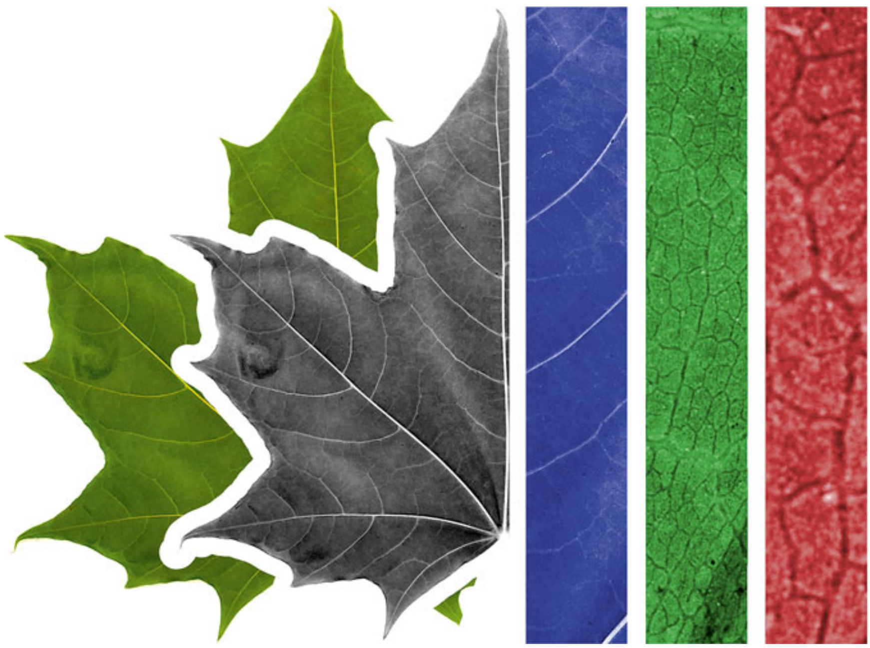
The Structural Basis of Biological Energy Generation



This illustration is based on a scanned image of a leaf. The left side of the illustration shows the original leaf, followed, to the right, by a black and white representation. Consecutive strips to the right show the same leaf at increasing resolution, thereby revealing increased structural detail. The illustration exemplifies how scientists can explore living systems at different scales that reveal different information and insights, which are represented by different colors.

Advances in Photosynthesis and Respiration
Including Bioenergy and Related Processes

VOLUME 39

The book series ADVANCES IN PHOTOSYNTHESIS AND RESPIRATION *Including Bioenergy and Related Processes* provides a comprehensive and state-of-the-art account of research in photosynthesis, respiration and related processes. Virtually all life on our planet Earth ultimately depends on photosynthetic energy capture and conversion to energy-rich organic molecules. These are used for food, fuel, and fiber. Photosynthesis is the source of almost all bioenergy on Earth. The fuel and energy uses of photosynthesized products and processes have become an important area of study, and competition between food and fuel has led to resurgence in photosynthesis research. This series of books spans topics from physics to agronomy and medicine; from femtosecond processes through season-long production to evolutionary changes over the course of the history of the Earth; from the photophysics of light absorption, excitation energy transfer in the antenna to the reaction centers, where the highly-efficient primary conversion of light energy to charge separation occurs, through the electrochemistry of intermediate electron transfer, to the physiology of whole organisms and ecosystems; and from X-ray crystallography of proteins to the morphology of organelles and intact organisms. In addition to photosynthesis in natural systems, genetic engineering of photosynthesis and artificial photosynthesis is included in this series. 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 and related energy processes. The purpose of this series is to improve understanding of photosynthesis and respiration at many levels both to improve basic understanding of these important processes and to enhance our ability to use photosynthesis for the improvement of the human condition.

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The Structural Basis of Biological Energy Generation

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 39: The Structural Basis of Biological Energy Generation

We are delighted to announce the publication of Volume *39* in this series. This is the fifth volume with the new cover and enhanced web presence. The series publisher, Springer, now makes the table of contents of all of the volumes freely available online. Links to each volume are given below. Readers may also see that this volume and the past few volumes have had significantly more color figures, and the color figures are now better integrated into the chapters, instead of being collected in one section of the book. This improvement was possible because of changes in how the books are produced. Another change is that references to chapters in books are now tracked by bibliographic services. This will help authors provide evidence of the importance of their work. We hope that these updates will maintain the importance of these edited volumes in the dissemination of the science of photosynthesis and bioenergy.

We are fortunate to have Martin F. Hohmann-Marriott, of Norway, to take the lead of editing a unique volume on *The Structural Basis of Biological Energy Generation.* It is first of its kind in the field of photosynthesis. Martin is an authority on bioenergetics of photosynthesis, and on the evolution of photosynthetic organisms. He has expertise on a variety of photosynthetic organisms including green sulfur bacteria, cyanobacteria, green algae and many others.

The Book

As stated in the Preface by Martin, this book provides an "overview of the structural foundation for bioenergetics in bacteria, algae and plants from the molecular to the organism level". It deals with how organisms channel energy into generating what we call "*the stuff of life*" giving rise to the living world around us. We learn about the details of the mechanisms that organisms employ to capture light energy, transport electrons and protons, and ultimately fix carbon. Biological energy generation also requires accessing the energy stored by photosynthetic reactions, and so mitochondria are covered in several chapters as well. The organisms covered in this book illustrate the range of mechanisms of biological energy generation rather than the range of organisms most familiar to people. This emphasis is a better representation of the diversity of biological energy generation. We are sure that this book will have a great impact in the field of photosynthesis for a long time.

Authors

The current book contains 24 chapters written by 49 authors from 15 countries. We thank all the authors for their valuable contribution to this book; their names (arranged alphabetically) are: N. **A**dir (Israel; Chap. 4); M. Asao (USA; Chap. 13); M. **B**arták (Czech Republic; Chap. 20); F. Baymann (France; Chap. 8); M. Benchimol (Brazil; Chap. 22); M. Berney (New Zealand; Chap. 15); E.J. Boekema (The Netherlands; Chap. 12); B. Böttcher (United Kingdom; Chap. 6); Z.L. Bouzon (Brazil; Chap. 16); H.-P. Braun (Germany; Chap. 12); L.S. Brown (Canada; Chap. 1); C. Büchel (Germany; Chap. 2); S.J. Butcher (Finland; Chap. 5); A.M. **C**ollins (USA; Chap. 13); G.M. Cook (New Zealand; Chap. 15); V. **D**askalakis (Cyprus; Chap. 10); L. David (Israel; Chap. 4); A. Dikiy (Norway; Chap. 11); O. Dobrovolska (Norway; Chap. 11); N.V. Dudkina (United Kingdom; Chap. 12); D. **G**argano (Norway; Chap. 23); M.L. Genova (Italy; Chap. 21); H.L. Gorton (USA; Chap. 19); P. Gräber (Germany; Chap. 6); K. Gundermann (Germany; Chap. 2); E. Hoffmann (Germany; Chap. 3); M.S. Kimber (Canada; Chap. 7); P.G. **K**roth (Germany; Chap. 18); J. **M**aple (Norway; Chap. 23); A. Marx (Israel; Chap. 4); Y. Matsuda (Japan; Chap. 18); A.E. McDonald (Canada; Chap. 9); J.A. Mears (USA; Chap. 24); S.G. Møller (USA; Chap. 23); T. **P**olívka (Czech Republic; Chap. 3); J. Pšenčík (Czech Republic; Chap. 5); W.M. **S**attley (USA; Chap. 13); E.C. Schmidt (Brazil; Chap. 16); M. Schmidt (Germany; Chap. 17); E. Shumilina (Norway; Chap. 11); K.-H. **T**ang (USA; Chap. 13); F. ten Brink (France; Chap. 8); C.S. Ting (USA; Chap. 14); R. Tuma (United Kingdom; Chap. 5); G.C. **V**anlerberghe (Canada; Chap. 9); C. Varotsis (Cyprus; Chap. 10); T.C. Vogelmann (USA; Chap. 19); C. **W**ilhelm (Germany; Chap. 17); and C.S. **Z**itta (Brazil; Chap. 16).

Our Books: Now 38 Volumes

We list below information on the 38 volumes that have been published thus far (see http://www.springer.com/series/5599 for the series web site). We are pleased to note that Springer, our publisher, is now producing complete *Tables of Contents* of these books. Electronic access to individual chapters depends on subscription (ask your librarian) but Springer provides free downloadable front matter as well as indexes. The available web sites of the books in the Series are listed below.

- **Volume 38 (2014): Microbial BioEnergy: Hydrogen Production,** edited by Davide Zannoni and Roberto De Phillipis, both from Italy. Fifteen chapters, XXXV + 366 pp, Hardcover, ISBN: 978-94-017-8553-2 (HB); ISBN 978-94-017-8554-9 (e-book) [http://www.springer.com/life+sciences/plant+sciences/book/978-94-017-8553-2]
- **Volume 37 (2014): Photosynthesis in Bryophytes and Early Land Plants,** edited by David T. Hanson, and Steven K. Rice, both from USA. Eighteen chapters, XXVII + 343 pp, Hardcover, ISBN: 978-94-007-6987-8 (HB); ISBN 978-94-007-6988-5 (e-book) [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-6987-8]
- **Volume 36 (2013): Plastid Development in Leaves during Growth and Senescence**, edited by Basanti Biswal, Karin Krupinska and Udaya Biswal, from India and Germany. Twenty-eight chapters, 837 pp, Hardcover, ISBN: 978-94-007-5723-3 (HB); ISBN 978-94-007-5724-0 (e-book) [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-5723-3]
- **Volume 35 (2012): Genomics of Chloroplasts and Mitochondria**, edited by Ralph Bock and Volker Knoop, from Germany. Nineteen chapters, 475 pp, Hardcover, ISBN: 978-94-007-2919-3 (HB) ISBN 978-94-007-2920-9 (e-book) [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-2919-3]
- **Volume 34 (2012): Photosynthesis – Plastid Biology, Energy Conversion and Carbon Assimilation**, edited by Julian Eaton-Rye, Baishnab C. Tripathy, and Thomas D. Sharkey, from New Zealand, India, and USA. Thirty-three chapters, 854 pp, Hardcover, ISBN: 978-94-007-1578-3 (HB) ISBN 978-94-007-1579-0 (e-book) [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-1578-3/]
- **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, ISBN:

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- **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.springer.com/life+sciences/plant+sciences/book/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, 451 pp, Hardcover, ISBN: 978-90-481-8530-6 [http://www.springer.com/life+sciences/plant+sciences/book/978-90-481-8530-6]
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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.

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 forthcoming books (not necessarily arranged in the order of future appearance):

- *Canopy Photosynthesis: From Basics to Applications* (Editors: Kouki Hikosaka, Ülo Niinemets and Niels P.R. Anten)
- *Non-Photochemical Quenching (NPQ) and Thermal Energy Dissipation In Plants, Algae and Cyanobacteria* (Editors: Barbara Demmig-Adams, Győző Garab and Govindjee)
- *Cytochromes* (Editors: William A. Cramer and Tovio Kallas)

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- Artificial Photosynthesis
- ATP Synthase and Proton Translocation
- Bacterial Respiration II
- Biohydrogen Production
- Carotenoids II
- Cyanobacteria II
- Ecophysiology
- Evolution of Photosynthesis
- 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 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 Govindjee 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.

Acknowledgments

We take this opportunity to thank and congratulate Martin F. Hohmann-Marriott for his outstanding editorial work; he has done a fantastic job, not only in editing, but also in organizing this book for all of us, and for his highly professional dealing with the reviewing process. We thank all the 49 authors of this book (see the list above): without their authoritative chapters, there would be no such volume. We give special thanks to Mr. Prakash Marudhu, SPi Global, India for directing the typesetting of this book; his expertise has been crucial in bringing this book to completion. We owe Jacco Flipsen, Andre Tournois, and Ineke Ravesloot (of Springer) thanks for their friendly working relation with us that led to the production of this book.

January 1, 2014

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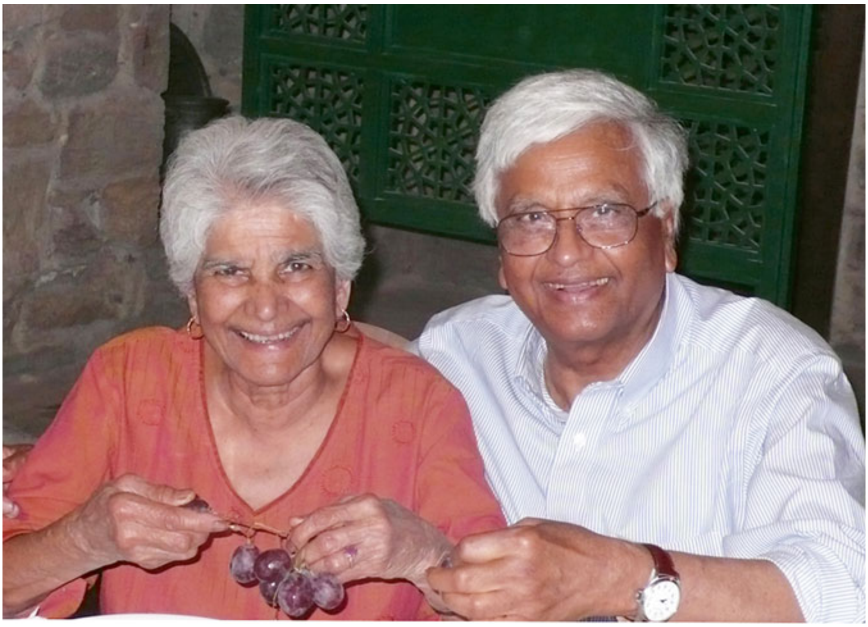
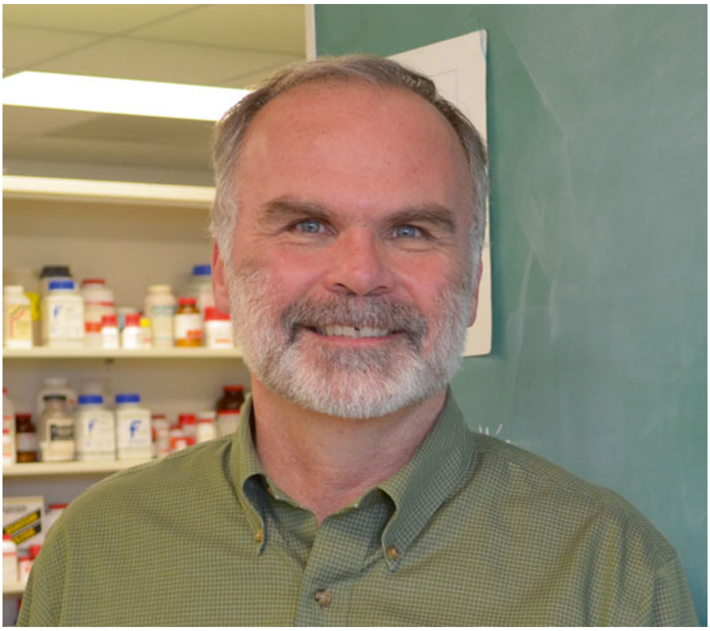
Series Editors



A 2013 photograph of Govindjee (on the right) with his wife Rajni. Photo by Zsuzsanna DeaÏk.

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 excitation energy transfer, light emission (prompt and delayed fluorescence, and thermoluminescence), primary photochemistry and 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 what is 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 relationship 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', and in 'Photosynthesis Education'. 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 (1956), Fulbright Senior Lecturer (1997), and Fulbright Specialist (2012); 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 & 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); **(2)** in 2008, through a special International Symposium on 'Photosynthesis in a Global Perspective', held in November, 2008, at the University of Indore, India; **(3)** Volume 34 of this Series "*Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*", edited by Julian Eaton-Rye, Baishnab C. Tripathy, and one of us (TDS), was dedicated to Govindjee, celebrating his academic career; and **(4)** in 2013, through two special volumes of Photosynthesis Research, celebrating his 80th birthday (Guest Editors: Suleyman Allakhverdiev, J.-R. Shen, and Gerald T. Edwards). Of special note is the article by Julian Eaton-Rye (2013). Govindjee at 80: more than 50 years of free energy for photosynthesis. Photosynthesis Research 116:111–144.

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). Each year a Govindjee and Rajni Govindjee Award (http://www.life.illinois.edu/plantbio/PlBiogiving.html; http://sib.illinois.edu/grants_Govindjee.htm) is being given to graduate students, by the Department of Plant Biology (odd years) or by the Department of Biochemistry (even years), 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, USA. After 2 years as a research technician in the federally funded Plant Research Laboratory at Michigan State University under the mentorship of Professor Klaus Raschke, Tom entered the PhD program in the same lab, and graduated in 1980. Postdoctoral research was carried out with Professor Graham Farquhar at the Australian National University, in Canberra, where he co-authored a landmark review on photosynthesis and stomatal conductance that continues to receive much attention 30 years after its publication. For 5 years, Tom worked at the Desert Research Institute together with Professor Barry Osmond, followed by 20 years as a 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 biochemistry and biophysics of gas exchange between plants and the atmosphere. Photosynthetic gas exchange, especially carbon dioxide uptake and use, and isoprene emission from plants, are the two major research topics in his laboratory. Among his contributions are measurements of the carbon dioxide concentration inside leaves, studies of the resistance to diffusion of carbon dioxide within the mesophyll of leaves of C_3 plants, and an exhaustive study of short-term feedback effects on carbon metabolism. As part of the study of short-term feedback effects, Tom's research group demonstrated that maltose is the major form of carbon export from chloroplasts at night, and made significant contributions to the elucidation of the pathway by which leaf starch is converted to sucrose 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 he has published many papers on the biochemical regulation of isoprene synthesis. Tom has coedited three books: T.D. Sharkey, E.A. Holland and

H.A. Mooney (Eds.) *Trace Gas Emissions from Plants*, Academic, San Diego, CA, 1991; R.C. Leegood, T.D. Sharkey, and S, von Caemmerer (Eds.) *Physiology and Metabolism, Advances in Photosynthesis (and Respiration)*, Volume 9 of this Series, Kluwer (now Springer), Dordrecht, 2000; and Volume 34 of this series *Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*, Advances in Photosynthesis and Respiration *Including Bioenergy and Related Processes,* Julian J. Eaton-Rye, Baishnab C. Tripathy and Thomas D. Sharkey (Eds) Springer. Tom joined the series founder Govindjee as Series Co-editor from volume 31 of this series. Tom is currently the Chairperson of the Department of Biochemistry and Molecular Biology, Michigan State University, East Lansing, Michigan. For further information see his web page at: http://www.bmb.msu.edu/faculty/sharkey/Sharkey/index.html.

Contents

Preface

This book, *The Structural Basis of Biological Energy Generation*, provides a detailed overview of the structural foundation for bioenergetics in bacteria, algae and plants from the molecular to the organism level. The authors of the chapters review our current understanding of how organisms channel energy gradients into generating the living world. Thus the book illustrates the mechanisms employed in these organisms to efficiently capture light energy, transport electrons and protons, and fix carbon.

In addition to chlorophyll-based photoconverters, a fundamentally different type of photoconverters, rhodopsins, convert light energy into a trans-membrane proton gradient using conformational changes of the carotenoid retinal. The molecular mechanisms that underlie the light conversion by rhodopsins is the topic of Chap. 1. The capture and utilization of light is the energetic basis of all organisms that inhabit ecosystems on the surface of Earth. A careful description of the molecular mechanisms that facilitate light harvesting is provided in chapters reviewing light-harvesting complexes of heterokont algae (Chap. 2), peridinin-chlorophyll proteins (Chap. 3), phycobilisomes (Chap. 4), and chlorosomes (Chap. 5). Current models for the biogenesis of chlorosomes and phycobilisomes are also reviewed in detail in Chaps. 4 and 5. An in-depth analysis of how light penetrates the complex organ for light capture by plants is provided in Chap. 19. The influence of morphological and environmental factors on photosynthesis in lichens is discussed in Chap. 20.

Several chapters provide molecular insights into electron and proton transport within protein complexes. Chapter 6 explores structure-function relationships of ATPases found in different groups of organisms. Coupling electron transfer to proton-translocation is the topic of a chapter on Cytochrome b_6f and *bc* complexes (Chap. 8). Electron transport to oxygen in quinone oxidases (Chap. 9) and cytochrome oxidases (Chap. 10) are explored using structural and computational approaches. Methionine sulfoxide reductase recovers proteins damaged by electron transport to oxygen (Chap. 11). In addition to their destructive action in mitochondria, reactive oxygen species are also an important signaling molecule in mitochondria (Chap. 24).

Biological systems employ compartmentalization to efficiently execute cellular functions. Protein complexes can provide sophisticated compartments for light-harvesting (Chaps. 4 and 5), carbon fixation (Chap. 7), and coordinated proton and electron transport (Chap. 12). In addition, membrane systems also compartmentalize the respiratory (Chaps. 15 and 21) and photosynthetic (Chap. 16) energy generation machinery. Structural and physiological insights into energy generation of bacteria and algae are provided in chapters with a focus on heliobacteria (Chap. 13), cyanobacteria (Chap. 14), mycobacteria (Chap. 15) and green algae (Chap. 17).

The ability to convert inorganic carbon into organic molecules is the defining characteristic of autotrophic organisms. Carboxysomes are complex protein assemblies with the function to locally increase the amount of inorganic carbon. The molecular structure of carboxysomes is reviewed in Chap. 7, and insights obtained from imaging carboxysomes in cyanobacteria are provided in Chap. 14. The mode of concentrating inorganic carbon is also the focus of a chapter on diatoms (Chap. 18). In addition, the potential utilization of fixed carbon for the production of biofuels and carotenoids in different green algae is reviewed in Chap. 17.

Mitochondria and chloroplasts are the result of endosymbiotic events. Therefore many functional elements can only be understood in an evolutionary context. This is especially true for the machinery employed in the biogenesis of chloroplasts (Chap. 23) and mitochondria (Chap. 24). Physiological and structural characteristics of the red algal chloroplast (Chap. 16), mitochondrion (Chap. 21) and the mitochondrion-derived hydrogenosome (Chap. 22) exemplify the transformation of bacteria into organelles specialized for light energy conversion and energy generation in the presence or absence of oxygen.

November 14, 2013

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The Editor

Martin F. Hohmann-Marriott was born on July 21, 1971 in Mannheim, Germany. He graduated with a Diplom in Biology from the Julius-Maximilians-Universität Würzburg, in 1998, having worked with Laurens Mets (University of Chicago, USA) and Ulrich Schreiber (Julius-Maximilians-Universität Würzburg) on his Diplom thesis.

Martin completed his PhD in Plant Biology in 2005, working with Robert E. Blankenship, Robert R. Roberson and Wim F. Vermaas at Arizona State University, Tempe, Arizona, USA. He had obtained Postdoctoral Fellowships from the National Research Council (USA), the Japan Society for Promotion of Science (Japan) and the Foundation for Research, Science and Technology (New Zealand). These fellowships enabled Martin to work with Richard D. Leapman (National Institute of Biomedical Imaging and Bioengineering, Bethesda MD, USA), Jun Minagawa (Hokkaido University, Sapporo, Japan) and Julian J. Eaton-Rye (University of Otago, New Zealand). Martin was appointed Associate Professor in the Department of Biotechnology at the Norwegian University of Science and Technology (Trondheim, Norway) in 2011. Here he lectures in courses on biochemistry, molecular genetics and bioinformatics.

Martin's research interest is in bioenergetics, especially the evolution of the photosynthetic machinery in different organisms. Martin has worked on the photosynthetic machinery and physiology of green sulfur bacteria, cyanobacteria, green algae and lately heterokont algae. His current research focus is renewable energy and the application of structural approaches to address open questions in bioenergetics.

At the Norwegian University of Science and Technology, Martin established the PhotoSynLab (http://photosynlab.org). PhotoSynLab is an 'open-science' laboratory that shares all protocols and publishes all experimental results online. PhotoSynLab is intended to apply synthetic biology approaches and laboratory automation to explore photosynthetic organisms.

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