Photosystem I

The Light-Driven Plastocyanin:Ferredoxin Oxidoreductase

Advances in Photosynthesis and Respiration

VOLUME 24

The scope of our series, beginning with volume 11, reflects the concept that photosynthesis and respiration are intertwined with respect to both the protein complexes involved and to the entire bioenergetic machinery of all life. *Advances in Photosynthesis and Respiration* is a book series that provides a comprehensive and state-of-the-art account of research in photosynthesis and respiration. Photosynthesis is the process by which higher plants, algae, and certain species of bacteria transform and store solar energy in the form of energy-rich organic molecules. These compounds are in turn used as the energy source for all growth and reproduction in these and almost all other organisms. As such, virtually all life on the planet ultimately depends on photosynthetic energy conversion. Respiration, which occurs in mitochondrial and bacterial membranes, utilizes energy present in organic molecules to fuel a wide range of metabolic reactions critical for cell growth and development. In addition, many photosynthetic organisms engage in energetically wasteful photorespiration that begins in the chloroplast with an oxygenation reaction catalyzed by the same enzyme responsible for capturing carbon dioxide in photosynthesis. This series of books spans topics from physics to agronomy and medicine, from femtosecond processes to season long production, from the photophysics of reaction centers, through the electrochemistry of intermediate electron transfer, to the physiology of whole orgamisms, and from X-ray crystallography of proteins to the morphology or organelles and intact organisms. The goal of the series is to offer beginning researchers, advanced undergraduate students, graduate students, and even research specialists, a comprehensive, up-to-date picture of the remarkable advances across the full scope of research on photosynthesis, respiration and related processes.

The titles published in this series are listed at the end of this volume and those of forthcoming volumes on the back cover.

Photosystem I

The Light-Driven Plastocyanin:Ferredoxin Oxidoreductase

Edited by

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Cover Figure Image. The trimeric structure of Photosystem I from cyanobacteria; the view direction is from the stromal side onto the membrane plane. The 12 proteins are shown in a backbone representation (PsaA, blue; PsaB, red; PsaC, pink; PsaD, turquoise; PsaE, light blue; PsaF, yellow; PsaI, dark pink; PsaJ, green; PsaK, gray; PsaL, brown; PsaM, orange and PsaX, light pink). The head groups of the chlorophylls are shown in yellow, their phytyl-tails have been omitted for clarity; the carotenoids are depicted in gray and the lipids in dark turquoise. Figure courtesy of Petra Fromme.

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From the Series Editor

Advances in Photosynthesis and Respiration

Volume 24, Photosystem I: The Light-Driven Plastocyanin: Ferredoxin Oxidoreductase

I am delighted to announce the publication, in *Advances in Photosynthesis and Respiration* (AIPH) Series, of ***Photosystem I: The Light-Driven Plastocyanin:Ferredoxin Oxidoreductase***, a book integrating biochemistry, biophysics and molecular biology of this photosystem that provides the necessary reducing power for carbon fixation in plants, algae and cyanobacteria. This volume was edited by a leading World authority John H. Golbeck of The Pennsylvania State University, University Park, PA, USA. Several earlier AIPH volumes (particularly Volume 10, authored by Bacon Ke) did include a good discussion of Photosystem I; however, the current book integrates all known aspects of this system, including its evolution. The current volume follows the 23 volumes listed below.

Published Volumes (1994–2005)

- *Volume 1:* ***Molecular Biology of Cyanobacteria*** (28 Chapters; 881 pages; 1994; edited by Donald A. Bryant, from USA);
- *Volume 2:* ***Anoxygenic Photosynthetic Bacteria*** (62 Chapters; 1331 pages; 1995; edited by Robert E. Blankenship, Michael T. Madigan and Carl E. Bauer, from USA);
- *Volume 3:* ***Biophysical Techniques in Photosynthesis*** (24 Chapters; 411 pages; 1996; edited by the late Jan Amesz and the late Arnold J. Hoff, from The Netherlands);
- *Volume 4:* ***Oxygenic Photosynthesis: The Light Reactions*** (34 Chapters; 682 pages; 1996; edited by Donald R. Ort and Charles F. Yocum, from USA);
- *Volume 5:* ***Photosynthesis and the Environment*** (20 Chapters; 491 pages; 1996; edited by Neil R. Baker, from UK);
- *Volume 6:* ***Lipids in Photosynthesis: Structure, Function and Genetics*** (15 Chapters; 321 pages; 1998; edited by Paul-André Siegenthaler and Norio Murata, from Switzerland and Japan);
- *Volume 7:* ***The Molecular Biology of Chloroplasts and Mitochondria in Chlamydomonas*** (36 Chapters; 733 pages; 1998; edited by Jean David Rochaix, Michel Goldschmidt-Clermont and Sabeeha Merchant, from Switzerland and USA);
- *Volume 8:* ***The Photochemistry of Carotenoids*** (20 Chapters; 399 pages; 1999; edited by Harry A. Frank, Andrew J. Young, George Britton and Richard J. Cogdell, from USA and UK);
- *Volume 9:* ***Photosynthesis: Physiology and Metabolism*** (24 Chapters; 624 pages; 2000; edited by Richard C. Leegood, Thomas D. Sharkey and Susanne von Caemmerer, from UK, USA and Australia);
- *Volume 10:* ***Photosynthesis: Photobiochemistry and Photobiophysics*** (36 Chapters; 763 pages; 2001; authored by Bacon Ke, from USA);
- *Volume 11:* ***Regulation of Photosynthesis*** (32 Chapters; 613 pages; 2001; edited by Eva-Mari Aro and Bertil Andersson, from Finland and Sweden);
- *Volume 12:* ***Photosynthetic Nitrogen Assimilation and Associated Carbon and Respiratory Metabolism*** (16 Chapters; 284 pages; 2002; edited by Christine Foyer and Graham Noctor, from UK and France);
- *Volume 13:* ***Light Harvesting Antennas*** (17 Chapters; 513 pages; 2003; edited by Beverley Green and William Parson, from Canada and USA);
- *Volume 14:* ***Photosynthesis in Algae*** (19 Chapters; 479 pages; 2003; edited by Anthony Larkum, Susan Douglas and John Raven, from Australia, Canada and UK);
- *Volume 15:* ***Respiration in Archaea and Bacteria: Diversity of Prokaryotic Electron Transport Carriers*** (13 Chapters; 326 pages; 2004; edited by Davide Zannoni, from Italy);
- *Volume 16:* ***Respiration in Archaea and Bacteria 2: Diversity of Prokaryotic Respiratory Systems***

(13 chapters; 310 pages; 2004; edited by Davide Zannoni, from Italy);

- *Volume 17:* ***Plant Mitochondria: From Genome to Function*** (14 Chapters; 325 pages; 2004; edited by David A. Day, A. Harvey Millar and James Whelan, from Australia);
- *Volume 18:* ***Plant Respiration: From Cell to Ecosystem*** (13 Chapters; 250 pages; 2005; edited by Hans Lambers, and Miquel Ribas-Carbo, 2005; from Australia and Spain);
- *Volume 19:* ***Chlorophyll a Fluorescence: A Signature of Photosynthesis*** (31 Chapters; 817 pages; 2004; edited by George C. Papageorgiou and Govindjee, from Greece and USA);
- *Volume 20:* ***Discoveries in Photosynthesis*** (111 Chapters; 1304 pages; 2005; edited by Govindjee, J. Thomas Beatty, Howard Gest and John F. Allen, from USA, Canada and Sweden (& UK));
- *Volume 21:* ***Photoprotection, Photoninhibition, Gene Regulation and Environment Photosynthesis*** (21 Chapters; 380 pages; 2005; edited by Barbara Demmig-Adams, Willam Adams III and Autar K. Mattoo, all from USA);
- *Volume 22:* ***Photosystem II: The Light-Driven Water:Plastoquinone Oxidoreductase*** (34 Chapters; 786 pages; 2005; edited by Thomas J. Wydrzynski and Kimiyuki Satoh, from Australia and Japan, respectively);
- *Volume 23:* ***Structure and Function of the Plastids*** (27 Chapters; 576 pages; 2005; edited by Robert Wise and J. Kenneth Hoober, both from USA)

The next volume in the AIPH Series, also scheduled for publication in 2006, is:

- *Volume 25:* ***Chlorophylls and Bacteriochlorophylls: Biochemistry, Biophysics, Functions and Applications*** (37 Chapters; number of pages not yet available; edited by Bernhard Grimm, Robert Porra, Wolfhart Rüdiger and Hugo Scheer, from Germany and Australia)

Further information on these books and ordering instructions can be found at <http://www. springeronline. com> under the Book Series 'Advances in Photosynthesis and Respiration'. Table of Contents of the earlier volumes (1–19) may be found at <http://www.life. uiuc.edu/govindjee/photosynSeries/ttocs.html>. Special discounts are available to members of the International Society of Photosynthesis Research, ISPR (<http://www.photosyn-thesisresearch.org/>).

About Volume 24: Photosystem I: The Light-Driven Plastocyanin:Ferredoxin Oxidoreductase

This book summarizes, in 40 authoritative chapters, the advances made in the last decade in the biophysics, biochemistry, and molecular biology of the enzyme known as Photosystem I, the light-driven plastocyanin:ferredoxin oxidoreductase. Photosystem I participates along with Photosystem II in harvesting solar energy to supply photosynthetic organisms with stored chemical energy in the form of ATP and stored reducing power in the form of NADPH for processes such as metabolism, growth, and reproduction. This volume is a unique compilation of chapters that include information on molecular architecture, protein-pigment interactions, excitation and electron transfer dynamics, protein-cofactor interactions, kinetics of electron transfer and bioassembly of proteins and cofactors. The volume begins with a series of historical perspectives that provide a solid background to the field, and ends with information on modelling of light-harvesting and electron transfer reactions, and the evolution of the reaction center. Particular attention is paid to spectroscopy, including the theory of the measurement and the interpretation of the data. The book is intended to be a comprehensive and up-to-date source of background information on the Photosystem I reaction center for seasoned researchers, those who are just entering the field, Ph.D. students, researchers and undergraduates in the fields of biophysics, biochemistry, microbiology, agriculture, and ecology.

This book complements "Photosystem II: The Light-Driven Water:Plastoquinone Oxidoreductase" edited by Thomas J. Wydrzynski and Kimiyuki Satoh. Electrons are transferred from water to plastoquinone by Photosystem II. Plastoquinol transfers electrons to Photosystem I via the cytochrome $b_6 f$ complex, and Photosystem I then reduces $NADP^+$.

Photosystem I: The Light-Driven, Plastocyanin: Ferredoxin Oxidoreductase is divided into the following topics: Historical Perspectives (4 chapters); Molecular Architecture (4 chapters); Pigment-Protein Interactions (3 chapters); Excitation Dynamics and Electron Transfer Processes (2 chapters); Modification of the Cofactors and their Environments (2 chapters); Spectroscopic Studies of the Cofactors (8 chapters); Kinetics of Electron Transfer (6 chapters); Biosynthetic Processes (3 chapters); Modeling of Photosystem I Reactions (4 chapters); Cyclic Photophosphorylation (1 chapter); Photoinhibition (1 chapter); and Evolution

(2 chapters). For details see Table of Contents (pp. xi–xxiii) of this extraordinary book.

This book is written by 80 international authorities from 13 countries. It is my privilege to publicly express my thanks to all of them (listed in alphabetical order):

Mikhail **A**ntonkine; James **B**arber; Roberto Bassi; Adam Ben-Shem; Thomas Bibby; Robert Blankenship; Egbert Boekema; Jacques Breton; Donald Bryant; Sergey K. **C**hamorovsky; Roberta Croce; Jan **D**ekker; Bruce A. Diner; Fredrich Drepper; James Duncan; P. Leslie Dutton; Alexander **F**ish; Petra Fromme; John H. **G**olbeck; Carlos Gómez–Moreno; Ingo Grotjohann; Anna **H**aldrup; Toshiharu Hase; Gary Hastings; Manuel Hervás; Michael Hippler; John K. Hurley; Poul Erik **J**ensen; Giles Johnson; Anne Joliot; Pierre Joliot; Navassard **K**arapetyan; Bacon Ke; David Knaff; Konstantin Kogan; Gerd Kothe; Roman Kouřil; Wolfgang **L**ubitz; Richard **M**alkin; Mahir D. Mamedov; Paul Mathis; David Mauzerall; Milagros Medina; Fernando P. Molina-Heredia; Tomas Morosinotto; Christopher C. Moser; José A. **N**avarro; Rachel Nechushtai; Nathan Nelson; Jon Nield; Oleg **P**oluektov; Velupillaimani M. **R**amesh; Fabrice Rappaport; Jason Raymond; Kevin Redding; Thomas Renger; Jean-David Rochaix; Miguel de la Rosa; Yumiko **S**akuragi; Anthony San Pietro; Kenneth Sauer; Sergei Savikhin; Henrik Vibe Scheller; Eberhard Schlodder; Peter Schürmann; Alexey Yu. Semenov; Pierre Sétif; Gaozhong Shen; Vladimir Shinkarev; Anatoli Ya. Shkuropatov; Vladimir A. Shuvalov; Kintake Sonoike; Dietmar Stehlik; Marion **T**hurnauer; Gordon Tollin; Arthur **v**an der Est; Rienk van Grondelle; L. G. Vasilieva; Andrew **W**ebber; and Andrei G. **Y**akovlev

The URL for this book is at:
http://www.life.uiuc.edu/Govindjee/newbook/Volume%2024.html

A Bit of History – From there to here

Just to give a flavor of history, I list below some discoveries. [For historical perspectives, I refer the readers to chapters 1–4 (Anthony San Pietro; Richard Malkin; Bacon Ke; and Paul Mathis & Kenneth Sauer) in this volume.]

- *Discovery of P700, reaction center of Photosystem I (PS I) in The Netherlands.* Bessel Kok (1918–1978; see Kok, Biochim. Biophys. Acta 22: 399–401, 1956), while in Wageningen, The Netherlands, discovered, in several photosynthetic organisms, a light-induced absorbance decrease that had its highest long-wavelength peak at 700 nm (labeled as P700).
- *Two-Light Effects in USA in Baltimre (MD) and Urbana (IL); hypothesis in Cambridge, UK*. Kok and George Hoch, from Baltimore, MD presented in 1960 (see McElroy WD and Glass B (eds) (1961) A Symposium on Light, and Life, pp 397–423. The Johns Hopkins Press, Baltimore, MD), a two-light reaction scheme at about the time Robin Hill and Fay Bendall, in UK, were publishing his now famous Z-scheme (Nature 186: 136–137, 1960). Kok (Plant Physiol. 34: 184–192, 1959) had already shown, in cyanobacteria, that red light oxidized P700 and orange light reduced oxidized P700. He had already related this two-light effect to the Emerson Enhancement effect, discovered earlier by Emerson et al. (Proc. Natl. Acad. Sci., USA, 43: 133–143, 1957).
- *Naming of Photosystem I in Leiden, The Netherlands*. Louis N. M. Duysens et al. (Nature, 190: 510–511, 1961) provided the crucial evidence for the two light reaction two-pigment system scheme, working in series. In the red alga *Porphyridium cruentum*, red light absorbed by chlorophyll *a* oxidized a cytochrome. When green light, absorbed by phycoerythrin, was superimposed, the oxidized cytochrome became reduced. Duysens et al. called the red light 'light 1,' and the chlorophyll *a*-containing system, 'system 1.' The other light, they had called 'light 2,' was absorbed by 'system 2.'
- *Crystal structure of Photosystem I in Berlin, Germany*. P. Jordan et al. (Nature, 411: 909–917, 2001) were the first to resolve the X-ray crystallographic structure of Photosystem I of a thermophilic cyanobacterium for a 3D structure at 2.5 Å resolution.

(For a time-line on oxygenic photosynthesis, see Govindjee and David Krogmann (2004) Photosynthesis Research 80: 15-57.)

Future AIPH Books

The readers of the current series are encouraged to watch for the publication of the forthcoming books (not necessarily arranged in the order of future appearance):

- **Biophysical Techniques in Photosynthesis II** (Editors: Thijs J. Aartsma and Jörg Matisyk);

- **Photosynthesis: A Comprehensive Treatise; Physiology, Biochemistry, Biophysics and Molecular Biology**, **Part 1** (Editors: Julian Eaton-Rye and Baishnab Tripathy); and
- **Photosynthesis: A Comprehensive Treatise; Physiology, Biochemistry, Biophysics and Molecular Biology, Part 2** (Editors: Baishnab Tripathy and Julian Eaton-Rye)
- **The Purple Photosynthetic Bacteria** (Editors: C. Neil Hunter, J. Thomas Beatty, Fevzi Daldal and Marion Thurnauer)

In addition to these contracted books, we are in touch with prospective Editors for the following books:

- Sulfur Metabolism in Photosynthetic Systems
- Molecular Biology of Cyanobacteria II.
- ATP Synthase
- Genomics and Proteomics
- Hydrogen Evolution
- Molecular Biology of Stress
- Global Aspects, Parts 1 and 2
- Artificial Photosynthesis

Readers are encouraged to send their suggestions for these and future volumes (topics, names of future editors, and of future authors) to me by E-mail (gov@uiuc.edu) or fax (1-217-244-7246).

In view of the interdisciplinary character of research in photosynthesis and respiration, it is my earnest hope that this series of books will be used in educating students and researchers not only in Plant Sciences, Molecular and Cell Biology, Integrative Biology, Biotechnology, Agricultural Sciences, Microbiology, Biochemistry, and Biophysics, but also in Bioengineering, Chemistry, and Physics.

Acknowledgments

I take this opportunity to thank and congratulate John H. Golbeck for his outstanding and painstaking editorial work. I thank all the 80 authors (see the list above) of volume 24 of the AIPH Series: without their authoritative chapters, there would be no such volume. We owe thanks to Jacco Flipsen, Noeline Gibson and André Tournois (both of Springer) for their friendly working relation with us that led to the production of this book. I thank Seema Koul (of Techbooks, New Delhi) for her outstanding work on this book; she communicated wonderfully well at every step of the process. Thanks are also due to Jeff Haas (Director of Information Technology, Life Sciences, University of Illinois at Urbana-Champaign, UIUC), Evan DeLucia (Head, Department of Plant Biology, UIUC) and my dear wife Rajni Govindjee for their constant support.

January 26, 2006

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A photograph of **Govindjee** (taken in 2004) with a letter box in the Department of Botany, University of Allahabad; this letter box was used by Govindjee during his pre-PhD days (1952–1956).

Govindjee, the Series Editor of 'Advances in Photosynthesis and Respiration', uses only one name; he was born on October 24, 1932, in Allahabad, India. His father, along with other reformers of that time, belonging to the 'Arya Samaj Movement', dropped their family names, since they reflected the 'caste' of the person. The family name was 'Asthana', a member of the 'Kayastha', who were mostly professionals, including being teachers. Govindjee (whose name was then written as Govind Ji) obtained his B.Sc. (Chemistry, Biology) and M.Sc. (Botany, Plant Physiology) in 1952 and 1954, from the University of Allahabad, India, both in the first division. He came to USA in September, 1956 to work with Robert Emerson; after Emerson's death on February 4, 1959, he became a graduate student of Eugene Rabinowitch, receiving his Ph.D. (Biophysics), in 1960, from the University of Illinois at Urbana-Champaign (UIUC), IL, U.S.A. He has since focused his research mainly on the function of "Photosystem II" (PS II, the water:plastoquinone oxidoreductase), particularly primary photochemical events, the unique role of bicarbonate on the acceptor side of PS II, and the mechanism of 'photoprotection' in plants and algae, using lifetime of chlorophyll a fluorescence measurements. His research on Photosystem I (the topic of this book) has included low temperature fluorescence spectroscopy (1963–1970), and one of the first measurements on its primary photochemistry (J.M. Fenton, M.J. Pellin, Govindjee, and K. Kaufmann (1979) Primary Photochemistry of the Reaction Center of Photosystem I. FEBS Lett. 100: 1–4.; and M.R. Wasielewski, J.M. Fenton, and Govindjee (1987) The Rate of Formation of P700 [$^{+}$]-Ao[$^{-}$] in Photosystem I Particles from Spinach as Measured by Picosecond Transient Absorption Spectroscopy. Photosynth. Res. 12: 181–190.). For further details, on his discoveries and research, see his biography in earlier Advances in Photosynthesis and Respiration volumes. His current focus, however, is on the "History of Photosynthesis Research" and in 'Photosynthesis Education'. He has served the UIUC as an Assistant Professor, Associate Professor and Professor (1961–1999). Since 1999, he has been Professor Emeritus of Biochemistry, Biophysics and Plant Biology at the UIUC. His honors include: Fellow of the American Association of Advancement of Science (1976); Distinguished Lecturer of the School of Life Sciences, UIUC (1978); Fellow and Life Member of the National Academy of Sciences (Allahabad, India, 1978); President of the American Society for Photobiology (1980–1981); Fulbright Senior Lecturer (1996–1997); and Honorary President of the 2004 International Photosynthesis Congress (Montréal, Canada).

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Preface

Photosystem I: The Light-Driven, Plastocyanin:Ferredoxin Oxidoreductase is the 24th volume in the series Advances in Photosynthesis and Respiration (Series Editor, Govindjee). It is one of the two volumes that deal with the photosynthetic reaction centers in oxygenic photosynthetic organisms. The other, Volume 22, is Photosystem II: The Light-Driven Water:Plastoquinone Oxidoreductase, edited by Thomas J. Wydrzynski and Kimiyuki Satoh.

The realization that two independent photochemical reactions are required in oxygenic photosynthesis came about through a series of biophysical observations, particularly with the discovery of the Enhancement Effect in oxygen evolution by Robert Emerson in 1957 that culminated in the codification of the 'Z-scheme' by Robin Hill and Fay Bendall in 1960. The terminology in use today was coined by Lou Duysens, who, in 1961, proposed a hypothetical scheme for photosynthesis composed of two photochemical pigment systems that were termed 'system I' and 'system II'. In the banner year of 1956, three components of what we know as Photosystem I were discovered: Bessel Kok found an absorption change at 700 nm that is now attributed to the oxidation of the primary donor, P700; Mordhay Avron and André Jagendorf isolated a $TPNH_2$ diaphorase, a soluble enzyme that is now known as $NADP^+$:ferredoxin oxidioreductase; and Anthony San Pietro and Helga Lang purified a soluble protein termed PPNR (photosynthetic pyridine nucleotide reductase), a soluble enzyme that is now known as ferredoxin (a story told in detail in Chapter 1). The last soluble component associated with Photosystem I was discovered in 1961 when Sakae Katoh and colleagues isolated plastocyanin, which was then proposed to function as a redox carrier in the Hill reaction and is now known to function as the soluble electron donor to $P700^+$. The physical separation from the membrane of the Photosystem I reaction center as a discrete pigment-protein complex was accomplished by Keith Boardman and Jan Anderson who, in 1964, made use of the detergent digitonin to isolate the 'D-144 particle'. This advance set the stage for dealing with Photosystem I as a distinct pigment-protein complex. By 1970, the focus had switched to the bound cofactors, and the race was on to find the primary electron acceptor, the story of which is provided by the original investigators in Chapters 2 through 4 of this volume.

This book comprises 40 chapters, authored by 80 international experts in the field. The highly diverse nature of Photosystem I is evident in the multiplicity of skills and techniques that have proven necessary to understand how the energy of a photon of visible light is converted into the stable products of oxidized plastocyanin (or cytochrome c_6) and reduced ferredoxin (or flavodoxin). This book is arranged into 11 sections. Following a section on '*Historical Perspectives*', the book is divided into sections that deal with '*Molecular Architecture*', '*Pigment-Protein Interactions*', '*Excitation Dynamics and Electron Transfer Processes*', '*Modification of the Cofactors*', '*Spectroscopic Studies of the Cofactors*', '*Kinetics of Electron Transfer*', '*Biosynthetic Processes*', '*Modeling of Photosystem I Reactions*', '*Related Processes*', and '*Evolution of Photosystem I*'.

The volume covers Photosystem I in sufficient depth so that it is useful not only for molecular biologists, biochemists and biophysicists, but also for plant physiologists, ecologists and those interested in applying lessons learned from natural photosynthesis to artificial photosynthetic systems. I had asked each author to provide an in-depth introduction so that each topic is accessible to the beginners. I had also asked that each author provide sufficient depth so that each of the topics is of value to seasoned researchers. I fully expect that the book will be a source of information not only for undergraduate and graduate students but also for postdoctoral scientists and those who are entering the field for the first time.

I have made no attempt, beyond the most cursory, to enforce a common nomenclature of the proteins or cofactors that comprise Photosystem I. Conventions establish themselves by consensus over time, and to large degree this has happened in this field. Nevertheless there are sub-discipline norms, and a note is made in the 'nomenclature' footnote of those chapters where the nomenclature differs from convention. This volume is not meant to be a textbook in the sense that authors of textbooks strive to give the final word, and to achieve closure, on a topic. On the contrary, no attempt is made to achieve a forced reconciliation or synthesis of controversial issues. Instead, the reader is shown exactly where the points of disagreement lie, and hence, where the boundary of the research frontier is drawn. Such is the nature of a thriving, dynamic discipline. Indeed, it is my hope that this book will stimulate not only the research necessary to solve these problems, but for others to enter this exciting field.

I would like to take this opportunity to acknowledge the authors for providing uniformly excellent chapters. Each author is a leading authority in his/her field, and each has generously offered the time and effort to make this book a success. I thank Petra Fromme for the striking view of the X-ray crystal structure of cyanobacterial Photosystem I which appears on the front cover. I would like to thank my mentors, Anthony San Pietro and Bessel Kok, and my closest colleagues and collaborators, Joseph Warden, Parag Chitnis, Lee McIntosh, Alyosha Semenov, Art van der Est, Dietmar Stehlik and (especially) Don Bryant, all of whom have contributed to the field as well as to my development as a research scientist. I wish to thank my students and postdoctoral scientists for their hard work on Photosystem I over the past 20 years. In particular, I would like to single out Ilya Vassiliev, with whom I have published 30 papers. Ilya was tragically struck by a car and died as this book was being sent to press. Finally, I very much appreciate the support my wife, Carolyn Wilhelm, who (as always) provides assistance and encouragement in all of my endeavors.

I also acknowledge the help received from Noeline Gibson and Jacco Flipson (of Springer, Dordrecht, The Netherlands), from Seema Koul (of TechBooks, New Delhi, India) and from Govindjee (of the University of Illinois at Urbana-Champaign).

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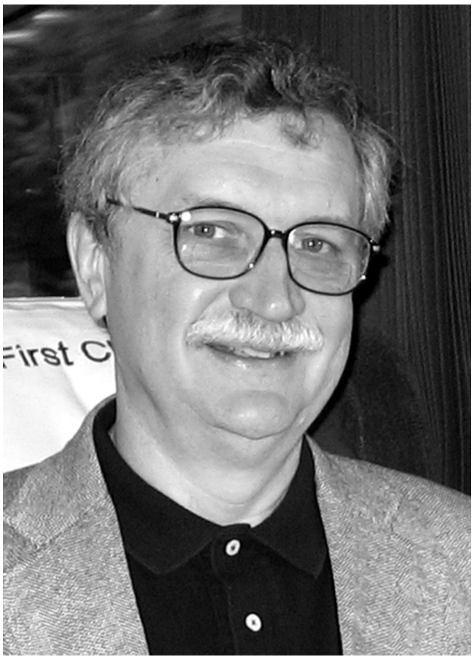

John H. Golbeck

John H. Golbeck is Professor of Biochemistry and Biophysics and Professor of Chemistry at The Pennsylvania State University (Penn State), University Park, PA. John's research interests lie in the assembly, structure, function, and modification of Type I reaction centers. John was born in Wisconsin in 1949. He received his Ph.D. in Biological Chemistry from Indiana University, Bloomington IN, under the supervision of Anthony San Pietro for work related to the bound Fe/S clusters in Photosystem I. His postdoctoral studies at Martin Marietta Laboratories, Baltimore, MD, with Bessel Kok centered around the identification of F_X (A_2) as a third bound Fe/S cluster in Photosystem I. After a five year (ad)venture into industrial research, John went back to university life as Professor in the Chemistry Dept. at Portland State University, Portland, OR, where he focused on isolating the P700-F_X core and on the resolution and reconstitution of the stromal ridge proteins, PsaC, PsaD and PsaE. In 1990, he moved to the Biochemistry Department at the University of Nebraska, Lincoln, NE, where he worked to identify the ligands to the F_A and F_B clusters of PsaC. Six years later, he accepted a position in the Dept. of Biochemistry and Molecular Biology at Penn State, where he studied quinone biosynthetic pathway mutants as a means to biologically introduce novel quinones into Photosystem I. Since 2004, he has held an appointment in the Department of Chemistry at Penn State. John spent sabbatical leaves at Rensselaer Polytechnic Institute (1984), the Centre d'Etudes Nucléaires de Saclay (1992), and most recently at the Freie Universität, Berlin (2002/2003). He has published 120 articles in refereed journals and 10 invited reviews and book chapters. His current research interests involve the genes and proteins that assemble the bound Fe/S clusters, the protein factors that confer redox potentials to organic and inorganic cofactors, and the structural makeup of Type I reaction centers from anaerobic bacteria. His long-term goal lies in modifying Photosystem I to produce H_2. John is a member of the American Society for Biochemistry and Molecular Biology, the Biophysical Society of America, and the International Society for Photosynthesis Research. He presently serves as Secretary for the International Society for Photosynthesis Research. Further information on him and his work can be found at his web site: http://www.bmb.psu.edu/faculty/golbeck/golbeck.html

Dedication: A Tribute to Lee McIntosh

Lee McIntosh (1950–2004)

With the death of Lee McIntosh on June 18, 2004, the scientific community lost an esteemed and valued colleague. Lee's passion for science was apparent to whomever he met, and it never wavered, even through the 5 years that he suffered from chronic lymphocytic leukemia. Lee was born in Los Angeles in 1950. He received his Ph.D. from the University of Washington, Seattle, WA, with Bastiaan J.D. Meeuse and he performed postdoctoral research at Harvard University, Boston, MA, with Laurie Bogorad, where he was a Maria Moors Cabot Postdoctoral Research Fellow. In 1983, Lee worked at the University of Geneva, Switzerland, under a European Molecular Biology Fellowship, and in 1981, he joined the Plant Research Laboratory at Michigan State University, East Lansing, MI. Lee received the Distinguished Faculty award in 2002. At the time of his passing, he was a Distinguished Professor of Biochemistry and Molecular Biology.

Lee's scientific accomplishments were many and varied. He was one of the pioneers in applying the techniques of modern molecular biology to understanding the biochemical mechanisms of photosynthesis. In a wonderful achievement at the time, Lee and his collaborators used directed mutagenesis to identify the electron donor to $P680^+$ as Tyr161 on the D1 polypeptide. Lee's primary interest was focused on plant mitochondria, particularly in the genetics and function of the alternative oxidase (AOX) in plant respiration. His work on Photosystem I involved modifying the ligands to the bound Fe/S clusters as a means of establishing the pathway of electron transfer through F_X, F_B, and F_A. A suppressor mutation of a cysteine mutant to F_A led to his last scientific paper, the identification of a gene that codes for a transcriptional repressor that controls the biosynthesis of Fe/S clusters in cyanobacteria.

Lee's long-term goal was to determine how organelles communicated with each other, particularly how signals were transduced from the mitochrondrion to the nucleus as a way of regulating mitochondrial energy and carbon metabolism. His discoveries were always made in the context of the larger picture, which was to understand at the molecular level the control of energy and carbon flow in plants. His approach was to modify specific proteins and to create new transgenic plant lines in the attempt to dissect the pathways by which nuclear genes are regulated by organelles. These transgenic plants allowed him to study the function of specific nuclear-encoded mitochondrial genes as well as the means by which the mitochondrion signals the nucleus.

Lee was a scientist of uncommon skill and uncompromising integrity. He never tired of pointing out that genetics (and not biochemistry or biophysics) is the engine for making new discoveries in biology. His favorite saying (uttered when a particularly bad idea was put forward) was '*you know, you really don't want to go down that path*'. Lee enjoyed his farm, Walnut Rise, where he and his son Angus Robin raised 30 to 40 Shetland sheep as breeding stock, and for their fleece.

His loss is mourned by all of us who had the pleasure of working with him.

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Color Plates

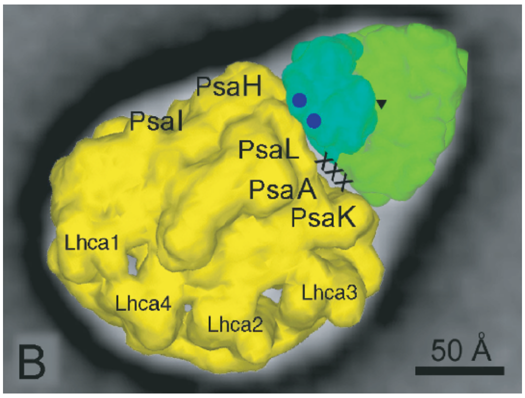

Fig. 1. Model of the PSI-LHCII complex. Assignment of the supercomplex by fitting of the high-resolution structures of PS I (yellow) and trimeric LHCII (green). One LHCII monomer is indicated in blue-green, blue dots mark the spots where the ends of the helices A and B are closest to PS I in projection and the center of the trimer is indicated by a triangle. The part of subunits PSI-A, -H, -I, -K and -L closest to the LHCII trimer has been indicated. Open space in the interfaces of PS I and LHCII is marked by crosses. (Modified from Kouřil et al., 2005.) See Chapter 5, p. 43.

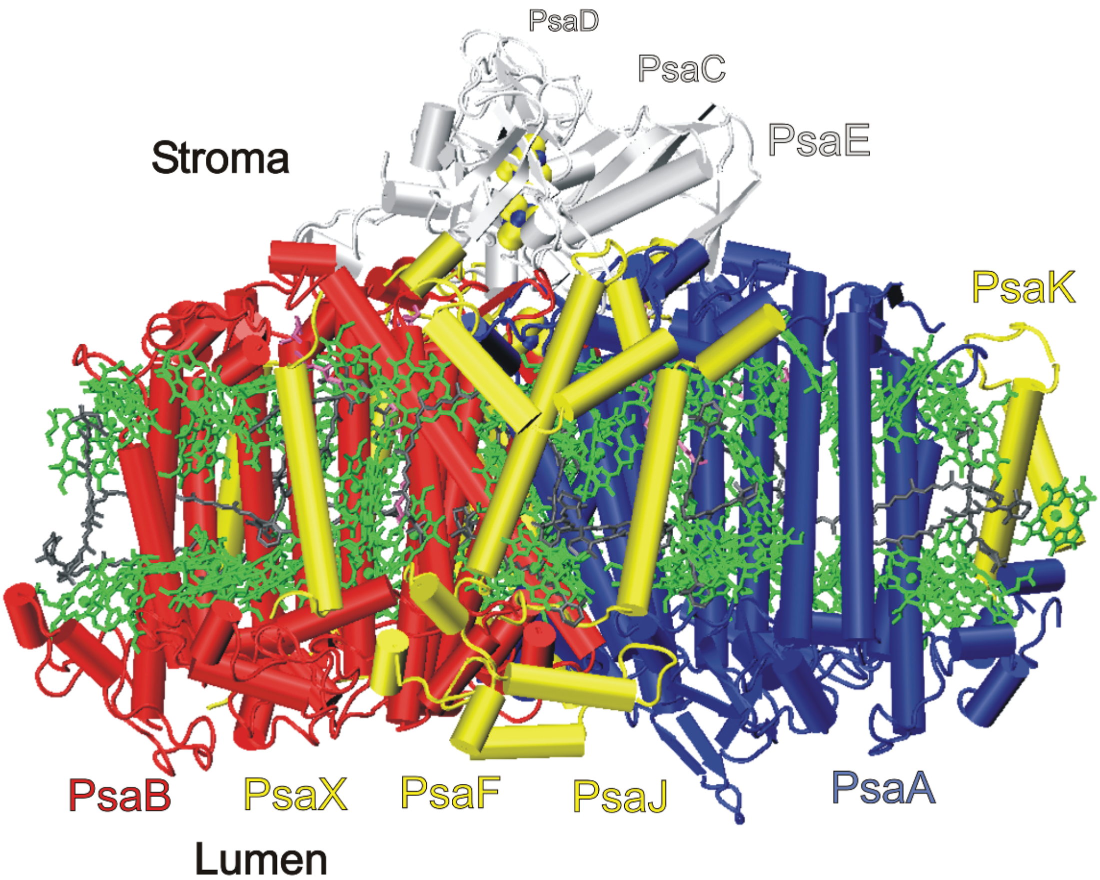

Fig. 2. Photosystem I. PS I with all cofactors as seen from within the membrane plane. The view leads from the distal side into the trimerization site. PsaA is shown in blue, PsaB in red, the small subunits with transmembrane helices in yellow, the stromal subunits in white, chlorophylls in green, carotenoids in grey, lipids in mauve, and Fe/S clusters with yellow/blue spheres. (P. Fromme and I. Grotjohann, unpublished.) See Chapter 6, p. 50.

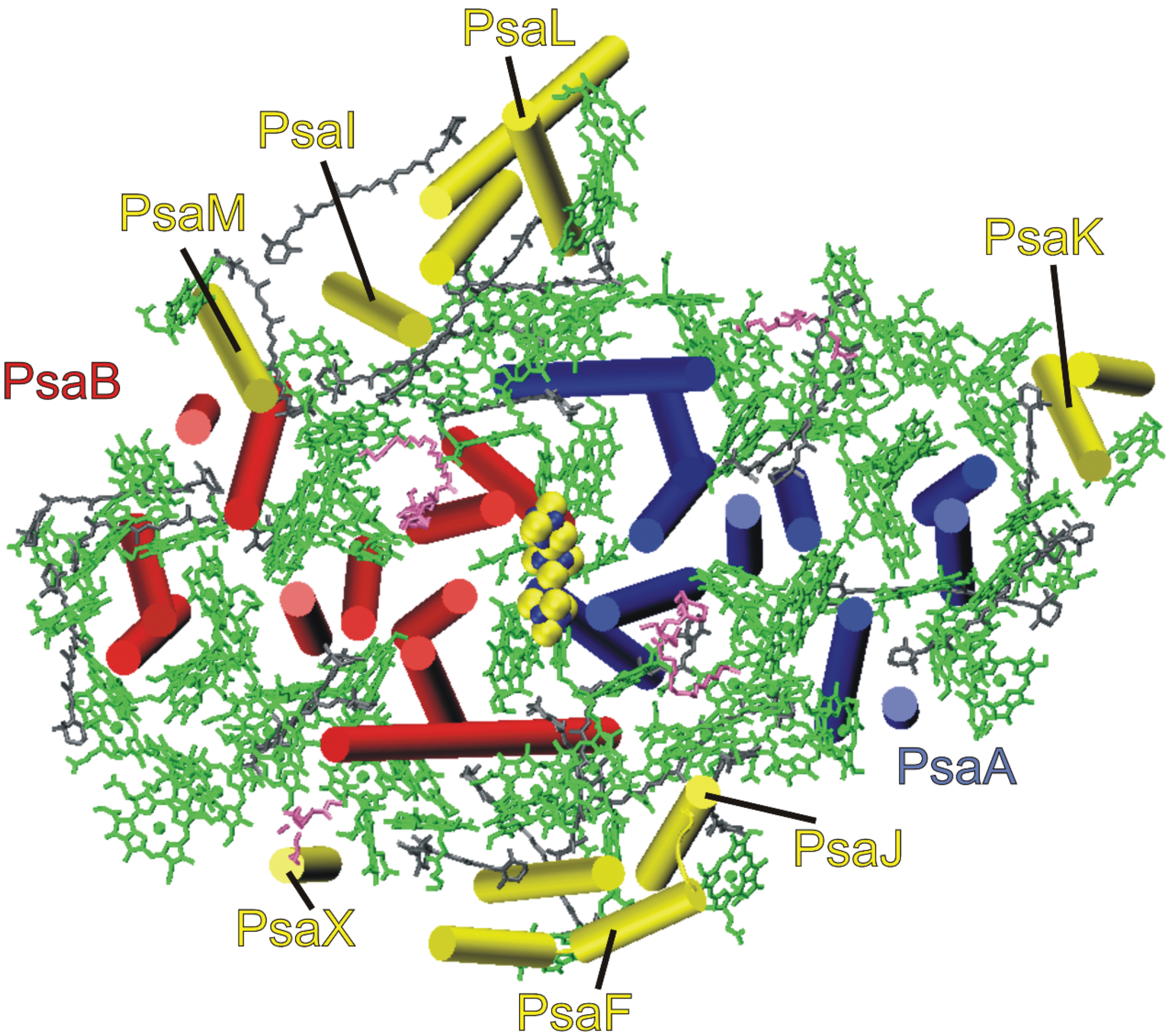

Fig. 2. (*cont.*) Photosystem I. View of the transmembrane helices of the protein backbone with all cofactors as seen from the stroma. The trimerization site can be found on the top of the picture. PsaA is shown in blue, PsaB in red, the small subunits with transmembrane helices in yellow, the stromal subunits in white, chlorophylls in green, carotenoids in grey, lipids in mauve, and Fe/S clusters with yellow/blue spheres. (P. Fromme and I. Grotjohann, unpublished.) See Chapter 6, p. 51.

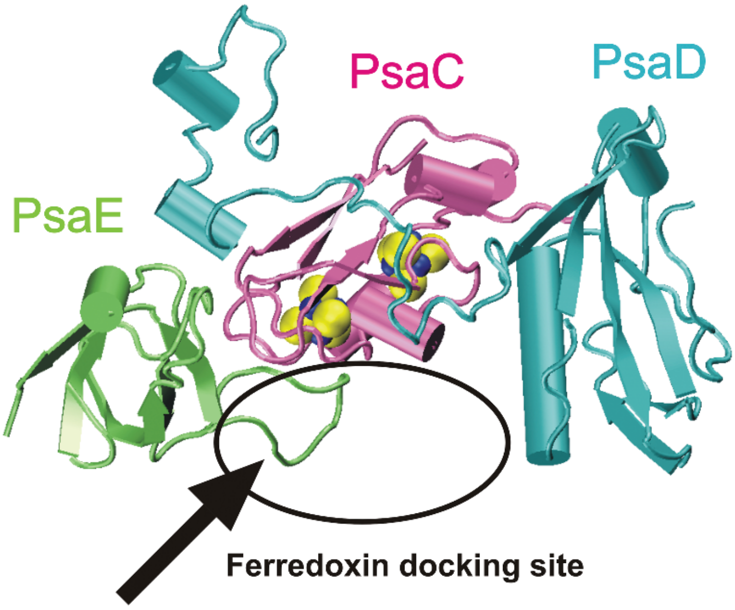

Fig. 1. The stromal subunits of Photosystem I. View from the stromal side of the thylakoid membrane. The subunits PsaC, PsaD, and PsaE form a protein cluster on the stromal side of PS I, which harbors the terminal part of the electron transfer chain. PsaC coordinates the Fe/S clusters F_A and F_B. PsaC is depicted in mauve, PsaD in cyan, and PsaE in lime. The docking site for ferredoxin is indicated. (P. Fromme and I. Grotjohann, unpublished.) See Chapter 6, p. 54.

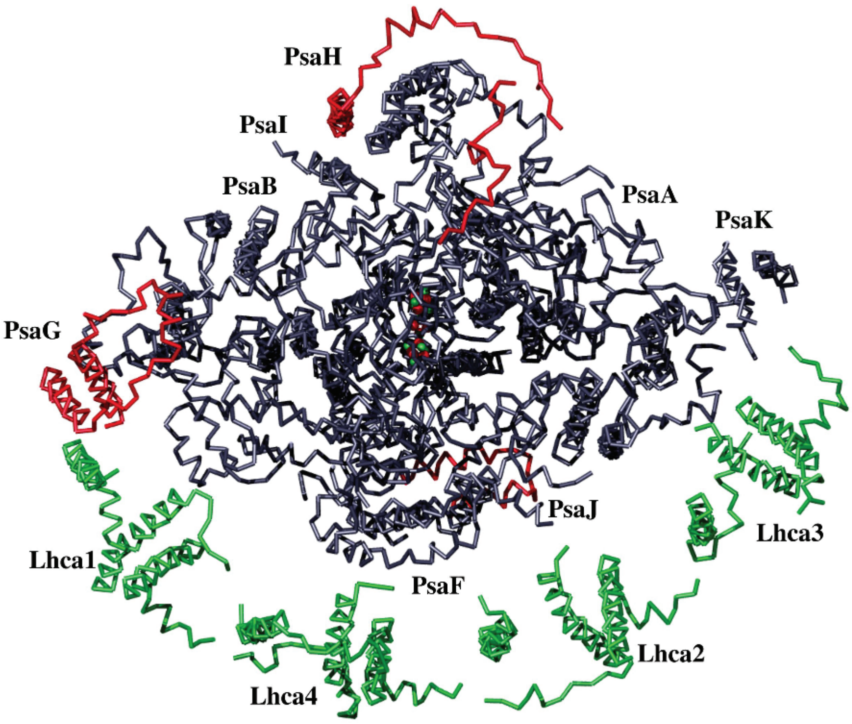

Fig. 2. The Cα backbone model of plant Photosystem I at 4.4 Å resolution. View from the stromal side of the thylakoid membrane. The four light-harvesting proteins are in green (Lhca1-4). Novel structural elements within the RC (core) not present in the cyanobacterial counterpart are colored red, the conserved features of the RC are in grey. The three [4Fe-4S] clusters are depicted as red (Fe) and green (S) balls. Subunits A, B, F, G, H, I, J and K of the RC are indicated. The assignment of the four different Lhca proteins is shown. (Modified from Ben-Shem et al., 2003.) See Chapter 7, p. 73.