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BOOK REVIEW

Thomas J. Wydrzynski and Kimiyuki Satoh (eds), Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase

Springer, Dordrecht, The Netherlands, 2006, 786 pp, $389.00, ISBN: 978-1-4020-4249-2

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The publication of Volume 22 in the *Advances in Photosynthesis and Respiration*[1] series titled ''Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase'' couldn't come at a better time. The reason is that the world is facing two simultaneous, interrelated issues dealing with the energy problem. The first issue is the eventual exhaustion of fossil-derived liquid and gas hydrocarbon fuels due to peaking of production and increasing demand in both developed and developing countries. Notwithstanding current aggressive exploration and advanced recovery efforts, peak oil production—the point at which one-half of the extractable oil has been consumed—may have either already occurred or it will occur sometime in the next couple of years. On top of this, the United Nation's International Energy Agency (IEA) predicts that within 35 years, the demand for energy will double among the world's expected 10×10^9 people. The question is where all of this energy will come from. Two obvious sources are nuclear and coal, but the severe drawback of how to handle and store nuclear waste, and the almost insurmountable problem of global warming, caused by the accumulation of greenhouse gases such as CO_2, makes these solutions problematical. The second issue is that the United Nation's intergovernmental panel on climate change (IPCC) estimates a 4°C rise in temperature by the end of this century. The ramifications in terms of loss of food production and landmass, as well as increase in flooding and incidence of disease, are certain to be profound. We clearly need to switch to a carbon-neutral energy system as quickly as possible. This will require the use of recyclable fuels that can be generated from renewable energy sources. In this regard, it would only take a small fraction of the 5.22×10^{24} J of solar energy that falls on the Earth each year to satisfy mankind's present and future energy needs. The issue is that although solar energy is plentiful and widely distributed, it is diffuse and extremely difficult to transform efficiently into other forms of energy. One approach to solving this problem is to learn from nature, which has evolved reaction centers over the course of 3.5×10^9 years to create a sustainable cycle of production and utilization. The key to our energy dilemma, then, is to uncover the problems that photosynthesis has had to solve and then apply these design principles to biomimetic systems.

The mechanism by which Photosystem II employs a photon of visible light to split the water molecule into O_2, H^+ and e^- is the central topic of this comprehensive book. While there have been numerous attempts to review and summarize progress in this field, this is the first time in recent memory that all of the leading experts have been brought together in one volume to weigh in on their particular areas of competence. What is especially engaging about this book is that the chapters are written in such a way that the topics are accessible to rank beginners who want to enter the field as well as to seasoned practitioners who need to brush up on current developments. This is as much a tribute to the excellent editing by Thomas J. Wydrzynski (of Australia) and Kimiyuki Satoh (of Japan) as to

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[1] Thomas J. Wydrzynski and Kimiyuki Satoh (Editors) (2006) Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase. In: Advances in Photosynthesis and Respiration (Series Editor: Govindjee), Volume 22, XLIV, 786 pp, Hardcover, ISBN: 978-1-4020-4249-2, Springer, Dordrecht, The Netherlands.

the high quality of writing by the authors of their individual chapters.

Part I begins with a chapter written by the editors that introduces the reader to the historical developments that have led to our current understanding of the overall structure, function and organization of Photosystem II. Here, those new to the field will have a chance to learn the rich and colorful story of how our knowledge of this reaction center has unfolded over time. The remainder of the book is constructed so that the chapters progress conceptually from the particular to the general.

Part II consists of 5 chapters devoted to the protein constituents of Photosystem II. Solar energy is diffuse, and so that the photosensitizer is not idle the majority of the time, antenna proteins have evolved to increase the optical cross-section. The problem that photosynthesis has solved is that a photon must be captured and the excitation must migrate with high efficiency to the photosensitizer before de-excitation processes such as fluorescence result in the destruction of the excited state. The proteins that constitute the necessary scaffold for the pigments and cofactors that accomplish photon capture and charge separation are described here. The topics covered include: the distal and extrinsic antennas, the CP47 and CP43 core antennas, the D1 and D2 core proteins, the low molecular weight extrinsic proteins that are considered enhancers of oxygen evolution, and the low molecular weight intrinsic proteins that have, for the most part, an undiscovered function.

Part III consists of 9 chapters, and is concerned with the organization of functional sites in Photosystem II. The central issue is that once charge separation has occurred, it must be stabilized over time by delocalization of the electron through a series of secondary electron acceptors and secondary electron donors. The terminal acceptor, a mobile quinone, functions as a one-electron, two-electron gate, and the final donor, the 4Mn–Ca cluster, serves to oxidize water with as-yet undisclosed chemistry. The extremely positive redox potential of the donor side requires additional cofactors to function properly. These topics are considered in chapters devoted to: primary electron transfer, the iron-quinone acceptor complex, the redox active tyrosines Y_Z and Y_D, the catalytic manganese center (organization of the metal ions, protein ligands, and structural and functional implications from spectroscopy), the Ca^{2+} and Cl^- cofactors, the effect of HCO_3^-, and the function of the side-path donors *cyt* b_{559}, Chl_Z, and β-carotene.

Part IV consists of 6 chapters devoted to a description of the structural basis of Photosystem II. The three-dimensional organization of the proteins and cofactors is a necessary step in understanding charge separation, charge stabilization and the mechanics of water splitting. Information about the ground state structures is obtained by electron microscopy, X-ray crystallography, and a number of allied spectroscopic techniques, while information about the excited state structures is available with the use of magnetic resonance techniques, primarily EPR and its derivatives ENDOR and ESEEM. The topics covered in this chapter are: molecular analysis of the binding site of cofactors by vibrational spectroscopy, the configuration of electron transfer cofactors by EPR spectroscopy, analysis of the Photosystem II core/antenna holocomplex by electron cryo-microscopy and three interpretations on the X-ray crystal structure of the Photosystem II core.

Part V is concerned with the molecular dynamics of Photosystem II. The issue of how the water splitting apparatus functions is one of nature's best-kept secrets. Structural information is a necessary precondition, but the dynamics of how each photon is trapped, equilibrated and utilized for charge separation, and the dynamics of how four successive oxidants are accumulated in order to extract the four non-equivalent electrons from two water molecules can best be understood using time-resolved methodologies. The topics covered in these four chapters include: regulation and efficiency of energy trapping and equilibration, the role of carotenoids in energy quenching, the flash-induced oscillatory pattern of oxygen evolution, and mechanistic considerations of oxygen production.

Part VI deals with the assembly and biodynamics of Photosystem II. The assembly of the reaction center is an exceedingly complicated process because most of the proteins are highly hydrophobic and membrane bound, and the hydrophobic cofactors (chlorophyll, pheophytin), hydrophilic cofactors (quinone and iron) and metallo cofactors (nonheme iron, cytochrome, 4Mn–Ca complex) must be inserted into the growing polypeptides at precisely the right instant in development. The reaction center self-assembles, but it also self-recognizes damaged components, and self-repairs. All of these steps must be regulated at the transcriptional, translational, and post-translational levels. These topics are covered in three chapters devoted to: the assembly of the catalytic Mn cluster, the mechanism of photoactivation and recovery, the transcriptional and translational regulation of gene expression, and the protein transport and post-translational processing.

The final section, *Part VII*, compares Photosystem II with natural and artificial systems. One way to approach the structure and function of Photosystem II is to try to deduce its evolutionary origin, another is to compare its structure and function to systems that do exactly the opposite—reduce oxygen to water. The ultimate triumph would be to understand Photosystem II sufficiently so that it could be mimicked in function by producing an artificial photosynthetic system capable of splitting water. These topics are dealt within 5 chapters devoted to: the evolutionary origin of Photoystem II, a mechanistic comparison with cytochrome c oxidase, an attempt to alter the bacterial reaction center to resemble Photosystem II, the design of proteins capable of carrying cofactors that participate in respiration and photosynthesis, and an attempt to mimick Photosystem II reactions artificially. Last, but not least, there is a touching perspective dedicated to the late Jerry Babcock, one of the leaders in this dynamic field.

While I have deliberately couched this review in terms of recommended reading for those interested in bioinspired design, the book is equally valuable to graduate students who are entering the field of basic research in Photosystem II as well as to established researchers considering moving into this exciting area of research. It should be considered required reading for all of those involved in the basic biochemistry, biophysics, molecular biology and physiology of photosynthetic reaction centers. Every topic of importance in the field is covered in chapters that are of uniformly high quality. I can't think of any topics that are superfluous or any topics that have been left out. My only criticism, one that applies to all of the books in the *Advances in Photosynthesis and Respiration Series*, is that all of the color plates are published in a separate section apart from the individual chapters. This is likely done to keep the cost to a minimum, but the time has come for this practice to change. Also, the publisher might have spent a little additional effort on compiling a more comprehensive index, which is arguably one of the most important features of a review volume.

A complete table of content of this book (with page numbers) is available at <http://www.life.uiuc.edu/govindjee/References/Volume%2022%20By%20Chapter.htm>, and a web site of the book is at <http://www.life.uiuc.edu/govindjee/newbook/Vol%2022.html>. Members of the ISPR (International Society of Photosynthesis Research; <http://www.photosynthesisresearch.org/>) receive 25% discount on this and other books.

My graduate students, who for good reason have a predilection to keep current on the 'other' photosystem (Photosystem I[2]), have asked that my copy of Volume 22 be placed in the student office for easy reference. That is quite a tribute. Certainly, detailed study of both photosystems, their similarities and their differences, is of global interest and this book should be considered a must-read component in that quest. I whole-heartedly recommend this book to all the major libraries in the World.

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[2] J. H. Golbeck (Editor) (2006) Photosystem I: The Light-Driven Plastocyanin: Ferredoxin Oxidoreductase. In: Advances in Photosynthesis and Respiration (Series Editor: Govindjee), Volume 24, XLVIII, 716 pp. Hardcover, ISBN: 978-1-4020-4255-3, Springer, Dordrecht, The Netherlands