Functional Genomics
and
Evolution of Photosynthetic Systems

Advances in Photosynthesis and Respiration

VOLUME 33

The scope of our series 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 organisms, and from X-ray crystallography of proteins to the morphology of 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.

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Functional Genomics and Evolution of Photosynthetic Systems

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Dedication

Teruo Ogawa

The editors dedicate this volume in the series *Advances in Photosynthesis and Respiration* to **Teruo Ogawa**, who has made numerous original contributions to the field of photosynthesis. Teruo began his graduate studies in the laboratory of Professor Kazuo Shibata in the early 1960s, at the Tokyo Institute of Technology. At that time, techniques for the biochemical separation of chlorophyll-protein complexes using detergents began to flourish. Teruo described the first electrophoretic separation of chlorophyll-protein complexes using sodium dodecyl sulfate. This and the concurrent work of Philip Thornber solidified the concept that chlorophyll is coordinated by protein in the photosynthetic membrane and marked a signal point in the path that has ultimately led to the high resolution crystal structures of the photosystems and light-harvesting complexes. Teruo continued this line of investigation joining the lab of Professor Leo Vernon as a postdoc at the Charles F. Kettering Research Laboratory in Yellow Springs, Ohio, working on the isolation of photosystem particles from cyanobacteria. Teruo rejoined Professor Shibata, who had become Head of the Plant Physiology Lab at RIKEN (The Institute of Physical and Chemical Research) to study the mechanism of stomatal movements. With the subsequent formation of a new unit at RIKEN, The Solar Energy Research Group, Teruo assumed a role as Associate Director and began what would become years of successful exploitation of cyanobacterial molecular genetics to understand photosynthetic function.

It was this effective utilization of molecular genetics, and the genomic sequence data of cyanobacteria that deserves special recognition in the context of the present volume. In 1994 Teruo was invited to become a Professor at Nagoya University, where he continued this genetics-based, soon to be genomics-based, understanding of photosynthetic physiology. An indicator of the prolific laboratory output, much of it personally executed, can be found at the Kazusa Institute's genomics website in the catalog of mutants registered by researchers around the world – the overwhelming majority were produced by Teruo and are archived as frozen stocks in the lab of Prof. Masahiko Ikeuchi at the University of Tokyo. The work was fruitful, especially in the area of defining the components of the inorganic carbon concentration mechanism. Overall, the research identified and functionally characterized the role of genes encoding (i) functionally distinct NADPH dehydrogenases, (ii) an iron transporter, (iii) a low-Mn sensing mechanism, (iv) two types of CO_2-uptake systems, and (v) genes encoding a sodium-dependent bicarbonate transporter. Finding functionally distinct NADPH dehydrogenases has led to a new concept regarding their roles, which have been traditionally associated with respiration, yet now appear to exist in diverse structural variations that provide functions ranging from carbon dioxide hydration to sodium pumping. Teruo 'retired' from his Professorship at Nagoya in 2003, but this only marked a change in the experimental modus operarandi, at least from the outsiders' perspective. He continued research abroad and also in Ikeuchi's lab at Tokyo University. He has donned lab coats in Professor Himadri Pakrasi's lab at Washington University, Professor Eva-Mari Aro's lab at the University of Turku, Dr. Hualing Mi's lab at the Shanghai Institute of Plant Physiology and Ecology and in Professor Matthias Rögner's lab at the Ruhr University. Genetic and proteomic studies on the mutants of *Synechocystis* sp. PCC 6803 and *Thermosynechococcus elongatus* with the people in these laboratories advanced the understanding of the structure and function of NDH-1 complexes and the carbon concentrating mechanism. One can count more than sixteen peer-reviewed articles, as well as a number of articles such as book chapters and reviews, all emerging during this 8 year period of 'retired' status.

From the Series Editors

Advances in Photosynthesis and Respiration

Volume 33: Functional Genomics and Evolution of Photosynthetic Systems

We (Tom Sharkey and I) are delighted to announce the publication, in the Advances in Photosynthesis and Respiration (AIPH) Series, of *Functional Genomics and Evolution of Photosynthetic Systems*. Robert (Rob) L. Burnap (of the Department of Microbiology and Molecular Genetics of the Oklahoma State University) and Willem (Wim) F.J. Vermaas (of the School of Life Sciences and the Center for Bioenergy and Photosynthesis of Arizona State University), two international authorities of Molecular Biology of Photosynthesis, have edited this volume. I have personally known both Rob and Wim for many years as scientists of remarkable insight into the field of photosynthesis. Rob is a pioneer in the studies of the metabolic signals resulting from the light reactions and how these signals control the expression and activity of the cyanobacterial carbon-concentrating mechanism. Wim is a pioneer of functional genomics. His major research focus is to understand the physiology of cyanobacteria based not only on genomic, but also on biochemical and biophysical information. His research leads him from *genome* through *proteome* to *metabolome*.

Our Books: 32 Volumes

We list below information on all the 32 volumes that have been published thus far. Beginning with volume 31, Thomas D. Sharkey, who had earlier co-edited volume 9 (Photosynthesis: Physiology and Metabolism) of this Series, has joined me as a co-Series Editor. [Note: Another book 'Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation, edited by Julian J. Eaton-Rye, Baishnab C. Tripathy, and Thomas D. Sharkey', volume 34 in the series, is in the press.]

We are pleased to note that Springer, our publisher, is now producing complete tables of contents of these books and electronic copies of individual chapters of these books; their web sites include free downloadable front matter as well as indexes. The available and anticipated web sites of the books in the Series are listed below. This volume and volume 34 will be the last two with the familiar white cover. A green cover better suited to the increasing web presence will be used for volume 35, which will be published early 2012. The name of the series will also be updated to Advances in Photosynthesis and Bioenergy.

- **Volume 32 (2010): C4 Photosynthesis and Related CO_2 Concentrating Mechanisms**, edited by Agepati S. Raghavendra, and Rowan Sage, from India and Canada. Nineteen chapters, 410 pp, Hardcover, ISBN 978-90-481-9406-3 [http://www.springerlink.com/content/978-90-481-9406-3/]
- **Volume 31 (2010): The Chloroplast: Basics and Applications**, edited by Constantin Rebeiz (USA), Christoph Benning (USA), Hans J. Bohnert (USA), Henry Daniell (USA), J. Kenneth Hoober (USA), Hartmut K. Lichtenthaler (Germany), Archie R. Portis (USA), and Baishnab C. Tripathy (India). Twenty-five chapters, 421 pp, Hard cover, ISBN: 978-90-481-8530-6 [http://www.springerlink.com/content/978-90-481-8530-6/]
- **Volume 30 (2009): Lipids in Photosynthesis: Essential and Regulatory Functions**, edited by Hajime Wada and Norio Murata, both from Japan. Twenty chapters, 506 pp, Hardcover, ISBN: 978-90-481-2862-4; e-book, ISBN: 978-90-481-2863-1 [http://www.springerlink.com/content/978-90-481-2862-4/]
- **Volume 29 (2009): Photosynthesis in Silico: Understanding Complexity from Molecules**, edited by Agu Laisk, Ladislav Nedbal, and Govindjee, from Estonia, The Czech Republic, and

USA. Twenty chapters, 508 pp, Hardcover, ISBN: 978-1-4020-9236-7 [http://www.springerlink.com/content/978-1-4020-9236-7/]

- **Volume 28 (2009): The Purple Phototrophic Bacteria**, edited by C. Neil Hunter, Fevzi Daldal, Marion C. Thurnauer and J. Thomas Beatty, from UK, USA and Canada. Forty-eight chapters, 1014 pp, Hardcover, ISBN: 978-1-4020-8814-8 [http://www.springerlink.com/content/978-1-4020-8814-8/]
- **Volume 27 (2008): Sulfur Metabolism in Phototrophic Organisms**, edited by Christiane Dahl, Rüdiger Hell, David Knaff and Thomas Leustek, from Germany and USA. Twenty-four chapters, 551 pp, Hardcover, ISBN: 978-4020-6862-1 [http://www.springerlink.com/content/978-1-4020-6862-1/]
- **Volume 26 (2008): Biophysical Techniques in Photosynthesis**, Volume II, edited by Thijs Aartsma and Jörg Matysik, both from The Netherlands. Twenty-four chapters, 548 pp, Hardcover, ISBN: 978-1-4020-8249-8 [http://www.springerlink.com/content/978-1-4020-8249-8/]
- **Volume 25 (2006): Chlorophylls and Bacteriochlorophylls: Biochemistry, Biophysics, Functions and Applications**, edited by Bernhard Grimm, Robert J. Porra, Wolfhart Rüdiger, and Hugo Scheer, from Germany and Australia. Thirty-seven chapters, 603 pp, Hardcover, ISBN: 978-1-40204515-8 [http://www.springerlink.com/content/978-1-4020-4515-8]
- **Volume 24 (2006): Photosystem I: The Light-Driven Plastocyanin: Ferredoxin Oxidoreductase**, edited by John H. Golbeck, from USA. Forty chapters, 716 pp, Hardcover, ISBN: 978-1-40204255-3 [http://www.springerlink.com/content/978-1-4020-4255-3]
- **Volume 23 (2006): The Structure and Function of Plastids**, edited by Robert R. Wise and J. Kenneth Hoober, from USA. Twenty-seven chapters, 575 pp, Softcover, ISBN: 978-1-4020- 6570-6; Hardcover, ISBN: 978-1-4020-4060-3 [http://www.springerlink.com/content/978-1-4020-4060-3]
- **Volume 22 (2005): Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase**, edited by Thomas J. Wydrzynski and Kimiyuki Satoh, from Australia and Japan. Thirty-four chapters, 786 pp, Hardcover, ISBN: 978-1-4020-4249-2 [http://www.springerlink.com/content/978-1-4020-4249-2]
- **Volume 21 (2005): Photoprotection, Photoinhibition, Gene Regulation, and Environment**, edited by Barbara Demmig-Adams, William W. Adams III and Autar K. Mattoo, from USA. Twenty-one chapters, 380 pp, Hardcover, ISBN: 978-14020-3564-7 [http://www.springerlink.com/content/978-1-4020-3564-7]
- **Volume 20 (2006): Discoveries in Photosynthesis**, edited by Govindjee, J. Thomas Beatty, Howard Gest and John F. Allen, from USA, Canada and UK. One hundred and eleven chapters, 1304 pp, Hardcover, ISBN: 978-1-4020-3323-0 [http://www.springerlink.com/content/978-1-4020-3323-0]
- **Volume 19 (2004): Chlorophyll *a* Fluorescence: A Signature of Photosynthesis**, edited by George C. Papageorgiou and Govindjee, from Greece and USA. Thirty-one chapters, 820 pp, Hardcover, ISBN: 978-1-4020-3217-2 [http://www.springerlink.com/content/978-1-4020-3217-2]
- **Volume 18 (2005): Plant Respiration: From Cell to Ecosystem**, edited by Hans Lambers and Miquel Ribas-Carbo, from Australia and Spain. Thirteen chapters, 250 pp, Hardcover, ISBN: 978-14020-3588-3 [http://www.springerlink.com/content/978-1-4020-3588-3]
- **Volume 17 (2004): Plant Mitochondria: From Genome to Function**, edited by David Day, A. Harvey Millar and James Whelan, from Australia. Fourteen chapters, 325 pp, Hardcover, ISBN: 978-1-4020-2399-6
- **Volume 16 (2004): Respiration in Archaea and Bacteria: Diversity of Prokaryotic Respiratory Systems**, edited by Davide Zannoni, from Italy. Thirteen chapters, 310 pp, Hardcover, ISBN: 978-14020-2002-5 [http://www.springerlink.com/content/978-1-4020-2002-5]
- **Volume 15 (2004): Respiration in Archaea and Bacteria: Diversity of Prokaryotic Electron Transport Carriers**, edited by Davide Zannoni, from Italy. Thirteen chapters, 350 pp, Hardcover, ISBN: 978-1-4020-2001-8 [http://www.springerlink.com/content/978-0-7923-2001-8/]
- **Volume 14 (2004): Photosynthesis in Algae**, edited by Anthony W. Larkum, Susan Douglas and John A. Raven, from Australia, Canada and UK. Nineteen chapters, 500 pp, Hardcover, ISBN: 978-0-7923-6333-0 [http://www.springerlink.com/content/978-0-7923-6333-0/]
- **Volume 13 (2003): Light-Harvesting Antennas in Photosynthesis**, edited by Beverley R. Green and William W. Parson, from Canada and USA. Seventeen chapters, 544 pp, Hardcover, ISBN: 978-07923-6335-4 [http://www.springerlink.com/content/978-0-7923-6335-4/]
- **Volume 12 (2003): Photosynthetic Nitrogen Assimilation and Associated Carbon and Respiratory Metabolism**, edited by Christine

H. Foyer and Graham Noctor, from UK and France. Sixteen chapters, 304 pp, Hardcover, ISBN: 978-07923-6336-1 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-6336-1]
- **Volume 11 (2001): Regulation of Photosynthesis**, edited by Eva-Mari Aro and Bertil Andersson, from Finland and Sweden. Thirty-two chapters, 640 pp, Hardcover, ISBN: 978-0-7923-6332-3 [http://www.springerlink.com/content/978-0-7923-6332-3]
- **Volume 10 (2001): Photosynthesis: Photobiochemistry and Photobiophysics**, authored by Bacon Ke, from USA. Thirty-six chapters, 792 pp, Softcover, ISBN: 978-0-7923-6791-8; Hardcover: ISBN: 978-0-7923-6334-7 [http://www.springerlink.com/content/978-0-7923-6334-7]
- **Volume 9 (2000): Photosynthesis: Physiology and Metabolism**, edited by Richard C. Leegood, Thomas D. Sharkey and Susanne von Caemmerer, from UK, USA and Australia. Twenty-four chapters, 644 pp, Hardcover, ISBN: 978-07923-6143-5 [http://www.springerlink.com/content/978-0-7923-6143-5]
- **Volume 8 (1999): The Photochemistry of Carotenoids**, edited by Harry A. Frank, Andrew J. Young, George Britton and Richard J. Cogdell, from UK and USA. Twenty chapters, 420 pp, Hardcover, ISBN: 978-0-7923-5942-5 [http://www.springerlink.com/content/978-0-7923-5942-5]
- **Volume 7 (1998): The Molecular Biology of Chloroplasts and Mitochondria in *Chlamydomonas***, edited by Jean David Rochaix, Michel Goldschmidt-Clermont and Sabeeha Merchant, from Switzerland and USA. Thirty-six chapters, 760 pp, Hardcover, ISBN: 978-0-7923-5174-0 [http://www.springerlink.com/content/978-0-7923-5174-0]
- **Volume 6 (1998): Lipids in Photosynthesis: Structure, Function and Genetics**, edited by Paul-André Siegenthaler and Norio Murata, from Switzerland and Japan. Fifteen chapters, 332 pp, Hardcover, ISBN: 978-0-7923-5173-3 [http://www.springerlink.com/content/978-0-7923-5173-3]
- **Volume 5 (1997): Photosynthesis and the Environment**, edited by Neil R. Baker, from UK. Twenty chapters, 508 pp, Hardcover, ISBN: 978- 07923-4316-5 **[**http://www.springerlink.com/content/978-0-7923-4316-5**]**
- **Volume 4 (1996): Oxygenic Photosynthesis: The Light Reactions**, edited by Donald R. Ort, and Charles F. Yocum, from USA. Thirty-four chapters, 696 pp, Softcover: ISBN: 978-0-7923-3684-6; Hardcover, ISBN: 978-0-7923-3683-9 [http://www.springerlink.com/content/978-0-7923-3683-9]
- **Volume 3 (1996): Biophysical Techniques in Photosynthesis**, edited by Jan Amesz and Arnold J. Hoff, from The Netherlands. Twenty-four chapters, 426 pp, Hardcover, ISBN: 978-0-7923-3642-6 [http://www.springerlink.com/content/978-0-7923-3642-6]
- **Volume 2 (1995): Anoxygenic Photosynthetic Bacteria**, edited by Robert E. Blankenship, Michael T. Madigan and Carl E. Bauer, from USA. Sixty-two chapters, 1331 pp, Hardcover, ISBN: 978-0-7923-3682-8 [http://www.springerlink.com/content/978-0-7923-3681-5]
- **Volume 1 (1994): The Molecular Biology of Cyanobacteria**, edited by Donald R. Bryant, from USA. Twenty-eight chapters, 916 pp, Hardcover, ISBN: 978-0-7923-3222-0 [http://www.springerlink.com/content/978-0-7923-3222-0/]

Further information on these books and ordering instructions can be found at http://www.springer.com/series/5599. Contents of volumes 1–29 can also be found at http://www.life.illinois.edu/govindjee/g/References.html.

Special 25% discounts are available to members of the International Society of Photosynthesis Research, ISPR http://www.photosynthesisresearch.org/: See http://www.springer.com/ispr

This Book

"*Functional Genomics and Evolution of Photosynthetic Systems*" is volume 33 of the Advances in Photosynthesis and Respiration Series. The preface of the book on pp. xxiii–xxv beautifully describes the context of this book, and the contents of this book on pp. xvii–xxi shows the breadth of this book.

According to the editors Rob Burnap and Wim Vermaas, "This book was inspired by the new possibilities brought about by the stunning number of genomic sequences that are currently, or will soon become, available for photosynthetic organisms. This new world of whole genome sequence data spans the phyla from photosynthetic microbes to algae to higher plants. These whole genome projects are intrinsically interesting, but also tell us about the variety of other molecular sequence databases including the recent 'meta-genomic' sequencing efforts that analyze entire communities of organisms. The fruits of these sequencing projects, as impressive as they are, are obviously only the beginning of the effort to decipher the biological meaning encoded within them. This book highlights progress in this direction. It includes discussion of promising approaches in analyzing the wealth of sequence information and the resultant insights these analyses are providing regarding the function and evolution of photosynthesis. This book aims toward a genome-level understanding of the structure, function, and evolution of photosynthetic systems and the advantages accrued from the availability of diverse sets of gene sequences for the major components of the photosynthetic apparatus. It provides a good introduction to some of the many aspects of the genomics of photosynthetic systems in relation to the variety of photosynthetic mechanisms that have evolved. This book will serve both the established researchers and educators who wish to understand this rapidly developing area as well as young scientists starting their research career."

Authors

The current book contains 15 chapters written by 44 authors from seven countries (Canada; China; Denmark; Germany; Spain; Sweden and USA), with most authors from the USA. We thank all the authors for their valuable contribution to this book; their names (arranged alphabetically) are:

Iwona **A**damska (Germany; Chapter 11); Birgit E. Alber (USA; Chapter 9); Jens Appel (USA; Chapter 15); Shaun **B**ailey (USA; Chapter 6); J. Thomas Beatty (Canada; Chapter 10; co-editor of volumes 20 and 28 of this Series); Devaki Bhaya (USA; Chapter 2); Donald A. Bryant (USA; Chapter 1, Chapter 3; editor of volume 1 of this Series); Robert L. Burnap (USA; Chapter 13; co-editor of this volume); Fei **C**ai (USA; Chapter 14); You Chen (USA; Chapter 5); Wei Chi (China; Chapter 7); Frederick M. Cohan (USA; Chapter 1); Johannes **E**ngelken (Spain, Chapter 11); Niels-Ulrik **F**rigaard (Denmark; Chapter 3); Christiane Funk (Sweden; Chapter 11); Amaya M. **G**arcia-Costas (USA; Chapter 3); John H. Golbeck (USA; Chapter 12; editor of volume 24 of this Series); Susan S. Golden (USA; Chapter 5); David González-Ballester (USA; Chapter 6); Arthur R. Grossman (USA; Chapter 6); Thomas E. **H**anson (USA; Chapter 9); Caroline S. Harwood (USA; Chapter 10); C. Kay Holtman (USA; Chapter 5); Bharat **J**agannathan (USA; Chapter 12); Steven J. **K**arpowicz (USA; Chapter 6); Cheryl A. Kerfeld (USA; Chapter 14); Christian G. Klatt (USA; Chapter 1, Chapter 3); Andrew S. **L**ang (Canada; Chapter 10); Tao Li (USA; Chapter 3); Marc Linka (Germany; Chapter 8); Zhenfeng Liu (USA; Chapter 3); Sabeeha S. **M**erchant (USA; Chapter 6; coeditor of volume 7 of this Series); Aparna **N**agarajan (USA; Chapter 13); Jörg **O**vermann (Germany; Chapter 3); Brian **P**alenik (USA; Chapter 4); Gustaf **S**andh (USA; Chapter 14); Gaozhong Shen (USA; Chapter 12); F. Robert **T**abita (USA; Chapter 9); Arnaud Taton (USA; Chapter 5); David M. **W**ard (USA; Chapter 1, Chapter 3); Andreas P.M. Weber (Germany; Chapter 8); Jason Wood (USA; Chapter 1); Lixin **Z**hang (China; Chapter 7); and Fangqing Zhao (USA; Chapter 3).

Future Advances in Photosynthesis and Respiration and Other Related Books

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

- The Bioenergetic Processes of Cyanobacteria: From Evolutionary Singularity to Ecological Diversity (Editors: Guenter A. Peschek, Christian Obinger, and Gernot Renger) [http://www.springer.com/life+sciences/book/978-94-007-0352-0]
- Chloroplast Biogenesis: During Leaf Development and Senescence (Editors: Basanti Biswal, Karin Krupinska and Udaya Chand Biswal)
- The Structural Basis of Biological Energy Generation (Editor: Martin Hohmann-Marriott)
- Genomics of Chloroplasts and Mitochondria (Editors: Ralph Bock and Volker Knoop)
- Photosynthesis in Bryophytes and Early Land Plants (Editors: David T. Hanson and Steven K. Rice)

In addition to the above contracted books, the following topics are under consideration:

- Algae, Cyanobacteria: Biofuel and Bioenergy
- Artificial Photosynthesis
- ATP Synthase and Proton Translocation
- Bacterial Respiration II
- Biohydrogen Production
- Canopy Photosynthesis

- Carotenoids II
- Cyanobacteria II
- The Cytochromes
- Ecophysiology
- Evolution of Photosynthesis
- FACE Experiments
- Global Aspects of Photosynthesis
- Green Bacteria and Heliobacteria
- Interactions between Photosynthesis and other Metabolic Processes
- Limits of Photosynthesis: Where do we go from here
- Photosynthesis, Biomass and Bioenergy
- Photosynthesis under Abiotic and Biotic Stress
- Plant Canopies and Photosynthesis
- Plant Respiration II

If you have any interest in editing/co-editing any of the above listed books, or being an author, please send an E-mail to Tom Sharkey (tsharkey@msu.edu) and/or to me at gov@illinois.edu. Suggestions for additional topics are also welcome.

In view of the interdisciplinary character of research in photosynthesis and respiration, it is our 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, Chemical Biology, Biological Physics, and Biophysics, but also in Bioengineering, Chemistry, and Physics.

We take this opportunity to thank and congratulate Rob Burnap and Wim Vermaas for their outstanding editorial work; they have done a fantastic job not only in editing, but also in organizing this book for all of us, and for their highly professional dealing with the reviewing process. We thank all the 44 authors of this book (see the list above): without their authoritative chapters, there would be no such volume. We give special thanks to A. Lakshmi Praba of SPi Global, India for directing the typesetting of this book; her efficiency and politeness in dealing with the authors and the editors has been crucial in bringing this book to completion. We owe Jacco Flipsen, Ineke Ravesloot and André Tournois (of Springer) thanks for their friendly working relationship with us that led to the production of this book. Further, I thank Tom Sharkey, my co-editor of this Series since volume 31, for his constant involvement and support.

As always, I am indebted to the offices of the Department of Plant Biology (Head: Feng Sheng Hu) and of the Information Technology, Life Sciences (Director: Jeff Haas) of the University of Illinois at Urbana-Champaign, for their continued support. I remain highly indebted to my dear wife Rajni Govindjee for her everlasting support on all matters of my life.

August 15, 2011

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Series Editors

A photograph of Govindjee wearing Andy Benson's bow-tie (for details, see Govindjee (2010) Photosynth. Res. 105:201–208, Fig. 12).

Govindjee, who uses one name only, was born on October 24, 1932, in Allahabad, India. Since 1999, he has been Professor Emeritus of Biochemistry, Biophysics and Plant Biology at the University of Illinois at Urbana-Champaign (UIUC), Urbana, IL, USA. He obtained his B.Sc. (Chemistry and Biology) and M.Sc. (Botany; Plant Physiology) in 1952 and 1954, from the University of Allahabad. He studied 'Photosynthesis' at the UIUC, under two pioneers of photosynthesis Robert Emerson, and Eugene Rabinowitch, obtaining his Ph.D. in 1960, in Biophysics. He is best known for his research on the excitation energy transfer, light emission, the primary photochemistry and the electron transfer in "Photosystem II" (PS II, water-plastoquinone oxido-reductase). His research, with many collaborators, has included the discovery of a short-wavelength form of chlorophyll (Chl) *a* functioning in the Chl *b*-containing system, now called PS II; of the two-light effect in Chl *a* fluorescence; and, with his wife Rajni Govindjee, of the two-light effect (Emerson Enhancement) in NADP reduction in chloroplasts. His major achievements, together with several other researchers, include an understanding of the basic relationships between Chl *a* fluorescence and photosynthetic reactions; an unique role of bicarbonate/carbonate on the electron acceptor side of PS II, particularly in the protonation events involving the Q_B binding region; the theory of thermoluminescence in plants; the first picosecond measurements on the primary photochemistry of PS II; and the use of Fluorescence Lifetime Imaging Microscopy (FLIM) of Chl *a* fluorescence in understanding photoprotection, by plants, against excess light. His current focus is on the 'History of Photosynthesis Research', in 'Photosynthesis Education', and in the 'Possible Existence of Extraterrestrial Life'. He has served on the faculty of the UIUC for ~ 40 years. Govindjee's honors include: Fellow of the American Association of Advancement of Science (AAAS); Distinguished Lecturer of the School of Life Sciences, UIUC;

Fellow and Lifetime member of the National Academy of Sciences (India); President of the American Society for Photobiology (1980–1981); Fulbright Scholar and Fulbright Senior Lecturer; Honorary President of the 2004 International Photosynthesis Congress (Montréal, Canada); the first recipient of the Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology, 2006; Recipient of the Communication Award of the International Society of Photosynthesis Research, 2007; and the Liberal Arts and Sciences Lifetime Achievement Award of the UIUC, 2008. Further, Govindjee was honored (1) in 2007, through two special volumes of Photosynthesis Research, celebrating his 75th birthday and for his 50-year dedicated research in 'Photosynthesis' (Guest Editor: Julian Eaton-Rye), and (2) in 2008, through a special International Symposium on 'Photosynthesis in a Global Perspective', held in November, 2008, at the University of Indore, India. Govindjee is coauthor of 'Photosynthesis' (John Wiley, 1969); and editor of many books, published by several publishers including Academic Press and Kluwer Academic Publishers (now Springer). Since 2007, each year a Govindjee and Rajni Govindjee Award is given to graduate students, by the Department of Plant Biology, at the UIUC, to recognize Excellence in Biological Sciences. For further information on Govindjee, see his web site at http://www.life.illinois.edu/govindjee.

Thomas D. (Tom) Sharkey obtained his Bachelor's degree in Biology in 1974 from Lyman Briggs College, a residential science college at Michigan State University, East Lansing, Michigan. After 2 years as a research technician, Tom entered a PhD program in the federally funded Plant Research Laboratory at Michigan State University under the mentorship of Klaus Raschke and finished in 1979 after just 3 years and 3 months. Post-doctoral research was carried out with Graham Farquhar at the Australian National University, in Canberra, Australia, where he coauthored a landmark review on photosynthesis and stomatal conductance that continues to get over 50 citations per year more than 25 years after its publication. For 5 years, he worked at the Desert Research Institute, Reno, Nevada. After Reno, Tom spent 20 years as Professor of Botany at the University of Wisconsin in Madison. In 2008, Tom became Professor and Chair of the Department of Biochemistry and Molecular Biology at Michigan State University. Tom's research interests center on the exchange of gases between plants and the atmosphere. The biochemistry and biophysics underlying carbon dioxide uptake and isoprene emission from plants form the two major research topics in his laboratory. Among his contributions are measurement of the carbon dioxide concentration inside leaves, an exhaustive study of short-term feedback effects in carbon metabolism, and a significant contribution to elucidation of the pathway by which leaf starch breaks down at night. In the isoprene research field, Tom is recognized as the leading advocate for thermotolerance of photosynthesis as the explanation for why plants emit isoprene. In addition, his laboratory has cloned many of the genes that underlie isoprene synthesis and published many papers on the biochemical regulation of isoprene synthesis. Tom has edited two books, the first on trace gas emissions from plants in 1991 and then volume 9 of this series (*Advances in Photosynthesis and Respiration*) on the physiology of carbon metabolism of photosynthesis in 2000. Tom is coeditor of volume 34, titled "*Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*" of this series with Julian Eaton-Rye and Baishnab Tripathy. Tom is listed in Who's Who and is a "Highly Cited Researcher" according to the Thomson Reuters Institute for Scientific Information.

Contents

Preface

Recent advances in the genomics of photosynthetic organisms, coupled with increased understanding of the photosynthetic mechanisms, provide new perspectives on the function and evolution of the photosynthetic machinery. A central theme of this book '*Functional Genomics and Evolution of Photosynthetic Systems*' is how the explosive growth in biological sequence data is leading to a better understanding of the operation and evolution of photosynthetic mechanisms. The book illustrates the interplay between genomic information, bioinformatic analysis and molecular methods to obtain a better understanding of photosynthesis and its development. This interplay has further informed us on the evolution and functional diversification of well-known structures, such as the photosynthetic antennae and reaction centers. Since many photosynthetic structures and pathways are increasingly well understood, even at the atomic level, the large amount of genomic sequence information can now be integrated with structural and mechanistic knowledge of photosynthetic mechanisms and physiology. While not meant to be fully comprehensive in terms of the topics covered, the book provides detailed views of specific cases and thereby illustrates important new directions that are being taken in this fast-moving field – a field that involves the integration of bioinformatics, molecular biology, physiology, and ecology. The book is intended for a wide audience but it is designed specifically for advanced undergraduate and graduate students and for researchers in photosynthesis who are interested in functional genomics, bioinformatics, and evolution of photosynthesis.

The book includes two broad perspectives that have benefitted from the *genomics revolution* – first, the perspective examining whole genome and metagenomic information, and second, the perspective looking into the individual photosynthetic complexes and enzyme systems. The first perspective, introduced in **Chapter 1**, emphasizes the importance of placing genomic information within eco-physiological context in order to understand the functionalities, such as photosynthetic capacity, encoded within the genomic DNA sequences. What level of genomic diversity exists at the species/genus levels? How do various genotypes partition into different ecological niches? The authors of Chapter 1 provide a current analysis of hot springs mat communities in Yellowstone National Park; this habitat contains many photosynthetic bacteria, several of which are comprehensively discussed elsewhere in this book.

Chapter 2 describes a multi-pronged strategy that led to the total genomic sequencing of a pair of cyanobacterial strains (ecotypes) that play dominant roles in the photosynthetic ecology of the hot spring mat ecosystem. This has permitted genomic comparisons, for example, to evaluate the role of insertion and deletions, events leading to genomic divergence. And, when integrated with ecophysiological information, this kind of analysis leads to an understanding of how specific genotypes become associated with particular ecological niches. Further, by using the genomic sequences as reference 'scaffolds' for comparison with metagenomic sequence information, ideas on the origins of sequence diversity within closely related populations begin to emerge.

Chapter 3 summarizes insights gained from an analysis of a massive set of genomic and metagenomic sequence data for the three major taxa comprising the so-called 'green bacteria'. As with the cyanobacteria from the hot springs, discussed in the first two chapters, the synergy between whole-genome sequencing and the more fragmentary, but more ecologically representative metagenomic data of the various green bacteria permits researchers to draw detailed conclusions on the probable evolution of specific metabolic processes and, at the same time, to place these findings in a more meaningful ecological context. Together, these analyses bring us closer to the answers to the question of what constitutes a bacterial species and what are the molecular mechanisms of adaptation to specific ecological niches. Studies of different phototrophs that occupy very different ecological niches, likewise, move us towards answers to these crucial questions of biology. Recent findings on the marine cyanobacteria in the taxonomic group

Synechococcus are presented in **Chapter 4**. Here, the author describes how genomic information has led to advanced gene expression analysis to understand niche specialization in terms of the patterns of gene expression under changing environmental conditions. This again sheds light on fundamental biological questions into how various genotypes partition into different ecological niches within the marine environment.

Very much has been, and will continue to be, learned from photosynthetic model systems. Chapters 5–7 illustrate this by showing the latest application of cutting-edge functional genomics approaches to three well-studied photosynthetic organisms, the cyanobacterium *Synechococcus*, the green alga *Chlamydomonas*, and the angiosperm *Arabidopsis*. In **Chapter 5**, an elegant molecular genetic approach is described to define the function of potentially all genes in the chromosome of the *Synechococcus* sp PCC 7942. Chapters 6 and 7 lead us away from the prokaryotic phototrophs and introduce the reader to the latest developments regarding photosynthesis in the eukaryotes, *Chlamydomonas* and *Arabidopsis*. A comprehensive discussion of the new insights into the photosynthesis genes of the recently sequenced *Chlamydomonas* genome is presented in **Chapter 6**; this chapter describes a multi-pronged approach involving high-throughput methods and path-finding bioinformatic analysis to discover and find function of photosynthesis genes using, among other techniques, comparative genomics. High-throughput techniques also figure prominently into the description of the current status of understanding the photosynthetic mechanism of the very well studied higher plant, Arabidopsis, as presented in **Chapter 7**.

Photosynthetic carbon metabolism has turned out to be much more varied and complex than could have been imagined immediately following the studies that originally defined the individual steps of the Calvin-Benson-Bassham cycle. Furthermore, photosynthetic metabolism in eukaryotes involves cooperation of multiple subcellular compartments including the chloroplast. **Chapter 8** probes the question of the evolution of photosynthetic metabolism in organisms containing chloroplasts. As originally surmised by microscopists in the late nineteenth century, it is now recognized that the chloroplasts of algae and plants derive from the ancient endosymbiotic capture of once free-living cyanobacteria – these endosymbionts have evolved within the cytoplasm of their hosts to become present-day chloroplasts. The authors of Chapter 8 address the thought-provoking question of how two separate metabolic systems (endosymbiont and host) became integrated into the finely-tuned, compartmentalized metabolic systems found in algae and plants. The topic of photosynthetic metabolism is broadened in **Chapter 9** where an insightful presentation is given of the remarkable diversity of carbon-fixing mechanisms. The Chapter richly benefits from the growing wealth of genomic information on both the structural and regulatory components of carbon fixation systems in autotrophic prokaryotes and eukaryotes.

The final six chapters provide the other broad perspective of the book: how the ever-growing volume of genetic data has illuminated the study of individual photosynthetic complexes and enzyme systems. This section of the book considers 'genome-enabled' and bioinformatic approaches for the understanding of the structure, function, and evolution of photosynthetic mechanisms. The evolution of the light-harvesting complexes of purple phototrophic bacteria is analyzed in **Chapter 10**, where a careful and comprehensive phylogenetic analysis illustrates the fundamentals of gene family evolution in this ancient protein family. Evidence consistent with convergent evolution of function and examples of horizontal gene transfer are presented. Similarly, the evolution of the large and widespread light-harvesting chlorophyll protein superfamily is tackled in **Chapter 11**. Based upon their analysis, the authors discuss the taxonomy of this superfamily and present a plausible model how the ancestral protein duplicated and diverged to adopt the various functional roles played, now seen among the individual members of the superfamily. Insights on the structure, function, and evolution of individual complexes and pathways have developed, for example, from bioinformatic analyses through the identification of conserved amino acids, in turn reflecting functional constraints on replacement through mutational events. The discussion of the conservation features can be enriched by connecting the sequence/structure information with known functional roles when these roles are known from actual experiments or by a discussion of hypotheses where conserved features have been identified, but experimental information is not yet established. The authors of **Chapter 12** examine our current knowledge on the evolution of Type I photosynthetic reaction centers and the selective forces that may have been at work during the evolution of structural asymmetry during the evolution of heterodimeric Photosystem I from the ancestral homodimeric versions that are presently represented in certain anaerobic phototrophs. This chapter also provides an excellent treatment of the literature on the current thinking about the evolution of photosynthesis on primordial Earth. In **Chapter 13**, the evolution of Photosystem II is discussed, including a description of techniques that allow the projection of amino acid residue conservation obtained from large sets of multiple sequence alignments on to the three-dimensional structure of the reaction center complex. The emerging topic of bacterial protein micro-compartments is discussed in **Chapter 14** with a presentation of the structural aspects of the carboxysome, which is part of the carbon concentrating mechanism in a wide range of prokaryotes, most notably the cyanobacteria. Finally, the function and evolution of the various hydrogenases found in Nature is considered in **Chapter 15**. A detailed presentation of structure, function, and genetics of the major hydrogenase protein families is given with an eye towards the ultimate biotechnological application of hydrogenases for solar energy production.

We emphasize that the impact of genomic and bioinformatic approaches on the field of photosynthesis is bidirectional: not only has the genomics revolution benefitted the field of photosynthesis, but the reciprocal is equally true. The photosynthetic community has the ability to make a unique contribution to the field of genomics and bioinformatics since a reasonably comprehensive knowledge-base of the various components (*e.g.*, reaction centers; see volumes 22, 24 and 28 in the Advances in Photosynthesis and Respiration Series) and pathways (*e.g.*, chlorophyll biosynthesis; see volume 31 in the same Series) of the different photosynthetic mechanisms has been established. It is often possible to add great depth to the ‘annotations’ of the sets of genes encoding photosynthetic structures. In this way, examples of how photosynthetic genomes function and evolve can provide more tangible insights into the broader issues of genome function, evolution, and speciation. Importantly, efforts to place genomic sequence data in the context of metagenomic community information are discussed in terms of long-standing questions of niche and speciation.

Finally, we thank the many people who have made this book project a reality. This includes the contributors of the chapters (see list of Contributors, pp. i-xxxiii) for their efforts and patience during the development of the book. Many thanks go to members of one of our groups (that of RLB), especially Hong Hwang and Anthony Kappell, for their contributions to the editing. RLB especially thanks his wife, Kathy (Ling), for her enduring support and patience during this and other projects. We also thank Jacco Flipsen, Ineke Ravesloot and Andre Tournois of Springer, and A. Lakshmi Praba of SPi Global for her friendly and valuable guidance during the typesetting and printing of this book.

We are grateful to Govindjee for inviting us to edit this work and for his constant guidance and support from its inception to the final release of this book. RLB acknowledges that his efforts on this book were supported by the US National Science Foundation under Grant MCB 0818371 and US Department of Energy grant DE-FG02-08ER15968 from Energy Biosciences Division.

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The Editors

Robert (Rob) L. Burnap first developed an interest in photosynthesis during a summer field course in marine biology at Woods Hole (Massachusetts, USA), while an undergraduate student at the University of Michigan from where he graduated in 1977. Entering the Master's program in biology at the University of California Los Angeles, he was influenced by the late J. Philip Thornber and by David Chapman, who team-taught a plant biochemistry course. Thornber infected him with an enthusiasm for experimental science and for studying chlorophyll-protein complexes. Chapman revealed to him that beneath the seemingly tedious nomenclature of taxonomic classification lay the workings of evolution and natural selection. Chapman also introduced him to what would later become the topic of his Ph.D. thesis: The taxonomically enigmatic and evolutionarily important photosynthetic protist, *Cyanophora paradoxa*. He joined the laboratory of Robert Trench, at the University of California Santa Barbara, a world expert on symbiosis and *Cyanophora paradoxa*. The result was a thesis, entitled "Biogenesis of the Endosymbiotic Cyanobacteria (Cyanelles) of *Cyanophora paradoxa*". That project began the life-long fascination with oxygenic photosynthesis as conducted by the originators of this earth-transforming process: the cyanobacteria. Following his PhD research, Rob joined the laboratory of Louis Sherman at Purdue University to focus on Photosystem II (PSII), the system that splits water. He studied the function of the manganese-stabilizing protein (PsbO) of PSII, finding that the protein was not essential for the function of the manganese cluster of the water oxidation complex, in contrast to what had been previously thought. That project ultimately led to a preoccupation with photoactivation; the light-driven assembly of the metal atoms of the water oxidation complex. As part of his postdoctoral research he spent time in Yorinao Inoue's lab at RIKEN in Japan, analyzing the PSII charge-separation properties of mutants using thermoluminescence and absorption spectroscopy with Hiroyuki Koike and sharing the lab with Teruo Ogawa, Masahiko Ikeuchi and others. During the time in the Sherman lab, Rob also discovered that the novel chlorophyll-protein complexes produced by cyanobacteria under iron-deficiency were related to the CP43 protein of PSII illustrating the evolutionary diversification of six transmembrane helix chlorophyll proteins beyond their canonical roles played in the reaction centers as proximal antennae. He joined the faculty of the Department of Microbiology and Molecular Genetics at the Oklahoma State University (OSU) in 1991. He has continued a study of the assembly and function of the water oxidation complex, which now takes on new mechanistic focus with the continued refinement of the PSII crystal structure – thanks to others in the community of photosynthesis researchers. Ten years ago, his lab developed DNA microarrays for the cyanobacterium *Synechocystis*, and the global perspective afforded by using these arrays has returned Rob's attention to some of the more holistic ideas from his PhD thesis on how organisms and their parts are integrated into functional bioenergetic/metabolic units. Specifically, he has been studying the metabolic signals resulting from the light reactions and how these signals control the expression and activity of the cyanobacterial carbon-concentrating mechanism. Rob has served as a rotating Program Director at the United States National Science Foundation where, besides his regular duties in the Division of Cellular Molecular Biochemistry, he helped develop a special program for fielding and funding innovative proposals in photosynthesis research. For further information on Rob, see his web page at: http://microbiology.okstate.edu/faculty/burnap/.

Willem (Wim) F.J. Vermaas developed an interest in photosynthesis and cyanobacteria during his Master's research at the Agricultural University in Wageningen (The Netherlands) with Jack J.S. van Rensen, working on Photosystem II (PS II) herbicides. The University actively encouraged global research experience, and subsequent graduate work was done by spending about a year each at the University of Illinois at Urbana-Champaign, USA (with Govindjee, working on the bicarbonate effect in PSII), Michigan State University (with Charles Arntzen, working on the mode of action of PSII herbicides), and the Technical University in Berlin, Germany (with Gernot Renger, working on competitive interactions between the native plastoquinone and PSII herbicides). After defending his dissertation at the Agricultural University in Wageningen in 1984 (with Jack J.S. van Rensen, Wim Vredenberg and Gernot Renger), he joined the Arntzen group at the Du Pont Experimental Station in Wilmington, Delaware, learning the tricks of genetic manipulation of *Synechocystis* sp. PCC 6803 from John G.K. Williams. During his time at Du Pont, he published the first deletion and site-directed mutations leading to significant impairments in cyanobacterial photosynthesis. Wim joined Arizona State University in 1986, and before his lab was set up he spent time in Yorinao Inoue's lab at RIKEN in Japan, working on the PSII composition of mutants and sharing the lab with Teruo Ogawa, Masahiko Ikeuchi and others. At ASU, he was part of the founding of the Photosynthesis Center, and continued his work on discovery of protein residues and regions important for redox and chlorophyll-binding function in PSII. Over the years this work evolved into placing photosynthesis within the context of the molecular physiology and the evolutionary history of the cyanobacterium. New insights at the time included a common evolutionary ancestry of the two photosystems based on the primary structure of the heliobacterial reaction center, as well as the realization that photosynthesis and respiration share electrons and complexes in cyanobacteria. The sequencing of the *Synechocystis* genome by Satoshi Tabata's group at the Kazusa Institute in 1995 provided an excellent genomic framework. The genome sequence also facilitated the investigation of photosynthesis-related areas including the synthesis of photosynthetic pigments in relation to photosynthetic proteins, and of proteins aiding in chlorophyll reutilization. Structural insights complemented the functional and genomic research, with collaborative work on electron tomography and on hyperspectral imaging providing a detailed structural framework for the photosynthetic and physiological function of cyanobacteria. With the development of a detailed "toolbox" for modification of *Synechocystis* over the years, Wim's interests gradually evolved to include the use of *Synechocystis* as a photosynthetic platform for more applied purposes, such as production of petroleum substitutes, including fatty acids that are subsequently converted to alkanes, from sunlight, CO_2 and water. This emphasis necessitates a better understanding of the photosynthate metabolism in cyanobacteria, which also has become an active area of research. However, many of the basic processes in cyanobacteria, such as the formation of thylakoid membranes, remain poorly understood, and research in these fundamental areas are likely to continue to be an important emphasis. Wim has received an NSF Presidential Young Investigator award, and is Fellow of the American Association for the Advancement of Science. He is on the Editorial Board of the Journal of Biological Chemistry, and has served as Associate Editor of Plant Molecular Biology and on the Editorial Boards of Photosynthesis Research and Plant Cell Physiology.

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