

Photosystem I – The Light-Driven Plastocyanin: Ferredoxin Oxidoreductase, vol. 24. John Golbeck (ed.). Series on Advances in Photosynthesis and Respiration (Series editor: Govindjee). Springer, Dordrecht. 2006. 713 pp. Price not mentioned.

The series 'Advances in Photosynthesis and Respiration' (Series editor Govindjee) is devoted to the comprehensive and up-to-date information on research carried out on these two topics and their relationship with each other as also their roles in the bioenergetic aspects of the life of photosynthetic bacteria, cyanobacteria, algae and plants. In oxygenic photosynthesis, two photosystems (Photosystem I (PS I) and Photosystem II (PS II)) function to transfer electrons from water to NADP. Volume 22 of the series, devoted to PS II (*The Light-Driven Water: Plastocyanin Oxidoreductase*) has already been reviewed (Sood, S. C. and Tripathy, B. C., *Curr. Sci.*, 2006, **90**, 858–859). Volume 24 of the series under review is devoted to PS I^a; it was the editor, John Golbeck, who has contributed much to the understanding of various aspects of PS I. With his intimate knowledge not only about the work on PS I but also on those who in the past 5–6 decades have been involved in different discoveries related to PS I, Golbeck had invited those authors who have contributed to the historical development of the subject. No wonder then that each of the chapters has been authoritatively written with an intimate knowledge of the subject. The authors have also given a personal touch while writing their chapters, and this makes the reading far more interesting. Golbeck deserves to be congratulated for bringing out such an informative volume on PS I that will be useful not only to researchers but also to students and teachers of the subject. Govindjee has always been choosy in selecting his editors for each volume of the series and he deserves to be complimented for having chosen Golbeck for this volume. (See an announcement of the book in *Photosynth. Res.*, 2006, **90**, 91–96.)

^aA useful website provides complete references of all the chapters in this book: <http://www.life.uiuc.edu/govindjee/References/Volume%2024%20By%20Chapter.htm>. Here, complete titles of all the chapters and names of all the authors are available.

The volume is divided into 11 sections spanning a total of 40 chapters authored by about 80 researchers. It begins with a dedication to Lee McIntosh who pioneered modern molecular techniques to understand the biochemical mechanisms of photosynthesis primarily using site-directed mutagenesis.

The first section consists of four chapters written by such well-known names as A. San Pietro, R. Malkin, B. Ke, P. Mathis and K. Sauer, who contributed to the understanding of enzymatic NADP reduction, bound iron sulphur clusters of PS I, identification of P 430 by spectroscopy and identification of other primary acceptors by time-resolved optical spectroscopy. These chapters capture the excitement of doing research on PS I during the 1960s and 70s. The information provided also shows the reader the logical approach that these early researchers used to obtain an understanding of PS I. Interestingly, San Pietro tells us as to how the name ferredoxin came to be used for the bacterial redox factor. Many students will find such information interesting. The volume has a small write-up in the beginning about Govindjee.

The second section focuses on the molecular architecture of PS I in cyanobacteria and plants. The chapters in this section discuss the state transitions-related association of LHC II, details of the structure of PS I in cyanobacteria obtained at 2.5 Å resolution and the crystal structure of plant PS I at 4.4 Å resolution. The chapters bring out some of the differences between the two: the cyanobacterial PS I consists of 12 protein subunits with about 127 cofactors, while the plant PS I has 14 protein subunits and about 200 cofactors, and is thus much larger. The organization of different protein complexes and their relation with each other have been described and depicted through colour photographs. The chapter by Antonkine and Golbeck also describes the ionic and hydrogen bond interactions between different subunits. The central role of the subunit PsaC in the assembly of stromal subunits, i.e. PsaC, PsaD and PsaE has been brought out here for the readers to appreciate. These chapters provide the most up-to-date information on the structural aspects of PS I.

The third section is devoted to pigment–protein interactions, the structure of LHC I and low molecular weight subunits of PS I of higher plants. Cyanobacteria are known to respond to iron deficiency by

accumulation of a chlorophyll *a* binding protein called IsiA that forms a ring of 18 subunits around the trimeric reaction centre core. J. Barber and coauthors have described in-depth, the structure and organization of this protein in *Synechocystis*. Other chapters in this section provide information on LHC I, the antenna complex of PS I, spectroscopic properties and different models for the LHC I polypeptides. The last chapter in this section is fully devoted to the 18 different subunits of low molecular mass of higher plant PS I, their functions and possible organization.

The fourth section describes ultrafast optical spectroscopy techniques used to investigate sub-picosecond electronic excitation equilibration in antenna chlorophylls and electron transfer up to the secondary electron acceptor A₁. There is a chapter that describes characteristics and functions of the long-wavelength chlorophylls of PS I, providing the absorption characteristics, fluorescence and CD spectra of these pigments. This section will certainly interest physicists and spectroscopists studying fast reactions, energy absorption, transfer and dissipation of excess energy by the pigments.

The next section (section 5) brings out how specific mutations in the ligands provided valuable information on the identification of ligands of P700, A₀, A₁ and iron sulphur centres of PS I. With the availability of models of the structure of PS I at higher resolutions, site-directed mutagenesis combined with spectroscopy becomes even more powerful in understanding the energy absorption and transfer processes. These aspects have been dealt with in the first chapter of this section. This is followed by studies of quinone biosynthesis in cyanobacteria using genetic approaches. These two chapters provide examples of how mutagenesis has helped in elucidating the structure and function of the PS I cofactors.

The sixth section is one of the larger ones with eight chapters and deals with spectroscopic studies of different cofactors involved in electron transfer processes of PS I. The chapters describe studies on optical spectroscopic, EPR (Electron Paramagnetic Resonance), and FTIR (Fourier Transform Infra Red) investigations of the primary electron donor P700 in PS I. The first chapter attempts to provide information on the possible involvement of both the cofactors (the two phylloquinones) located on the two op-

posing branches of the electron transport pathway. Evidence using site-directed mutations has been provided to substantiate the proposal that electron transport in PS I may use both the branches on the two sides of the reaction centre protein. In this section, a chapter is devoted to the comparison of primary charge separation between P700 and the primary electron acceptor complex A–A₀ in plant PS I and the equivalent components in the bacterial reaction centres. A chapter on electrogenic reactions in PS I discusses the methods for measurement of membrane potentials and compares the situation in PS I, PS II and the bacterial reaction centre. The last two chapters in this section provide information on high-field EPR and transient EPR spectroscopy studies of the electron transfer intermediates in PS I. This large section would be particularly interesting to biophysicists interested in spectroscopic studies of the intermediates of electron transport in PS I.

Section 7 examines the kinetics of electron transfer in PS I, with the first two chapters dealing at length with the reduction of phyloquinone from P-700. It includes various methods used in such studies, the directionality of the electron flow, namely whether both the A and B branches are used, and a discussion of the evidence in this respect. I liked the first chapter by A. van der Est, although it appears to have the most editorial errors. He concludes that the observed slow phase of the forward electron transport is associated with the A branch, just as the cyclic electron transport that occurs at low temperatures arises in the A branch. The next chapter coauthored by van der Est and Redding provides a detailed analysis of the evidence obtained by different laboratories to understand the bidirectionality of electron flow in PS I. On the basis of alteration in the protein environment through mutagenesis, it appears that both A and B branches may be active in PS I reaction centres. This is an interesting and important area of research and the first two chapters in this section have done a good job of analysing all the evidence. I have personally thoroughly enjoyed reading this section and particularly the first two chapters. The remaining chapters have summarized information on the movement of electrons from the quinones to the bound iron sulphur clusters and then to ferredoxin/flavodoxin, resulting finally in the reduction of NADP. The

last chapter in this section discusses electron transfer on the donor side of PS I, namely reduction of P700 from plastocyanin/cytochrome C₆.

The synthesis and assembly of PS I is the main theme of section 8. The chapters in this section provide information on nucleus and chloroplast encoded genes encoding the different subunits, post-transcriptional processing of RNA, trans-splicing, translation and finally assembly of the subunits. In a separate chapter, Golbeck and Shen describe the assembly of bound iron sulphur clusters, while the last chapter in this section summarizes information on the assembly of the PS I reducing site.

Section 9 is devoted to modelling of photosynthetic processes, with the first chapter dealing with the thermodynamics of PS I. In this chapter, D. Mauzerall discusses and assesses methods of obtaining free energy and enthalpy of different steps in the electron transfer chain of PS I. The methods of determining redox potentials of the components have been discussed with their merits and demerits. Based on information from the literature, redox potentials and kinetics have been presented and efficiency of the processes discussed. The next chapter discusses the application of Marcus theory to PS I electron transfer and will be of interest to biophysicists. The next two chapters in this section dwell upon the modelling of optical spectra and functional modelling of the electron transfer in PS I reaction centres. This section should interest the bioenergeticists and teachers of biology, biochemistry and biophysics.

Section 10 discusses two important related processes of PS I, namely the cyclic electron flow around PS I involving electron transfer from NADPH to plastocyanin, and ferredoxin to plastocyanin, and the high-light-associated photoinhibition and its recovery. The role of cyclic electron transport, charge recombination and enzymes for scavenging reactive oxygen species, produced due to over excitation of the photosystems, has been discussed for the protection of PS I. Researchers in the area of stress physiology and environmentalists would find this section quite informative and interesting.

The last section of the book deals with the evolutionary aspects of different components of PS I and traces the possible evolution of the present oxygenic 130 cofactor involving heterodimeric multi-

subunit complex, beginning with the ancient homodimeric reaction centre with its antenna and important electron transfer cofactors. The homodimeric to heterodimeric change has been proposed to be due to gene duplication. Interestingly, the 11 transmembrane helices containing reaction centre that probably arose from either 11 or 5 transmembrane containing reaction centre has remained the same. The increased complexity, involving additional subunits, appears to be due to gene recruitment from other sources. The second chapter in this section, which is also the last chapter of the book, deals with coevolution of plastocyanin and cytochrome C₆. These two proteins, that have different primary sequence as well 3D structure, have almost identical function. It is proposed that the iron containing Cyt C₆ might have been discovered first when iron was more easily available, in the reducing atmosphere of the earth, than copper. Plastocyanin, the copper containing protein, may have been discovered later when increased oxygen concentration in the atmosphere decreased the bioavailability of iron, but increased the availability of copper. The last chapters are of interest to all biologists.

This book is a valuable addition to the literature on photosynthesis in general and PS I in particular, as it provides detailed information and analysis of the important experimental observations made by various researchers all over the world for the understanding of the various aspects of PS I, the plastocyanin-ferredoxin oxidoreductase. In particular, the book shows how development took place over several decades; it is a useful volume not only for researchers and Ph D students, but for teachers of biology, biochemistry and biophysics. I strongly recommend this book to all universities and research institutions that work on plant biology. Govindjee and Golbeck deserve to be complimented for bringing out such a valuable volume.

PRAFULLACHANDRA VISHNU SANE

C-739/B, Sector-C,
Mahanagar Extension,
Lucknow 226 006, India
e-mail: rajsane@hotmail.com