Advances in Photosynthesis and Respiration 37
Including Bioenergy and Related Processes

David T. Hanson
Steven K. Rice *Editors*

Photosynthesis in Bryophytes and Early Land Plants

Springer

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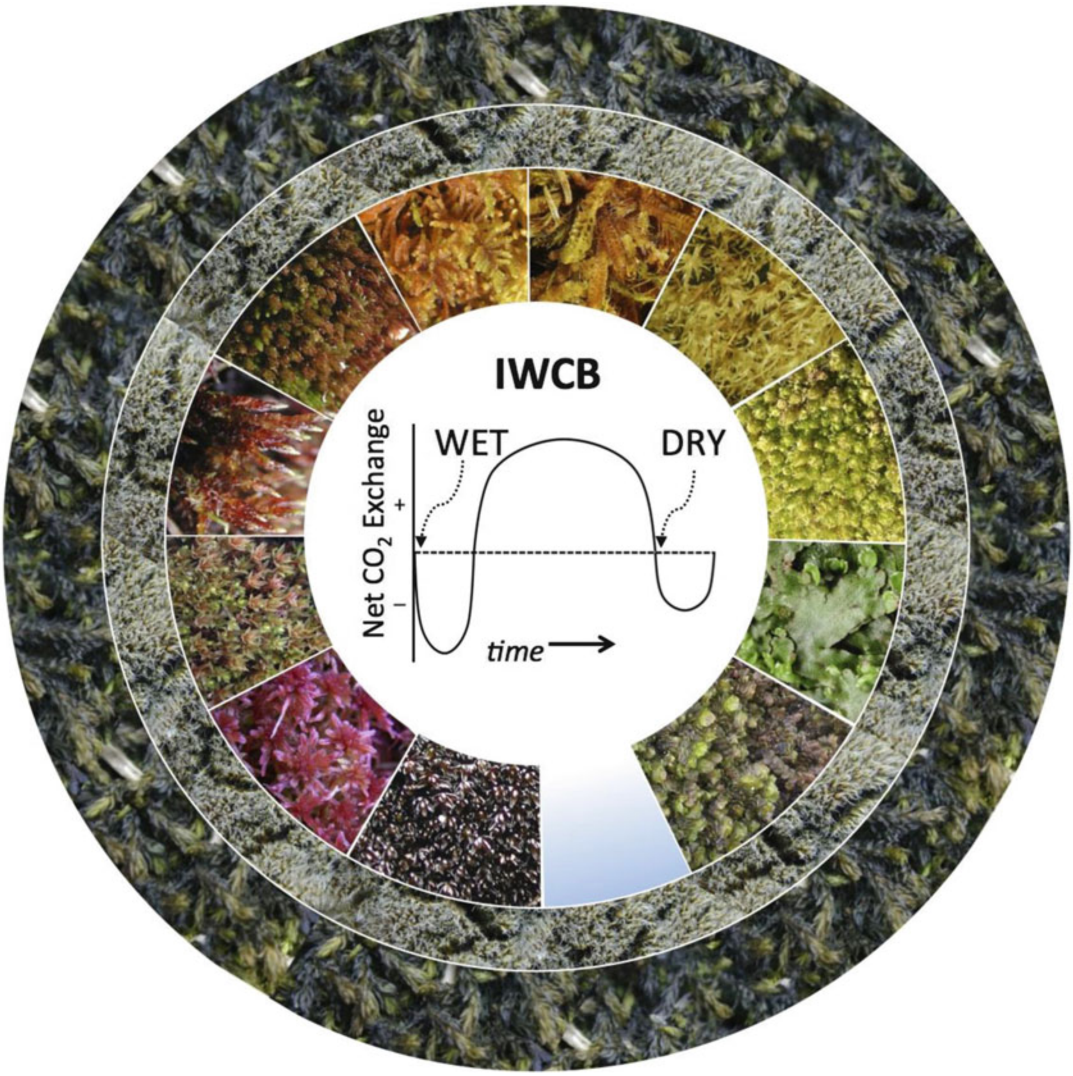

Bryophyte Color Wheel Bryophytes present diverse photosynthetic physiology and morphology, as evidenced by differences in the organization of the shoot system and by their varied pigmentation. Yet the vast majority are desiccation tolerant, represented by the Integrated Water-Carbon Budget (IWCB) model showing the photosynthetic response following hydration of a dry bryophyte (see Coe et al., Chap. 16, this volume). Bryophytes are arranged on a color wheel starting from the red on the left above the horizontal and progressing clockwise through orange, yellow, green, blue and violet with secondary colors also shown. No known bryophyte expresses blue pigmentation. Clockwise from red, species shown include *Calliergon sarmentosum*, *Bryum muehlenbeckii*, *Cratoneuron commutatum*, *Barbilophozia floerkei*, *Barbula enderesii*, *Bryum capillare*, *Conocephalum conicum*, *Frullania dilatata*, *Andreaea alpestris*, *Sphagnum warnstorfii* and *Bryum arcticum*, *with Grimmia funalis* in the white ring and *Cinclidotus riparius* in the black ring. Photographs by Michael Lüth and composition by Steven Rice.

Advances in Photosynthesis and Respiration
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VOLUME 37

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 plant 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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Photosynthesis in Bryophytes and Early Land Plants

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 37: Photosynthesis in Bryophytes and Early Land Plants

We are delighted to announce the publication of Volume 37 in this series. This is the third 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 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.

This Book

This volume, *Photosynthesis of Bryophytes and Early Land Plants*, was conceived and edited by David T. (Dave) Hanson (University of New Mexico, Albuquerque, New Mexico, USA) and Steven K. (Steve) Rice (Union College, Schenectady, New York, USA). We are grateful to them for their timely submission of the book and to all the 33 authors, who contributed to this book that describes photosynthesis in bryophytes, plants that were, perhaps, the first to colonize the land, and that today are found in some of the harshest environments on land. Often, photosynthesis research focuses on land plants such as spinach and now *Arabidopsis*. Further, most often, photosynthesis is studied in aquatic organisms such as bacteria and algae (e.g., *Chlamydomonas*). This book focuses on the evolutionary transition between aquatic photosynthesis and terrestrial photosynthesis. As plants colonized the land, water availability, intense sunlight, and diffusion of CO_2 became important issues that determined which organisms would be successful. This book describes the latest information about how land plants adapted to the aerial environment. Fascination by one of us (TDS) with this topic began when Dave Hanson worked jointly in his laboratory and that of Linda Graham (see Chap. 2, this book). He is very grateful that Dave and Steve were willing to draw together so many experts to create this valuable look at the transition of photosynthesis from aquatic environments to aerial environments.

Authors

The book contains 18 chapters written by 33 authors from 8 countries [Australia (5); Canada (1); Estonia (2); Germany (4);

UK (6); The Netherlands (1); and USA (13)]. We thank all the authors for their valuable contribution to this book; their names (arranged alphabetically) are:

Maaike Y. **Bader** (Germany; Chap. 15); Jayne Belnap (USA; Chap. 16); Jessica Bramley-Alves (Australia; Chap. 17); Kirsten K. **Coe** (USA; Chap. 16); Martha Cook (USA; Chap. 2); J. Hans C. Cornelissen (The Netherlands; Chap. 5); David J. Cove (UK; Chap. 11); Andrew C. Cuming (UK; Chap. 11); Dianne **Edwards** (UK; Chap. 3); Lawrence B. **Flanagan** (Canada; Chap. 14); Linda **Graham** (USA; Chap. 2); Janice M. Glime (USA; Chap. 12); Tomáš **Hájek** (Czech Republic; Chap. 13); David T. Hanson (USA; Chaps. 1, 6, 10, 18); Diana H. **King** (Australia; Chap. 17); Martina Königer (USA; Chap. 8); Louise A. **Lewis** (USA; Chap. 2); Rebecca E. **Miller** (Australia; Chap. 17); Ülo **Niinemets** (Estonia; Chap. 9); Zach **Portman** (USA; Chap. 10); Michael C.F. Proctor (UK; Chap. 4); John A. **Raven** (UK; Chap. 3); Karen Renzaglia (USA; Chap. 6); Steven K. Rice (USA; Chaps. 1, 5, 10, 18); Sharon A. Robinson (Australia; Chap. 7, 17); Jed P. **Sparks** (USA; Chap. 16); Wilson **Taylor** (USA; Chap. 2); Mari Tobias (Estonia; Chap. 9); Juan Carlos **Villarreal** (Germany; Chap. 6); Sebastian **Wagner** (Germany; Chap. 15); Melinda J. Waterman (Australia; Chap. 7); Charles Wellman (UK; Chap. 2); Gerhard **Zotz** (Germany; Chap. 15).

Our Books: Now 37 Volumes

We list below information on the 36 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 for nearly all volumes. The available web sites of the books in the Series are listed below.

- **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.springerlink.com/content/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.springerlink.com/content/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.springerlink.com/content/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: 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 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.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 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/]
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- **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://nwww.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/]
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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):

- Microbial BioEnergy: Hydrogen Production (Editors: Davide Zannoni and Roberto de Phillipis)
- The Structural Basis of Biological Energy Generation (Editor: Martin Hohmann-Marriott)
- Canopy Photosynthesis: From Basics to Applications (Editors: Kouki Hikosaka, Ülo Niinemets and Niels P.R. Anten)
- Saga of Non-Photochemical Quenching (NPQ) and Thermal Energy Dissipation In Plants, Algae and Cyanobacteria (Editors: Barbara Demmig-Adams, Győző Garab and Govindjee)
- ATP Synthase and Proton Translocation (Editor: Wayne Frasch)
- Cytochromes (Editors: William A. Cramer and Tovio Kallas)
- Photosynthesis for Bioenergy (Editors: Elizabeth A. Ainsworth and Stephen P. Long)

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- Algae, Cyanobacteria: Biofuel and Bioenergy
- Artificial Photosynthesis
- 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 at 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 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 Dave Hanson and Steve Rice 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 33 authors of this book (see the list above): without their authoritative chapters, there would be no such volume. We give special thanks to I. Mohamed Asif, SPi Global, India, his 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.

April 5, 2013

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Govindjee

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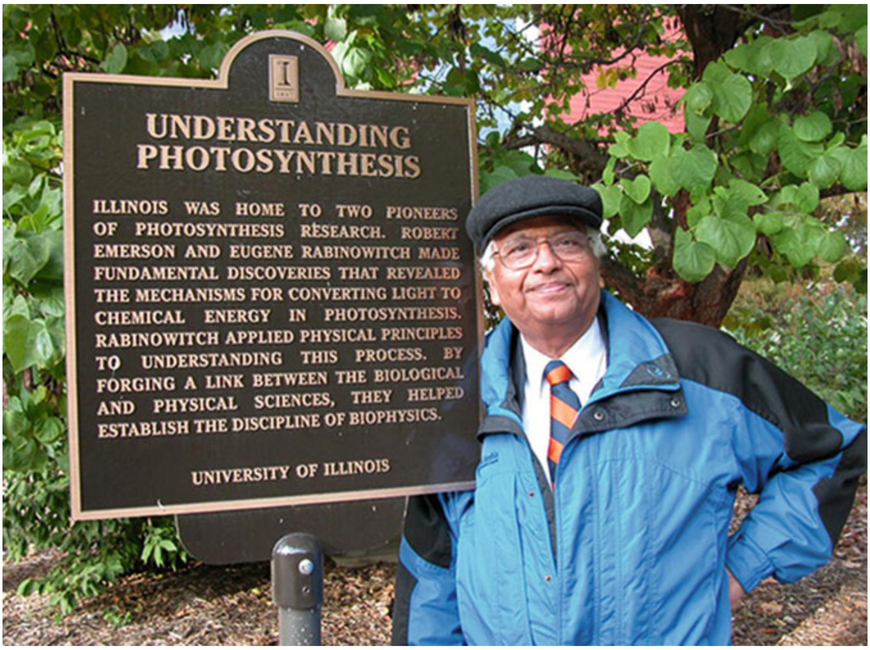
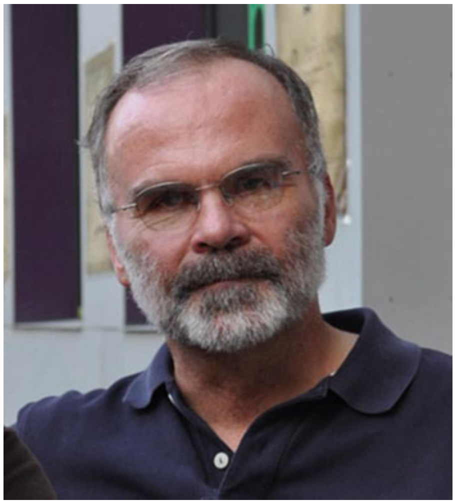
Series Editors



Govindjee with the plaque honoring his professors Robert Emerson and Eugene Rabinowitch.

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 first use of Fluorescence Lifetime 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', as well as 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 (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 and Sciences Lifetime Achievement Award of the UIUC, 2008. Further, Govindjee was honored (**1**) in 2007, through 2 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; and (**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. Currently, a special issue of *Photosynthesis Research* is being edited by Suleyman Allakhverdiev, Gerald Edwards and Jian-Ren Shen, celebrating his 80th birthday. 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 (http://www.life.illinois.edu/plantbio/PlBiogiving.html; http://sib.illinois.edu/grants_Govindjee.htm) is being given to graduate students, by the UIUC, to recognize Excellence in Biological Sciences. For further information on Govindjee, see his website 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 Ph.D. program in the Department of Energy Plant Research Laboratory at Michigan State University under the mentorship of Klaus Raschke and finished in 1979. Post-doctoral research was carried out with Graham Farquhar at the Australian National University, in Canberra, where he coauthored a landmark review on photosynthesis and stomatal conductance. 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 co-edited three books, the first on trace gas emissions from plants in 1991 (with Elizabeth Holland and Hal Mooney) and then volume 9 of this series (with Richard Leegood and Susanne von Caemmerer) on the physiology of carbon metabolism of photosynthesis in 2000 and volume 34 (with Julian Eaton-Rye and Baishnab C. Tripathy) entitled *Photosynthesis*: *Plastid Biology*, *Energy Conversion and Carbon Assimilation*. Tom has been co-series editor of this series since volume 31.

Contents

Preface

Why would anyone let you study moss? This question was put to one of us (David Hanson) by a well-known and well-respected plant biologist (who will not be named) in the middle of the 1990s when he was graduate student. This was not a question originating from malice, but rather benign ignorance and a genuine concern for the career of an aspiring biologist. It is also likely that many authors in this volume have had similar questions put to them since bryophyte photosynthesis, and even bryophyte biology in general, has suffered from a perceived lack of relevance or importance until recent decades. Much of the bryophyte dismissal came from out-dated views that bryophytes were just reduced vascular plants, an evolutionary dead-end with remnants that were essentially inconsequential ecologically except for the genus *Sphagnum*. Fortunately, these views have been turned on their head.

Bryophytes are now widely recognized as the earliest divergent land plants from phylogenetic evidence and ever-growing fossil data. This has cemented their important position in understanding the evolution of land plants. Ecologically, *Sphagnum* is still king and is probably the most important single genus of all land plants, playing a major, if not controlling, role in ecosystem function over 2–3 % of the continental surface. However, critical roles of other bryophytes as members of vast biological crust communities and as major components of high latitude and altitude ecosystems is undeniable, and their roles in many other ecosystems are more likely to be poorly understood rather than not being important. The value of bryophytes for understanding cellular and developmental biology of plants has also become much clearer and has helped immensely in the effort to garner respect for these misunderstood organisms. After centuries of relative neglect, it appears that the era of bryophyte biology is well underway.

This volume of *Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes* brings together experts on bryophyte photosynthesis whose research spans the genome and cell, through whole plant and ecosystem function, and combines that with historical perspectives on the role of algal, bryophyte and vascular plant ancestors during the terrestrialization of the Earth. Many of the authors in this volume are responsible for ushering in a new era for bryophyte biology, while others are emerging as leaders for the future. There are also others in the field from both of these categories that we were not able to include in this volume, and we see that as evidence of a strong and growing field. Here we have tried to take a wide view on existing areas of research involving photosynthesis in bryophytes and early land plants (actual interpretations from fossil data, not just examination of modern representatives).

We begin this volume with an introductory chapter, followed by three multi-chapter sections, and we end the book with a final prospective chapter. The introduction (Chap. 1) provides an overview of why research in bryophyte photosynthesis is important; it is also a general guide to where each topic is addressed in the book. We hope that this will help newcomers to the field navigate to the material that is of greatest interest to them. In the first section of this volume, after the introduction, authors consider fossil, biogeochemical, systematic and comparative physiological evidence to understand three phases of terrestrialization: the transition to the land from aquatic algal ancestors (Chap. 2); the physiological adaptation of early land plants (Chap. 3); and the diversification of plants and environments (Chap. 4). The second section starts out with a discussion of the challenges involved in measuring photosynthesis of bryophytes and presents our view of what the best practices should entail (Chap. 5).

The section then introduces new perspectives and reviews photosynthetic physiology across spatial and temporal scales in six additional chapters that focus on the unique strategies of bryophytes in relation to carbon acquisition (Chap. 6), photoprotection (Chap. 7), chloroplast movement (Chap. 8), canopy structure (Chaps. 9 and 10) along with genetics and genomics of bryophytes (Chap. 11). This section also discusses novel approaches used in the investigation of bryophyte photosynthesis. The last section emphasizes the ecological setting, showing how the photosynthetic physiology of bryophytes plays out within aquatic (Chap. 12), peatland (Chaps. 13 and 14), tropical (Chap. 15), dryland (Chap. 16) and Antarctic (Chap. 17) settings with discussions of implications of global change. The volume ends with a forward-looking view (Chap. 18) of exciting opportunities for future work along with a list of some other books and websites that are valuable resources for researchers interested in bryophyte photosynthesis. Overall, the 18 well-illustrated chapters reveal unique physiological approaches to achieving carbon balance and dealing with environmental limitations and stresses that present an alternative, yet successful strategy for land plants.

We are grateful for the effort and patience of the authors and series editors in helping to bring this volume to fruition. The authors of this volume helped lay the foundations for this field of work and inspired both of us during our higher education and subsequent careers. We hesitate to single out specific authors in such a distinguished list, but we hope others will agree with us and take a moment to recognize and reflect upon the massive contributions of Michael Proctor and John Raven (to date!). We are especially grateful for their contributions to the field and to this volume. In addition, Govindjee and Tom Sharkey have long recognized the value of studying bryophyte photosynthesis and the value of their encouragement and advice is immeasurable. It has been a great pleasure to work with such an enthusiastic and knowledgeable group. We hope readers will be as invigorated as we are by this volume and will be inspired to participate in the advancement of research in bryophyte photosynthesis and respiration. Just remember, bryophytes rule! If you were unaware of this fact before reading this volume, we hope you are persuaded by the time you finish it.

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The Editors

David T. Hanson was born on April 25, 1972 in Baltimore, Maryland, USA. He is Associate Professor in the Department of Biology and Associate Curator of Bryophytes in the Museum of Southwestern Biology at the University of New Mexico in Albuquerque, New Mexico. He received his Bachelor of Science degree with Honors in Botany from the University of Iowa, Iowa City, Iowa. It was there that David's passion for bryophytes was ignited under the guidance of Prof. Diana G. Horton. His Honors thesis examined whether species of the genus *Atrichum* had sun and shade leaf forms based on the height of photosynthetic lamellae, and this initiated his life-long interest in both bryophytes and photosynthesis. During the summer of 1994, between undergraduate and graduate school, David was fortunate to take "Bryophytes" with one of the best known bryologists of his time, Prof. Howard Crum, along with "Boreal Flora" taught by the legendary Prof. Ed Voss at the University of Michigan Biological Station, cementing his love of the Northwoods, *Sphagnum* and bathtub Marys. These experiences colored his subsequent Ph.D., received in 1999, from the Botany Department at the University of Wisconsin-Madison, where he pursued research in photosynthesis, isoprene emission, and bryophyte biology under the guidance of Prof. Thomas D. Sharkey (co-editor of this series) and Prof. Linda E. Graham (contributor to this volume). His post-doctoral fellowship at the Australian National University from 2000 to 2002 was a joint appointment to work with Prof. T. John Andrews and Prof. Murray R. Badger on Rubisco kinetics and CO_2 concentrating mechanisms in hornworts and algae. David was appointed as Assistant Professor at the University of New Mexico started in 2002 and promoted to Associate Professor in 2008. In the area of bryophyte research, David is best known for his work on the evolution of isoprene emission from mosses and function of the hornwort pyrenoid. However, in 2006 he developed a new method for conducting high-frequency, online $^{13}CO_2$ gas exchange and since then his research has centered on using stable isotopes of CO_2 to study diffusion through photosynthetic tissues. This has led to several papers demonstrating an *in vivo* role for CO_2 transporting aquaporins. David is currently the Chair of the 2014 Gordon Conference on CO_2 Assimilation in Plants: Genome to Biome along with Prof. Christoph Peterhansel.

Steven K. Rice was born on April 12, 1961 in Ann Arbor, Michigan, USA, and is currently Professor in the Department of Biological Sciences and co-Program Director of the Bioengineering Program at Union College in Schenectady, New York. He received his Bachelor of Science degree in Biology from Yale University in 1983 and spent 5 years teaching science in museum and school settings. Following his deepening interests in plant biology, Steven returned to school at Duke University to earn his Master's of Science (1991) and Ph.D. (1994) degrees in Botany. At Duke, his interest in bryophyte structure-function relationships was stimulated by Brent Mishler, who co-advised his dissertation (with ecologist Norman Christensen) on "Form, Function and Phylogeny of Aquatic *Sphagnum*", and by Lewis Anderson, who led him on many collecting trips to the Coastal Plain, teaching Steven the idiosyncrasies of *Sphagnum* biology in that region. Following a postdoctoral position at University of North Carolina-Chapel Hill with the ecologist Robert Peet, and a teaching position at Wake Forest University, Steven came to Union College in 1998 as an Assistant Professor. He was promoted to Associate Professor in 2004 and to Professor in 2011. In his research he employs integrative and comparative approaches to understand the ecological and evolutionary significance of variation in plant form in bryophytes. His studies focus on understanding structure-function relationships with particular emphasis on how variation in structure influences water balance, carbon balance and plant productivity. With co-authors (N. Neal, J. Mango and K. Black), he received the 2012 Sullivant Award from the American Bryological and Lichenological Society for the best bryology publication in *The Bryologist*.

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Author Index

Chapter 1

What Can We Learn From Bryophyte Photosynthesis?

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Summary

Bryophytes have been evolving in terrestrial and aquatic environments longer than any other group of land plants, surviving and thriving through an incredible range of climatic and environmental variation. Several of the bryophyte growth forms we find today closely resemble those found in ancient fossils whereas many of the other early land plant forms lack modern representatives. What is it about bryophyte growth form and physiology that has allowed them to persist through time and radiate into every terrestrial ecosystem, even dominating some of them? What can we learn from modern bryophytes to address this question and to predict how plants will respond to future environmental change? In this chapter, we briefly examine these questions as a preview to the volume as a whole.

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I. Introduction

Bryophytes have barely been tapped as a resource for understanding photosynthesis and respiration on land despite the fact that the bryophyte life form has achieved ecological success in varied environments that span every continent, occur across dramatic gradients of temperature and water availability and were present at the early stages of the transition from aquatic habitats to land, potentially as early as the Cambrian (see Chaps. 2 and 3). Critical aspects of life cycle evolution were involved in adapting bryophyte ancestors to life on land (e.g., protection of the embryo in protective maternal tissue, elaboration of two distinct multicellular stages specialized for different functions), but the colonization of land also required structural and physiological adaptations to succeed in habitats with high solar radiation, a drying atmosphere, high temperature fluctuations, and limited access to dissolved nutrients (Chaps. 4 and 7).

Although the primary architecture of the photosynthetic machinery was conserved from their algal ancestors, early land plants, as with contemporary bryophytes, likely facilitated carbon capture over short and long temporal scales in several ways. These include the reduction of external water films on leaf surfaces, which impede diffusion of carbon dioxide, the evolution of ventilated thalli or leaf structures, and the evolution of carbon concentrating mechanisms. In addition, they evolved desiccation tolerance, which allowed plants to equilibrate with a drying atmosphere and retain metabolic function upon rehydration along with adaptations to achieve positive carbon balance during wet—dry cycles. Bryophyte population and community structure also indirectly influences photosynthesis through alteration of canopy boundary layers and, thereby, retention of water and soil respired CO_2. The multiple scales over which bryophyte photosynthesis is measured (shoot, canopy, community) also raises the question of what is a functional photosynthetic unit in bryophytes, i.e. what can be treated as an analogue to the vascular plant leaf (Chaps. 5 and 9)? The amazing variation in form and function and the diverse range of micro-habitats that bryophytes occupy makes them an ideal, yet rarely utilized, system for studying the role of photosynthesis and respiration in the adaptive radiation of plants.

II. Terrestrialization

Terrestrialization is the adaptive radiation of aquatic organisms onto land. The organisms we consider here are grouped by function rather than by phylogeny. Interestingly, despite the existence of all major lineages of aquatic photosynthetic organisms, from cyanobacteria to green algae, being present when terrestrial photosynthetic organisms were becoming wide-spread, only one small corner of that aquatic diversity came to dominate land. For roughly the last 500 million years, descendants of Charophycean green algae, collectively called embryophytes, or land plants, have adaptively radiated onto land with greater success than any other lineage. Thus, the story of terrestrialization by photosynthetic organisms has been effectively limited to a single lineage. Bryophytes are at the base of this lineage, and in this volume we examine what features of bryophyte photosynthesis may have allowed them to be so successful.

A. Photosynthesis on Land

Despite their current dominance of terrestrial environments, land plants (embryophytes) are one of several groups of photosynthetic organisms that have terrestrial representatives. It is likely that cyanobacteria, many varieties of algae, and even lichens colonized land before or concurrently with land plants and each of these groups have extant terrestrial representatives

Abbreviation: Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase