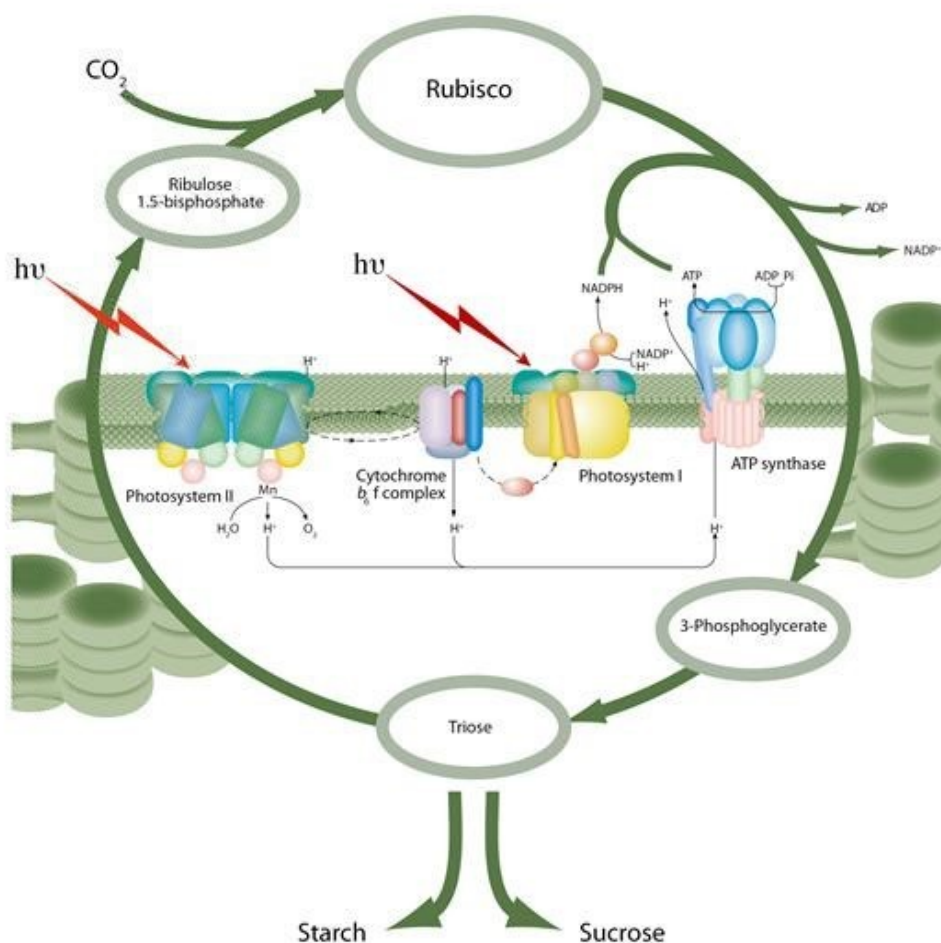


Photosynthesis

Plastid Biology, Energy Conversion and Carbon Assimilation



Edited by

Julian J. Eaton-Rye

Baishnab C. Tripathy

and

Thomas D. Sharkey



Springer

Photosynthesis

Plastid Biology, Energy Conversion and Carbon Assimilation

Advances in Photosynthesis and Respiration

VOLUME 34

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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 to evolutionary time scales, 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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Edited by

Julian J. Eaton-Rye

University of Otago

Dunedin

New Zealand

Baishnab C. Tripathy

Jawaharlal Nehru University

New Delhi

India

and

Thomas D. Sharkey

Michigan State University

East Lansing

Michigan

USA



Springer

Editors

Julian J. Eaton-Rye
Department of Biochemistry
University of Otago
P.O. Box 56
Dunedin 9054
New Zealand
julian.eaton-rye@otago.ac.nz

Baishnab C. Tripathy
School of Life Sciences
Jawaharlal Nehru University
New Delhi 110067
India
bctripathy@mail.jnu.ac.in

Thomas D. Sharkey
Department of Biochemistry and Molecular
Biology
Michigan State University
410 Biochemistry Building
East Lansing, MI 48824, USA
tsharkey@msu.edu

ISBN 978-94-007-1578-3 (HB) ISBN 978-94-007-1579-0 (e-book)

DOI 10.1007/978-94-007-1579-0

Springer Dordrecht Heidelberg London New York

Library of Congress Control Number: 2011939834

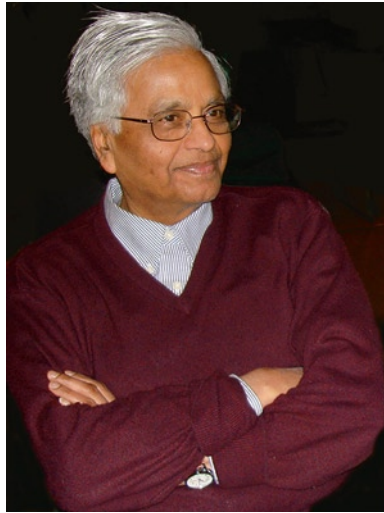
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Dedication



*Govindjee's passion for photosynthesis has been inspirational for students and researchers for over 50 years. At the start of his 80th year this volume of the *Advances in Photosynthesis and Respiration* series is dedicated to Govindjee to especially acknowledge not only his unique discoveries in Photosystem II, but also his commitment to educating students and researchers throughout the World (Photo taken in 2009 by Ram Singh).*

Govindjee has provided unparalleled educational resources to the field of photosynthesis through his three *Scientific American* articles (1965; 1974; 1990; translated in Russian and in Japanese), and outstanding editorship of authoritative books on Photosynthesis (*Bioenergetics of Photosynthesis*, 1975; *Photosynthesis*, two volumes, 1982 (translated in Russian, 1987); *Light Emission by Plants and Bacteria*, 1986; *Chlorophyll a Fluorescence: A Signature of Photosynthesis*, 2004; reprinted in 2010; *Photosynthesis in Silico: from Molecules to Ecosystems*, 2009; and *Abiotic Stress in Plants*, 2010). Under his leadership, as the chief editor of *Photosynthesis Research*, he made this publication a World-class journal; it took a quantum jump (five-fold) in the number of pages published per year. He then founded the unique 'Historical Corner' of *Photosynthesis Research*, and by his sheer persuasion attracted all the leaders in the field to write on their discoveries. This culminated in a unique book 'Discoveries in Photosynthesis'. Govindjee is also the founding Editor of the '*Advances in Photosynthesis and Respiration*'

Series; under his leadership more than 30 highly-acclaimed authoritative volumes on all aspects of photosynthesis: from molecules to the whole plant have been published; they are available in all leading libraries and photosynthesis research laboratories of the World. In addition, Govindjee's 1969 book on '*Photosynthesis*' remains a classic as it was used in the past to teach photosynthesis to thousands of students around the World. Lastly, together with Larry Orr, Govindjee has produced the highly cited and heavily used web site '*Photosynthesis and the World Wide Web*' for education. We refer the readers to Chapter 31 (by George C. Papageorgiou), Chapter 32 (by Julian J. Eaton-Rye) and Chapter 33 (by Robert M. Clegg) on Govindjee's research during 1956–1969, 1970–1999, and 2000–2010, respectively; also see the Preface of this book and Govindjee's Biographical Sketch that follows. These achievements have been made possible by Govindjee's personal enthusiasm and dedicated service to photosynthesis research and education. His unparalleled commitment and knowledge have

made him a true advocate, and ambassador, of photosynthetic research and education around the World.

Biographical Sketch

Govindjee, born in 1932, obtained his BSc (Chemistry, Biology) and MSc (Botany) in 1952 and 1954, from the University of Allahabad, India. He was a graduate student of Robert Emerson and of Eugene Rabinowitch, receiving his Ph.D. (Biophysics), in 1960, from the University of Illinois at Urbana-Champaign (UIUC). He has focused mainly on “*Photosystem II*” (PS II, the Water:Plastoquinone Oxidoreductase) throughout his career; research on PS II has included discoveries on excitation energy transfer, light emission, primary photochemistry and electron transfer. His early research included the discovery of a short-wavelength form of chlorophyll (Chl) *a* functioning in the Chl *b*-containing system, now called PS II (in 1960, with Eugene Rabinowitch); and the two-light effect (Emerson Enhancement) in NADP-reduction in chloroplasts (1962–1964, with Rajni Govindjee and George Hoch). In collaboration with his ~25 graduate students and postdoctoral associates, he has worked on the origins of the different spectral fluorescing forms of Chl *a* and the temperature dependence of excitation energy transfer down to 4 K (1963–1970); established basic relationships between Chl *a* fluorescence and photosynthetic reactions (1968–1988); discovered a unique role of bicarbonate on the acceptor side of PS II, particularly in protonation events involving the Q_B binding region (1970–1998); formulated the

theory of thermoluminescence in plants (1983, with Don C. De Vault); made the first picosecond measurement on the primary photochemistry of PS II (1989–1997, with Michael Seibert and Michael Wasielewski); and pioneered the use of the lifetime of Chl *a* fluorescence in understanding photoprotection against excess light (with Adam Gilmore). His current focus, however, is on the “*History of Photosynthesis Research*” and in “*Photosynthesis Education*” in addition to his dedicated research on the application of FLIM (Fluorescence Lifetime Imaging Microscopy) to photosynthetic systems to understand photoprotection in plants and algae (with Robert Clegg of UIUC) and on fluorescence spectroscopy of cyanobacterial cells during fluorescence induction (with Ondrej Prasil in The Czech Republic).

Govindjee 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 and Life Member of the National Academy of Sciences, India (1978); President of the American Society of Photobiology (1980–1981); Fulbright Senior Lecturer (1996–1997); Honorary President of the 13th International Photosynthesis Congress (Montréal, 2004); the first recipient of the Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology (2006); recipient of the ISPR (International Society of Photosynthesis Research) Communication Award (2007); and the LAS (Liberal Arts and Sciences) Lifetime Achievement Award of the University of Illinois at Urbana-Champaign (2008). He is also listed among the Eminent Indian Botanists, Past and Present (2010).

From the Co-Series Editor

Advances in Photosynthesis and Respiration

Volume 34: Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation

I am delighted to announce the publication, in the *Advances in Photosynthesis and Respiration* (AIPH) Series, of *Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*. Julian Eaton-Rye and Baishnab Tripathy (coeditors of Vol. 34) conceived a comprehensive look at photosynthesis and I (TDS) joined them in the late stages to put together this volume. Julian and Baishnab had in mind a volume to be dedicated to Govindjee for his extraordinary contributions to both discoveries and education about photosynthesis. (See the Dedication page, his Biographical Sketch, the Preface of this book, and Chapters 31, 32 and 33 in this volume.) Volume 31 of the series marked a turning point, with Govindjee inviting a co-series editor beginning with that volume. Govindjee's invitation to me represents his strong desire to keep the series comprehensive and reflects his view that, while photosynthesis begins with the absorption of a photon, a full understanding of photosynthesis can take investigators on many journeys, some of which can lead to intricacies of carbon metabolism and sugar synthesis while others undertake studies of the role of photosynthesis in ecology and even its very significant role in global change. I can now tell the story of Govindjee's incredible efforts on behalf of this series from the inside. Editors of the previous 30 volumes will recount how Govindjee can be a task-master, making sure that books are produced in a timely manner and making sure the quality is upheld at every step of the process. Above all else, Govindjee cares about photosynthesis. The coeditors of Volume 34 are pleased to reflect on the history of Govindjee's contributions to photosynthesis.

Our Books: Thirty-Three Volumes

Below is listed information on all the past 33 volumes. We are pleased to note that Springer is now producing complete table of contents of these books and electronic copies of individual chapters of these books (<http://www.springer.com/series/5599>); their web sites include free downloadable front matter as well as indexes. All the available and anticipated web sites of books in this series *Advances in Photosynthesis and Respiration* are listed, within square brackets, at the end of each entry. This volume (34) will be the last 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.

- **Volume 33 (2012): Functional Genomics and Evolution of Photosynthetic Systems**, edited by Robert L. Burnap and Willem F.J. Vermaas, from USA; Fifteen chapters, 428 pp, <http://www.springer.com/life+sciences/book/978-94-007-1532-5> [<http://www.springerlink.com/content/978-90-481-1532-5/>]
- **Volume 32 (2011): C₄ Photosynthesis and Related CO₂ Concentrating Mechanisms**, edited by Agepati S. Raghavendra and Rowan Sage, from India and Canada. Nineteen chapters, 425 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 Hooper (USA), Hartmut K. Lichtenthaler (Germany), Archie R. Portis (USA), and Baishnab C. Tripathy (India). Twenty-five chapters, 451 pp, Hardcover, 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, 525 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, 1053 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 Hooper, 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 [<http://www.springerlink.com/content/978-1-7923-2399-6/>]
 - **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.springerlink.com/content/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: Photobiology 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 USA and UK. 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 Ames 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: Volume 34

“Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation” was conceived as a comprehensive treatment touching on most of the processes important for photosynthesis. Most of the chapters provide a broad coverage that, it is hoped, will be accessible to advanced undergraduates, graduate students, and researchers looking to broaden their knowledge of photosynthesis. For biologists, biochemists, and biophysicists, this volume will provide quick background understanding for the breadth of issues in

photosynthesis that are important in research and instructional settings. This volume will be of interest to advanced undergraduates in plant biology, and plant biochemistry and to graduate students and instructors wanting a single reference volume on the latest understanding of the critical components of photosynthesis.

Solar energy is the source of almost all life on this Earth. An important factor in increasing the production of biomass, bioenergy and biofuels, which is needed to solve the global energy crisis, is the overall efficiency of photosynthesis. To manipulate overall efficiency we must understand the basic reactions of photosynthesis. This volume (*Photosynthesis: Plastic Biology, Energy Conversion and Carbon Assimilation*) in the *Advances in Photosynthesis and Respiration* series provides a comprehensive view of the current understanding of photosynthesis; it is divided into several sections to help the readers see the broad categories of photosynthetic processes. The first twenty-nine chapters in this volume cover the topics central to our current understanding of *Photosynthesis*.

A look back can be very informative and help make sense of the present. A historical perspective comes out in many of the chapters. The term “historical” can have different meaning to different people. A history of photosynthesis research (Chapter 30) caps the chapters on various aspects of photosynthesis in the volume; it traces the development of concepts in photosynthesis.

A strong theme in many of the chapters is a different type of history, the course of evolution that led to the current photosynthetic organisms that exist today. A strong evolutionary thread runs through various chapters; evolutionary insights aid in understanding why photosynthesis today has so many of its special properties. In this volume, readers will find discussions of the origins of photosynthesis as well as the future of photosynthesis, including the prospects for engineering artificial photosynthesis. Readers will learn about bacteria that use just parts of the photosynthetic system found in plants and how duplication and specialization in a small number of progenitor pigments, and proteins, gave rise to the vast array of pigments and proteins that are found in photosynthetic systems today. As Theodosius Dobzhansky wrote in 1973, “*Nothing in biology makes sense except in light of evolution.*” Photosynthesis is a rich area for the study of evolution.

This volume has a number of chapters that tell fascinating stories tracing the evolution of photosynthetic processes including the photosystems (Chapter 1), plastids (Chapter 2), carbon metabolism (Chapter 26), and sucrose metabolism (Chapter 27). Evolutionary perspectives can be found in many of the other chapters as well.

This book is appropriately dedicated to Govindjee, the founding series editor, on the occasion of a new board of advisors and a new co-editor (officially starting from Volume 31). Govindjee’s contributions are enormous, and are included in the last three chapters (Chapters 31, 32 and 33) of this book. In my opinion, Govindjee is, perhaps, the best-known photosynthesis researcher alive today.

Authors

The current book contains 33 chapters written by 76 international authors from 20 different countries (Australia, Canada, China, Finland, France, Germany, Greece, Hungary, India, Israel, Italy, Japan, New Zealand, The Netherlands, Russia, Spain, Sweden, Switzerland, United Kingdom, and the United States of America). The series editors give a special thank you to each and every author for their valuable contribution to the successful production of this unique book:

Iwona Adamska (Germany; Chapter 14); Elizabeth A. Ainsworth (USA; Chapter 29); Suleyman I. Allakhverdiev (Russia; Chapter 12); Yagut Allahverdiyeva (Finland; Chapter 13); Naohiro Aoki (Australia and Japan; Chapter 28); Eva-Mari Aro (Finland; Chapter 13); Neil R. Baker (UK; Chapter 23); Olivier Bastien (France; Chapter 9); Roberto Bassi (Italy; Chapter 5); Carl J. Bernacchi (USA; Chapter 29); Basanti Biswal (India; Chapter 10); Udaya C. Biswal (India; Chapter 10); Robert E. Blankenship (USA; Chapter 1); Maryse A. Block (France; Chapter 9); Robert Carpentier (Canada; Chapter 12); Wah Soon Chow (Australia; Chapter 24); Robert MacDonald Clegg (USA; Chapter 33); Gabriel Cornic (France; Chapter 23); Roberta Croce (The Netherlands; Chapter 6); Antoine Danon (France; Chapter 15); Ildikó Domonkos (Hungary; Chapter 11); Julian J. Eaton-Rye (New Zealand; Chapters 20, 32); Johannes Engelken (Germany and Spain; Chapter 14); Denis Falconet (France; Chapter 2); Wayne D. Frasch (USA; Chapter 22); Hideya

Fukuzawa (Japan; Chapter 25); Robert T. Furbank (Australia; Chapter 28); Zoltán Gombos (Chapter 11; Hungary); Mounia Heddad (Switzerland; Chapter 14); Jane F. Hill (USA; Chapter 30); Tatsuro Hirose (Japan; Chapter 28); Martin F. Hohmann-Marriott (New Zealand; Chapter 1); Kenneth J. Hooper (USA; Chapter 16); Tassilo Hornung (USA; Chapter 22); Norman P. A. Hüner (Canada; Chapter 19); Robert Ishmukhametov (USA; Chapter 22); Alexandra G. Ivanov (Canada; Chapter 19); Lixia Jin-Day (USA; Chapter 22); Juliette Jouhet (France; Chapter 9); Jacques Joyard (France; Chapter 9); Toivo Kallas (USA; Chapter 21); Aaron Kaplan (Israel; Chapter 25); Vyacheslav V. Kilmov (Russia; Chapter 12); Vladimir D. Kreslavski (Russia; Chapter 12); Andrew D.B. Leakey (USA; Chapter 29); Hartmut K. Lichtenthaler (Chapter 4; Germany); Steve P. Long (USA; Chapter 29); Dmitry A. Los (Russia; Chapter 12); John E. Lunn (Germany; Chapter 27); Elspeth MacRae (New Zealand; Chapter 27); Eric Marechal (France; Chapter 9); James Martin (USA; Chapter 22); Mamoru Mimuro (Japan; Chapter 12); Iain L. McConnell (USA; Chapter 20); Prasanna Mohanty (Russia and India; Chapter 12); Pranab K. Mohapatra (India; Chapter 10); Tomas Morosinotto (Italy; Chapter 5); Teruo Ogawa (China; Chapter 25); Donald R. Ort (USA; Chapter 29); Ulrike Oster (Germany; Chapter 8); Gunnar Öquist (Sweden; Chapter 19); George C. Papageorgiou (Greece; Chapters 18, 31); Gopal K. Pattanayak (USA; Chapter 3); Mukesh K. Ravel (India; Chapter 10); Gernot Renger (Germany; Chapter 17); Wolfhart Rüdiger (Germany; Chapter 8); Prafullachandra Vishnu Sane (India; Chapter 19); Thomas D. Sharkey (USA; Chapter 26); David Spetzler (USA; Chapter 22); Balázs Szalontai (Hungary; Chapter 11); Baishnab C. Tripathy (India; Chapter 3); Jack J. S. van Rensen (The Netherlands; Chapter 20); Klaas J. van Wijk (USA; Chapter 7); Sean E. Weise (USA; Chapter 26); Justin York (USA; Chapter 22); Xinguang Zhu (China; Chapter 29).

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- Bacterial Respiration II
- Biohydrogen Production
- Carotenoids II
- Cyanobacteria II
- The Cytochromes
- Ecophysiology
- Evolution of Photosynthesis
- Excitation Energy Transfer in Photosynthesis
- The 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 Govindjee at gov@illinois.edu, and/or to me (tsharkey@msu.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 Agricultural Engineering, Bioengineering, Chemistry, and Physics.

We take this opportunity to thank and congratulate Julian Eaton-Rye and Baishnap Tripathy for their outstanding editorial work; they have done a fantastic job not only in editing, but also in organizing this book for Springer, and for their highly professional dealing with the typesetting process. We have thanked all the 76 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, Project Manager, SPi Content Solutions – SPi Global, India for directing the typesetting of this book; her expertise 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 relation with us that led to the production of this book. Thanks are also due to Govindjee, the Series Founding Editor. Some of the text above was originally written by him and adapted by me. Govindjee has been involved and keenly interested at every stage to bring this book to fruition.

Thomas D. Sharkey
Series Co-Editor, Advances in
Photosynthesis and Respiration
Department of Biochemistry and Molecular
Biology
Michigan State University
East Lansing, MI 48824, USA
tsharkey@msu.edu

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Preface

During 1945–1956, Govindjee's Ph.D. mentor, Eugene Rabinowitch, wrote a comprehensive three-volume treatise on photosynthesis; however, today the amount of knowledge makes such a project out of the reach of a single author. Perhaps Govindjee recognized this when he produced his own excellent multi-author two-volume *Photosynthesis* in 1982. However, the *Advances in Photosynthesis and Respiration* series, under Govindjee's editorial leadership, has provided an ongoing authoritative presentation of photosynthesis and related research over the past 17 years. This book, volume 34 in the series, differs from many of its predecessors in that its scope includes topics in many branches of photosynthesis. This is no accident as the book is dedicated to Govindjee and reflects his far reaching interests and many of the chapters provide excellent introductions to different branches of the subject that are suitable for senior students or for researchers wishing to introduce themselves to aspects other than their own research specialty. The selection of topics also reflects the research interests of Govindjee. These include chapters on photosynthetic water splitting by photosystem II, fluorescence emission by the photosynthetic apparatus, thermoluminescence and the regulation of photosystem II electron transport by bicarbonate.

The material in this book is divided into *eight parts*. The *first part* is a single chapter that introduces the photosynthetic world in all its diversity. The chapter provides a unique perspective on the many ways nature has harvested light to drive photosynthesis and the variety of photosynthetic reaction centers served by these antenna both in prokaryotic and eukaryotic photosynthetic organisms. The *second part* covers nine topics in plastid biochemistry and physiology. Following from the material covered in the first introductory chapter, section two opens with a chapter on the origin, evolution and division of plastids: this is followed by four chapters that introduce chlorophyll and carotenoid biosynthesis, the assembly of pigments into light-harvesting pigment-protein complexes and the diversity of the chlorophyll-binding proteins of plants and cyanobacteria. Section two continues with chapters on the appli-

cation of proteomics to photosynthesis research, the intricacies of cell signaling between the plastid and the nucleus and the role of the plastid envelope membrane in glycerolipid biosynthesis. Section two concludes with a chapter on leaf senescence and the interconversion of chloroplasts into gerontoplasts.

In *Part III* the subject matter turns to the response of the photosynthetic apparatus to different environmental stress factors. Individual chapters cover the susceptibility and adaptations to low-temperature stress, high temperatures, too much light and environmentally-induced oxidative stress. In *Part IV* the emphasis is on energy conversion and it is in these nine chapters that the topics most closely aligned with the research career of Govindjee are covered. The first of these chapters focuses on light absorption by chlorophyll and the unique biological functions of the accessory chlorophylls *b* and *c*. The next chapter focuses on the apparatus and mechanism of Photosystem II and presents a current understanding of water splitting in oxygenic photosynthesis. Govindjee's many seminal contributions to our understanding of Photosystem II began with establishing basic relationships between chlorophyll *a* fluorescence and photosynthetic reactions: these relationships are explored in the subsequent chapter that addresses fluorescence emission by the photosynthetic apparatus. Together with Don DeVault, Govindjee also formulated the theory of thermoluminescence and this is the next topic in this section of the book. Govindjee also discovered the role of bicarbonate in Photosystem II where it acts as a ligand to the non-heme iron of the photosystem; this subject has a long history going back to early experiments by Otto Warburg and this story is told in a chapter exploring the regulation of Photosystem II electron transport by bicarbonate. The remaining chapters of this section review the pivotal role of the cytochrome b_6/f complex in photosynthetic electron transport, the mechanism of energy transduction by the F_1F_0 ATP synthase, electron transport in leaves and finally the currently available technologies for developing artificial photosynthetic systems for the planet's future energy needs.

The *fifth part* of this book turns to the topics of carbon assimilation as well as sucrose synthesis and transport. The uptake of CO₂ by cyanobacteria and microalgae is covered and the diversity of carbon fixing mechanisms together with the operation and control of the Calvin-Benson-Bassham cycle are discussed in a chapter devoted to autotrophic carbon fixation. This section concludes with a chapter providing a unique evolutionary perspective on photosynthetic sucrose biosynthesis and a chapter detailing sucrose transport in higher plants. The *sixth and the seventh parts* each contain a single chapter. The first looks at photosynthesis in the context of climate change and considers photosynthesis in a CO₂ rich atmosphere. The second provides a detailed history of the early pioneers of photosynthesis research. The book concludes with the last section (*Part VIII*) detailing Govindjee's extensive research, teaching and service contributions to the photosynthesis community.

We thank all the contributors to this volume. We have endeavored to edit these chapters to the best of our abilities and we apologize where we have missed something. We hope our readers enjoy learning more about photosynthesis from reading the contributions included here. We thank Govindjee for his inspiration to so many in the field of photosynthesis to do good science, to remember those whose contributions our own work has built on and to take up his example of excellence in teaching to our undergraduate and postgraduate students.

Julian J. Eaton-Rye

Department of Biochemistry
University of Otago
P.O. Box 56
Dunedin
New Zealand

Tel: +64 3 479 7865

Fax: +64 3 479 7866

e-mail: julian.eaton-rye@otago.ac.nz

Baishnab C. Tripathy

School of Life Sciences
Jawaharlal Nehru University
New Delhi 110067
India

Tel: +91-11-26704524

Fax: +91-11-26742558

e-mail: betripathy@mail.jnu.ac.in

Thomas D. Sharkey

Michigan State University
Department of Biochemistry and Molecular
Biology
410 Biochemistry Building
East Lansing, MI 48824
USA

Tel: +1 517 353-3257

e-mail: tsharkey@msu.edu

The Editors



Julian J. Eaton-Rye is currently in the Department of Biochemistry at the University of Otago in New Zealand. He completed a BSc Honors degree in Botany from the University of Manchester, UK in 1981 and obtained his Ph.D. (Plant Physiology) in 1987 at the University of Illinois at Urbana-Champaign under the supervision of Govindjee. His Ph.D. thesis research addressed the role of the bicarbonate cofactor in Photosystem II and showed that the reduction of the secondary plastoquinone electron acceptor and the turnover of the two-electron gate were impaired in bicarbonate-depleted membranes consistent with bicarbonate acting as a ligand to the non-heme iron of Photosystem II and participating in the protonation reactions associated with plastoquinone reduction on the acceptor side of the photosystem. He then obtained a Japan Society for the Promotion of Science postdoctoral fellowship (through the Royal Society, UK) and worked with Professor Norio Murata at the National Institute for Basic Biology in Okazaki, Japan (1987–1989). In Professor Murata's laboratory he studied the binding of the manganese-stabilizing protein (MSP or more usually nowadays, PsbO) to isolated Photosystem II complexes and demonstrated the requirement of an

N-terminal domain of MSP for the binding of this protein to Photosystem II. In 1989 he moved to the Center for Early Event in Photosynthesis at Arizona State University to take up a postdoctoral position in the laboratory of Professor Wim Vermaas. In Professor Vermaas' laboratory he began working with the cyanobacterial model organism *Synechocystis* sp. PCC 6803, and produced the first site-directed mutations in the chlorophyll *a*-binding core antenna protein CP47 targeting putative chlorophyll ligands and the large hydrophilic loop of this protein that interacts with MSP. In 1993, he moved to Brookhaven National Laboratory as a Senior Research Fellow in the laboratory of Geoffrey Hind and demonstrated, using isoelectric focusing and kinase activity assays, that the then candidate Light-Harvesting Complex II protein kinase was in fact a *substrate* of a then as yet unidentified thylakoid-membrane-associated kinase. Since his appointment to a lectureship in the Department of Biochemistry at the University of Otago in 1994 his research group has studied the role of either the luminal "extrinsic proteins" of Photosystem II or low-molecular-weight membrane-spanning "auxiliary" Photosystem II subunits found at the monomer-monomer interface of the Photosystem II supercomplex. His laboratory

is also actively studying the role of three additional Photosystem II lipoproteins (Psb27, CyanoP and CyanoQ) that are present in isolated Photosystem II complexes from *Synechocystis* sp. PCC 6803 but are absent from the current atomic resolution structures from the thermophilic cyanobacteria *Thermosynechococcus elongatus* and *T. vulcanus*. This work has produced the first X-ray-derived crystal structure of CyanoQ and NMR solution structures of Psb27 and CyanoP. With respect to other professional activities Julian currently serves

on the Executive Committee of the International Society of Photosynthesis and the International Scientific Committee of the Triennial International Symposium on Phototrophic Prokaryotes. He is also a consulting editor for the Advances in Photosynthesis and Respiration book series and an Associate Editor of the New Zealand Journal of Botany. He served as the President of the New Zealand Society for Plant Biologists (2006–2008) and will serve as the President of the New Zealand Institute of Chemistry in 2012.



Baishnab C. Tripathy was born in Kutilo, Cuttack, located on the east eastern coast of India. After 11 years of primary, middle and high school education in a rural setting, he joined Ravenshaw College, Cuttack in 1967, and subsequently Buxi Jagabandhu Bidyadhar (BJB) College, Bhubaneswar in 1969, where he received a BSc (Major: Botany) in 1971. Then he obtained an MSc (Botany) in 1973 from Utkal University, Orissa, India. In 1981, he was awarded a Ph.D. degree, from Jawaharlal Nehru University (JNU), New Delhi, India, for his work on the ‘Primary production and role of metal ions on the primary processes of photosynthesis’ under the supervision of Professor Prasanna Mohanty, who had obtained his Ph.D. under Govindjee in 1972. During 1981–1983, he was a post-doctoral research associate, with Professors Elizabeth Gross and John S. Rieske, at the Ohio State University, Columbus, Ohio, USA, where he worked on ‘*The role of cations on chlorophyll a fluorescence and on electron transport from plastocyanin to cytochrome c through complex III of mitochondria*’. From December 1983 till March 1987, he worked with Professor Constantin A Rebeiz, at the University of Illinois at Urbana-Champaign, Illinois, USA on ‘*Chloroplast biogenesis and biochemistry of chlorophylls*’. In 1987, he joined as an Assistant Professor of Photobiology in the School of Life Sciences, JNU, where he was promoted to an

Associate Professor and finally as a Professor in 2002. At JNU, Baishnab teaches and does research in plant physiology and photobiology. His research work has significantly contributed to our knowledge of plant tetrapyrroles and chloroplast biogenesis. His work on plant senescence in relation to chlorophyll metabolism has demonstrated the presence of different sets of enzymes i.e., kinetin-sensitive and kinetin-insensitive that are responsible for the degradation of chlorophyll and protochlorophyllide, respectively. His demonstration of the role of the meristematic layer in the intra- and inter-cellular signaling system in relation to chloroplast development of wheat and rice plants grown under red or red plus blue light, are novel and interesting. At the National Aeronautics and Space Administration (NASA), USA, he has published research papers on photosynthetic responses of plants growing in space. In addition to research articles, he has contributed several chapters to books and has edited books on photosynthesis. He has mentored a large number of Ph.D., MPhil and MSc students. Baishnab is on the editorial board of “*Horticulture, Environment and Biotechnology*”. He is a member of the Board of Directors of the Rebeiz Foundation for Basic Research, is a fellow of the National Academy of Sciences, India, of the Indian National Science Academy and of the National Academy of Agricultural Sciences, India.