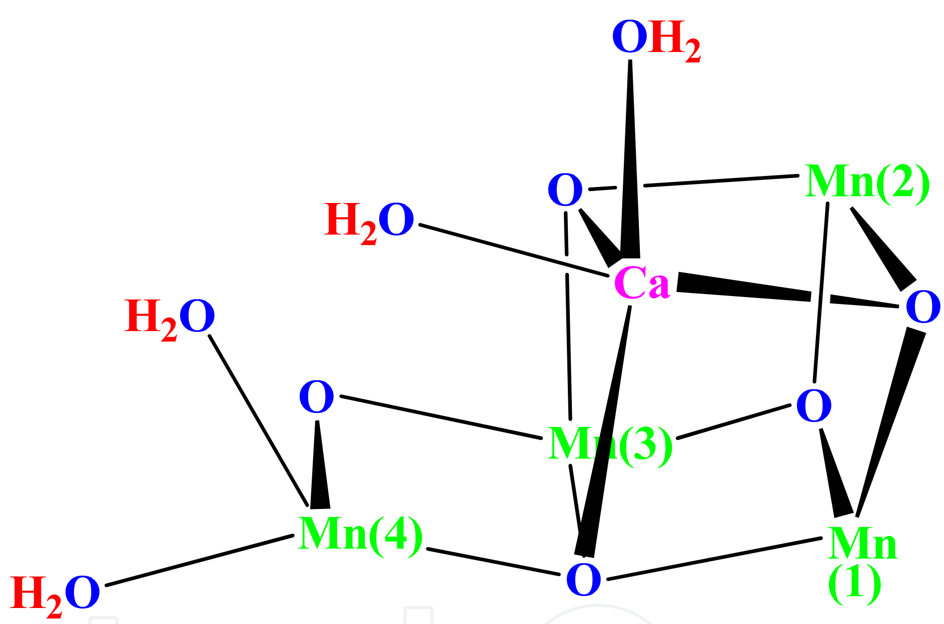

Fig. 4. The structure of water oxidizing complex (WOC) (Umena et al., 2011).

Light-dependent reactions occur in the thylakoid membranes of the chloroplasts in plants and use light energy to synthesize ATP and NADPH. Cyclic and non-cyclic are two forms of the light-dependent reaction. In the non-cyclic reaction, the photons are captured in the light-harvesting antenna complexes of photosystem II by different pigments (Fig. 5 and Fig. 6).

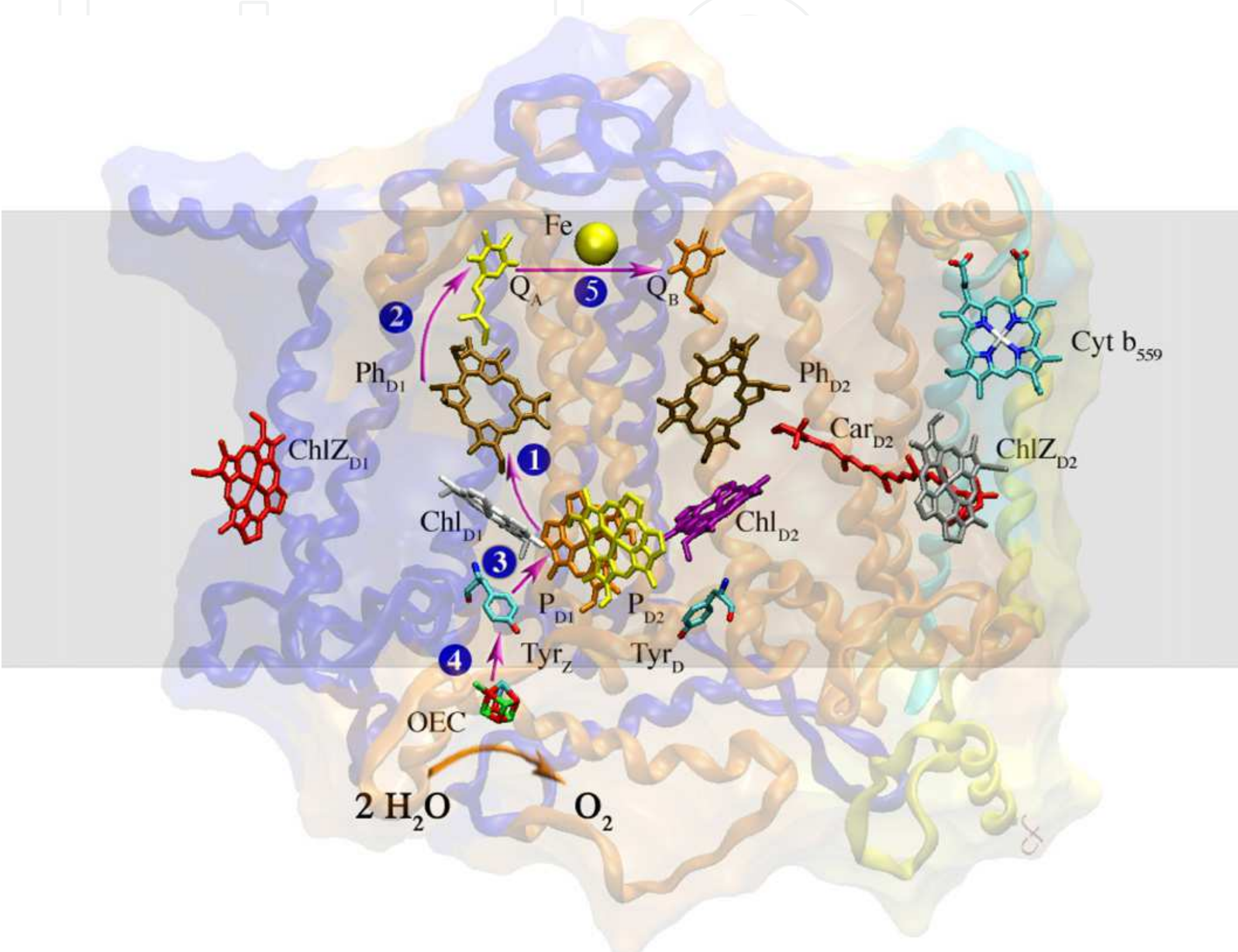

Fig. 5. Map of the main cofactors of PSII. The arrows show the electron transfer steps and the numbers indicate the order in which they occur. The figure was reproduced from Herrero et al., 2010.

When a chlorophyll molecule in reaction center of the photosystem II obtains sufficient excitation energy from the adjacent antenna pigments, an electron is transferred to the primary electron-acceptor molecule, pheophytin, through a process called photoinduced charge separation. These electrons are shuttled through an electron transport chain, the so-called *Z-scheme* shown in Fig. 7, that initially functions to generate a chemiosmotic potential across the membrane.

Z-scheme diagram of oxygenic photosynthesis demonstrates the relative redox potentials of the co-factors in the linear electron transfer from water to $NADP^+$.

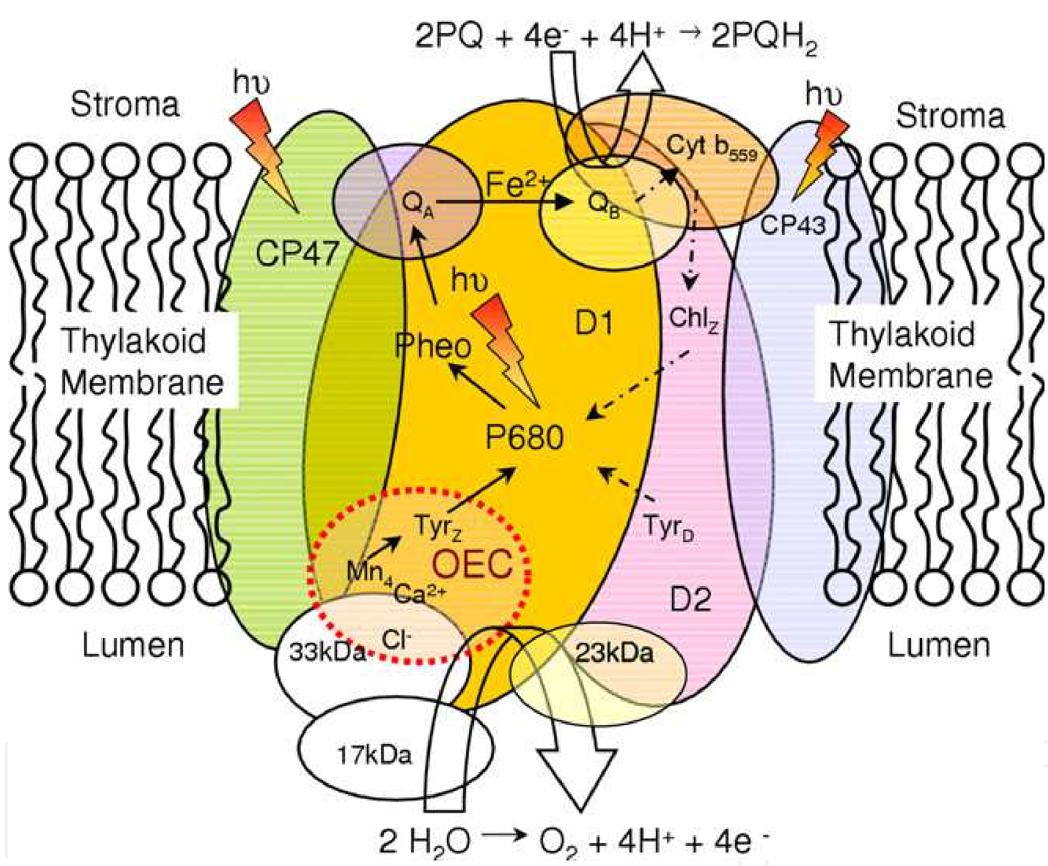

Fig. 6. Schematic representation of photosystem II and its components embedded in the thylakoid membrane. The figure was reproduced from Sproviero et al., 2008.

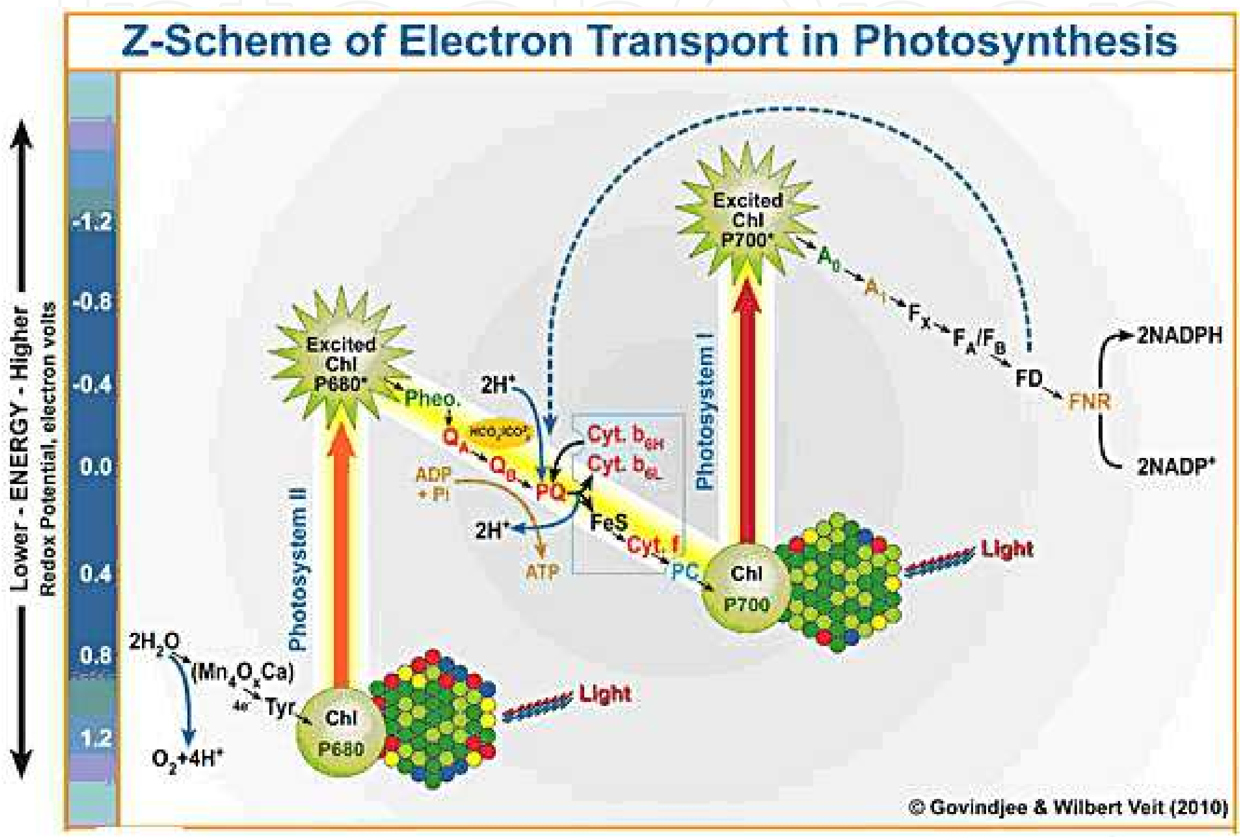

Fig. 7. Z-Scheme of Electron Transport in Photosynthesis (the picture provided by Govindjee and Wilbert Veit in http://www.life.illinois.edu/govindjee/photoweb/subjects.html#antennas).

An ATP synthase enzyme uses the chemiosmotic potential to make ATP during photophosphorylation, whereas NADPH is a product of the terminal redox reaction in the *Z-scheme*. Photosystem I operates at the final stage of light-induced electron transfer. It reduces $NADP^+$ via a series of intermediary acceptors that are reduced upon excitation of the primary donor P_{700} and oxidize plastocyanin. The cyclic reaction is similar to that of the non-cyclic, but differs in the form that it generates only ATP, and no reduced $NADP^+$ (NADPH) is created. The stored energy in the NADPH and ATP is subsequently used by the photosynthetic organisms to drive the synthesis in the Calvin - Benson cycle in the light-independent or dark reactions (Fig. 8).

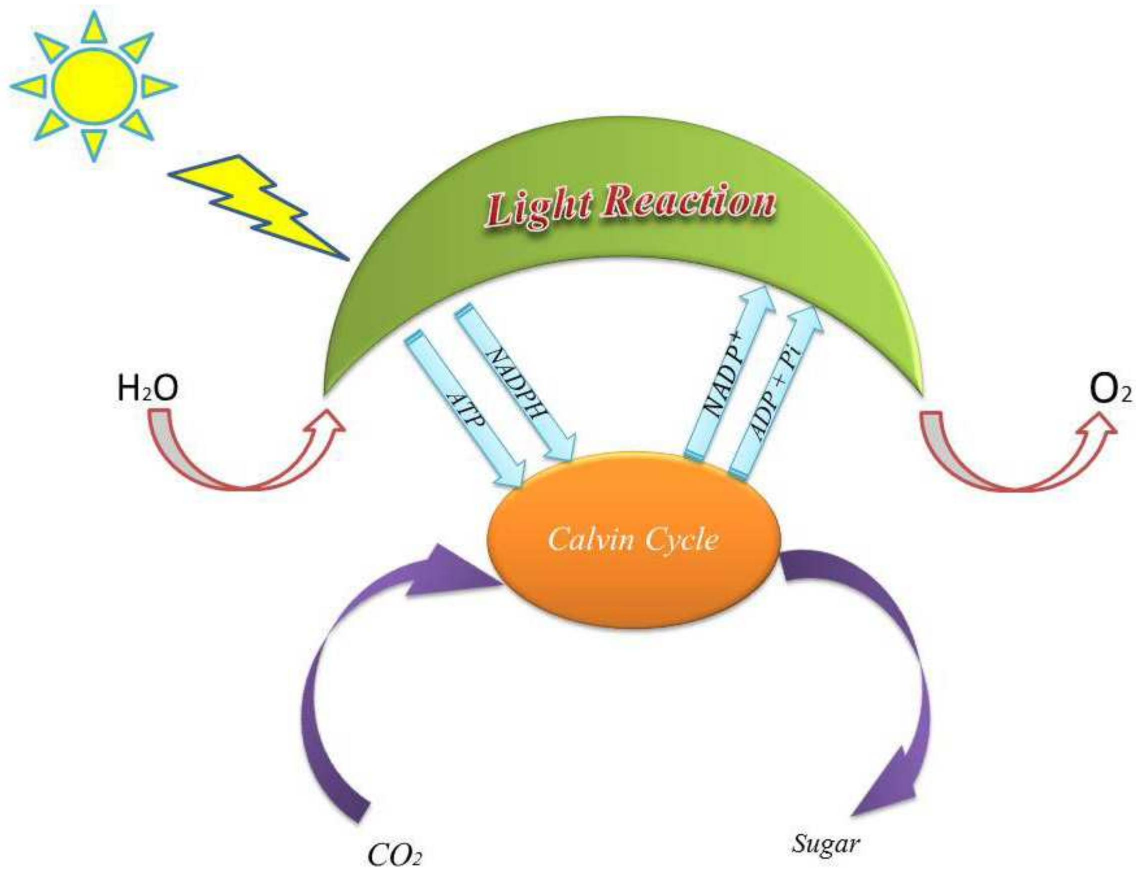

Fig. 8. Schematic representation of photosynthesis.

In these reactions, the enzyme RuBisCO captures CO_2 from the atmosphere and in a process that requires the newly formed NADPH, releases three-carbon sugars, which are later combined to form sucrose and starch. The overall equation for the light-independent reactions in green plants is:

$$3\ CO_2 + 9\ ATP + 6\ NADPH + 6\ H^+ \rightarrow C_3H_6O_3\text{-phosphate} + 9\ ADP + 8\ P_i + 6\ NADP^+ + 3\ H_2O$$

2. Why is photosynthesis important?

It is believed that photosynthesis is the most important biological process on earth. Our food, energy, environment and culture, directly or indirectly, depend on the important process. Really, the relationship between living organisms and the balance of atmosphere and life on earth needs knowledge of the molecular mechanisms of photosynthesis. The process also provides paradigms for sustainable global energy production and efficient energy transformation. Research into the nature of photosynthesis is necessary because by understanding photosynthesis, we can control it, and use its strategies for the improvement of human's life.

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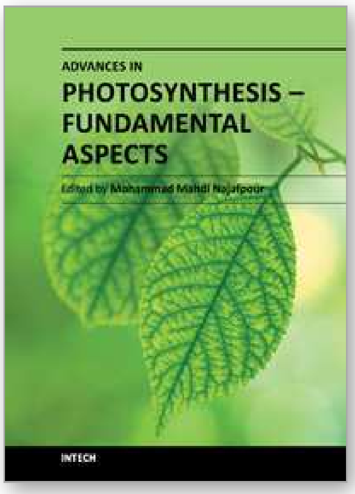

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Photosynthesis is one of the most important reactions on Earth. It is a scientific field that is the topic of many research groups. This book is aimed at providing the fundamental aspects of photosynthesis, and the results collected from different research groups. There are three sections in this book: light and photosynthesis, the path of carbon in photosynthesis, and special topics in photosynthesis. In each section important topics in the subject are discussed and (or) reviewed by experts in each book chapter.