C_4 Photosynthesis
and
Related CO_2 Concentrating Mechanisms

Advances in Photosynthesis and Respiration

VOLUME 32

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

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C_4 Photosynthesis and Related CO_2 Concentrating Mechanisms

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Cover images: **Single cell C_4 photosynthesis in Chenopodiaceae**. C_4 is developed with the intracellular location of two distinct groups of chloroplasts (indicated by the red fluorescence) held in position by the cytoskeleton (green fluorescence). Borszczowia type (left): One type of chloroplast is more abundant in the proximal end and another type towards the distal end. Bienertia type (right): Dimorphic chloroplasts partition between the peripheral cytoplasm and a central cytoplasmic compartment. These features of single cell C_4 photosynthesis are described in detail by Edwards and Voznesenskaya (Chapter 4). Images were provided by Simon D.X. Chuong, Vincent R. Franceschi and Gerald E. Edwards. Adapted from Chuong et al. (2006), from *Plant Cell* (volume 18, pp 2207–2223).

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From the Series Editor

Advances in Photosynthesis and Respiration
Volume 32: C_4 Photosynthesis and Related CO_2 Concentrating Mechanisms

We (Tom Sharkey and I) are delighted to announce the publication, in the Advances in Photosynthesis and Respiration (AIPH) Series, of *C_4 Photosynthesis and Related CO_2 Concentrating Mechansims*. Two distinguished international authorities in the field of photosynthesis have edited this volume: Agepati S. Raghavendra (University of Hyderabad, Hyderabad, India) and Rowan F. Sage (University of Toronto, Toronto, Canada). Ragha, as Raghavendra is called by his friends, has contributed significantly to the topics in this volume and photosynthesis in general, e.g., to the discovery of several C_4 plants, C_3–C_4 intermediates, regulation of C_4 phosphoenolpyruvate, requirement of mitochondrial respiration for optimizing photosynthesis, and mitochondrial enrichment in bundle sheath cells as the basis of reduced photorespiration in C_3–C_4 intermediates. Rowan Sage has worked over a remarkably broad range of topics, from biochemistry to ecology of photosynthesis and has been interested in C_4 and its attributes since his Ph.D. research on co-occurrence of C_3 and C_4 weeds. His work has shown that there have been at least 60 independent origins of C_4 photosynthesis, making it the most convergent of evolutionary phenomena known to humanity. His work on C_4 evolution led to his participation in the C_4 rice engineering project; his current research includes the evolution and engineering of C_4 photosynthesis, the impact of temperature and CO_2 variation on the biochemical processes governing C_3 and C_4 photosynthesis, and cold-tolerance in high-yielding C_4 grasses such as *Miscanthus*. This last project is geared toward developing a bioenergy economy based on high-yielding C_4 plants, a very important goal for the benefit of all humanity.

Our Books: 31 Volumes

We list below information on all the 31 volumes that have been published thus far; beginning with volume 31, Thomas D. Sharkey, who had earlier edited volume 9 of this series of book, has joined us as its co-series editor. We are pleased to note that Springer is now producing complete table of content of these books and electronic copies of individual chapters of these books; their web sites include free downloadable front matter as well as indexes. As of July 12, 2010, the only volumes that are not yet complete are: volumes 1, 13, 14, 15 and 17. All the available web sites are listed, within square brackets, at the end of each entry.

- *Volume 31* (2010): ***The Chloroplast: Basics and Applications,*** edited by Constantin Rebeiz, Christoph Benning, Hans J. Bohnert, Henry Daniell, J. Kenneth Hoober, Hartmut K. Lichtenthaler, Archie R. Portis, and Baishnab C. Tripathy. Twenty-five chapters, 500 pp, Hardcover, ISBN: 978-90-481-8530-6 available June 2010
- *Volume 30* (2009): ***Lipids in Photosynthesis: Essential and Regulatory Functions,*** edited by Hajime Wada and Norio Murata, both from Japan. Twenty chapters, 506 pp, Hardcover, ISBN:978-90-481-2862-4;e-book, ISBN:978-90-481-2863-1 [http://www.springerlink.com/content/978-90-481-2862-4]
- *Volume 29* (2009): ***Photosynthesis In silico: Understanding Complexity from Molecules,*** edited by Agu Laisk, Ladislav Nedbal, and Govindjee, from Estonia, The Czech Republic, and USA. Twenty chapters, 508 pp, Hardcover, ISBN:978-1-4020-9236-7 [http://www.springerlink.com/content/978-1-4020-9236-7]

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

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

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.uiuc. edu/govindjee/photosynSeries/ttocs.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

"*C_4 Photosynthesis and Related CO_2 Concentrating Mechanisms*" is volume 32 of the Advances in Photosynthesis and Respiration. The preface of the book on page xix beautifully describes the context of this book; and the contents of this book on page xiii shows the breadth of this book. A unique aspect of this book is tributes to two pioneers: Jagadish Chandra Bose; and Constance E. Hartt just before the topic of the book is introduced. The C_4 pathway, also known as the Hatch and Slack pathway, of photosynthesis was discovered and characterized more than 4 decades ago. The C_4 photosynthesis has had profound impact not only on food production, but on global ecology, and on the

evolutionary development of the modern biosphere, including our own origin and the rise of our civilization. Recent studies have provided new perspectives on the diversity and evolutionary origin of C_4 plants; these plants have independently evolved over 50 times; there are even multiple examples of single-celled C_4 photosynthesis (see the cover of this book). The evolutionary rise of C_4 plants has altered the face of the Earth, and has contributed to the origin of the grassland biota we know today. With new molecular tools, many of the genes controlling C_4 photosynthesis have now been elucidated, allowing us to begin engineering the C_4 pathway into C_3 plants and to domesticate wild C_4 species as new energy crops for our future. This book provides a state-of-the-art overview of basic and applied aspects of C_4 plant biology; its emphasis is on physiology, biochemistry, molecular biology, biogeography and evolution. Further, this book provides a review of developments in the bioengineering of C_4 rice and novel biofuels. We expect that this book will serve as an advanced textbook for graduate students, and a reference for researchers, in several areas of the life sciences, including plant biology, cell biology, biotechnology, agronomy, horticulture, ecology, and evolutionary biology.

Tom Sharkey, who is an expert on the topic of this book, writes "The discovery of C_4 metabolism touched off many investigations about both the commonalities and variation among CO_2-concentrating mechanisms. The decades from the 1960s to the 1980s saw significant new insights into carbon dioxide acquisition by photosynthesizing organisms. These included advances in understanding the biophysical constraints for CO_2 uptake in C_3 plants, the active uptake of CO_2 and bicarbonate by algae and bacteria, and of course, C_4 metabolism. Since these discoveries, tremendous advances have been made and two world experts, Agepati S. Raghavendra (of India) and Rowan Sage (of Canada), have now edited this volume that makes all of the latest advances available to the interested reader. Clearly, C_4 and related metabolism provides tremendous opportunity to better understand photosynthesis and the possibilities to further adapt it to the needs of people."

Authors

The current book contains 19 chapters written by 32 international authors from ten different countries (Argentina; Australia; Canada; Germany; India; Ireland; Russia; Turkey; United Kingdom and the United States of America). They are (arranged alphabetically): Carlos S. Andreo (Argentina); Hermann Bauwe (Germany); Andrew A. Benson (USA); James O. Berry (USA); George Bowes (USA); Andrea Bräutigam (Germany); Jim N. Burnell (Australia); Chris J. Chastain (USA); María F. Drincovich (Argentina); Gerald E. Edwards (USA); John R. Evans (Australia); Oula Ghannoum (Australia); Govindjee (USA); Udo Gowik (Germany); Mike B. Jones (Ireland); Ferit Kocacinar (Turkey); Stanislav Kopriva (UK); David S. Kubien (Canada); María V. Lara (Argentina); Andrew Maretzki (USA); Verónica G. Maurino (Germany); Timothy Nelson (USA); Colin P. Osborne (UK); Minesh Patel (USA); Agepati S. Raghavendra (India); Eric H. Roalson (USA); Rowan F. Sage (Canada); Susanne von Caemmerer (Australia); Elena V. Voznesenskaya (Russia); Andreas P. M. Weber (Germany); Peter Westhoff (Germany); and Amy Zielinski (USA).

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):

- Photosynthesis: Perspectives on Plastid Biology, Energy Conversion and Carbon Metabolism (Editors: Julian Eaton-Rye, Baishnab Tripathy, and Thomas D. Sharkey)
- Functional Genomics and Evolution of Photosynthetic Systems (Editors: Robert Burnap and Willem Vermaas)
- The Bioenergetic Processes of Cyanobacteria: From Evolutionary Singularity to Ecological Diversity (Editors: Guenter A. Peschek, Christian Obinger, and Gernot Renger)

- Chloroplast Biogenesis: During Leaf Development and Senescence (Editors: Basanti Biswal, Karin Krupinska, and Udaya Chand Biswal)
- The Structural Basis of Biological Energy Generation (Editor: Martin Hohmann-Marriott)
- Genomics of Chloroplasts and Mitochondria (Editors: Ralph Bock and Volker Knoop)
- Photosynthesis in Bryophytes and Early Land Plants (Editors: David T. Hanson and Steven K. Rice)

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

- Artificial Photosynthesis
- ATP Synthase and Proton Translocation
- Biohydrogen Production
- Carotenoids II
- Cyanobacteria
- The Cytochromes
- Ecophysiology
- Evolution of Photosynthesis
- Genomics of Chloroplasts and Mitochondria
- Global Aspects of Photosynthesis
- Green Bacteria and Heliobacteria
- Interactions Between Photosynthesis and Other Metabolic Processes
- Limits of Photosynthesis
- Photosynthesis, Biomass and Bioenergy
- Photosynthesis Under Abiotic Stress
- Plant Canopies and Photosynthesis

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

In view of the interdisciplinary character of research in photosynthesis and respiration, it is my earnest hope that this series of books will be used in educating students and researchers not only in plant sciences, molecular and cell biology, integrative biology, biotechnology, agricultural sciences, microbiology, biochemistry, chemical biology, biological physics, and biophysics, but also in bioengineering, chemistry, and physics.

We take this opportunity to thank and congratulate Agepati S. Raghavendra and Rowan F. Sage 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 and their help in preparing this editorial. We thank all the 32 authors of this book (see the list above): without their authoritative chapters, there would be no such volume. We give special thanks to R. Samuel Devanand for directing the typesetting of this book: his 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 Jeff Haas (Director of Information Technology, Life Sciences, University of Illinois at Urbana-Champaign, UIUC), Feng Sheng Hu (Head, Department of Plant Biology, UIUC), Tom Sharkey (my co-Series Editor), and my dear wife, Rajni Govindjee for constant support.

August 15, 2010

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The Founding Series Editor

Govindjee

Govindjee 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 Robert Emerson, and Eugene Rabinowitch, obtaining his Ph.D. in 1960, in Biophysics. He is best known for his research on the excitation energy transfer, light emission, the primary photochemistry and the electron transfer in "*Photosystem II*" (PS II, water-plastoquinone oxido-reductase). His research, with many collaborators, has included the discovery of a short-wavelength form of chlorophyll (Chl) *a* functioning in the Chl *b*- containing system, now called PS II; of the two-light effect in Chl a fluorescence; and of the two-light effect (Emerson enhancement) in NADP reduction in chloroplasts. His major achievements include an understanding of the basic relationships between Chl *a* fluorescence and photosynthetic reactions; an unique role of bicarbonate on the electron acceptor side of PS II, particularly in the protonation events involving the Q_B binding region; the theory of thermoluminescence in plants; the first picosecond measurements on the primary photochemistry of PS II; and the use of fluorescence lifetime imaging microscopy (FLIM) of Chl *a* fluorescence in understanding photoprotection, by plants, against excess light. His current focus is on the "*History of Photosynthesis Research*", in '*Photosynthesis Education*', and in the '*Possible Existence of Extraterrestrial Life*' He has served on the faculty of the UIUC for ~40 years. Govindjee's honors include: Fellow of the American Association of Advancement of Science (AAAS); Distinguished Lecturer of the School of Life Sciences, UIUC; Fellow and Lifetime Member of the National Academy of Sciences (India); President of the American Society for Photobiology (1980-1981); Fulbright Scholar and Fulbright Senior Lecturer; Honorary President of the 2004 International Photosynthesis Congress (Montréal, Canada); the first recipient of the Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology, 2006; Recipient of the Communication Award of the International Society of Photosynthesis Research, 2007; and the Liberal Arts and Sciences Lifetime Achievement Award of the UIUC, 2008. Further, Govindjee was honored (1) in 2007, through two special volumes of *Photosynthesis Research*, celebrating his 75th birthday and for his 50-year dedicated research in 'Photosynthesis' (Guest Editor: Julian Eaton-Rye); (2) in 2008, through a special International Symposium on 'Photosynthesis in a Global Perspective', held in November, 2008, at the University of Indore, India. Govindjee is coauthor of 'Photosynthesis' (Wiley, 1969); and editor of many books, published by several publishers including Academic and Kluwer (now Springer). For further information on Govindjee, see his web site at http://www.life.illinois.edu/govindjee.

Series Editor

Thomas D. Sharkey

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 federally funded Plant Research Laboratory at Michigan State University under the mentorship of Klaus Raschke and graduated in 1980 after just 3 years and 3 months. 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 that continues to get over 50 citations per year more than 25 years after its publication. For 5 years he worked at the Desert Research Institute, Reno, Nevada, where Rowan Sage, co-editor of this volume, joined him as a post-doc. After Reno, Tom spent 20 years as professor of botany at the University of Wisconsin in Madison. In 2008, Tom became professor and chair of the Department of Biochemistry and Molecular Biology at Michigan State University. Tom's research interests center on the exchange of gases between plants and the atmosphere. The biochemistry and biophysics underlying carbon dioxide uptake and isoprene emission from plants form the two major research topics in his laboratory. Among his contributions are measurement of the carbon dioxide concentration inside leaves, an exhaustive study of short-term feedback effects in carbon metabolism and a significant contribution to elucidation of the pathway by which leaf starch breaks down at night. In the isoprene research field, Tom is recognized as the leading advocate for thermotolerance of photosynthesis as the explanation for why plants emit isoprene. In addition, his laboratory has cloned many of the genes that underlie isoprene synthesis and published many papers on the biochemical regulation of isoprene synthesis. Tom has edited two books, the first on trace gas emissions from plants in 1991 and then volume 9 of this series on the physiology of carbon metabolism of photosynthesis in 2000. Tom is listed in *Who's Who* and is a "highly cited researcher" according to the Thomson Reuters Institute for Scientific Information, and is grateful to Rowan Sage for contributing to that honor by his early productivity.

Contents

Part III: Molecular Basis of C_4 Pathway

Part V: C_4 Engineering and Bioenergy

Preface

C_4 photosynthesis is carbon concentrating system that uses a metabolic cycle centered around phosphoenolpyruvate (PEP) carboxylation to concentrate CO_2 into an internal compartment where Rubisco (Ribulose bis-phosphate carboxylase oxygenase) has been localized. In doing so, it greatly reduces photorespiratory inhibition of photosynthesis and increases the carboxylation capacity of Rubisco over what would be possible in C_3 plants under similar conditions. Approximately 7,500 plant species in 19 families of vascular plants use the C_4 photosynthetic pathway as an alternative to the C_3 pathway. Even though C_4 plants make up to only about 3% of angiosperm species, they account for one-fourth of global terrestrial productivity, and are the most productive and resource-use efficient plants exploited by humanity.

With the discovery of the C_4 pathway in the 1960s by Marshall (Hal) D. Hatch, C. Roger Slack and colleagues, humans quickly recognized its superior performance relative to C_3 photosynthesis. This recognition led to a surge in research of all things C_4, and by the mid-1970s, the general patterns of ecology, physiology, systematics and biochemistry of the C_4 pathway had been described. This rapid expansion of knowledge of C_4 photosynthesis following the first publication of the C_4 pathway in 1967 stands out as one of the most exciting eras in the plant sciences.

As the C_4 photosynthesis was characterized, plant biologists were able to explain in mechanistic terms many patterns long recognized by humanity. The classic example is the function of Kranz anatomy, which was first described in the 1880s by the Austrian/German botanist Gottlieb Haberlandt, but had no known purpose. The C_4 discovery demonstrated that the enlarged bundle sheath of Kranz anatomy is the internal compartment where CO_2 is concentrated around Rubisco by the C_4 metabolic cycle. The geographical separation of warm-season "sour" grasses from cool season "sweet" grasses that was long noticed by pastoralists became clear – sour grasses are C_4 species, while the sweet grasses were C_3 species. Weed biologists quickly realized that there was a physiological explanation for the severity of the world's worst weeds; it turned out that most of the severe weeds utilized the C_4 pathway and thus were highly productive in the presence of C_3 crops. Furthermore, with the discovery of the photorespiratory pathway in the late 1960s, plant biologists were able to explain the biogeographical segregation between C_3 and C_4 grasses and sedges, and thus the reason for the long-noted pattern that Kranz species occur in warm climates became known. In short order, the discovery of C_4 photosynthesis revolutionized our understanding of the biological world and our place in it, and in doing so, provided society a means to better manipulate the natural world to meet the food, fiber and fuel needs of human society.

The four decades since the discovery of the C_4 pathway have produced a widening arc of discovery that has spread well beyond the plant sciences to influence a wide range of biological disciplines, as well as fields outside of biology such as geology and anthropology. With the advent of modern phylogenetics, it has become possible to precisely identify the lineages where C_4 photosynthesis independently arose. This understanding laid the foundation for the realization that C_4 photosynthesis is one of the most convergent of evolutionary phenomenon, having independently evolved at least 60 times. Molecular phylogenetics, along with advances in the use of isotopic tracers, provide strong evidence for the first origin of the C_4 pathway some 25 million years ago, at a time when the climate of the earth was becoming cooler and drier, and atmospheric CO_2 levels were falling to values lower than currently observed. The rise of functional and comparative genomics have provided physiologists with important new tools for identifying genes, enzymes and regulatory systems that are essential for C_4 function. In the past decade, these tools have allowed for

the identification of the evolutionary changes within the genome during the evolution of the C_4 pathway. With these discoveries, scientists now have some of the key elements needed to engineer C_4 photosynthesis into C_3 plants, potentially bringing the greater productivity of the C_4 pathway to a wide range of plants used in agriculture and forestry. Because of the magnitude and complexity of the task, C_4 engineering will require unprecedented coordination between specialists in basic research disciplines (plant physiology, genetics and genomics, molecular and systems biology, and bioinformatics) and related applied fields such as crop breeding, agronomy, and weed science. Many scientists, both old and new, will need to become familiar with a wide range of topics concerning C_4 photosynthesis. As such, a new text is needed that provides up-to-date summaries of the latest developments in C_4 plant biology. To this end, we and the authors of the chapters in this volume of the *Advances in Photosynthesis and Respiration* series provide in-depth summaries of the state of our understanding of the structure, function, evolution and potential for novel applications of C_4 plants.

Since the discovery of the C_4 pathway in the 1960s, there have been three major treatises on C_4 photosynthesis. The first was *Photosynthesis and Respiration* (1971) edited by M.D. Hatch, C.B. Osmond and R.O. Slatyer (Wiley-Interscience Publishers). This book arose out of a highly influential conference held in December 1970 at the Australian National University in Canberra where many of the disparate elements of the C_4 story first came together. As summarized by the editors, this meeting "permitted a consensus of opinion on matters of interest or controversy regarding the new and rapidly advancing areas" of C_4 photosynthesis and photorespiration. One seminal feature of this meeting and the resulting book was the first realization of the significance of photorespiration for the existence and success of the C_4 pathway. To this day, the importance of this meeting is heralded by old-timers and youngsters alike, as demonstrated at the 2007 C_4-CAM International Congress held in Cambridge, England where the attendees honored the early pioneers of C_4 research by singing "*The C-Two Three Through Four Pathway*" first sung by the participants of the 1970 conference.

The second notable treatise was *C_3–C_4: Mechanisms, and Cellular and Environmental Regulation, of Photosynthesis* by Gerry Edwards and David Walker (Blackwell Scientific, 1983). This book was notable in that it provided the first in depth, textbook style-summary of the C_3, C_4 and CAM pathways as understood at that time. For the second generation of C_4 plant biologists who came of age in the late-1970s and 1980s, this book was the C_4 bible, the text to memorize, and later, when they were academics, the book to assign to their students. For nearly 20 years, one could not be a C_4 biologist without having intimate familiarity of *C_3–C_4*, for its breadth of scope addressed everything from the detailed biochemistry to ecological performance of C_3, C_4 and CAM species. Even today, nearly 30 years later, *C_3–C_4* remains one of the most straight-forward and understandable introduction to C_4 plant biology for students as they move beyond the simple treatments in plant physiology textbooks.

The third and most recent comprehensive overview on C_4 photosynthesis was prepared a decade ago by one of us (R.F.S.) and Russ Monson (*C_4 Plant Biology*, Academic, San Diego, CA, USA, 1999). This book was noted for its breadth, and the depth with which its authors reviewed the biochemical, physiological, evolutionary, ecological, agronomic and anthropological aspects of C_4 plant biology. Notable contributions from this volume included a series of cogent arguments for why the C_4 pathway existed, when it had evolved and how it had influenced the rise of humanity. The first comprehensive phylogenetic pattern of the world's C_4 flora was presented, along with the first detailed theoretical model of C_4 photosynthesis. The distribution of the C_4 flora around the world, and underlying ecological and physiological drivers for the distribution were reviewed, and for the first time, a complete compilation of the many types of Kranz anatomy was presented. As C_3–C_4 have been to the C_4 plant scientists coming of age in the 1980s and 1990s, *C_4 Plant Biology* became the main text for the most recent generation of plant biologists, many of whom are represented in this volume either as authors, or colleagues whose research is summarized in the many chapters.

Since *C_4 Plant Biology,* there has been rapid progress in our understanding of the C_4 pathway,

with new emerging concepts, particularly in relation to evolution, novel single-cell C_4 plants, molecular biology of gene expression, genetic engineering of C_4 traits and novel ways to exploit C_4 plants for food and fuel. The high-throughput techniques of molecular biology are responsible for many of the new insights, but the widening realization that C_4 plants had a great impact on the evolution of the biosphere in recent geological time has brought new approaches and perspectives to the study of C_4 plants. Thus, zoologists, geologists and anthropologists have provided important contributions to our understanding of C_4 plant biology, and knowledge of C_4 photosynthesis is considered important for specialists in each of these disciplines. The need to summarize these recent developments in C_4 research for a broad audience that extends beyond the traditional core of plant physiologists has been a major impetus in the development of this book.

This current book on C_4 plants and algae is broadly divided into four parts. Part I starts with two tributes: one to Jagadish Chandra Bose (Chapter 1) and a second to Constance Hartt (Chapter 2), two of the early discoverers of C_4-like characteristics in plants. This is followed by an introduction to the book (Chapter 3). Part II addresses new physiological and developmental perspectives of the C_4 pathway. This part has the largest number of chapters (seven in total), reflecting the expansion in our knowledge of this traditional core area of C_4 research. Topics covered in this part include: single-cell C_4 systems in terrestrial and aquatic plants (Chapters 4 and 5); photorespiration (Chapter 6); nitrogen/sulphur metabolism (Chapter 7); nitrogen and water use efficiency (Chapter 8); the development of leaves and the specialized anatomy required for C_4 photosynthesis (Chapter 9); and finally, a review of the temperature responses of C_4 photosynthesis (Chapter 10).

Part III, with five chapters (11–15), provides descriptions of the molecular basis of the C_4 pathway. The intercellular and intracellular transport processes unique for C_4 leaves are described in Chapter 11, while the different patterns of gene expression in mesophyll and bundle sheath cells are outlined in Chapter 12. The molecular and biochemical properties of the key enzymes of C_4 pathway, namely PEP carboxylase, pyruvate orthophosphate dikinase and C_4 acid decarboxylases, are presented in Chapters 13–15. Part IV contains reviews of the multiple origins of the C_4 pathway in the monocots (Chapter 16) and the geologic history of C_4 plants (Chapter 17). In Part V, Chapter 18 focuses on novel applications of C_4 photosynthesis and how our current knowledge can be exploited for engineering of C_4 rice. The very last chapter (Chapter 19) addresses the use of C_4 species as energy crops.

We are confident that the present volume will follow in the footsteps of the earlier treatises and serve as an important milestone in the literature on C_4 pathway. The information provided here should stimulate further research and pave the way for interdisciplinary interactions, and may be key in inspiring a new generation of researchers to build on the successes of their fore-bearers. The book would be a useful tool in diversifying the research on C_4 photosynthesis and in exploiting C_4 plants for the benefit and advancement of all humanity.

We dedicate this volume to the memory of the many scientists whose early efforts created the knowledge base that made the C_4 discovery possible. While the scientific endeavor is punctuated by significant discoveries that are often attributed to one or a few individuals, it is the efforts of those who have gone before, many of whom are never recognized for their contributions that made the great discoveries such as C_4 photosynthesis possible. In this volume, we have specifically recognized Jagadish Chandra Bose and Constance Hartt, but to this list we would like to add Gottlieb Haberlandt, who first published the term Kranz anatomy (*Kranz-typus*) and recognized that there could be a functional specialization of the mesophyll and bundle sheath cell types. While many know of Haberlandt and Kranz anatomy, few in the C_4 community know his first name, the circumstances of his life, and that he is also considered the father of plant tissue culture. A fascinating aspect of the C_4 story is how independent lines of inquiry suddenly converged in 1966–1968 to produce the understanding that holds today. Names worth recalling from these different lines of inquiry include Heinrich Moser (Austria), Roger Black (Australia) and Tana Bisalputra (Australia and Canada) whose anatomical work between 1934 and 1960 drew

attention to Kranz anatomy in the dicots. Bisalputra may have played a key role in linking the early use of the term "Kranz" with the newly described C_4 physiology, for he brought his knowledge of the early anatomical literature to the lab of Bruce Tregunna in Vancouver, Canada, and published with Tregunna and John Downton the paper that first applied the term "Kranz" anatomy to C_4 photosynthesis (*Canadian Journal of Botany* **47**: 915, 1969). From the cell biology perspective, the possible significance of the distinct cell structure of maize was discussed in some depth in 1944 by M.M. Rhoades and A. Carvalho in a light microscopy analysis. Following the introduction of the electron microscope, A.J. Hodge, J.D. McLean and F.V. Mercer described the ultrastructure of maize chloroplasts in 1955, and W.M. Laetsch and co-workers followed with studies on sugarcane and C_4 dicots in the 1960s. On the gas exchange front, an important node was the lab of Roger Musgrave and students (D.N. Baker, D.N. Moss and J.D. Hesketh) and later, Hesketh's group which included Mabrouk El-Sharkaway and H. Muramoto in Arizona. These workers, along with Y. Murata and J. Iyami in Japan produced an extensive body of photosynthesis data in the early-to-mid 1960s that drew attention to the distinctive characteristics of what would soon be known as C_4 photosynthesis. On the biochemical front, two important contributions preceded the work of Hatch and Slack. One was from the research team of Hugo Kortschak, Constance Hartt and George Burr at the Hawaiian Sugar Planter's Association, and the other was the team of Yuri Karpilov in the former Soviet Union. These groups independently demonstrated C_4 acid flux in maize and sugarcane in the 1950s. Unfortunately, Karpilov's work did not come to the attention of western scientists until the late 1960s, after the C_4 pathway had been described. The Hawaiian results proved instrumental in stimulating Hal Hatch and Roger Slack to begin their experiments on sugarcane in the early-to-mid-1960s, which quickly led to the elucidation of the C_4 pathway (see Hatch in *Photosynthesis Research* **73**: 251–256, 2002). Also of note, Barry Osmond produced a significant paper in 1967 showing that dicots also exhibited the C_4-type of metabolism. This work, along with the studies by Hatch and Slack, allowed John Downton and Bruce Tregunna to produce a series of papers in 1968–1970 that pulled the C_4 story together by linking C_4 biochemistry, C_4 anatomy, and the biogeography of C_4 plants.

It is the efforts of these and the many other researchers who made the telling of the C_4 story possible. Their history deserves a dedicated volume, for the discovery of the C_4 story is a compelling example of how disparate and perhaps mundane observations converge in an instant in time with a profound realization that impacts the human condition. With much of this early research now available on-line, we urge the new generation of C_4 plant biologists to examine the contributions of the early pioneers of the C_4 story, both to see how prescient their work was in retrospect, but also to appreciate the context in which they studied. Unlike us, they had no idea of the big discovery that lay just around the corner.

We thank all the authors who made this book possible with their excellent contributions. We owe special thanks to the reviewers who read the drafts and helped to improve the chapters. In particular, we thank Govindjee for his significant assistance, from the beginning of this project until final publication of the manuscripts, and as the founding series editor, author, and critical advisor on formatting/editorial issues. We also welcome Thomas D. Sharkey who has joined this series, from volume 31, as a co-series editor. We appreciate the help and services of Jacco Flipsen, Noeline Gibson (who has now retired), Ineke Ravesloot at the Springer office in Dordrecht, the Netherlands and R. Samuel Devanand, SPi Technologies, India.

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The Editors

Agepati S. Raghavendra

Agepati Srinivasa Raghavendra was born on 17 November 1950 in India. He is now a Professor and J.C. Bose National Fellow at the Department of Plant Sciences, School of Life Sciences, University of Hyderabad, Hyderabad, India. He earned a B.Sc. (1969), an M.Sc. (1971) and a Ph.D. (1975), all from Sri Venkateswara (S.V.) University, Tirupati. Availing the Humboldt Foundation Fellowship, he worked with leading plant physiologists/biochemists in Germany, including Ulrich Heber, Hans Walter Heldt, Peter Westhoff and Renate Scheibe. He also collaborated with scientists from Japan, France, Germany and U.K. for extended periods. He started his career as scientist at Central Plantation Crops Research Institute (Indian Council of Agricultural Research, ICAR), Vittal in 1974; worked as Assistant Professor, Botany Department, S.V. University (1976–1982); Deputy Director and Head, Plant Physiology Division, Rubber Research Institute, Kottayam (1982–1985); and Associate Professor (1985), Professor (1996–current), Department of Plant Sciences, and Dean, School of Life Sciences (2004–2010), all at University of Hyderabad. Ragha, as he is called by his friends, contributed significantly towards the discovery of several C_4 plants, C_3–C_4 intermediates; regulation of C_4-phosphoenolpyruvate carboxylase, essentiality of mitochondrial respiration for optimizing photosynthesis, mitochondrial enrichment in bundle sheath cells as the basis of reduced photorespiration in C_3–C_4 intermediates and mechanisms of stomatal closure. He has published more than 190 research papers, and authored a number of reviews and book chapters, besides a highly referred book (*Photosynthesis: A Comprehensive Treatise*, Cambridge University Press. 1998 and 2000). He established an active research group to study photosynthetic carbon assimilation initially at the S.V. University and later at the University of Hyderabad. His current research interests include biochemistry of C_4 photosynthesis, chloroplast–mitochondria interactions and signal transduction in stomatal guard cells. Ragha is on the editorial board of the journal *Photosynthesis Research* and was on the advisory editorial board of the *Advances in Photosynthesis and Respiration*, both published by Springer, Germany. Currently, he is editor-in-chief of *Journal of Plant Biology*. In recognition of his research contributions, Ragha was elected Fellow of all the three Indian Science Academies (Indian National Science Academy, Indian Academy of Science, and the National Academy of Sciences), besides the National Academy of Agricultural Sciences and the prestigious Third World Academy of Sciences, Trieste, Italy.

Rowan F. Sage

Rowan Frederick Sage was born on September 2, 1958 in Reno, Nevada USA, and now lives in Toronto, Canada where he is a Professor of Botany in the Department of Ecology and Evolutionary Biology, University of Toronto, St. George Campus, Toronto, Ontario, Canada. He received a B.Sc. degree in 1980 from Colorado College, in Colorado, USA and his Ph.D. in 1986 from the University of California, Davis under the supervision of Professor Robert W. Pearcy. His Ph.D. dissertation addressed the nitrogen use efficiency of C_4 photosynthesis in the ecologically similar weeds *Chenopodium album* (C_3) and *Amaranthus retroflexus* (C_4). From Davis, he returned to Reno for a post-doctoral appointment in the labs of Thomas D. Sharkey and Jeffrey Seemann at the Desert Research Institute, where he studied the biochemical limitations on C_3 photosynthesis in response to temperature and CO_2. After 2 years in Reno (1986–1987), he accepted his first faculty appointment at the University of Georgia, where he remained for 5 years (1988–1993). In 1993, he joined the faculty at the University of Toronto, where he reactivated his C_4 research. At the University of Toronto, he served as associate chair (1996–2003) and chair (2004–2006) of the Botany department. Initially, the C_4 research during his Toronto years addressed whether Rubisco limits C_4 photosynthesis at cooler temperatures, rather than pyruvate–phosphate dikinase, which at the time was the prevailing hypothesis. Following the publication of *C_4 Plant Biology* in 1999, which he edited with Russ Monson, Rowan embarked on a 10-year program to study the evolution of C_4 photosynthesis in the dicots. A highlight of this work was the compilation of every known C_4 evolutionary lineage, which at the latest count shows at least 60 independent origins of C_4 photosynthesis, making it one of the most convergent of evolutionary phenomena known to humanity. Rowan's work on C_4 evolution led to his participation in the C_4 Rice Engineering project, which was initiated by John Sheehy at the International Rice Research Institute in 2006. His current research includes the evolution and engineering of C_4 photosynthesis, the impact of temperature and CO_2 variation on the biochemical processes governing C_3 and C_4 photosynthesis, and cold-tolerance in high-yielding C_4 grasses such as *Miscanthus*. This last project is geared toward developing a bioenergy economy in Canada based on high-yielding C_4 plants. In addition to his research and teaching (of physiological ecology and global change ecology), he is a handling editor for *Global Change Biology* and *Oecologia*, an associate editor for the *Journal of Integrative Plant Sciences*, and serves on the editorial board of *Plant, Cell and Environment*, *Plant and Cell Physiology*, and *Photosynthesis Research*.

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