Harvey J.M. Hou · Mohammad Mahdi Najafpour
Gary F. Moore · Suleyman I. Allakhverdiev
Editors

Photosynthesis: Structures, Mechanisms, and Applications

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Editors
Harvey J.M. Hou
Department of Physical Sciences
Alabama State University
Montgomery, AL, USA

Gary F. Moore
School of Molecular Sciences, Center
for Applied Structural Discovery
at the Biodesign Institute
Arizona State University
Tempe, Arizona, USA

Mohammad Mahdi Najafpour
Center for Research in Climate Change
and Global Warming
Institute for Advanced Studies
in Basic Sciences
Zanjan, Iran

Suleyman I. Allakhverdiev
Institute of Plant Physiology
Russian Academy of Sciences
Moscow, Russia

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Foreword

A huge energy crisis is before us, and, in my opinion, the field of photosynthesis is being borne again; we are indeed seeing its reincarnation in what we may call "sustainability." Those who would solve the energy crisis need all the information on different parts of the process of photosynthesis. They would want to know how to replicate it, how to mimic it, how to modify it, and how to exploit it to our benefit using all sorts of tools from various disciplines of science: biology, physics, chemistry, mathematics (for modeling), and engineering. This book *Photosynthesis: Structures, Mechanisms, and Applications*, edited by four international authorities, Harvey Hou (USA), Mahdi Najafpour (Iran), Gary Moore (USA), and Suleyman Allakhverdiev (Russia), is one of the first books in that direction. Harvey Hou is a leading scientist and pioneer in assessing the thermodynamic parameters of photosynthesis and in developing manganese/semiconductor catalysts for artificial photosynthesis. Mahdi Najafpour is an active and successful expert in exploring transition-metal compounds as water-oxidizing catalysts. Gary Moore is a prominent specialist in artificial photosynthesis and solar-to-fuel technology. Suleyman Allakhverdiev is an established world leader in the field of photosystem II and artificial photosynthesis. This book appears at a particularly appropriate time with a balanced combination of topics related to both basic and applied aspects of photosynthesis (see the Preface and the Table of Contents). It is in the right direction toward the goal of finding a solution to the energy crisis facing us all—because of growing world population and climate change. The book deals not only with possible ways and means to understand and improve natural photosynthesis, but it also includes possibilities around the corner (maybe by 2050) for what some of us call "artificial photosynthesis." For several highly innovative ideas being discussed where photosynthesis plays an important role, I refer the readers to a paper by Donald R. Ort (with 24 top international authorities): *Redesigning photosynthesis to sustainably meet global food and bioenergy demand*, Proceedings of the National Academy of Science USA 112 (28): 8529-8536. I strongly recommend this highly informative and innovative book to all the major libraries in the world as well as to all researchers engaged in solving problems related to bioenergy.

I end my remarks by citing the hope Jules Verne (1875) gave us—we should, of course, modify it after reading this remarkable book, *Photosynthesis: Structures, Mechanisms, and Applications*: “I believe that one day water will one day be used as a fuel because the hydrogen and oxygen which constitute it, used separately or together, will furnish an inexhaustible source of heat and light. I therefore believe that, when coal (oil) deposits are oxidized, we will heat ourselves by means of water. Water is the fuel of the future.” I am an optimist and have faith in the next generation of scientists to solve the problems of global warming and of both food and energy facing us today. For background on all aspects of photosynthesis, I refer the readers to now 42 volumes in the Springer series *Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes* (see http://www.springer.com/series/5599).

University of Illinois at Urbana-Champaign Govindjee
Urbana, IL, USA
URL: http://www.life.illinois.edu/govindjee/

Preface

Photosynthesis powers our biosphere and offers an intellectual challenge to deepen our understanding of this globally important process. It is an inherently interdisciplinary field of research, involving times that span from geologic to sub-femtosecond scale. The process occurs in plants, algae, and cyanobacteria and has evolved over 3 billion years. Photosynthesis currently produces more than 100 billion tons of dry biomass annually, equating to a global energy storage rate of ~100 TW. However, addressing the environmental, socioeconomic, and geopolitical issues, associated with increasing global human energy consumption, will require the identification and development of new technologies capable of using renewable carbon-free or carbon-neutral energy sources. Among the renewable sources, solar is indeed quite promising as it alone is sufficient to meet global human energy demands well into the foreseeable future. In this context, photosynthesis inspires us to transform our current technological energy infrastructure to one that utilizes sunlight for the direct production of fuels and other industrially important chemicals.

Recent advances in understanding the detailed structures of photosynthetic systems have set the stage for dynamic functional studies. Likewise, sophisticated spectroscopic techniques have revealed important mechanistic details. In this book, we provide examples of such important advances and progress. The book contains chapters written by experts and leaders in their respective fields, representing an international collaborative effort including 52 leading experts and scientists in photosynthesis research from 27 laboratories in 13 countries including Bulgaria, Canada, China, Germany, India, Iran, Japan, New Zealand, Russia, Slovakia, Sweden, the UK, and the USA. We envision this book to serve as a resource for both young and established researchers as well as students in colleges and universities at the graduate as well as advanced undergraduate level.

Several new topics on photosynthesis are covered in this book; these include structural and mechanistic information on biological photosynthetic systems and on human engineered constructs that are inspired by their biological counterparts. The notion that biology can inspire technology is an embedded theme, and the chapters are organized in terms of the temporal sequence of events occurring in the process of photosynthesis. For example, chapters on the topic of light harvesting are followed by those on charge separation at the reaction centers, followed by charge stabilization and then chemical reactions and protection mechanisms. The book concludes with more specialized topics including artificial photosynthetic constructs and their potential applications in future technologies.

The opening chapter, by Mohammad Mahdi Najafpour, Harvey J. M. Hou, and Suleyman I. Allakhverdiev, provides an introduction and overview of natural and artificial photosynthesis. Chapter 2, by Pu Qian, and Chap. 3, by Erica Belgio and Alexander V. Ruban, evaluate the structure and function of native and recombinant light-harvesting systems from purple photosynthetic bacteria and higher plants. The next three Chaps. (4, 5, 6 and 7) focus on the charge transfer mechanisms of photosystem II and the oxygen-evolution complex: Chap. 4 is by Jessica Wiwczar and Gary W. Brudvig; Chap. 5 by Alice Haddy, Vonda Sheppard, Rachelle Johnson, and Eugene Chen; and Chap. 6 by Mahir D. Mamedov and Alexey Yu. Semenov. The structure, function, and organization of photosystem I are reviewed and discussed in Chap. 7 by Wu Xu and Yingchun Wang. The following seven Chaps. (8, 9, 10, 11, 12, 13 and 14) deal with the regulation and protection mechanisms of photosynthesis under diverse environmental conditions: Chap. 8 is by Seiji Akimoto and Makio Yokono; Chap. 9 by Leonid V. Kurepin, Alexander G. Ivanov, Mohammad Zaman, Richard P. Pharis, Vaughan Hurry, and Norman P.A. Hüner; Chap. 10 by Marek Zivcak, Katarina Olsovska, and Marian Brestic; Chap. 11 by Anjana Jajoo; Chap. 12 by Krishna Nath, James P. O'Donnell, and Yan Lu; Chap. 13 by Beth Szyszka, Alexander G. Ivanov, and Norman P.A. Hüner; and Chap. 14 by Amarendra N. Misra, Ranjeet Singh, Meena Misra, Radka Vladkova, Anelia Dobrikova, and Emilia L. Apostolova. Several stimulating new approaches on the topic of artificial photosynthesis are presented in the next five Chaps. (15, 16, 17, 18 and 19): Chap. 15 is by Mohammad Mahdi Najafpour, Saeideh Salimi, Małgorzata Hołyńska, Fahime Rahimi, Mojtaba Tavahodi, Tatsuya Tomo, and Suleyman I. Allakhverdiev; Chap. 16 by Mohammad Mahdi Najafpour, Seyed Esmael Balaghi, Moayad Hossaini Sadr, Behzad Soltani, Davood Jafarian Sedigh, and Suleyman I. Allakhverdiev; Chap. 17 by Harvey J.M. Hou; Chap. 18 by Art Van Der Est and Prashanth K. Poddutoori; and Chap. 19 by Babak Pashaei and Hashem Shahroosvand. The final chapter, Chap. 20, by Gary F. Moore, offers concluding remarks and a forward-looking perspective regarding research in natural as well as artificial photosynthesis.

We acknowledge all the authors for their contributions that have made this book possible. The book chapters were reviewed by Seiji Akimoto, Erica Belgio, Marian Brestic, Gary Brudvig, Alice Haddy, Anjana Jajoo, Leonid Kurepin, Krishna Nath, Pu Qian, Art Van Der Est, and Wu Xu. The complete book was reviewed by the four editors and revised by the authors. We are deeply thankful to Govindjee for his valuable advice and continued support. We are very grateful to André Tournois, Jacco Flipsen, and Mariska van der Stigchel of Springer for their help during the production of this book. Finally, the support from Alabama State University (to HJMH), the Institute for Advanced Studies in Basic Sciences (to MMN), Arizona State University (to GFM), and the Russian Science Foundation (grant no. 14-14-00039, to SIA) is greatly appreciated.

Montgomery, AL, USA	Harvey J.M. Hou
Zanjan, Iran	Mohammad Mahdi Najafpour
Tempe, AZ, USA	Gary F. Moore
Moscow, Russia	Suleyman I. Allakhverdiev

Contents

Contributors

Seiji Akimoto Graduate School of Science, Kobe University, Kobe, Japan

Suleyman I. Allakhverdiev Controlled Photobiosynthesis Laboratory, Institute of Plant Physiology, Russian Academy of Sciences, Moscow, Russia

Institute of Basic Biological Problems, Russian Academy of Sciences, Pushchino, Moscow, Russia

Faculty of Biology, Department of Plant Physiology, M. V. Lomonosov Moscow State University, Moscow, Russia

Emilia L. Apostolova Institute of Biophysics and Biomedical Engineering, Bulgarian Academy of Sciences, Sofia, Bulgaria

Seyed Esmael Balaghi Faculty of Basic Sciences, Department of Chemistry, Azarbaijan Shahid Madani University, Tabriz, Iran

Erica Belgio School of Biological and Chemical Sciences, Queen Mary University of London, London, UK

Department of Autotrophic Microorganisms – ALGATECH, Institute of Microbiology ASCR, Třeboň, Czech Republic

Marian Brestic Department of Plant Physiology, Slovak University of Agriculture, Nitra, Slovakia

Gary W. Brudvig Department of Chemistry, Yale University, New Haven, CT, USA

Eugene Chen Department of Chemistry and Biochemistry, University of North Carolina at Greensboro, Greensboro, NC, USA

Anelia G. Dobrikova Institute of Biophysics and Biomedical Engineering, Bulgarian Academy of Sciences, Sofia, Bulgaria

Alice Haddy Department of Chemistry and Biochemistry, University of North Carolina at Greensboro, Greensboro, NC, USA

Małgorzata Hołyńska Fachbereich Chemie and Wissenschaftliches Zentrum für Materialwissenschaften (WZMW), Philipps-Universität Marburg, Marburg, Germany

Harvey J.M. Hou Department of Physical Sciences, Alabama State University, Montgomery, AL, USA

Norman P.A. Hüner Department of Biology and the Biotron Center for Experimental Climate Change Research, Western University, London, ON, UK

Vaughan Hurry Umeå University, Umeå, Sweden

Alexander G. Ivanov Department of Biology and the Biotron Center for Experimental Climate Change Research, Western University, London, ON, Canada

Institute of Biophysics and Biomedical Engineering, Bulgarian Academy of Sciences, Sofia, Bulgaria

Anjana Jajoo School of Life Science, Devi Ahilya University, Indore, MP, India

Rachelle Johnson Department of Chemistry and Biochemistry, University of North Carolina at Greensboro, Greensboro, NC, USA

Leonid V. Kurepin Department of Biology and the Biotron Center for Experimental Climate Change Research, Western University, London, ON, Canada

Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, Umeå, Sweden

Yan Lu Department of Biological Sciences, Western Michigan University, Kalamazoo, MI, USA

Mahir D. Mamedov A.N. Belozersky Institute of Physical-Chemical Biology, Lomonosov Moscow State University, Moscow, Russia

Amarendra N. Misra Centre for Life Sciences, School of Natural Sciences, Central University of Jharkhand, Ranchi, India

Meena Misra Centre for Life Sciences, School of Natural Sciences, Central University of Jharkhand, Ranchi, India

Gary F. Moore School of Molecular Sciences and the Biodesign Institute Center for Applied Structural Discovery (CASD), Arizona State University, Tempe, AZ, USA

Mohammad Mahdi Najafpour Department of Chemistry, Institute for Advanced Studies in Basic Sciences (IASBS), Zanjan, Iran

Center of Climate Change and Global Warming, Institute for Advanced Studies in Basic Sciences (IASBS), Zanjan, Iran

Krishna Nath Department of Biological Sciences, Western Michigan University, Kalamazoo, MI, USA

James P. O'Donnell Department of Biological Sciences, Western Michigan University, Kalamazoo, MI, USA

Katarina Olsovska Department of Plant Physiology, Slovak University of Agriculture, Nitra, Slovakia

Babak Pashaei Department of Chemistry, University of Zanjan, Zanjan, Iran

Richard P. Pharis Department of Biological Sciences, University of Calgary, Calgary, AB, Canada

Prashanth K. Poddutoori Department of Chemistry, Brock University, St. Catharines, ON, Canada

Pu Qian Department of Molecular Biology and Biotechnology, The University of Sheffield, Sheffield, UK

Fahime Rahimi Department of Chemistry, Institute for Advanced Studies in Basic Sciences (IASBS), Zanjan, Iran

Alexander V. Ruban School of Biological and Chemical Sciences, Queen Mary University of London, London, UK

Moayad Hossaini Sadr Faculty of Basic Sciences, Department of Chemistry, Azarbaijan Shahid Madani University, Tabriz, Iran

Saeideh Salimi Department of Chemistry, Institute for Advanced Studies in Basic Sciences (IASBS), Zanjan, Iran

Davood Jafarian Sedigh Department of Chemistry, Institute for Advanced Studies in Basic Sciences (IASBS), Zanjan, Iran

Alexey Yu Semenov A.N. Belozersky Institute of Physical-Chemical Biology, Lomonosov Moscow State University, Moscow, Russia

Hashem Shahroosvand Department of Chemistry, University of Zanjan, Zanjan, Iran

Vonda Sheppard Department of Chemistry and Biochemistry, University of North Carolina at Greensboro, Greensboro, NC, USA

Ranjeet Singh Centre for Life Sciences, School of Natural Sciences, Central University of Jharkhand, Ranchi, India

Biotechnology Department, Beej Sheetal Research Pvt. Ltd., Jalna, India

Behzad Soltani Faculty of Basic Sciences, Department of Chemistry, Azarbaijan Shahid Madani University, Tabriz, Iran

Beth Szyszka Department of Biology and the Biotron Center for Experimental Climate Change Research, Western University, London, ON, Canada

Mojtaba Tavahodi Department of Chemistry, Institute for Advanced Studies in Basic Sciences (IASBS), Zanjan, Iran

Tatsuya Tomo Faculty of Science, Department of Biology, Tokyo University of Science, Tokyo, Japan

Art Van Der Est Department of Chemistry, Brock University, St. Catharines, ON, Canada

Freiburg Institute of Advanced Studies (FRIAS), Albert-Ludwigs-Universität Freiburg, Freiburg, Germany

Radka Vladkova Institute of Biophysics and Biomedical Engineering, Bulgarian Academy of Sciences, Sofia, Bulgaria

Yingchun Wang State Key Laboratory of Molecular Developmental Biology, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing, China

Jessica Wiwczar Department of Molecular Biophysics and Biochemistry, Yale University, New Haven, CT, USA

Wu Xu Department of Chemistry, University of Louisiana at Lafayette, Lafayette, LA, USA

Makio Yokono Institute of Low Temperature Science, Hokkaido University, Sapporo, Japan

Mohammad Zaman Ballance Agri-Nutrients Limited, Tauranga, New Zealand

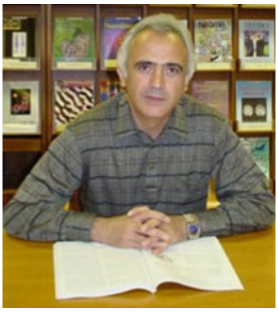
Marek Zivcak Department of Plant Physiology, Slovak University of Agriculture, Nitra, Slovakia

About the Editors

Harvey J.M. Hou, born in 1962 in China, is a professor in the Department of Physical Sciences at Alabama State University, Montgomery, Alabama, USA. He received his B.Sc. in physical chemistry in 1984 from Wuhan University and completed his Ph.D. in analytical chemistry in 1993 at Peking University (Beijing, China) with Xiaoxia Gao. He had his postdoctoral training at the Chinese Academy of Sciences with Peisung Tang and Tingyun Kuang, at Iowa State University with Parag Chitnis, and at Rockefeller University with David Mauzerall. Since 1995, he has served as a faculty member at the Chinese Academy of Sciences, Gonzaga University, the University of Massachusetts at Dartmouth, and Alabama State University. He began his research career in photosynthesis in 1993, working on photosystem II (PS II). In 1996, he visited the laboratory of Jacque Breton in France and studied the orientation of pigments in PS II. In the laboratory of Parag Chitnis, he examined the organization of PS I. Working with David Mauzerall, he systematically investigated the thermodynamics of electron transfer reactions in photosynthesis using pulsed photoacoustics. His work has uncovered a significant entropy change of reaction in PS I; further, he has demonstrated that the entropy change in PS I is dramatically different from that in PS II. Since he established his laboratory in 2002, he has maintained his long-term collaboration with David Mauzerall on the thermodynamics in cyanobacterial PS I and in heliobacteria. In 2006, he began collaboration with Gary Brudvig at Yale University and Dunwei Wang at Boston College on artificial photosynthesis and has developed a manganese/semiconductor system for solar energy storage. His research group has also investigated the responses of cyanobacteria and cranberry plants to environment. He co-chaired a symposium at the 15th International Congress of Photosynthesis Research, chaired the 28th Annual Eastern Regional Photosynthesis Conference, and co-organized the 38th Annual Midwest/Southeast Photosynthesis Meeting.

Mohammad Mahdi Najafpour received his Ph.D. in inorganic chemistry from Sharif University of Technology, Tehran, Iran, in 2009. Mahdi is a recipient of several awards and fellowships, notably the gold medal of the National Chemistry Olympiad in 2004, "Top Student" award of Sharif University of Technology in 2007, and fellowship of government for a research stay in Germany as a visiting scientist in 2009; he ranked first in the Khwarizmi Youth Festival in 2010, received Professor Ashtiani's award in 2012, was selected for the Third World Academy of Sciences (TWAS) young affiliateship in 2014, and awarded the Al-Biruni Award by the Academy of Sciences of Iran in 2015. Currently, he is an associate professor of chemistry at the Institute for Advanced Studies in Basic Sciences (IASBS) (Zanjan, Iran). As a nanobioinorganic chemist, Mahdi believes that, with learning strategies from natural systems, design of modern catalysts for all reactions using only earth-abundant, low-cost, and environmentally friendly metal ions is possible. Mahdi and his research group explore transition-metal compounds as water-oxidizing catalysts for artificial photosynthesis. He is the author of over 150 publications in these and other areas.

Gary F. Moore is an assistant professor in the School of Molecular Sciences and the Biodesign Institute Center for Applied Structural Discovery at Arizona State University. He is also guest faculty at Berkeley Lab. He obtained his B.Sc. (2004) from the Evergreen State College and his Ph.D. (2009) under Ana L. Moore from Arizona State University where he was a National Science Foundation fellow. Gary completed his postdoctoral training as a Camille and Henry Dreyfus Foundation energy fellow at Yale University (2009–2011) working with the research groups of Gary W. Brudvig, Robert H. Crabtree, Victor S. Batista, and Charles A. Schmuttenmaer. He began his independent research career as a principal investigator and staff scientist at Berkeley Lab (2011) working with the Joint Center for Artificial Photosynthesis before starting his current position at Arizona State University (2014). His group includes an interdisciplinary team of researchers that conduct use-inspired research with applications to photocatalysis, hard-to-soft matter interfaces, molecular electronics, chemical sensing, and proton-coupled electron transfer. He is a frequently invited speaker to international seminars, conferences, and workshops on the science and social policy of artificial photosynthesis and solar-to-fuel technologies.



Suleyman I. Allakhverdiev is the head of the Controlled Photobiosynthesis Laboratory at the Institute of Plant Physiology of the Russian Academy of Sciences (RAS), Moscow; chief research scientist at the Institute of Basic Biological Problems RAS, Pushchino, Moscow Region; professor at M.V. Lomonosov Moscow State University, Moscow, Russia; head of the Bionanotechnology Laboratory at the Institute of Molecular Biology and Biotechnology of the Azerbaijan National Academy of Sciences, Baku, Azerbaijan; and invited adjunct professor at the Department of New Biology, Daegu Gyeongbuk Institute of Science and Technology (DGIST), Daegu, Republic of Korea. He is originally from Chaykend (Karagoyunly/Dilichanderesi), Armenia, and he obtained both his B.S. and M.S. in physics from the Department of Physics, Azerbaijan State University, Baku. He obtained his Dr. Sci. degree (highest/top degree in science) in plant physiology and photobiochemistry from the Institute of Plant Physiology, RAS (2002, Moscow), and Ph.D. in physics and mathematics (biophysics) from the Institute of Biophysics, USSR (1984, Pushchino). His Ph.D. advisors were Academician Alexander A. Krasnovsky and Dr. Sci. Vyacheslav V. Klimov. He worked for many years (1990–2007) as visiting scientist at the National Institute for Basic Biology (with Prof. Norio Murata), Okazaki, Japan, and in the Départment de Chimie-Biologie, Universite du Quebec at Trois Rivieres (with Prof. Robert Carpentier), Quebec, Canada (1988–1990). He has been a guest editor of many (more than 30) special issues in international peer-reviewed journals. At present, he is a member of the editorial board of more than 15 international journals. Besides being editor-in-chief of SOAJ *NanoPhotoBioSciences*, associate editor of the *International Journal of Hydrogen Energy*, section editor of *BBA Bioenergetics*, and associate editor of *Photosynthetica*, he also acts as a referee for major international journals and grant proposals. He has authored (or co-authored) more than 350 research papers, 6 patents, and 7 books. He has organized several (more than 10) international conferences on photosynthesis. His research interests include the structure and function of photosystem II, water-oxidizing complex, artificial photosynthesis, hydrogen photoproduction, catalytic conversion of solar energy, plants under environmental stress, and photoreceptor signaling.

Photosynthesis: Natural Nanomachines Toward Energy and Food Production

1

Mohammad Mahdi Najafpour, Harvey J.M. Hou, and Suleyman I. Allakhverdiev

Summary

Photosynthesis is of the most important reactions on Earth and it is a scientific field that is intrinsically interdisciplinary. This chapter provides a brief discussion on the importance of photosynthesis and potential future applications of photosynthesis as a blueprint for artificial photosynthetic systems.

Keywords

Plant • Chloroplast • Photosystem I • Photosystem II • Water oxidation • Water splitting • ATP synthase • Chlorophyll • Electron transport • S-state cycle • Artificial photosynthesis

Contents

1.1 Introduction

Nature uses unique and powerful strategies to capture the solar energy in an amazing process: Photosynthesis (from Greek, photo: light and synthesis: putting together). The phenomenon is the most important photobiological reaction on our planet and occurs in plants, algae and cyanobacteria. All creatures need energy to their life. Phototrophy is a process used by organisms to trap photons and store energy as chemical energy in the form of adenosine triphosphate (ATP), which transports energy within cells (Fenchel et al. 2012). There are three types of phototrophy: anoxygenic photosynthesis,

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M.M. Najafpour (✉)
Department of Chemistry, Institute for Advanced Studies in Basic Sciences (IASBS), Zanjan 45137-66731, Iran

Center of Climate Change and Global Warming, Institute for Advanced Studies in Basic Sciences (IASBS), Zanjan 45137-66731, Iran
e-mail: mmnajafpour@iasbs.ac.ir

H.J.M. Hou
Department of Physical Sciences, Alabama State University, Montgomery, AL 36104, USA

S.I. Allakhverdiev
Controlled Photobiosynthesis Laboratory, Institute of Plant Physiology, Russian Academy of Sciences, Botanicheskaya Street 35, Moscow 127276, Russia

Institute of Basic Biological Problems, Russian Academy of Sciences, Pushchino, Moscow, Region, 142290, Russia

Faculty of Biology, Department of Plant Physiology, M. V. Lomonosov Moscow State University, Leninskie Gory 1-12, Moscow 119991, Russia

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oxygenic photosynthesis, and rhodopsin-based phototrophy (Fenchel et al. 2012). Photosynthesis usually converts carbon dioxide into different organic compounds using solar energy. Although, some anoxygenic photosynthetic organisms such as heliobacteria can't fix carbon photoautotrophically.

In anoxygenic photosynthesis used by green bacteria, phototrophic purple bacteria, and heliobacteria, light energy is captured and stored as ATP, without the production of oxygen (Bryant and Frigaard 2006; Blankenship et al. 1995; Feiler and Hauska 1995). This means water is not used as the primary electron donor. Such organisms use a single photosystem, which restricts them to cyclic electron flow only, and they are therefore unable to produce O_2 from the oxidization of H_2O. Anoxygenic phototrophs have photosynthetic pigments called bacteriochlorophylls. Bacteriochlorophyll a and b have maxima wavelength absorption at 775 nm and 790 nm, respectively.

In contrast, oxygenic photosynthesis in plants, algae and cyanobacteria results not only in the fixation of carbon dioxide (CO_2) from the atmosphere, but also release of molecular oxygen to the atmosphere (Blankenship 2013; Allen et al. 2011). The name of cyanobacteria is based on the bluish pigment phycocyanin, which is used to harvest light for photosynthesis in these cells. Plants, algae and cyanobacteria not only capture approximately 3000 EJ and produce more than 100 billion tons of dry biomass annually (Blankenship et al. 1995), but also they form oxygen, which is necessary for many organisms. The transition from anoxygenic to oxygenic photosynthesis in the eubacterial lineage was an important innovation in evolution and the vast majority of the scientific community is in agreement regarding the correlation between this event and the beginning of oxygen accumulation on Earth (Canfield 2005). The evidence from chemical markers (Kazmierczak and Altermann 2002; Summons et al. 1999), stromatolite fossils (Olson and Blankenship 2004), and microfossils (Schopf 1975) attest that cyanobacteria arose before 2.5 billion years ago (Konhauser et al. 2011; Gould et al. 2008). Before cyanobacteria, the atmosphere had much more carbon dioxide and organisms used hydrogen or hydrogen sulfide as sources of electron (Olson 2006), but the new oxygen-rich atmosphere was a revolution for complex life.

1.2 Organization and Function of Photosynthetic Nanomachines

In plants and algae, photosynthesis takes place in chloroplasts. Each plant cell contains about 10–100 chloroplasts (Fig. 1.1). The chloroplasts in modern plants are the descendants of these ancient symbiotic cyanobacteri (Gould et al. 2008). Chloroplast is one of three types of plastids, indicated by its high concentration of chlorophyll (Fig. 1.1a) (McFadden 2001). The plastids in plant cells are highly dynamics structures and divide during reproduction. Their behavior is strongly influenced and regulated by environmental factors like light color and intensity. They are composed of two inner and outer phospholipid membrane and an intermembrane space between them. Within the membrane is an aqueous fluid called the stroma, which contains stacks (grana) of thylakoids (Fig. 1.1b). The thylakoids are flattened disks, bounded by a membrane with a lumen or thylakoid space within it. The thylakoid membrane forms the photosystems (Fig. 1.1b, c, d). On the other hand, Cyanobacteria have an internal system of thylakoid membranes where the outer membrane, plasma membrane, and thylakoid membranes each have specialized roles in the cyanobacterial cell (McFadden 2001).

The process of photosynthesis starts with the absorption of light by pigments (Fig. 1.2) located in PSII (Blankenship 2013). Then, the energy is transferred to the reaction center, which are special chlorophyll ($P_{680}{}^{+}$). Energy transfer between the antenna pigments transports the excitation to the reaction center and is an important part of the photosynthetic process. Excitons trapped by a reaction center provide the energy for the primary photochemical reactions and causes the oxidation of its adjacent tyrosine (Yz) and

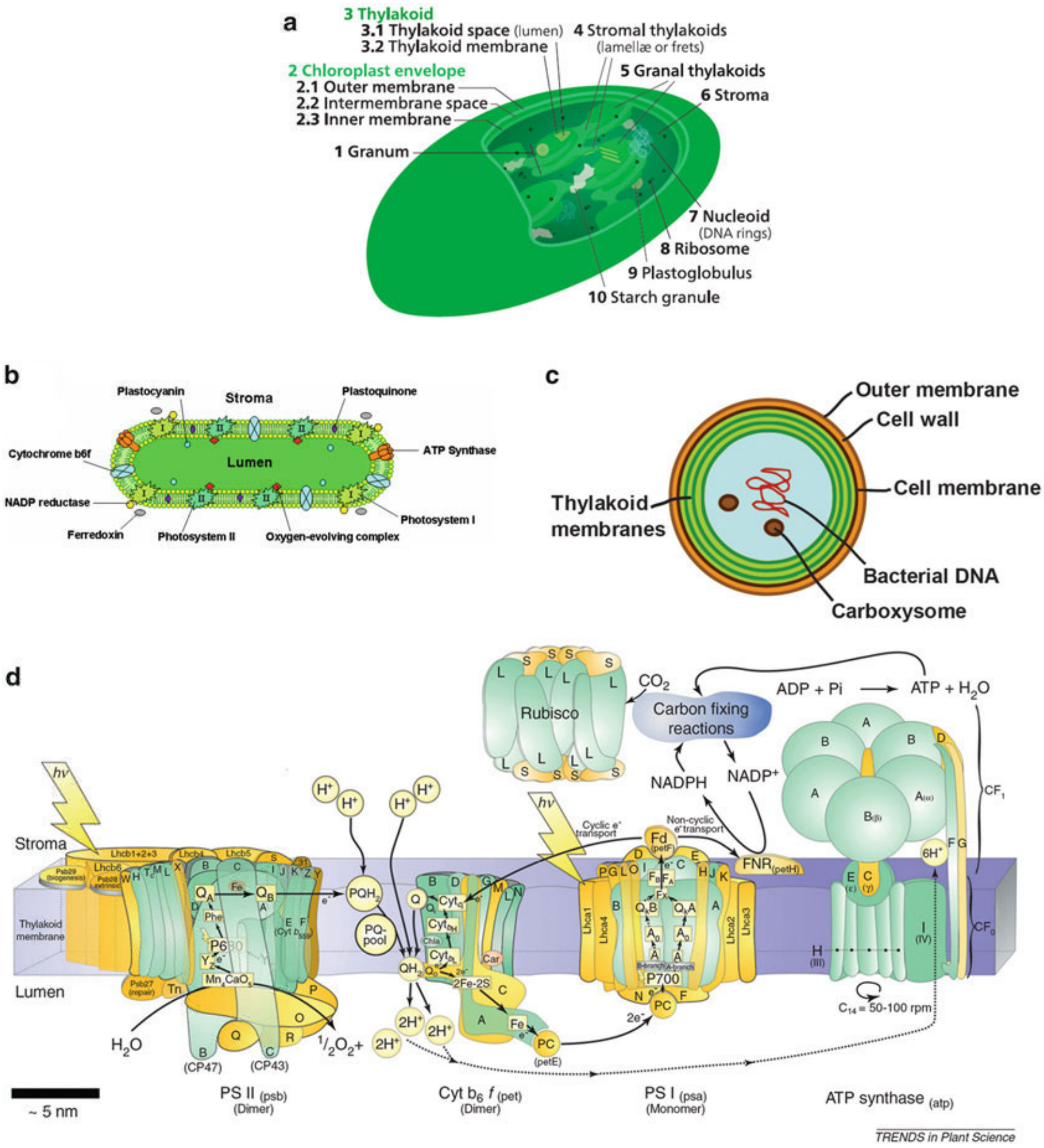

Fig. 1.1 Structures of a typical higher-plant chloroplast (**a**), thylakoid (**b**), thylakoids inside a cyanobacterium (**c**), and major protein complexes in a chloroplast (**d**). PSII; cytochrome b6f (Cyt b6f); PSI; ATP synthase; and Rubisco. Subunits are given single-letter names, omitting the three-letter prefix that denotes the complex of which each forms part. These prefixes are: psa for PSI; psb for PSII; pet (photosynthetic electron transport) for the cytochrome b6f complex and secondary electron carriers; atp for the ATP synthase; and rbc for Rubisco. Polypeptide subunits encoded in the chloroplast are coloured *green*; polypeptide subunits encoded in the nucleus are coloured *yellow*. Each major complex, such as PSI, PSII or ATP synthase, can be considered as a nano machine (see the scale in the image) (Reprinted with permission from Allen et al. 2011. Copyright (2011) by Elsevier)

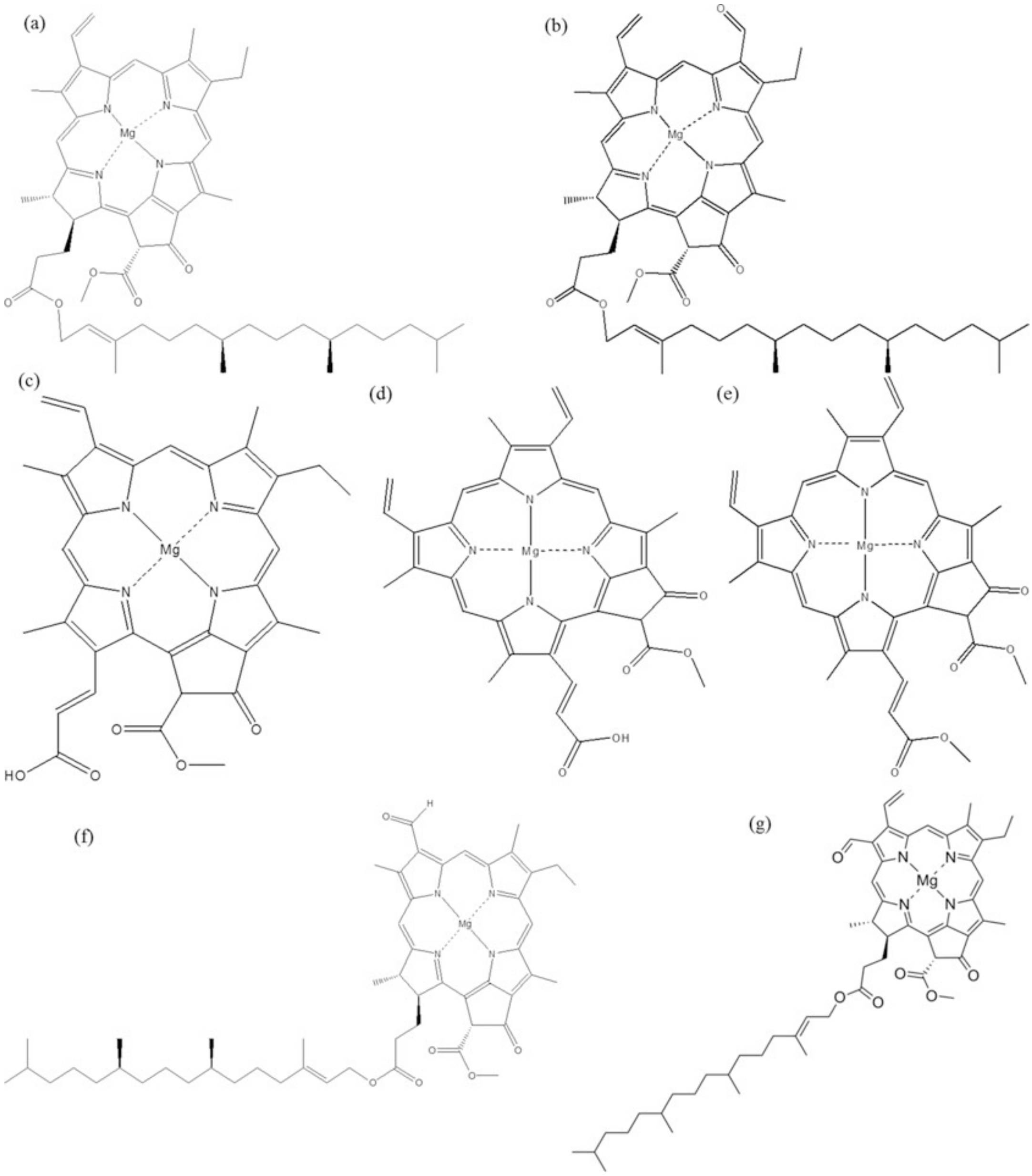

Fig. 1.2 Chemical structures of chlorophylls (**a**) chlorophyll a; (**b**) chlorophyll b; (**c**) chlorophyll c1; (**d**) chlorophyll c2; (**e**) chlorophyll c3; (**f**) chlorophyll d; (**g**) chlorophyll f

afterwards, the Yz^+ is reduced to Yz by the electron captured from the water oxidation complex (WOC) or the oxygen-evolving complex (OEC) (Ferreira et al. 2004; Umena et al. 2011). Two photosystems are connected by a series of intermediate carriers named plastoquinol, cytochrome b6f, and plastocyanin. Electrons transfer from P_{680} via Pheo QA to QB to give plastoquinol after two turnovers. Cytochrome b6f acts as an electron carrier mediates electron transfer between the two carriers plastoquinol and plastocyanin. The electron due the P_{680} excitation is carried to PSI to restore the function of chlorophyll P_{700}. The light absorption and electron

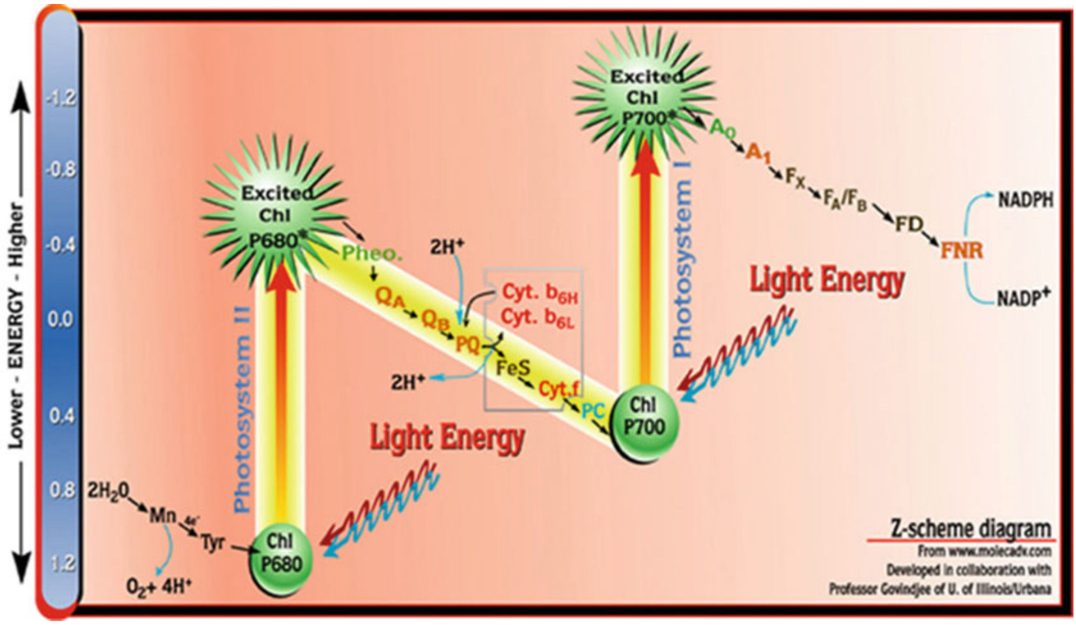

Fig. 1.3 Z-Scheme of electron transport in photosynthesis. Abbreviations used are (from *left* to the *right* of the diagram): Mn for a manganese complex containing 4 Mn atoms, bound to Photosystem II (PSII) reaction center; Tyr for a particular tyrosine in PSII; O2 for oxygen; H+ for protons; P680 for the reaction center chlorophyll (Chl) in PSII: it is the primary electron donor of PSII; Excited (Chl) P680 for P680* that has the energy of the photon of light; Pheo for pheophytin molecule (the primary electron acceptor of PSII; it is like a chlorophyll a molecule where magnesium (in its center) has been replaced by two "H"s); QA for a plastoquinone molecule tightly bound to PSII; QB for another plastoquinone molecule that is loosely bound to PSII; FeS for Rieske Iron Sulfur protein;Cyt. f for Cytochrome f; Cytb6 (L and H) for Cytochrome b6 (of Low and High Energy); PC for copper protein plastocyanin; P700 for the reaction center chlorophyll (Chl; actually a dimer, i.e., two molecules together) of PSI; it is the primary electron donor of PSI; Excited (Chl) P700 for P700* that has the energy of the photon of light; Ao for a special chlorophyll a molecule (the primary electron acceptor of PSI); A1 for a phylloquinone (Vitamin K) molecule; FX, FA, and FB are three separate Iron Sulfur Centers; FD for ferredoxin; and FNR for Ferredoxin NADP oxido Reductase (FNR). Three major protein complexes are involved in running the "Z" scheme: (1) PSII; (2) Cytochrome bf complex (containing Cytb6; FeS; and Cytf) and (3) PSI. The diagram does not show where and how ATP is made (Images from Govindjee and Wilbert Veit)

transition in PSI lead to production of NADPH. In the reactions, Ferredoxin and Ferredoxin NADP oxido Reductase are intermediates. Overall, the net reaction is electron transition resulting from water oxidation in PSII to $NADP^+$ and formation of NADPH form in PSI. These electrons are shuttled through an electron transport chain, the so-called Z-scheme shown in Fig. 1.3.

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) by a complicated mechanism:

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

1.3 Structures and Mechanisms of the Water Oxidation Nanomachines

Recently, the crystal structure of the PSII WOC at atomic resolution was determined (Umena et al. 2011; Suga et al. 2015). In this structure, one calcium and four manganese ions are bridged by five oxygen atoms. The structure also shows four water molecules, two of which are

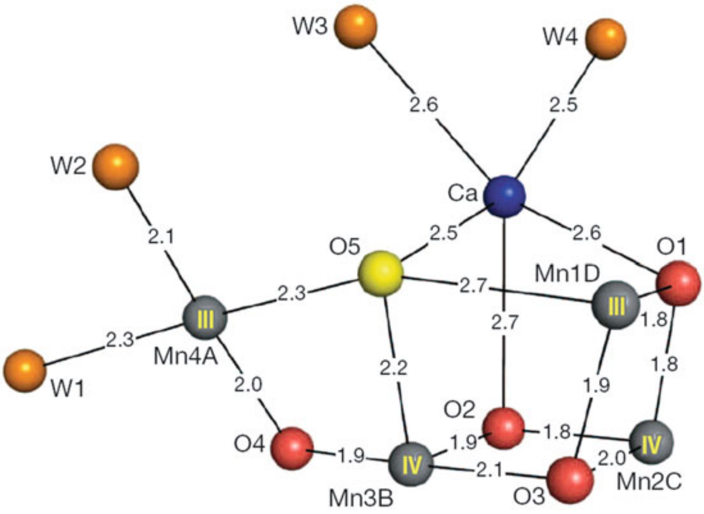

Fig. 1.4 The structure of PSII WOC (Suga et al. 2015) (Reprinted with permission from Suga et al. 2015. Copyright (2015) by McMilan publications)

suggested as the substrates for water oxidation (Fig. 1.4).

Joliot et al. (1969) showed that short flashes produced an oscillating pattern in the oxygen evolution and a maximum of water oxidation to oxygen production occurred on every fourth flash. Because water oxidation needs the removal of four electrons, these patterns were very interesting. Kok was the first scientist to propose an explanation for the observed oscillation of the oxygen evolution pattern (Kok et al. 1970). Kok's hypothesis was that in a cycle of water oxidation, a succession of oxidizing equivalents is stored on each separate and independent water oxidizing complex, and when four oxidizing equivalents have been accumulated 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. 1.5) (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 by $P_{680}{}^{+}$ (Blankenship 2013).

Light is also used to synthesize ATP and NADPH in photosynthesis. 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 PSII by different pigments (Blankenship 2013). The NADPH and ATP is used by the photosynthetic organisms to drive the synthesis in the Calvin – Benson cycle in the light-independent or dark reactions (Fig. 1.6) [22].

By the Calvin – Benson, 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 (Lundqvist and Schneider 1991):

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

There is a Mg(II) ion in the active site of RuBisCO, which stabilizes formation of an enediolate carbanion equivalent that is

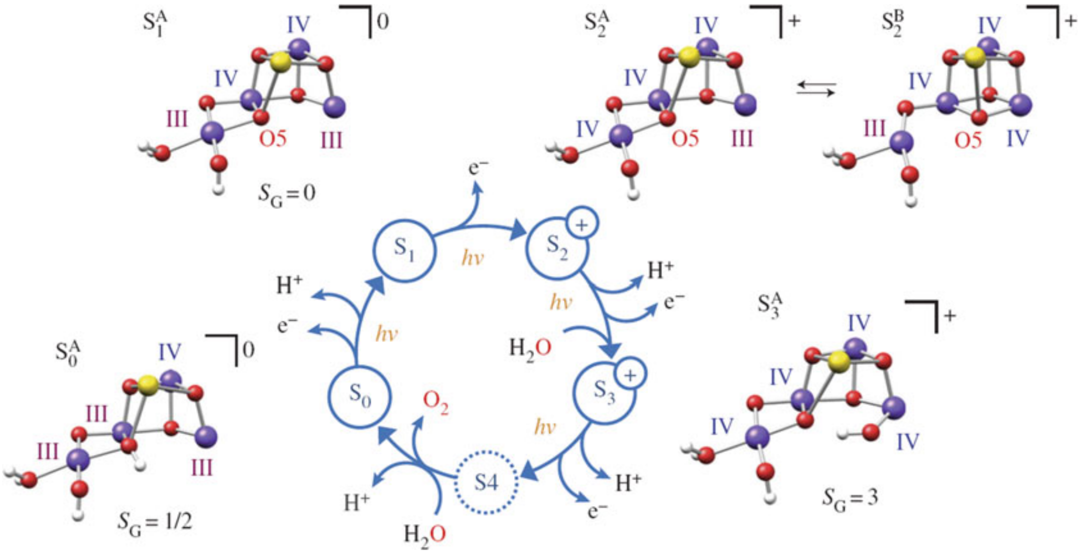

Fig. 1.5 S-state cycle of photosynthetic water oxidation (Kok cycle). Starting in the dark-stable S1 state, absorption of a photon and subsequent electron transfer leads to oxidation of tyrosine YZ, which in turn removes an electron from the WOC advancing it from state Si to Si + 1. The electron transfer steps are accompanied by charge-compensating deprotonation steps. A plausible set of oxidation-state combinations of the four Mn ions is shown for the various Si states. Models show the optimized geometry, protonation pattern and Mn oxidation states of the inorganic core. The cofactor exists in two forms in the S2 state, an open cubane (S2A) and a closed cubane (S2B) structure, which differ in their core connectivity by the reorganization of O5 (Reprinted with permission from Cox et al. 2013. Copyright (2013) by the American Chemical Society)

subsequently carboxylated by CO_2 (Lundqvist and Schneider 1991).

1.4 Applications of Artificial Photosynthetic Nanomechines

Our food, energy, environment and culture, directly or indirectly, depend on the photosynthesis. Because the solar energy absorbed by Earth is huge, approximately 3,850,000 exajoules per year, which is more energy in one hour than the world used in one year!, recently, artificial photosynthesis has been used as a model for how a sustainable supply of energy could be obtained. The term artificial photosynthesis is a general term (Najafpour et al. 2015; Tachibana et al. 2012; Nocera 2012). Recently, the phenomenon have been a blueprint to obtain a sustainable fuel for human as artificial photosynthesis, which is a general term to cover all strategies to mimic the photosynthetic process especially to provide a solar-based sustainable energy supply in the future (Fig. 1.6) (Najafpour et al. 2015; Tachibana et al. 2012; Nocera 2012). In other words, photosynthesis can provide paradigms for sustainable global energy production and efficient energy transformation (Najafpour et al. 2015; Tachibana et al. 2012; Nocera 2012; Ort et al. 2015; Lin et al. 2014; Blankenship et al. 2011). As an excellent example, artificial leaf, which is a machine that can harness sunlight to split water into molecular hydrogen and oxygen without needing any external connection, is being developed (Nocera 2012). The artificial leaf (Fig. 1.6) may be comparable to real leaves, which converts the energy of sunlight into chemical form, and represents one of the most promising directions in solar fuel and food production. In addition, several inspiring cases using different approaches in artificial photosynthesis are presented and discussed in Chaps. 15, 16, 17, 18, 19 and 20 in this book.

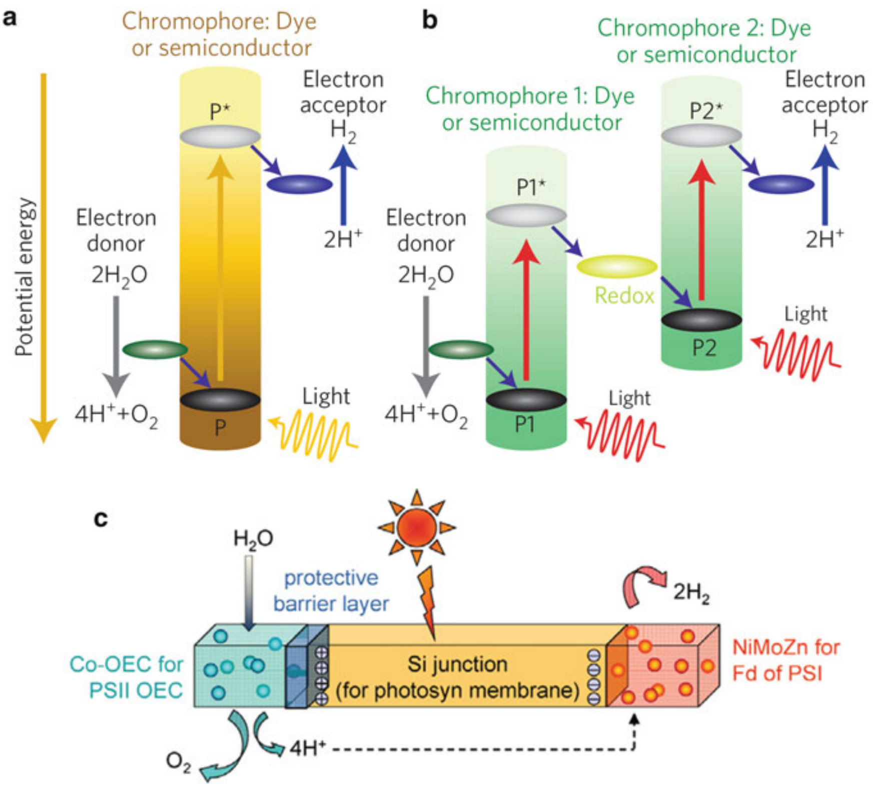

Fig. 1.6 An artificial photosynthetic system: single-step reactions (**a**), and two-step (Z-scheme) reactions (**b**). P: chromophore of a single-step reaction system; P*: excited state of P; P1: the first chromophore of a two-step reaction system; P1*: excited state of P1; P2: second chromophore of a two-step reaction system; P2*: excited state of P2 (Adapted with permission from ref. 24. Copyright (2013) by McMillan publications. Construction of an artificial leaf. The photosynthetic membrane is replaced by a Si junction, which performs the light capture and conversion to a wireless current. The oxygen-evolving complex and ferredoxin reductase of the photosynthetic membrane are replaced by Co-OEC and NiMoZn OER and HER catalysts, respectively, to perform water splitting (**c**). Adapted with permission from (Nocera 2012). Copyright (2012) by the American Chemical Society)

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Structure and Function of the Reaction Centre – Light Harvesting 1 Core Complexes from Purple Photosynthetic Bacteria

2

Pu Qian

Summary

Reaction centre-light harvesting 1 core complex is a fundamental unit in photosynthetic bacterium. It is the place where light energy is collected and used to power photosynthetic redox reaction, leading to the synthesis of ATP ultimately. The reaction centre is surrounded by elliptical LH1 complex. The subunit of the LH1 ring is a heterodimer of α-, β-polypeptide pair, to which pigment molecules, BChl *a* or BChl *b* and carotenoid are non-covalently bonded. There are at least three different types of the RC-LH1 core complexes found in photosynthetic bacteria so far. The core complex from *Rps. palustris* is a monomer. Its LH1 ring consists of 15 pairs of α/β-polypeptide with an extra protein 'W' located between two α-polypeptides, forming an incomplete ring. The gap of the LH1 ring was proposed as a gate to facilitate quinone/quinol exchange between reaction centre and cytochrome *bc*1 complex. A dimeric core complex was found in PufX-containing species, such as *Rba. sphaerides*. Two RCs are associated by 28 α/β-apoprotein pairs and two pufX proteins, forming an S-shaped RC-LH1-PufX core complex. The pufX protein causes incomplete LH1 ring and dimerization of the core complex. Monomeric RC-LH1 from *Tch. tepidum* has a complete elliptical LH1 ring that is composed of 16 pair α/β-apoprotein pairs without pufX-like protein. Sixteen Ca^{2+} are coordinated on C-terminal region of the α/β-polypeptide to stabilize the core complex and cause BChl *a* Qy absorption redshift to 915 nm. Carotenoid, spirilloxthanin contacts with α/β-apoproteins intimately to form an inter subunit interaction within the core complex, providing a further stability of the complex.

Keywords

Photosynthesis • Photosynthetic bacteria • Reaction center • Light harvesting 1 core complex • RCLH1 • Carotenoid • Bacteriochlorophyll

Contents

P. Qian (✉)
Department of Molecular Biology and Biotechnology, The University of Sheffield, Sheffield, UK
e-mail: p.qian@sheffield.ac.uk

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2.1 Introduction

Purple photosynthetic bacteria refer to a unique group of microorganism that use sun light as their energy source. The light energy is absorbed by pigment molecules, such as bacteriochlorophyll (BChl) and carotenoids (Car), which are non-covalently bound to so-called light harvesting complexes. In general, there are two major classes of light harvesting complex in the purple photosynthetic bacteria, light harvesting complex 1 (LH1) and light harvesting complex 2 (LH2). The LH2, sometime called peripheral antenna complex, is composed of oligomer of two short polypeptides (α and β) with associated pigments, Car and BChl *a* or BChl *b*. The α/β-polypeptide pair, therefore, is a building block of this cylinder-like complex (Koepke et al. 1996; McDermott et al. 1995). The building block of the LH1 is constructed similar as molecular architecture as that in the LH2 complexes. The LH1 complex is always intimately interacted with the reaction centre (RC) in a fixed stoichiometry. The term of core complex usually refers to the combination of the RC and the light harvesting complex 1 in the purple photosynthetic bacteria. A short name, such as RC-LH1 or RC-LH1-PufX is often used in literatures. As its name implies that the photosynthetic core complex or RC-LH1 is the central part of bacterial photosynthesis. This chapter will focus on the recent development on structural determination of the RC-LH1 core complexes from the purple photosynthetic bacteria by starting with basic background of bacterial photosynthesis and building blocks of the core complex. For the readers who are interesting in general works on the purple photosynthetic bacteria, two recent books edited by Blankenship, R. E. and Hunter, C. N. provide more detailed and comprehensive information on the bacterial photosynthesis. (Blankenship 2014; Hunter et al. 2009).

2.2 The Purple Photosynthetic Bacteria

The purple photosynthetic bacteria, much like the name suggested, are a group of dark coloured bacteria, with different morphologies such as rod, spirilla, cocci or vibrios, which can convert light energy to chemical energy to maintain their metabolism. The pigment molecules that are involved in the light absorption are usually BChl *a* or BChl *b* and carotenoids. It is these pigments that give the purple bacteria such gorgeous colours, from purple, red to green, depending on the amount and type of different carotenoids in an individual purple bacterium.

The purple photosynthetic bacteria can be divided into two groups, i.e., purple non-sulphur bacteria and purple sulphur bacteria according to their tolerance and utilization of sulphide (Imhoff et al. 1984). The purple sulphur bacteria use sulphur or sulphide, such as hydrogen sulphide H_2S as an electron donor for carbon dioxide reduction in its respiration, while the purple non-sulphur bacteria use organic electron-donor, such as succinate or malate instead. Usually, sulphide is toxic for the purple non-sulphur bacteria although the most species of the purple non-sulphur bacteria can still grow at low level of sulphide (<0.5 mM). Different from higher plant or cyanobacteria photosynthesis, photosynthesis in the purple bacteria does not give off oxygen, and it only occurs under anoxic conditions, which is called as anoxygenic photosynthesis. Therefore, an environment having abundance of oxygen hinders their photosynthetic growing. That is why they are typically found in hot sulphuric spring (for purple sulphur bacteria especially) or stagnant water.

The purple non-sulphur bacteria, such as *Rhodobacter* (*Rba.*) *sphaeroides*, *Rhodopseudomonas* (*Rps.*) *palustris, Blastochloris (Blc.) virids* can grow photoheterotrophically or even photoautotrophically and chemoheterotrophs in darkness as well. It is therefore relatively easy to grow them in laboratory conditions. Having such