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Oxygenic Photosynthesis: An Introduction[#]

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The article briefly describes the current status of understanding of the molecular mechanisms involved in the oxygenic photosynthesis: energy and electron transfer in photosynthetic species, energy transduction, etc. The reference list includes a large number of review articles, book and book chapters intended to learning of the subject more deeply and independently.

Keywords: *photosynthesis, photosystem II, photosystem I, Cyt b_6f complex, ATP-synthase*

The primary source of energy for life in our planet is the Sun. The energy in sunlight is introduced into the biosphere by a process known as photosynthesis, the physico-chemical process by which plants, algae and certain bacteria convert light energy into chemical energy of organic compounds, with concomitant use of these components in the bioenergetic processes. Photosynthesis developed very early in the history of life. It is generally believed that the earth was formed about 4.6 billion years ago. Life on earth began about 3.5 billion years ago with the first photosynthetic organisms to appear being the photosynthetic bacteria and primitive algae. There are fossil records showing evidence for photosynthetic activity as far back as 3.5 billion years ago (Broda, 1975; van Gorkom, 1987; Wilmotte, 1994; Wolfe and Hoober, 1995; Whitmarsh and Govindjee, 1999; Ke, 2001). By combining light energy and available sources of chemicals, these organisms evolved into the first photosynthetic species. Fossil fuel such as coal and crude oil was created by decaying organic matter of photosynthetic organisms and accumulates millions of years.

In plants, algae and cyanobacteria, the photosynthetic processes results in the fixation of carbon dioxide (CO_2) from the atmosphere that is used to synthesize carbohydrates and release of molecular oxygen to the atmosphere. This process is known as oxygenic photosynthesis. Some photosynthetic bacteria can use light energy to extract electrons from molecules other than water. The ultimate source of electrons in this type of photosynthesis is sulphur compounds or simple organic molecules. Photosynthesis preformed by these organisms is known as anoxygenic photosynthesis. These organisms are of ancient origin, presumed to have evolved at least 3.5 billion years ago, before oxygenic photosynthetic organisms (van Gorkom, 1987; Whitmarsh and Govindjee, 1999; Ke, 2001). Examples of organisms belonging to anoxygenic photosynthesis are the filamentous green bacteria, the green sulphur bacteria, the purple bacteria and the heliobacteria.

In spite of such differences some fundamental principles concerning to structure and energy conversion are, however, shared between different photosynthetic groups. These are represented schematically in the Figure 1.

The first step in photosynthesis is the absorption of photon by a pigment molecule of photosynthetic antenna resulting in conversion of the photon energy to an excited electronic state of pigment molecule. The antenna consists of hundreds of pigment molecules (chlorophylls, bacteriochlorophylls, carotenoids, etc.) that are bounded to proteins within the photosynthetic membrane. The excited electronic state is transferred over the antenna molecules as an exciton. Some excitons are converted back into photons and emitted as fluorescence, some converted to heat. For most of the excited pigment molecules the most useful decay pathway is "energy transfer" to a photochemical reaction centers, and it is of vital importance to photosynthesis. Excitons trapped by a reaction center provide the energy for the primary photochemical reaction of photosynthesis – the photoinduced transfer of an electron. Subsequent electron transfer reactions occur in the dark which results in accumulation of chemical bound energy. Electron transfer reactions in photosynthesis involve electron carriers or electron-transfer

[#]The article represents an overview of oxygenic photosynthesis and is a first in the series of review articles dealing with photosynthesis of plants, algae and cyanobacteria aimed to be writing for undergraduate students.

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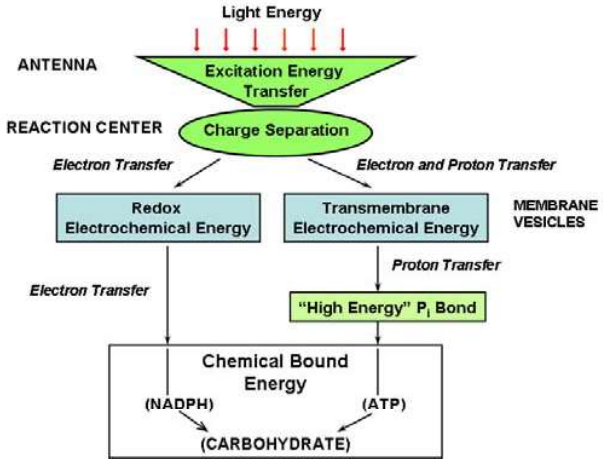

Figure 1. Energy transformation in photosynthesis: photosynthesis is shown as a series of reactions that transform energy from one to another (Whitmarsh and Govindjee, 1999).

proteins, among others, (bacterio)chlorophylls, quinones, cytochromes, and iron-sulfur proteins.

Research on the photosynthesis has been performed since the seventeenth century leading to a considerable basis of knowledge. The earliest studies of photosynthesis involve the nature of the components used and produced by plants. One well known result in the earliest study of photosynthesis was finding that plants could restore air that had been "injured" by a burning candle. It happened in 1771, when Joseph Priestley performed experiments, which demonstrated that plants releases molecular oxygen (today it is clear that a main source of oxygen in the earth atmosphere is photosystem II, one of major components of photosynthetic membrane of cyanobacteria, algae and higher plants). Although the importance of this process was immediately realized, it took another 150 years before some insight into the molecular mechanisms of photosynthesis began to evolve.

The late 1940's and early 1950's, which showed a rapid development of biochemical and physical techniques, also witnessed an unprecedented expansion of photosynthesis research, based on the application of these techniques. Due to work of Calvin and Benson in the forties and fifties it became clear that carbon dioxide fixation occurs by a sequence of enzymatic processes that can in principle function in the dark. Duysens's studies established the role of pigments in harvesting and transferring the energy of light, and gradually it became clear that the primary energy conversion steps consist of electron transfer reactions that take place in an entity called the reaction center. Around 1960 the basic difference between oxygenic and bacterial photosynthesis became known: bacteria have only one type of reaction center, whereas oxygenic species have two, one which produces a strong oxidant able to split water to molecular oxygen and protons.

During the last 50 years many important developments have taken place in photosynthesis science. The efforts of scientists have now provided a picture of the mechanisms of the photosynthetic reactions and the structure of different functional units of the photosynthetic apparatus. The application of advanced physical instrumentation combined with biochemical and molecular biology techniques, has provided a wealth of information concerning the primary reactions of photosynthesis and structure of the energy converting units of photosynthesis.

Photosynthetic reaction centers

Key steps in photosynthesis are the absorption of solar energy by antenna pigments and efficient transfer of excitation energy to photochemical reaction centers, where the energy is trapped in the form of stable charge separation. Photosynthetic reaction center is defined as the smallest unit which is able to convert light to electrochemical energy of separated charges by photo-induced electron transfer. It is membrane bound protein complexes which contain electronic cofactors – electron donor and acceptor, and accessory pigments. Charge separation in reaction centers resulted in series of electron transfer reactions and in the end accumulation of chemical bound energy.

All reaction centers which are found in contemporary photosynthetic organisms can be classified into two groups. One is iron-sulphur or type I reaction center that has iron-sulfur clusters as electron acceptors and is found in *Chlorobiaceae* (green sulfur bacteria), *Heliobacteriaceae* and in photosystem I of oxygenic photosynthesis. The other is (bacterio)pheophytin-quinone or type II reaction centre that contains a (bacterio)pheophytin and pair of quinones as electron acceptor. The reaction centers of purple bacteria, *Chloroflexaceae* (filamentous green bacteria) and photosystem II of oxygenic photosynthesis belong to the latter group (Wolfe and Hoober, 1995; Ke, 2001). Recent structural data obtained from X-ray analysis of type I and II reaction centers supports the hypothesis of the evolution of all photosynthetic reaction centers from one common ancestor (Ke, 2001; Zouni et al., 2001; Kamiya and Shen, 2003; Ferreira et al., 2004; Loll et al., 2005; Nelson and Yocum, 2006; Amunts et al., 2007).

Utilization of solar energy by oxygenic species

Higher plants, algae and cyanobacteria use photosynthesis to convert light energy into chemical energy and reducing equivalents, adenosine triposphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH), which are used in the CO_2 fixa-

tion to produce carbohydrates $(CH_2O)_n$ (Ke, 2001). The key to utilization of reducing power is ferredoxin. The ATP formed by the energy coupling reactions is also consumed in a variety of reactions unrelated to carbon metabolism. From the chemical point of view, the overall reactions of oxygenic photosynthesis may be described by the basic equation:

$$6CO_2+12H_2O+\text{Light Energy}\rightarrow C_6H_{12}O_6+6O_2$$

Oxygenic photosynthesis is driven by visible light (wavelengths from 400 to 700 nm) that is absorbed by different pigment molecules, chlorophyll *a* and *b*, carotenoids and phycobilins. The pigment molecules are bound to polypeptides forming pigment-protein complexes. Two types of antenna complexes, the inner (core) antenna consisting of pigment-proteins that are an integral part of the reaction center complex, and outer (peripheral) antenna complexes are distinguished in oxygenic species. In plants and green algae the light absorbing pigment molecules are chlorophyll *a*, chlorophyll *b* and carotenoids. The cyanobacteria and red algae have a different outer antenna system. In cyanobacteria and red algae, the phycobiliproteins are assembled into supromolecular aggregates called phycobilisomes, which are attached to the photosynthetic membrane surface and transfer electronic excitation energy (via chlorophyll) to the reaction centers to initiate photochemical reactions. Carotenoids and phycobiliproteins serve as accessory pigments, to absorb light energy not absorbed in the spectral region of chlorophyll absorption and transfer this energy to chlorophylls. The efficiency of singlet-singlet energy transfer from certain carotenoids to chlorophyll may be very high ranging from 70% to nearly 100%. Phycobilisomes can funnel the absorbed energy to the reaction center with more than 95% efficiency (Ke, 2001).

Oxygenic photosynthesis serves as a vital link between the light energy of the sun and all living creatures. Carbon dioxide and water, which both are energy poor compounds, are converted to the energy rich compounds, carbohydrates and molecular oxygen. In the cells of photosynthesizing organisms the compounds formed are utilized as building blocks for synthesis of other important molecules like proteins, lipids and nucleic acids. Other organisms, human and animals use the energy rich substances made by photosynthesizing organisms for food and respiration.

Oxygenic photosynthesis is a main source of oxygen in the earth atmosphere. Molecular oxygen liberated as a result of water splitting reactions. The water splitting reactions by photosynthetic organisms was an important event for life cycle on the earth. Water is never ending source of electrons and protons utilized by photosynthesis for carbon fixation. This is of extreme importance, since when electrons are extracted from water, molecular oxygen is formed as a by-product. More than 2.5 billion years ago, photosynthetic cyanobacteria developed the capacity to split water into the molecular oxygen and protons (van Gorkom, 1987; Wilmotte, 1994; Wolfe and Hoober, 1995; Ke, 2001), which had the major advantage that substrate was abudant, essentially unlimited, and photosynthetic species that developed mechanisms to master this chemistry became dominant. Appearance of the oxygenic photosynthesis leads to a gradual change in the atmosphere from being reducing to being oxidizing. This was a catastrophic environmental change for the dominating life on earth at that time. Before this event, all organisms on earth were adapted to an anaerobic environment. However, as oxygen started to accumulate in the atmosphere, the existing organisms either died or adapted to the new environment. Life had to adapt to the new oxygen rich environment and try to make the best use of it. However, more efficient energy metabolism systems could evolve, where molecular oxygen was used as the terminal oxidant in respiration. This provided the foundations for the thermodynamically more efficient aerobic respiration and for the development of higher organisms. Today oxygenic photosynthesis occurs in almost all the eukaryotic photosynthetic species, plants and algae, and in cyanobacteria.

One more important effect, which followed with the development of oxygenic photosynthesis and the accumulation of oxygen in the atmosphere, was the formation of the ozone layer that protects living organisms from destructive ultraviolet (UV) radiation from the sun. Protected from harmful UV radiation, life could finally climb out of the water, beginning with the plants about 400 million years ago (Ke, 2001).

Chloroplasts and thylakoid membranes

In higher organisms, plants and algae, all the molecular complexes involved in photosynthetic energy conversion are concentrated in special cell organelles, chloroplasts (Figure 2) (Taiz and Zeiger, 2002). The chloroplasts are self-replicating and contain own genetic material. The chloroplasts genome encodes a large portion of the proteins necessary for photosynthetic function and for replication (Erickson, 1995; Roell and Cruissem, 1995). However, many proteins involved in the photosynthesis are nuclear encoded and post-translationally imported into the chloroplasts (Gray, 1995). The chloroplast is separated from rest of the plant cell by a double membrane. Internal space of the organelle, stroma, is filled with a system of lamellae and flat-

tened thylakoids. The stroma contains soluble enzymes, plastid encoded DNA and protein synthesis apparatus.

The thylakoid membranes are located in the aqueous stroma phase of chloroplasts in plants and algae and in cytosol of the cyanobacterium. Thylakoids form a physically continuous three-dimensional network enclosing an aqueous space called the lumen and are differentiated into two distinct physical domains: flattened disk-like stacked structures, called grana and interconnecting single membrane regions, stroma lamellae. Each chloroplast contains about 10 to 100 such grana. Stroma lamellae connect between grana, so that a continuous closed membrane system is formed. Since all grana are interconnected by the unstacked stroma lamellae, the lumen of each thylakoid region is also connected with the lumen of all other thylakoid region. Thus the inner space of the thylakoid membrane, lumen, is completely separated from the stroma, which is vitally important for the proper functioning of the energy conversion system of photosynthesis (Gantt, 1994; Staehelin and van der Stay, 1995; Ke, 2001; Dekker and Boekema, 2005).

The cyanobacteria are prokaryotes and thus do not have organelles like chloroplasts. However, the whole cyanobacterial cell in it self closely resembles the chloroplast (Douglas, 1994; Gantt, 1994). The photosynthetic apparatus in the cyanobacteria is also located to a highly folded internal membrane system, the thylakoid. This has the same function as the thylakoid membranes of the chloroplasts, but they are not differentiated in grana stacks and stroma lamellae. The cyanobacterial cell is divided in two compartements by the thylakoid membrane, the cytoplasm and the thylakoid lumen. Cyanobacteria have a simpler genetic system than plants and algae that enable them to be easily modified genetically. Because of this cyanobacteria have been used as a model to understand photosynthesis in plants. By genetically altering photosynthetic proteins, researchers can investigate the relationship between molecular structure and mechanism in photosynthesis (Barry et al., 1994).

Molecular complexes of thylakoid membranes

The photosynthetic energy conversion of oxygenic organisms is divided in two distinct phases, the light reactions and the dark reactions. Light reactions are almost exclusively confined to the membranes. During the light reactions, light energy is used for generation of reducing power and energy rich compounds in the form of NADPH and ATP. Fixation of CO_2 and biosynthesis of carbohydrates from carbon dioxide occurs in the chloroplasts stroma via the Calvin cycle. This process carries the name of dark reaction since it does not require light, although reducing equivalents (NADPH) and chemical energy (ATP) generated by "light reactions" are necessary for CO_2 fixation. Most, if not all, enzymes involved in dark reactions are soluble, but there is evidence that some of them can function as membrane bound complexes (Andersson and Anderson, 1980; Süss et al., 1993; 1995).

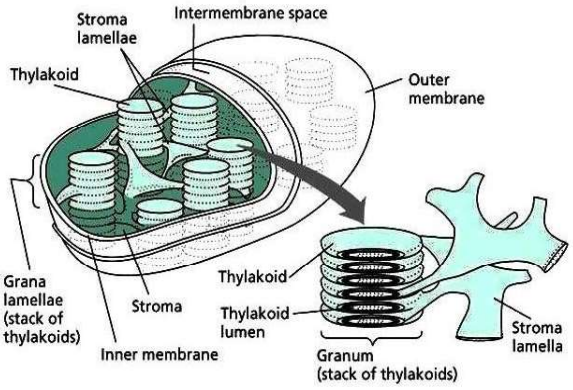

Figure 2. Topological representation of plant chloroplast: The chloroplast is about 6Å long. Inside of chloroplast is a complicated membrane system, known as photosynthetic membrane or thylakoid membrane that contains most of proteins required for the light reactions. The proteins required for fixation of CO_2 are located outside the photosynthetic membrane in the surrounding aqueous phase. The photosynthetic membrane is composed mainly of glycerol lipids and protein (Taiz and Zeiger, 2002).

The energy converting apparatus of the photosynthesing oxygenic species organized in several different multisubunit protein complexes associated with thylakoid membranes. These protein assemblies, the photosystem II and I, each with antenna, the cytochrome b_6f (Cyt b_6f) complex, the ATP-synthase, and the $NADP^+$, bind and organize pigments and other cofactors, which together with mobile electron carriers in the stroma (ferredoxin, ferredoxin-$NADP^+$ reductase), lumen (plastocyanin) and the plastoquinol cooperate in the convertion of radiant energy (Ke, 2001). The protein complexes that catalyze electron transfer and energy transduction are unevenly distributed in thylakoid. Photosystem II (PSII) is largely found in the grana stacks while photosystem I (PSI) and ATP-synthase are located in the stroma exposed regions and the cytochtome b_6f complex is evently distributed in grana and grana margins (Andersson and Anderson, 1980; Melis, 1991; Staehelin and van der Stay, 1995; Ke, 2001; Danielsson, 2005). A schematic view of the protein complexes and the redox centers involved in the electron transfer and proton translocation in the thylakoid membrane is shown in Figure 3.

In plants (algae and cyanobacteria) two photosystems, photosystem II and photosystem I operate

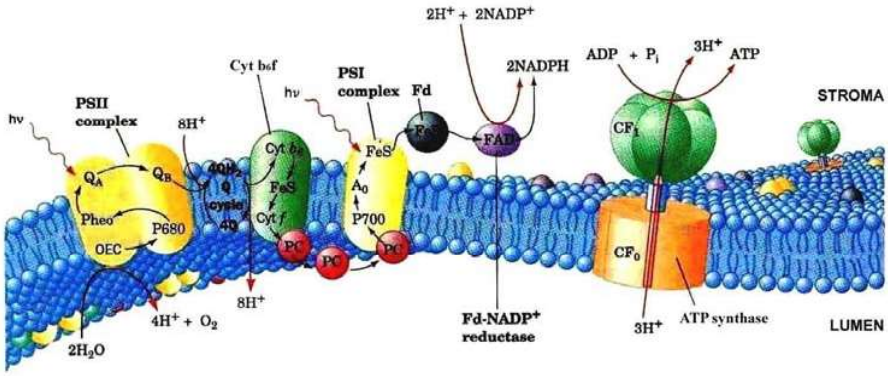

Figure 3. A schematic representation of the protein complexes of the thylakoid membrane involved in the photosynthetic light reactions of oxygenic photosynthesis: photosystem II (PSII), the cytochrome b_6f (Cyt b_6f) complex, photosystem I (PSI) and ATP-synthase. The first three enzymes are connected through the reduction and oxidation of the plastoquinole pool and through the electron carrier plastocyanin (PC). Upon light absorption, the primary donor chlorophylls (P_{680} in PSII and P_{700} in PSI) are excited and oxidized, which initiates a series of redox reactions in each photosystem. The photosystems work in series so that they together with three other electron carriers, plastoquinole pool, Cyt b_6f complex, and water soluble plastocyanin molecule can perform electron translocation from the water-splitting site on the lumenal side of PSII to the ferredoxin-$NADP^+$ reductase on the stromal side of PSI: plastoquinole moves electrons from PSII to heme containing Cyt b_6f, while the plastocyanin transfer electrons from Cyt b_6f to PSI. During the electron transfer processes, protons are released into the lumen by the water splitting reaction and with reactions inside Cyt b_6f. These reactions create an electrochemical gradient over the thylakoid membrane. The free energy of this proton gradient is utilized by the ATP-synthase for ATP production as the protons are translocated back to stroma. ATP is released into the stroma where the Calvin cycle proceeds (Voet and Voet, 2004).

in series. This enables these organisms to use water as a source of electrons. The combined action of these photosystems results in transfer of an electron across the thylakoid membrane from H_2O ($E_{m,\ pH\ 7.0}$ = +0.82 V) to $NADP^+$ ($E_{m,\ pH\ 7.0}$ = −0.32 V), using two photons, one in each photosystem, per electron transferred. The energetics of the electron transfer is usually represented in a redox potential scale as Z-scheme of photosynthesis (Hill and Bendall, 1960; Hil, 1965; Ke, 2001). In this scheme the two photoreactions are connected via an electron transport chain containing plastoquinol pool, Cyt b_6f and plastocyanin (Figure 4).

On the acceptor side of PSI, the light driven 2-electron reduction of $NADP^+$ occurs whereas on the donor side of photosystem II the 4-electron oxidation of H_2O to molecular oxygen takes place. Thus two photochemical reactions of oxygenic photosynthesis couples the 1-electron charge separation in reaction centers to multielectron redox chemistry of subsequent electron transfer reactions.

Photosystem II

Photosystem II is the first in the series of three complexes that couple photochemical excitation of electrons to electron transfer from H_2O to $NADP^+$ in higher plants, algae and cyanobacteria. According to the function carrying-out in photosynthesis, PSII is often referred as a "light driven water-plastoquinole oxidoreductase". Photosystem II has an outer antenna dominated by light harvesting complex II (LHCII), which binds chlorophylls *a* and *b* and carotenoids, and inner antenna of chlorophyll *a* binding proteins CP47 and CP43. The D_1 and D_2 polypeptides form the heterodimer of core of PSII reaction center that carries most of cofactors involved in electron transfer. Most proteins in the PSII complex are membrane spanning, but the three extrinsic proteins involved in oxygen evolution are located on the lumenal side of the thylakoid membrane. In higher plants and green algae these proteins are nuclear encoding subunits of PsbO (33 kDa), PsbP (23 kDa) and PsbQ (16 kDa), which together form the lumenally exposed water splitting center and closely associated with the Ca-$(Mn)_4$ cluster. Cyanobacterial PSII contains PsbO, but a PsbV (Cytochrome c_{550}) and PsbU (12 kDa) replace the PsbP and Q subunits in eukaryotes. The primary electron donor in photosystem II, P_{680} is a chlorophyll multimer. Upon excitation, it is oxidized and electrons through the intermediary electron carriers, pheophytin and plastoquinones Q_A and Q_B are transferred to the plastoquinol. PQH_2-pool serves as a reservoir for the electrons coming from photosystem II. While Q_A is a one electron acceptor, Q_B is reduced first to a semiquinone (Q_B^-) and thereafter, by accepting two protons from

stroma and another electron from photochemical reaction, to a hydroquinol (Q_BH_2). Moreover, Q_BH_2 has a low affinity for its binding site and is readily displaced by another plastoquinone, Q_B from the diffusible PQH_2-pool.

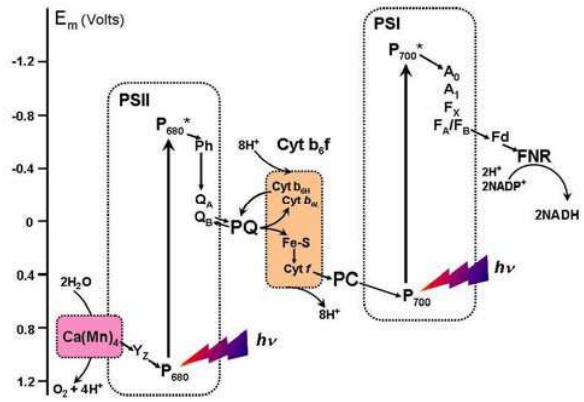

Figure 4. Z-scheme diagram of oxygenic photosynthesis demonstrates the relative redox potentials of the co-factors in the linear electron transfer from water to NADP. The relative redox potentials show that P_{680} and P_{700} are highly oxidising. Their excited forms (P_{680}* and P_{700}*) of the reaction centre pigments are highly reducing and located in the upper part of the diagram. To reduce $P_{680}^{\bullet+}$ electrons are transferred from water, through Y_Z. $P_{700}^{\bullet+}$ is reduced by electrons from PSII, transferred via plastoquinole, through Cyt b_6f complex and plastocyanin (PC).

The primary electron donor of PSII, $P_{680}^{\bullet+}$ is a very powerful oxidant that is finally reduced at the expense of water, which is oxidized in the water splitting center, attached to PSII at the lumen of thylakoid membrane (Knaff, 1977; Klimov and Krasnovsky, 1981; Govindjee et al., 1986; Mathis and Rutherford, 1987; Debus, 1992; Renger, 1992; Seibert, 1993; Barry et al., 1994; Diner and Babcock, 1995; Ke, 2001; Nelson and Yokum, 2006). This occurs by extracting of an electron from the cluster of Ca-$(Mn)_4$ via the tyrosine residue denoted as Y_Z (tyrosine-161 on the D_1-protein). Release of oxygen is a result of concerted four-electron oxidation of two molecules of water. This process is coupled to the reduction of $P_{680}^{\bullet+}$ via the formation of neutral $Y_Z^{\bullet}$ radical. In turn, $Y_Z^{\bullet}$ is reduced by cluster of Ca-$(Mn)_4$, that is the catalytic center for water oxidation. The coupling of the four electron water oxidation reactions to the one electron charge separation events of the reaction center is achieved with the accumulation of oxidizing equivalents within the Ca-$(Mn)_4$-cluster. This four step process followed by oxidation of water is called S-state cycle of PSII which is include five successive intermediate states denoted as S_0, S_1,…,S_4. The S_0 state is the most reduced state. Removal of electron from S_0 leads to the S_1 state which is dark-stable. The further sequential removal of three more electrons results in formation of S_2, S_3 and S_4 states. The S_4 state is an unstable, transient state that spontaneously converts to the S_0 with concomitant release of molecular oxygen.

Photosystem I

Photosystem I operate 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. Thus PSI is often referred as a "light driven plastocyanin-NADP oxidoreductase". The PSI antenna is organized similar to PSII antenna with outher light harvesting complex I (LHCI) antenna and inner chlorophyll *a* binding antenna. The pigment composition of PSI is very different from PSII, mainly containing chlorophyll *b*. The reaction center of PSI is formed by a special pair of chlorophylls, P_{700}, near the lumenal side of membrane. A second chlorophyll molecule (A_0), phylloquinone (A_1) and three iron sulfur clusters (F_X, F_A and F_B) function as electron acceptors. Upon excitation P_{700} reduces a chlorophyll species referred to as A_0. From this very low-potential chlorophyll anion (E_m < –1.0 V) an electron transferred to the next acceptor, A_1 and then subsequent electron acceptors, iron-sulfur centers denoted as F_X, F_B and F_A. The electrons are finally transferred from the RC to ferredoxin (Fd), a small (10 kDa) protein with a 2Fe-2S cluster as active centre (Golbeck, 1987; Mathis and Rutherford, 1987; Golbeck, 1994; Malkin, 1995; Brettel, 1997; Brettel and Leibl, 2001; Fromme et al., 2001; Gobets and van Grondelle, 2001; Ke, 2001; Scheller et al., 2001; Setif, 2001; Vassiliev et al., 2001; Webber and Lubitz, 2001; Xu et al., 2001; Nelson and Yokum, 2006). Although most proteins in the PSI complex are also membrane-spanning, a few, the iron-sulfur proteins that contain F_A, F_B, and the Fd-docking proteins are located toward the stromal side of the thylakoid membrane. Ferredoxin interacts with the thylakoid membrane at two distinct sites. It accepts electrons from the reducing side of PSI, then is reoxidized by the thylakoid-bound FAD-flavoprotein, ferredoxin-NADP reductase (FNR) which forms a one-to-one complex with Fd. The reduced FNR, then oxidized by NADP.

Why two photochemical reactions?

The overall reaction driven by the light reactions of PSII and PSI during the linear electron flow is the reduction of $NADP^+$ with electrons derived from water. The midpoint potential (E_m) of the $NADP^+$/NADP redox couple is 0.38 V at pH 8.0 (E_m

$_{(pH\ 7.0)}$ – 59 mV/pH unit), which is prevailing pH in the stroma. The potential of the H_2O/O_2 couple is +0.93 V at a lumenal pH of 5.0. The difference ΔE_m of -1.31 V (126.4 kJ/mol) represents a chemical potential generates per electron transferred through the linear electron flow of oxygenic photosynthesis and stored in the molecular oxygen and NADP.

The efficiency of PSII in converting solar energy to redox energy is approximately 45%. This estimation is based on the comparison between the energies of absorbed photons with the redox energies stored in the final products. Photosystem II can be driven by 680 nm photons equal to 1,82 eV per photon, which is converted into the H_2O/O_2 and Q_B^- /Q_BH_2 redox couples with a difference in midpoint potential equivalents to 0.82 eV per electron. That is, 45% of the incident photon energy is converted to chemical potential in the final, stable products of the photochemistry. For similar reason the overall efficiency of PSI is also in order 45%. With this 45% efficiency, the transfer of one electron through Z-scheme requires photon energy of 2.91 eV which corresponds to wavelengths of 426 nm or shorter. Consequently, in theory, it is energetically possible to drive the reduction of $NADP^+$ by H_2O by using only one light reaction which is driven by light in the visible region of solar spectrum.

However, oxygenic species engages two photosystems operating in series, rather than one, which suggests the existence of benefits with such an arrangement. A clear advantage with two photosystems, as compared to one photon oxidation of water and production of NADPH becomes evident upon inspection of the solar spectrum. PSII and PSI use photons of 680 and 700 nm to produce charge separation, respectively. The antennae pigments of the photosystems harvest light at shorter wavelengths. The light energy is transferred and accompanied by small energy losses, towards the low-energy traps of the reaction centers. By using photons of longer wavelengths for the final photochemistry, PSII and PSI can harvest light from the major part of the solar spectrum. If only one photosystem driven by 426 nm photons, were to be involved, the useful part of the solar spectrum would be narrowed. Thus, the strategy to split one high-energy reaction into two reactions involving lower energies, results in a substantial extension of the photosynthetically useful part of the solar spectrum.

Cytochrome b_6f complex

In thylakoid membranes electron transfer between PSII and PSI occurs via the plastoquinol pool, cytochrome b_6f complex and water soluble protein plastocyanin. The Cyt b_6f complex contains four large subunits (18 to 32 kDa), including Cyt f, Cyt b_6, the Rieske iron-sulfur (2F-2S) protein, and subunit IV, as well as four small hydrophobic subunits, PetG, PetL, PetM, and PetN. The two b-hemes of Cyt b_6 (Cyt b_{6L} and Cyt b_{6H}) and the subunit IV span the thylakoid membrane, while the Rieske 2Fe-2S protein and Cyt f are located near the lumen side. The function of the Cyt b_6f complex in thylakoid membrane is to oxidize plastoquinole formed by PSII and transfer these electrons to plastocyanin (Hore, 1993; Kallas, 1994; Hauska et al., 1995; Hore, 2000; Ke, 2001; Kurisu et al., 2003). Accordingly, the Cyt b_6f complex has therefore also been called the "plastoquinole-plastocyanin oxidoreductase". The PQH_2 is first oxidized by the Rieske center. Within the Cyt b_6f complex, one electron subsequently is transferred from plastoquinol to a Rieske 2Fe-2S protein and then Cyt f in a series, which can release electron to the plastocyanin. The plastocyanin, which is small (10.5 kDa) copper containing protein, is located to the lumenal surface of the thylakoid membrane and drives one electron from Cyt f to the PSI complex where reduces $P_{700}^{\bullet+}$ (Gross, 1995; Sigfridsson, 1998; Hore, 2000; Ke, 2001). After loss of one electron by PQH_2, the resulting semiquinone loses an electron on to the two b-hemes in series. The b-hemes operate in the so-called "Q-cycle", similar to that in the mitochondrial or bacterial cytochrome bc_1 complex, and provide a translocation of additional protons across the membrane into the lumenal space. When the plastoquinole becomes fully oxidized, it loses two electrons and also releases two protons to the lumen phase. Thus with splitting two water molecules by PSII to form one oxygen molecule, eight protons are translocated across the membrane (Ke, 2001).

ATP-syntase

From the Z-scheme it is seen that PSII generates a strong oxidant in $P_{680}^{\bullet+}$, which is able extract electrons from water, while PSI generates a strong reductant in P_{700}*, which can reduce $NADP^+$. The overall electron flow from the water-splitting center on the lumen toward $NADP^+$ on the stroma is linear and vectorial. The consequence of this vectorial electron flow, or displacement of electric charges, is creation of an electric potential across the membrane, with positive charges on the inside and negative on the outside. First, protons formed by the oxidation of water are released to the inside, resulting in an acidification of the thylakoid lumen space. In addition, protons are extracted from the outside, leading to the formation of PQH_2, and are ultimately released on the lumenal side during the reoxidation of this PQH_2. The proton release in the water splitting reaction by PSII, and proton pumping from stroma to lumen by PQH_2/Cyt b_6f create a proton gradient and electrochemical potential across the thylakoid membrane.

The generated potential energy is utilized by

ATP-synthase for synthesis of ATP. This complex has two essential parts, CF_1, the chloroplast ATP coupling factor, and CF_0, the membrane spanning portion of the holoenzyme. Each CF_1 and CF_0 contains several polypeptides and has remarkably similar structures. These enzyme systems are ubiquitously distributed in membrane systems where electron transfer reactions are coupled to ATP synthesis. The critical subunits of CF_1 are designated α, β, γ, δ, and ε. The enzyme is comprised of three copies of α and β, and single copies of δ and ε. The CF_0 portion of the ATP-synthase is an oligomer comprised of four different intrinsic protein subunits that self-assemble in the membrane bilayer to form H^+ conducting "pore" as well as the site to which CF_1 binds.

ATP-synthase pumps the proton in the opposite direction to electron transport, from lumen to stroma, and in the stroma, ADP is phosphorylated to ATP (Avron, 1987; Frash, 1994; McCarty, 1995; Ke, 2001). The light driven reactions catalyzed by PSII and PSI result in formation of the energy-rich mobile molecules NADPH and ATP. The stored energy in the NADPH and ATP is subsequently used by the photosynthetic organisms to drive the synthesis in the Calvin cycle.

Energetic efficiency of photosynthesis

Oxygenic photosynthesis is globally the most fundamental biochemical process that provides energy, organic matter, and oxygen for nearly all biotic processes, which is essential for life. It captures and converts the energy we need to live and grow, bringing it into our ecosystem for us to use in the form of food, and in the form of fuel, fossil and otherwise.

The quantum requirement for oxygenic photosynthesis, according to Z-scheme, is 8 quanta for each molecule of oxygen released (four quanta required by PSII and four by PSI), and requiring 8 moles of photons or 381 kcal energy for each mole of CO_2 reduced. The reduction of one mole of CO_2 molecule to glucose requires 112 kcal of energy. The quantum yield measurements show that the quantum yields of PSII and PSI reaction centers are near 100%. If 8 red quanta are absorbed (381 kcal/mol) for each CO_2 molecule reduced (112 kcal/mol), the calculated maximum energy efficiency (free energy stored / light energy absorbed) for carbon reduction is ~30% (Ke, 2001).

However under normal growing conditions the actual performance of the plants is far below these theoretical values. The annual flux of sunlight energy toward the earth's surface is estimated to be 1.2×10^{21} kcal. A large fraction of this energy is either reflected by the atmosphere (~ 4×10^{20} kcal) or absorbed by it (~ 2×10^{20} kcal). About 1.8×10^{20} kcal of sunlight energy falls on land. Of the total, the energy stored by green plants and algae has been estimated to be 6×10^{17} kcal. From this amount the energy from substances suitable for use as fuel amounts to 8×10^{15} kcal, food stuff amounts to 4×10^{15} kcal, and agricultural waste amounts to 2×10^{16} kcal. Based on the total energy (1.8×10^{20} kcal) from sun, falling on the earth's surface, only 6×10^{17} kcal, less than 0.4% appears to be efficiently utilized by photosynthesis (Ke, 2001). The factors that conspire to lower the quantum yield of photosynthesis include limitations imposed by biochemical reactions in the plant and environmental conditions that limit photosynthetic performance.

Why study photosynthesis?

Knowledge of the molecular mechanisms of oxygenic photosynthesis is essential for understanding the relationship between living organisms and the balance of atmosphere and life on earth. In spite of only small part of energy that reaches the earth is captured photosynthesis is still premier solar energy conversion process on earth. It provides paradigms for sustainable global energy production and efficient energy transformation.

Approximately 80% of the world energy consumption is based on three sources of fossil fuel, coal, oil and natural gas. These fuels are mostly used to generate electricity for industry and home, run vehicles with combustion engines, gives heat at home. Over the course of the last 100 years, the world consumption of energy based on fossil fuels has increased immeasurable due to constantly growing requirements of world industry. At the moment, the total fossil fuel reserve, a remnant of ancient photosynthetic products is driving the modern industrial civilization and estimated to be $\sim10^{19}$ kcal. Current world annual consumption of fuel is $\sim5\times10^{16}$ kcal. Consequently the current fuel reserve at the present rate of consumption will be last about 150-200 years. It is still unclear where most of energy will come from in the longer-term future. A fundamental problem of the energy industry is that traditional fossil fuel is only renewable on a very long time scale, that the rate of formation fossil fuels in the nature is many orders of magnitude slower than the rate of their consumption. Therefore, the reserves that can be recovered in an energetically feasible manner are shrinking rapidly, in parallel with an increasing worldwide energy demand. Therefore, in times of deforestation, acidification, and other negative effects due to lack of respect for and understanding of the earth and larger ecosystems, combined with rapidly growing population with increasing demands on living standards, study of photosynthesis is highly relevant.

The eventual solution for the fuel-energy is

developments of new energy technologies using energy of sun. The promising can be man made devices on the basis of photosynthesis, more precisely creating artificial photosynthesis. Scientists around the world study the photosynthetic structure and functions relation and try to understand photosynthesis in order to use the knowledge for energy conversion in the bio-mimetic systems. It is important to establish an artificial model of photosynthesis not only for understanding and simulating the photosynthesis, but also to construct artificial photosynthesis, which is attracting a great deal of interest to convert solar energy into fuels. The idea is to create artificial systems that exploit the basic chemistry of photosynthesis in order to produce fuels for engines and electricity. If one ever wants to mimic the natural processes of photosynthesis, the key physical chemical and biological elements of the process should be fully understood. Duplication of that catalytic activity in industrial setting would have considerable economic benefit but will require a solid understanding of the mechanism of the biological catalysis. Understanding its unique chemistry is not only important in its own right, but could have implications for the agricultural industry since photosynthetic processes are a main site of damage during environmental stress.

Methodology

The main focus in the studies of photosynthesis is to identifying pigment and subunit composition, electronic cofactors (their functions and arrangements on the proteins), amino acid sequences of main proteins and identifying amino acid residues surrounding redox cofactors. This has lead to the development of different biochemical and physical methods, a large variety of preparation, each with particular properties of purity, activity and stability as well as techniques during the last decades. Certain knowledge obtained from the protein amino acid sequencing and computer modeling of the protein folding geometry. Together with traditional, the advanced physical methods of XAS (X-ray Absorption Spectroscopy), FT-IR (Fourier Transform Infra Red), ultra-fast optic spectroscopy and large varieties of EPR (Electron Paramagnetic Resonance) spectroscopy have also widely applied to this field allowing one to identify the redox active components in photosynthetic species and providing the information about electronic structure, local environment and distance between them. The knowledge obtained from the spectroscopy, and research on biochemistry, biophysics and molecular biology together with highly purified preparations build up the basis for the determination at high resolution X-ray structures most of the proteins involved in the complexes PSII, PSI and Cyt b_6f and geometry most of cofactors. Recently an essential progress is achieved in determination of those photosynthetic structures by X-ray crystallography (Zouni et al., 2001; Kamiya and Shen, 2003; Kurisu et al., 2003; Ferreira et al., 2004; Loll et al., 2005; Nelson and Yocum, 2006; Amunts et al., 2007).

Photosynthesis Community (Govindjee, 2007; Orr and Govindjee, 2007)

The photosynthetic science is coordinated by the international society of photosynthesis research (ISPR), the International Congresses of Photosynthesis, specialized conferences dedicated to different topics of research of photosynthesis and the results of photosynthesis research are subject of the proceedings of Congress and conferences, and international journals such as Photosynthesis Research, Biochemistry, Journal of Biological Chemistry, Biochimica et Biophysica Acta (Bioenergetics), Biophysical journal, Plant Physiology, Photosynthetica, etc.

The ISPR was founded August 22, 1995 at the 10^{th} International congress of photosynthesis at Montpellier, France. The purposes of ISPR are to:

(1) encourage the growth and to promote the development of photosynthesis as a pure and applied science;
(2) to facilitate publication of research in photosynthesis;
(3) to sponsor the organization of a triennial international conferences;
(4) to promote international cooperation in photosynthesis research and education.

ISPR membership spans six continents and its members work across academia, education and training, as well as in government, industrial and commercial research environments. The Society plays a key role in uniting the photosynthesis research community internationally. Membership of ISPR is open to those concerned with all aspects (molecular, genetic, cellular and organismal) of the biochemistry, biophysics and physiology of photosynthesis in plants in agriculture and forestry, natural ecosystems and the marine and global environment. An official journal of ISPR is the journal of Photosynthesis Research and official meeting of ISPR is an International Congress of Photosynthesis (ICP). In spite of the ISPR was formed late, at 1995, the ICP was organized every three years since 1968. International Congress of Photosynthesis covers the achievements in photosynthesis research of every last three years. In the other hand every congress is accompanied by several specialized satellite discussion meetings related to the important problems of photosynthesis organized by leading scientists in the field. Organization of the Congresses and conferences aims to provide a dy-

namic exchange of information and new research finding in all areas, a celebration of the achievements of the photosynthesis community, providing a forum for the discussion of recent developments, advances in current concepts and understanding, as well as relevant applications.

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