Advances in Photosynthesis and Respiration 36
Including Bioenergy and Related Processes

Basanti Biswal
Karin Krupinska
Udaya C. Biswal *Editors*

Plastid Development in Leaves during Growth and Senescence

Springer

Plastid Development in Leaves During Growth and Senescence

This book deals with *plastid development in leaves during growth and senescence*. Leaves undergo various phases during their development finally leading to senescence and death. Deciduous trees form new leaves in spring, a process paralleled by development of photosynthetically active chloroplasts. In autumn, leaves undergo spectacular changes in colour ranging form yellow, red up to brown, a process paralleled by degradation of chlorophyll and dismantling of chloroplasts. We introduce this book with the above photographs taken by Karin Krupinska, showing at the left emerging and young leaves of *Tilia europaea* and at the right senescing leaves of *Acer tataricum* L.

Advances in Photosynthesis and Respiration
Including Bioenergy and Related Processes

VOLUME 36

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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Plastid Development in Leaves During Growth and Senescence

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This book is dedicated to the memory of

Prasanna Mohanty (1934–2013)

A dear friend, an eminent plant biologist, a pioneer of photosynthesis research, and a loving teacher

From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 36: Plastid Development in Leaves During Growth and Senescence

We are delighted to announce the publication of Volume 36 in this series. The series *Advances in Photosynthesis and Respiration* was updated in Volume 35 to include the subtitle: *Including Bioenergy and Related Processes*. The front cover, which had a distinctive white background and a colored illustration, was changed to a web-friendly green background. Further, the series publisher, Springer, has made the front matter of all of the volumes freely available online. Links to each volume are given below. Readers may also notice that this volume and the past few volumes have had color figures integrated into the chapters, instead of being collected in one section of the book. This improvement was possible because of changes in the method of book production. Another change is that references to chapters in books will soon be 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

Volume 36 deals with *Plastid Development in Leaves During Growth and Senescence*. We refer the readers to the excellent Preface (see pp. xxvii–xxix) by three outstanding editors of this book: Basanti Biswal (Sambalpur University, Jyoti Vihar, Odisha, India), Karin Krupinska (University of Kiel, Kiel, Germany), and Udaya Biswal (Sambalpur University, Jyoti Vihar, Odisha, India). These three, which include the wife (Basanti) and husband (Udaya) team of the Biswals and Karin Krupinska, are established authorities in the field of plant biology (see their biographies on pp. xxxi–xxxvi). An understanding of this aspect of plant life is important for all projects dealing with the production of increased biomass and bioenergy. Chloroplast development is a key process in the life of a plant. Recent advances in plant biology reveal that chloroplasts also determine the development, the structure, and the physiology of the entire plant. A number of books have emphasized the biogenesis of the chloroplast, but few have dealt with the events associated with the transformation of a mature chloroplast into a gerontoplast during senescence. This book, which has 28 chapters, is unique because it describes the process of chloroplast maturation and its subsequent transformation into a gerontoplast during senescence, a process required for nutrient recycling in plants. The book includes a state-of-the-art survey of the current knowledge of the regulation and mechanisms of chloroplast development. Authors critically discuss the signaling process, the expression potential of plastid DNA, the interaction of cellular organelles, and the molecular mechanisms associated with the assembly and the disassembly of organellar complexes. Finally, how chloroplast development is modulated by environmental

signals is discussed. We hope the readers will find this volume not only enlightening and fascinating but of practical use in their own endeavors. We are grateful to Basanti, Udaya, and Karin for their timely submission of this 28-chapter book and to all the 57 authors who contributed to this outstanding book in an area that had been somewhat neglected.

Authors

The current book contains 28 chapters written by 57 authors from 13 countries (Argentina (5); Croatia (3); France (2); Germany (8); Hungary (1); India (14); Italy (1); Japan (8); Spain (3); Sweden (2); Switzerland (2); UK (6); and USA (2)). We thank all the authors for their valuable contribution to this book; their names (arranged alphabetically) are listed below:

Mats X. Andersson (Chap. 8); Henrik Aronsson (Chap. 3); Basanti Biswal (Chaps. 1, 2, and 28); Udaya C. Biswal (Chaps. 1 and 2); Maryse Block (Chap. 7); Thomas Börner (Chap. 11); Naini Burman (Chap. 25); Cristian A. Carrion (Chap. 18); Maria L. Costa (Chap. 18); Vijay Dalal (Chap. 27); Emmanuelle Dubots (Chap. 7); Hrvoje Fulgosi (Chap. 26); Facundo M. Gomez (Chap. 18); John C. Gray (Chap. 9); Juan J. Guiamet (Chap. 18); Yukako Hihara (Chap. 5); Stefan Hörtensteiner (Chap. 16); Hiroyuki Ishida (Chap. 19); Paul Jarvis (Chap. 12); Padmanava Joshi (Chap. 28); Kengo Kanamaru (Chap. 10); Yusuke Kato (Chap. 20); Renu Khanna-Chopra (Chap. 17); Jitendra P. Khurana (Chap. 25); Karin Krupinska (Chaps. 1 and 14); Hartmut K. Lichtenthaler (Chap. 15); Karsten Liere (Chap. 11); Qihua Ling (Chap. 12); Nikola Ljubesic (Chap. 26); Eric Maréchal (Chap. 7); Mercedes Martín (Chap. 23); Dana E. Martínez (Chap. 18); Karin Meierhoff (Chap. 4); Bijaya K. Mishra (Chap. 2); Amarendra N. Misra (Chap. 28); Maria Mulisch (Chap. 14); Sergi Munné-Bosch (Chap. 22); Lalitendu Nayak (Chap. 28); Larry D. Noodén (Chap. 13); Kamlesh Kant Nutan (Chap. 17); Ashwani Pareek (Chap. 17); Matthew Paul (Chap. 24); Thomas Pfannschmidt (Chap. 22); Mukesh K. Raval (Chap. 2); Harry Roy (Chap. 6); Bartolomé Sabater (Chap. 23); Wataru Sakamoto (Chap. 20); Katalin Solymosi (Chap. 3); Kintake Sonoike (Chap. 5); Mamoru Sugita (Chap. 10); Baishnab C. Tripathy (Chap. 27); Raphael Trösch (Chap. 12); Shinya Wada (Chap. 19); Peter Westhoff (Chap. 4); Astrid Wingler (Chap. 24); Mercedes Wrischer (Chap. 26); and Michela Zottini (Chap. 21).

Our Books: 35 Volumes

We list below information on all the 35 volumes that have been published thus far (see http://www.springer.com/series/5599). 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. As of July 2011, Tables of Contents are available for all the volumes. The website URLs of the books in the series are listed below.

- **Volume 35 (2012)** ***Genomics of Chloroplasts and Mitochondria***, edited by Ralph Bock and Volker Knoop, both from Germany. Nineteen chapters, 475 pp, Hardcover, ISBN: 978-94-007-2919-3 (HB) ISBN978-94-007-2913-0 (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; 33 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, http://www.springer.com/life+sciences/

book/978-94-007-1532-5 (http://www.springerlink.com/content/978-90-481-1532-5/)

- **Volume 32 (2011): C4 Photosynthesis and Related CO_2 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/)
- **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://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 (http://www.springerlink.com/content/978-1-4020-3217-2/)
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- **Volume 14 (2004): Photosynthesis in Algae**, edited by Anthony W. Larkum, Susan Douglas and John A. Raven, from Australia, Canada and UK. Nineteen chapters, 500 pp, Hardcover, ISBN: 978-0-7923-6333-0 (http://www.springerlink.com/content/978-0-7923-6333-0/)
- **Volume 13 (2003): Light-Harvesting Antennas in Photosynthesis**, edited by Beverley R. Greenand William W. Parson, from Canada and USA. Seventeen chapters, 544 pp, Hardcover, ISBN: 978-07923-6335-4 (http://www.springerlink.com/content/978-0-7923-6335-4/)
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- **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/)
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Further information on these books and ordering instructions can be found at http://www.springer.com/series/5599. Contents of Volumes 1–31 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.

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):

- The Structural Basis of Biological Energy Generation (Editor: Martin Hohmann-Marriott)
- Photosynthesis in Bryophytes and Early Land Plants (Editors: David T. Hanson and Steven K. Rice)
- Canopy Photosynthesis: From Basics to Applications (Editors: Kouki Hikosaka, Ülo Niinemets and Niels P.R. Anten)
- Non-Photochemical Quenching (NPQ) and Energy Dissipation in Plants, Algae and Cyanobacteria (Editors: Barbara Demmig-Adams, Gyozo Garab, William W. Adams III, and Govindjee)
- Microbial BioEnergy: Hydrogen Production (Editors: Davide Zannoni and Roberto De Philippis)
- Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling (Editors: William Cramer and Toivo Kallas)

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

- Algae, Cyanobacteria: Biofuel and Bioenergy
- Artificial Photosynthesis
- ATP Synthase and Proton Translocation
- Bacterial Respiration II
- Biohydrogen Production
- Carotenoids II
- Cyanobacteria II
- Ecophysiology
- Evolution of Photosynthesis
- FACE Experiments
- Global Aspects of Photosynthesis
- Green Bacteria and Heliobacteria
- Hydrogen Evolution
- 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/coediting any of the above-listed books or being an author, please send an e-mail to Govindjee 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

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 Basanti Biswal, Karin Krupinska, and Udaya Biswal for their outstanding editorial work and for their highly professional dealing with the reviewing process; they have done a fantastic job not only in editing but also in organizing this book for all of us. We thank all the 57 authors of this book (see the list above); without their authoritative chapters, there would be no such volume. We give special thanks to Marjorie Ann P. Pacleb, of SPi Global, for directing the typesetting of this book; her expertise has been crucial in bringing this book to completion. We owe Jacco Flipsen, Ineke Ravesloot, and André Tournois (of Springer) thanks for their friendly working relation with us that led to the production of this book.

January 26, 2013 **Govindjee**

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Series Editors

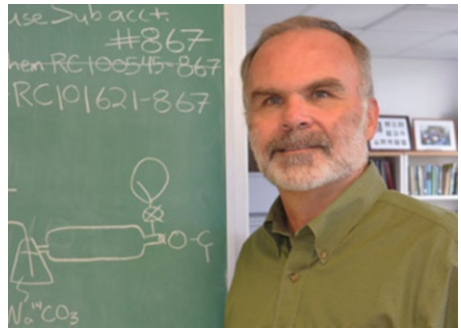
A 2012 Photograph of Govindjee. On a motorboat in Cayuga lake, Ithaca, New York. Photo by Morten Christiansen.

Govindjee, who uses one name only, was born on October 24, 1932, in Allahabad, India. We celebrated his 80th birthday last year. 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 had studied at Allahabad under Shri Ranjan, who had been a student of F.F. Blackman in UK. Govindjee 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, primary photochemistry, and electron transfer in "Photosystem II" (PS II, water-plastoquinone oxidoreductase). His research, with many collaborators, has included the discovery of a short-wavelength form of chlorophyll (Chl) *a* functioning in the Chl*b*-containing system, now called PS II; of the two-light effect in Chl*a* fluorescence; and, with his wife Rajni Govindjee, of the two-light effect (Emerson enhancement) in NADP reduction in chloroplasts. His major achievements, together with several other researchers, include an understanding of the basic relationships between Chl*a* fluorescence and photosynthetic reactions; a 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, algae and cyanobacteria; 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 and algae, against excess light.

His current focus is on the "History of Photosynthesis Research," on "Photosynthesis Education," and on the "Possible Existence of Extraterrestrial Life." He has served on the faculty of the UIUC for approximately 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, Fulbright Senior Lecturer and Fulbright Specialist; 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)** in 2012, through dedication to him of Volume 34 of this series, celebrating his 80th year; and **(4)** through a book *Photosynthesis (Overviews on Recent Progress and Future Perspectives)* (edited by S. Itoh, P. Mohanty, and K.N. Guruprasad, released in 2012, and published by IK International Publishers, New Delhi, India), honoring him for *his outstanding research and teaching of photosynthesis and for being a global leader for stimulating photosynthesis research throughout the world*.

Govindjee is coauthor of *Photosynthesis* (John Wiley, 1969) and editor of many books, published by several publishers including Academic Press and Springer. Since 2007, each year a Govindjee and Rajni Govindjee Award for Excellence in Biological Sciences is given to graduate students by the Department of Plant Biology at the UIUC. For further information on Govindjee, see his website http://www.life.illinois.edu/govindjee.



A 2012 photograph of Thomas D. Sharkey standing next to the chalk board in his laboratory at Michigan State University.

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 working for 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 Professor Klaus Raschke and graduated in 1980. Postdoctoral research was carried out with Professor Graham Farquhar at the Australian National University, in Canberra, where he coauthored 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 and then for 20 years as Professor of Botany at the University of Wisconsin in Madison. In 2008, he 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 of 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: (1) *Trace Gas Emissions from Plants* (T.D. Sharkey, E.A. Holland, and H.A. Mooney (eds.), Academic Press, San Diego, CA, 1991); (2) Volume 9 of this series; and (3) Volume 34 of this series. Tom joined the founder of this Series Govindjee as Coeditor from Volume 31. He is a "highly cited researcher" according to the Thomson Reuters Institute for Scientific Information. 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.bch.msu.edu/faculty/sharkey.htm.

Contents

Part II: Chloroplast Biogenesis During Leaf Development

Preface

Chloroplasts, the green plastids, harvest sunlight to convert CO_2 to organic carbon while producing oxygen from water. In addition, they manufacture phytohormones, amino acids, lipids, and thiol compounds. Because of their metabolic network and interaction with other cellular organelles, they play an important role in plant growth and development. The development of chloroplasts from proplastids is tightly coordinated with plant growth, whereas dismantling of chloroplasts in senescing leaves (chloroplast-to-gerontoplast transition) is an intrinsic feature of plant senescence, the terminal phase of plant development. Although studies on chloroplast development have mostly focused on photosynthesis, it is known to be also important for regulating plant growth and development. Another significance of chloroplast development, during the life of the plant, is the response to environmental stress. The chloroplast is known to be a sensor of changes in the environment. For example, some of the intermediates of biosynthetic pathways of pigments, specifically of chlorophylls, are photodynamic in nature and therefore make plants sensitive to abiotic stresses. Moreover, energy distribution within the photosynthetic apparatus and redox changes of the components involved in electron transport are sensitive toward the continuously changing environment including abiotic and biotic stresses. The sensitivity toward changes in environmental factors is likely to change with development. Possible changes in redox homeostasis, energy imbalance, and perturbation in metabolic networks during biogenesis and senescence of chloroplasts are likely to contribute to stress responses and adaptation of the whole plant.

Although chloroplast development is recognized as one of the major events in the development of plants, only few books have addressed this topic in the last decade. The books by J.T.O. Kirk and R.A.E. Tilney-Bassett (*The Plastids: Their Chemistry, Structure, Growth and Inheritance*, 1967, Freeman, London); by N.R. Baker and J. Barber (*Chloroplast Biogenesis*, 1984, Elsevier, Amsterdam); and by J.R. Ellis (ed.) (*Chloroplast Biogenesis*, 1984, Cambridge University Press, Cambridge and New York) are now outdated. Volume 23 of this series, *The Structure and Function of Plastids* (edited by R.R. Wise and J.K. Hoober, 2007), covers only a few topics (Chaps. 2, 7, 9, 15, 17, and 22) on chloroplast development, obviously not the focus of that volume. The books published thus far have emphasized primarily chloroplast biogenesis (buildup) during the greening process, but the events associated with yellowing at the end of leaf development have generally been neglected. Chloroplast development during leaf senescence when mature chloroplasts are transformed into senescing chloroplasts (gerontoplasts) had been de-emphasized for historical reasons. The process of senescence was ill-defined for a long time, but the advances made in plant molecular biology in the recent past have facilitated expansion of the knowledge of this process, of its mechanism, as well as its regulation. The availability of genome sequences of plants, specifically that of Arabidopsis, and extensive molecular genetic studies with it as a model system have allowed us to address several complex problems associated with the conversion of mature chloroplasts to gerontoplasts. A large volume of literature on the genetic program of leaf development and senescence, including gene expression and regulation, signaling systems, regulated dismantling of cellular fabrics, and molecular disassembly of the chloroplast during senescence, is now available. The progress in the field of plant senescence during the last decade has been discussed in several books and reviews. These include *Plant Cell Death Processes* (edited by L. D. Noodén, 2004, Academic

Press/Elsevier, San Diego, CA), *Senescence Processes in Plants* (edited by S. Gan, 2007, Wiley), and *Senescence Processes and Their Regulation* (edited by K. Krupinska and K. Humbeck, 2008, in *Plant Biology*) (Special Issue: Plant Senescence), German Botanical Society and The Royal Botanical Society of the Netherlands. They provide extensive information on the molecular mechanisms and regulation of the catabolic processes associated with chloroplast senescence and death. A broader view on chloroplast biogenesis and development was presented in the book *Chloroplast Biogenesis: From Proplastid to Gerontoplasts*, authored by U.C. Biswal, Basanti Biswal, and M.K. Raval (2003, Springer).

In the current volume, we present an updated and comprehensive overview of the knowledge on plastid biology during the entire life span of the leaf, ranging from chloroplast biogenesis to the transition into gerontoplasts. This volume, with 28 chapters, is unique in the series Advances in Photosynthesis and Respiration *Including Bioenergy and Related Processes* since the chapters describe the way the photosynthetic machinery (the green chloroplast) is built and subsequently transformed into another machinery (the yellow chloroplast/the gerontoplast) responsible for nutrient recycling. Authors (see List of Contributors, pp. xxxvii–xl) of the chapters (see Table of Contents, pp. xvii–xxv) are established scientists from different countries working in the area.

This book is divided into six parts. Part I, with two chapters, provides an introduction to chloroplast development, with a brief description of developmental transients, mechanisms, signaling, and regulation of the process. Chapter 1 outlines not only the current knowledge of chloroplast development but includes a discussion of the dynamic role of the organelle in integrating plant growth and development. In spite of the massive use of molecular biological tools, many questions concerning organelle development remain unanswered, suggesting limitations of these tools. It is time now to look for answers beyond the genetic basis of chloroplast development. Chapter 2 includes a discussion of the limitations of genomics, proteomics, and metabolomics and of the application of thermodynamic principles to understanding the developmental process.

The development of tools of bioinformatics and the rapid progress in plant molecular biology have significantly contributed to the expansion of knowledge in the area of biogenesis of the organelle during leaf development. The recent crystallographic studies of chloroplast complexes provide the molecular framework and geometry of the association of components of the complexes that have facilitated studies in elucidating the structural assembly of organelle complexes. In fact, the recent study of the structure of the intermediates of Rubisco (see Chap. 6) at atomic resolution during the biogenesis of this enzyme complex is a big step forward in our understanding of the assembly processes of multimeric protein complexes. The development of proplastids and etioplasts, which are the precursors of the mature organelle, into chloroplasts is discussed in Part II in seven chapters (Chaps. 3, 4, 5, 6, 7, 8, and 9) that critically review the current literature on the synthesis, trafficking, assembly, and regulation of thylakoid complexes and Rubisco. In Part III, Chaps. 10, 11, and 12 focus on the dynamic nature, expression, regulation, and stability of the plastid genome during its development as well as on targeting of nuclear-encoded plastid proteins.

Genetically programmed dismantling of chloroplast during leaf senescence, the regulated transformation of a mature chloroplast to a gerontoplast, constitutes one of the major current areas of study of plastid biology. Part IV contains eight chapters (Chaps. 13, 14, 15, 16, 17, 18, 19, and 20) that deal with the definition and concept of plant senescence, ultrastructural changes of thylakoid membranes, degradation of proteins and pigments, and their degradation pathways, mechanisms, and regulation. Part V includes four chapters (Chaps. 21, 22, 23, and 24) that describe the organellar control of chloroplast development and the role of chloroplasts in

regulating leaf senescence involving interorganellar signaling. Finally, the last part (Part VI) includes four chapters (Chaps. 25, 26, 27, and 28) that deal with responses of the developing chloroplast to environmental signals. These chapters critically dissect the mechanisms and control of the modulation of chloroplast biogenesis and of senescence during leaf growth and development in different environmental settings.

We thank all our contributors and reviewers of the different chapters of this volume and hope that this volume will be a valuable source of information and reference for those working in photosynthesis and plant developmental biology in general. As the book consists of extensive illustrations and graphics, it may also be used as a textbook by graduate and advanced undergraduate students.

We are grateful to Govindjee, who appreciated our comprehensive concept of chloroplast biology and invited us to edit this volume of the series, and to Thomas D. Sharkey, who is his co-series editor. Govindjee's valuable comments, continuous support, and timely advice during the preparation of this volume were of great help and inspiration to us.

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