

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 from 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

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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

Edited by

Basanti Biswal
Sambalpur University
Odisha
India

Karin Krupinska
University of Kiel
Kiel
Germany

and

Udaya C. Biswal
Sambalpur University
Odisha
India

 Springer

Editors

Basanti Biswal
School of Life Sciences
Sambalpur University
Jyoti Vihar, Sambalpur 768019
Odisha, India
basanti1952@gmail.com

Karin Krupinska
Institute of Botany
University of Kiel
Olshausenstraße 40
Kiel 24098, Germany
kkrupinska@bot.uni-kiel.de

Udaya C. Biswal
School of Life Sciences
Sambalpur University
Jyoti Vihar, Sambalpur 768019
Odisha, India
biswaluc@yahoo.co.in

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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 Ljubescic (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 Winkler (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 CO₂ Concentrating Mechanisms**, edited by Agepati S. Raghavendra and Rowan Sage, from India and Canada. Nineteen chapters, 425 pp, Hardcover, ISBN 978-90-481-9406-3 (<http://www.springerlink.com/content/978-90-481-9406-3/>)
 - **Volume 31 (2010): The Chloroplast: Basics and Applications**, edited by Constantin Rebeiz (USA), Christoph Benning (USA), Hans J. Bohnert (USA), Henry Daniell (USA), J. Kenneth Hooper (USA), Hartmut K. Lichtenthaler (Germany), Archie R. Portis (USA), and Baishnab C. Tripathy (India). Twenty-five chapters, 451 pp, Hardcover, ISBN:978-90-481-8530-6(<http://www.springerlink.com/content/978-90-481-8530-6/>)
 - **Volume 30 (2009): Lipids in Photosynthesis: Essential and Regulatory Functions**, edited by Hajime Wada and Norio Murata, both from Japan. Twenty chapters, 506 pp, Hardcover, ISBN: 978-90-481-2862-4; e-book, ISBN: 978-90-481-2863-1 (<http://www.springerlink.com/content/978-90-481-2862-4/>)
 - **Volume 29 (2009): Photosynthesis In Silico: Understanding Complexity from Molecules**, edited by Agu Laisk, Ladislav Nedbal, and Govindjee, from Estonia, The Czech Republic, and USA. Twenty chapters, 525 pp, Hardcover, ISBN: 978-1-4020-9236-7 (<http://www.springerlink.com/content/978-1-4020-9236-7/>)
 - **Volume 28 (2009): The Purple Phototrophic Bacteria**, edited by C. Neil Hunter, Fevzi Daldal, Marion C. Thurnauer and J. Thomas Beatty, from UK, USA and Canada. Forty-eight chapters, 1053 pp, Hardcover, ISBN: 978-1-4020-8814-8 (<http://www.springerlink.com/content/978-1-4020-8814-8/>)
 - **Volume 27 (2008): Sulfur Metabolism in Phototrophic Organisms**, edited by Christiane Dahl, Rüdiger Hell, David Knaff and Thomas Leustek, from Germany and USA. Twenty-four chapters, 551 pp, Hardcover, ISBN: 978-4020-6862-1 (<http://www.springerlink.com/content/978-1-4020-6862-1/>)
 - **Volume 26 (2008): Biophysical Techniques 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/>)
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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://www.springerlink.com/content/978-1-4020-4249-2/>)
 - **Volume 21 (2005): Photoprotection, Photoinhibition, Gene Regulation, and Environment**, edited by Barbara Demmig-Adams, William W. Adams III and Autar K. Mattoo, from USA. Twenty-one chapters, 380 pp, Hardcover, ISBN: 978-14020-3564-7 (<http://www.springerlink.com/content/978-1-4020-3564-7/>)
 - **Volume 20 (2006): Discoveries in Photosynthesis**, edited by Govindjee, J. Thomas Beatty, Howard Gest and John F. Allen, from USA, Canada and UK. One hundred and eleven chapters, 1304 pp, Hardcover, ISBN:978-1-4020-3323-0(<http://www.springerlink.com/content/978-1-4020-3323-0/>)

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- 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)

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- 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

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/tocs.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)

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

Department of Plant Biology, Department of Biochemistry and Center of Biophysics & Computational Biology, University of Illinois at Urbana-Champaign, Urbana 61801, IL, USA
gov@life.illinois.edu

Thomas D. Sharkey
Department of Biochemistry and Molecular Biology, Michigan State University, East Lansing 48823, MI, USA
tsharkey@msu.edu

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

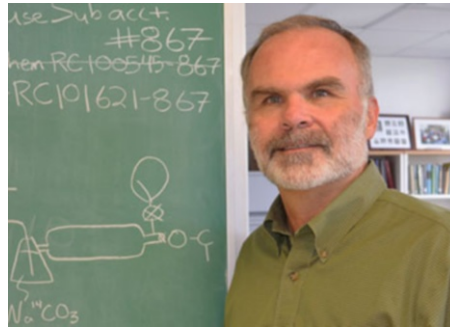
collaborators, has included the discovery of a short-wavelength form of chlorophyll (Chl) *a* functioning in the Chl*b*-containing system, now called PS II; of the two-light effect in Chl*a* fluorescence; and, with his wife Rajni Govindjee, of the two-light effect (Emerson enhancement) in NADP reduction 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 resis-

tance 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>.

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Preface

Chloroplasts, the green plastids, harvest sunlight to convert CO₂ 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. Hooper, 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 chloro-

plast 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 inter-organellar 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.

Basanti Biswal

School of Life Sciences, Sambalpur
University, Jyoti Vihar, Sambalpur 768019,
Odisha, India
basanti1952@gmail.com

Karin Krupinska

Institute of Botany, University of Kiel,
Olshausenstraße 40, Kiel 24098, Germany
kkrupinska@bot.uni-kiel.de

Udaya Chand Biswal

School of Life Sciences, Sambalpur
University, Jyoti Vihar, Sambalpur 768019,
Odisha, India
biswaluc@yahoo.co.in

The Editors



Basanti Biswal was born in Parlakhemundi in the Gajapati district of Odisha, India. During 1956–1966, she attended schools in Cuttack and Bhubaneswar, Odisha, and then joined Buxi Jagabandhu Bidyadhar (BJB) College, Bhubaneswar. She received her B.Sc. (major in Botany) in 1970 from Khallikote College, Berhampur, and her M.Sc. (Botany) in 1973 from Berhampur University, Odisha. She was awarded a Ph.D. in 1984 and a D.Sc. in 2010 from Sambalpur University, Odisha, for her work on “Chloroplast Development and Senescence.” Before obtaining her Ph.D., under the supervision of Professor Udaya Chand Biswal, Basanti had worked as an Associate Scientist in 1981 with Professor Hans Mohr at the University of Freiburg, Germany; there, she had worked on “Chlorophyll Biosynthesis in Pinus.” In 1985, she was a Research Associate of the Council of Scientific and Industrial Research (CSIR), New Delhi, and then in 1986, she became a Lecturer in the School of Life Sciences, Sambalpur University, where subsequently she was promoted to a Reader and finally a Professor in 2007. At Sambalpur University, she has been involved in teaching and research in developmental biology, plant physiology,

biochemistry, and photobiology. Her research work has significantly contributed to an understanding of the mechanism of regulation of chloroplast development and senescence. Her early work in the 1980s, when the regulation of senescence was not clearly understood, provided important information on the nuclear control of chloroplast demolition during senescence. She has also demonstrated the role of photoreceptors, such as the phytochrome and blue light receptors, in modulating leaf senescence, both in lower and higher plants. Currently, Basanti is working on “Stress Modulation of Leaf Senescence and Photosynthetic Response to Environmental Stress.” She has had extensive collaboration with several laboratories in India and abroad. In 1990, she was a Visiting Professor in the Department of Chemistry, Nebraska University, Lincoln, USA, and has worked with Professor Pill-Soon Song on the involvement of G-proteins in phytochrome-mediated signaling in plants. While on a Commonwealth Fellowship (1992–1993), she collaborated with Dr. Howard Thomas of the Institute of Grassland and Environmental Research, Aberystwyth, UK, and with Professor Lyndon J. Rogers of the Department of Biochemistry, University

of Aberystwyth, UK, on the stability of the D1 protein of Photosystem II of chloroplasts during leaf senescence of *Festuca pratensis*. In 1994, she visited Professor Horst Senger's laboratory in Philipps University, Marburg, Germany, supported by a DAAD (Deutscher Akademischer Austauschdienst) visiting fellowship program. In 1997, Basanti was invited by Professor Akira Watanabe of the Department of Biological Sciences, University of Tokyo, to work in the area of molecular biology of plant development with the support of a Japanese Society for the Promotion of Science (JSPS) fellowship. She worked there on the involvement of sugar and calcium signaling in regulating the expression of senescence-associated genes. In 2007 and again in 2009, she visited the University of Kiel in Germany for collaborative research work with Professor Rüdiger Schulz. In 2011, she visited the University of Alcalá in Spain

for collaborative research with Professor Bartolomé Sabater. In addition to many original research papers, Basanti has written several invited reviews and book chapters and has coauthored a research monograph *Chloroplast Biogenesis: From Proplastid to Gerontoplast* (Springer). She has mentored several Ph.D. and M.Phil. students at Sambalpur University. Basanti has served as a member of the editorial board of the *Journal of Photochemistry and Photobiology B: Biology* (Elsevier). She is also acting as the Editor-in-Chief of the Indian Photobiology Society Newsletter, Kolkata, India. Currently, Basanti is one of the consulting editors of the series *Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes* (Springer). In 1997, Basanti received the prestigious Samant Chandra Sekhar Award of the Government of Odisha and is now a Fellow of the National Academy of Sciences, India.



Karin Krupinska was born in Kassel, Germany. She now lives close to Kiel, Germany, where she is a Professor of Plant Cell Biology in the Institute of Botany at the Christian-Albrechts-University. She received her doctoral degree in 1984 from Philipps University in Marburg, Germany, under the supervision of Horst Senger. Her dissertation addressed the thylakoid membrane organization in chloroplasts from synchronous cultures and pigment mutants of the green alga *Scenedesmus obliquus*. In 1986, Karin received an EMBO (European Molecular Biology Organisation) fellowship for postdoctoral research in the laboratory of Diter von Wettstein at the Carlsberg Research Centre in Copenhagen, Denmark. During her stay in Carlsberg, she identified the cytochrome b_{559} genes in the barley plastid genome and was able to overexpress them. After 2 years in Copenhagen (1986–1987), she went to Kiel, where she studied light- and age-dependent changes in the transcription of plastid genes in barley (*Hordeum vulgare* L.) as a postdoctoral research associate in the laboratory of Klaus Apel at the Institute of Botany. Three years later, she accepted an appointment as a Junior Research Leader at the Center of Applied Plant Molecular Biology in the Institute of Botany at the University of Hamburg, Germany, where she remained for 5 years (1990–1995). During these years, she studied functional and molecular

changes occurring during senescence of flag leaves of barley under field conditions. In 1995, she accepted her first appointment as a Professor of Botany at the University of Cologne (*Köln*), Germany, where she stayed until 1998. Since 1998, she has been a Professor in the Institute of Botany at the University of Kiel, where she has served for 5 years (2000–2005) as Chair of the institute. Since 2000, she has been the Head of the Central Microscopy research facility of the Faculty of Mathematics and Natural Sciences at the Christian-Albrechts-University of Kiel. From 2002 to 2008, she was the leader of the Research Training Group on Natural Antioxidants. Her area of focus in this project was the functional significance of tocopherols during leaf senescence. Karin has organized several symposia on plant senescence processes, for example, the 2007 Third European Workshop on Plant Senescence (Salzau, Germany); participants of this meeting contributed to a special issue of *Plant Biology* coedited by Klaus Humbeck and herself (*Plant Biology* 10, Supplement 1, 2008). Since January 2011, Karin has been the leader of the European Marie Curie Initial Training Network CropLife that includes eleven research groups from six European countries (Denmark, France, Germany, United Kingdom, Poland, and Switzerland). Within this project, the important impact of leaf senescence on crop productivity is being

investigated. Karin has served as a cochair of the Gordon Research Conference on Plant Senescence (held in Stonehill College near Boston, Massachusetts, USA, July 2012). Besides leaf senescence, her long-term research concerns the function and molecular composition of plastid nucleoids. A milestone of her research was the discovery that the plastid nucleoid-associated protein WHIRLY1 is located in both the chloro-

plasts and the nucleus within the same cell. A major focus of her research is the role of WHIRLY1 in plastid-to-nucleus signaling which might involve translocation of the protein from plastids to the nucleus. Further current research activities of Karin include identification of transcription factors involved in the regulation of senescence in barley leaves and their distribution within the cell.



Udaya Chand Biswal, after his school education, joined, in 1962, Ravenshaw College, now Ravenshaw University, Odisha, India. He obtained his bachelor degree in 1966 with Honors in Botany. Subsequently, during his 2-year M.Sc. program, Professor Gadadhar Misra, a renowned photobiologist, introduced him to the biology of yellow leaves (senescing leaves) for his research project. This work, which he had conducted for his M.Sc. project, was published in 1973 in the Botanical Gazette (G. Misra and U.C. Biswal (1973) Factors concerned in leaf senescence. I. Effects of age, chemicals, petiole, and photoperiod on senescence in detached leaves of *Hibiscus rosa-sinensis* L, Bot Gazette 134(1) 5–11.) at a time when leaf senescence and chloroplast dismantling during the process did not draw serious attention by plant biologists. The publication cited above, however, inspired Udaya to work in this area in subsequent years of his scientific career. In 1971, he joined as a Lecturer in the Department of Botany at Berhampur University, Odisha, India. He then went for his doctoral studies to the School of Life Sciences at the Jawaharlal Nehru University (JNU) in New Delhi, India. In 1977, he was awarded the Ph.D. degree from JNU for his work on aging-induced alterations in the structure and function of chloroplasts of detached barley leaves under the joint guidance of Professors

Prasanna Mohanty and Gauri S. Singhal. During 1980–1982, Udaya worked with Professor Hans Mohr at the University of Freiburg in Germany. With Mohr, he worked on the changes in the pigment composition and ultrastructure of chloroplasts during senescence of the cotyledons of *Sinapis alba* and their regulation by phytochrome. This collaborative work was sponsored by the Humboldt Foundation of Germany. From 1984 until his retirement in 2005, Udaya served as a Professor in the School of Life Sciences, Sambalpur University, Odisha. At Sambalpur University, he developed an active group with research scholars from Physics, Chemistry, and Biological Science background to study photosynthesis with an interdisciplinary approach. The group has contributed significantly to the knowledge of the alterations in primary photochemical reactions of thylakoids of higher plants during senescence and stress response. Udaya's group has demonstrated that Photosystem II (PS II), specifically the oxygen-evolving complex (OEC), is the major target of both senescence and stress. In the early 1980s, his laboratory proposed theoretical models on the structure of PS II, when the structural details of the photosystem at atomic resolution were not available. After his retirement from professorship, he has continued his research in collaboration with Basanti Biswal (coeditor of this volume)

on the photosynthetic response of senescing plants to UV radiation, cell wall catabolism, and sugar signaling involved during senescence and stress response. Udaya has worked with Professor Rüdiger Schulz of the University of Kiel, Germany, on “Quinol Oxidase of Thylakoid Membranes of *Synechocystis* PCC 6803,” during his visits there in 2007 and 2009; this collaboration was supported by the Humboldt Foundation. In addition to his many research publications, Udaya has authored several book chapters, reviews, as well as a research monograph *Chloroplast Biogenesis*. In 1989, he, along with G. Britton, edited the book

Trends in Photosynthesis Research (Agro Botanical Publishers, India). Udaya was on the editorial board of the *Journal of Photochemistry and Photobiology B: Biology* (Elsevier). He has served as the President of the Indian Photobiology Society, Kolkata (2005–2007), and then joined as the Vice-Chancellor of Sambalpur University in 2007. For his achievements in the field of research in plant sciences, he received the Samant Chandra Sekhar Award in Life Sciences in 1995 and the prestigious Prana Krushna Parija National Award in 2008. He is a Fellow of the National Academy of Sciences, India.

Contributors

Mats X. Andersson

Department of Biological
and Environmental Sciences, University
of Gothenburg, PO Box 461, SE-405 30
Gothenburg, Sweden
mats.andersson@bioenv.gu.se

Henrik Aronsson

Department of Biological and
Environmental Sciences, University
of Gothenburg, PO Box 461, SE-405 30
Gothenburg, Sweden
henrik.aronsson@bioenv.gu.se

Basanti Biswal

School of Life Sciences, Sambalpur
University, Jyoti Vihar, Sambalpur 768019,
Odisha, India
basanti1952@gmail.com

Udaya C. Biswal

School of Life Sciences, Sambalpur
University, Jyoti Vihar, Sambalpur 768019,
Odisha, India
biswaluc@yahoo.co.in

Maryse A. Block

CEA-Grenoble, iRTSV/LPCV, 17 Rue des
Martyrs, F-38054 Grenoble, France
maryse.block@cea.fr

Thomas Börner

Institut für Biology/Genetik, Humboldt-
Universität zu Berlin, Chausseestr. 117,
10115 Berlin, Germany
thomas.boerner@rz.hu-berlin.de

Naini Burman

Interdisciplinary Centre for Plant Genomics
and Department of Plant Molecular Biology,
University of Delhi, South Campus,
New Delhi 110021, India
nainiburman21@gmail.com

Cristian A. Carrión

Instituto de Fisiología Vegetal,
Universidad Nacional de La Plata-
CONICET, cc 327, 1900 La Plata,
Argentina
ccarrion@agro.unlp.edu.ar

Maria L. Costa

Instituto de Fisiología Vegetal,
Universidad Nacional de La Plata-
CONICET, cc 327, 1900 La Plata,
Argentina
lorenzacosta@quimica.unlp.edu.ar

Vijay Dalal

School of Life Sciences,
Jawaharlal Nehru University,
New Delhi 110067, India

Emmanuelle Dubots

Department of Medicine, Biochemistry Unit,
University of Fribourg, CH-1700 Fribourg,
Switzerland
edubots@gmail.com

Hrvoje Fulgosi

Ruder Bošković Institute, Laboratory for
Electron Microscopy, Division of Molecular
Biology, Bijenička Cesta 54,
HR-10 000 Zagreb, Croatia
fulgosi@irb.hr

Facundo M. Gomez

Instituto de Fisiología Vegetal, Universidad
Nacional de La Plata-CONICET, cc 327,
1900 La Plata, Argentina
facugomez@agro.unlp.edu.ar

John C. Gray

Department of Plant Sciences, University
of Cambridge, Downing Street, Cambridge
CB2 3EA, UK
jcg2@cam.ac.uk

Juan J. Guiamet

Instituto de Fisiología Vegetal, Universidad Nacional de La Plata-CONICET, cc 327, 1900 La Plata, Argentina
jguiamet@fcnym.unlp.edu.ar

Yukako Hihara

Department of Biochemistry and Molecular Biology, Faculty of Science, Saitama University, Saitama-shi, Saitama 338-8570, Japan

Stefan Hörtensteiner

Institute of Plant Biology, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland
shorten@botinst.uzh.ch

Hiroyuki Ishida

Graduate School of Agricultural Science, Tohoku University, Sendai, Miyagi 981-8555, Japan
hiroyuki@biochem.tohoku.ac.jp

Paul Jarvis

Department of Biology, Adrian Building, University of Leicester, University Road, Leicester LE1 7RH, UK
rpj3@le.ac.uk

Padmanava Joshi

Department of Physics, Anchal College, Padampur, 768036, Bargarh, Odisha, India
padmanava.joshi@gmail.com

Kengo Kanamaru

Laboratory of Biological Chemistry, Graduate School of Agricultural Science, Kobe University, 1-1 Rokkoudai-cho, Nada-ku, Kobe, Hyogo 657-8501, Japan
kng@kobe-u.ac.jp

Yusuke Kato

Institute of Plant Science and Resources, Okayama University, 2-20-1 Chuo, Kurashiki, Okayama 710-0046, Japan

Renu Khanna-Chopra

Stress Physiology and Biochemistry Laboratory, Water Technology Centre, Indian Agricultural Research Institute (IARI), New Delhi 110012, India
renu.chopra3@gmail.com

Jitendra P. Khurana

Interdisciplinary Centre for Plant Genomics and Department of Plant Molecular Biology, University of Delhi, South Campus, New Delhi 110021, India
khuranaj@genomeindia.org

Karin Krupinska

Institute of Botany, University of Kiel, Olshausenstraße 40, 24098 Kiel, Germany
kkrupinska@bot.uni-kiel.de

Hartmut K. Lichtenthaler

Botanisches Institut (Molecular Biology and Biochemistry of Plants), Karlsruhe Institute of Technology (KIT), University Division, Kaiserstr. 12, D-76133 Karlsruhe, Germany
hartmut.lichtenthaler@kit.edu

Karsten Liere

Institut für Biologie/Genetik, Humboldt-Universität zu Berlin, Chausseestr. 117, 10115 Berlin, Germany
karsten.liere@rz.hu-berlin.de

Qihua Ling

Department of Biology, Adrian Building, University of Leicester, University Road, Leicester LE1 7RH, UK
ql24@le.ac.uk

Nikola Ljubešić

Ruder Bošković Institute, Laboratory for Electron Microscopy, Division of Molecular Biology, Bijenička Cesta 54, HR-10 000 Zagreb, Croatia, Zagreb, Croatia

Eric Maréchal

CEA-Grenoble, iRTSV/LPCV, 17 Rue des Martyrs, F-38054 Grenoble, France
emarechal@cea.fr

Mercedes Martín

Department of Plant Biology, University of Alcalá, Alcalá de Henares, 28871 Madrid, Spain
mercedes.martin@uah.es

Dana E. Martínez

Instituto de Fisiología Vegetal, Universidad Nacional de La Plata-CONICET, cc 327, 1900 La Plata, Argentina
danamartinez@conicet.gov.ar

Karin Meierhoff

Department of Developmental and Molecular Biology of Plants, Heinrich-Heine-University of Düsseldorf, Universitätsstr. 1, 40225 Düsseldorf, Germany
Karin.Meierhoff@uni-duesseldorf.de

Bijaya K. Mishra

School of Chemistry, Sambalpur University, Jyoti Vihar, Sambalpur 768019, Odisha, India
bijayam@hotmail.com

Amarendra N. Misra

Centre for Life Sciences, School of Natural Sciences, Central University of Jharkhand, Ratu-Lohardaga Road, Brambe, Ranchi 835205, India
misra.amarendra@gmail.com

Maria Mulisch

Institute of Botany, Central Microscopy, University of Kiel, Olshausenstraße 40, 24098 Kiel, Germany
mmulisch@bio.uni-kiel.de

Sergi Munné-Bosch

Departament de Biologia Vegetal, Facultat de Biologia, Universitat de Barcelona, Avinguda Diagonal 643, 08028 Barcelona, Spain
smunne@ub.edu

Lalitendu Nayak

Department of Physics, Anchal College, Padampur, 768036, Bargarh, Odisha, India
lalitendu_nayak@rediffmail.com

Larry D. Noodén

Biology-MCDB/EEB, University of Michigan, 830 North University Avenue, Ann Arbor, MI 48109-1048, USA
ldnum@umich.edu

Kamlesh Kant Nutan

School of Life Sciences, Stress Physiology and Molecular Biology Laboratory, Jawaharlal Nehru University, New Delhi 110067, India

Ashwani Pareek

School of Life Sciences, Stress Physiology and Molecular Biology Laboratory, Jawaharlal Nehru University, New Delhi 110067, India
ashwanipareek@gmail.com

Matthew Paul

Plant Science, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, United Kingdom
matthew.paul@rothamsted.ac.uk

Thomas Pfannschmidt

Université Joseph Fourier Grenoble, Laboratoire de Physiologie et Végétale, (LPCV) UJF/CNRS (UMR5168)/INRA, (USC1359)/CEA GRENoble, 17 rue des Martyrs, 38054 Grenoble CEDEX9, France
Thomas.Pfannschmidt@ujf-grenoble.fr

Mukesh K. Raval

Department of Chemistry, Gangadhar Meher College, Sambalpur 768004, Odisha, India
mraval@yahoo.com

Harry Roy

Biology Department, Rensselaer Polytechnic Institute, Troy 12180, NY, USA
royh@rpi.edu

Bartolomé Sabater

Department of Plant Biology, University of Alcalá, Alcalá de Henares, 28871 Madrid, Spain
bartolome.sabater@uah.es

Wataru Sakamoto

Institute of Plant Science and Resources, Okayama University, 2-20-1 Chuo, Kurashiki, Okayama 710-0046, Japan
saka@rib.okayama-u.ac.jp

Katalin Solymosi

Department of Plant Anatomy, Eötvös University, Pázmány P. s. 1/C, H-1117 Budapest, Hungary
solymosikata@hotmail.com

Kintake Sonoike

Faculty of Education and Integrated Arts
and Sciences, Waseda University,
2-2 Wakamatsu-cho, Shinjuku-ku, Tokyo
162-8480, Japan
sonoike@waseda.jp

Mamoru Sugita

Center for Gene Research, Nagoya
University, Nagoya 464-8602, Japan
sugita@gene.nagoya-u.ac.jp

Baishnab C. Tripathy

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

Raphael Trösch

Department of Biology, Adrian Building,
University of Leicester, University Road,
Leicester LE1 7RH, UK
rmt18@le.ac.uk

Shinya Wada

Graduate School of Agricultural Science,
Tohoku University, Sendai, Miyagi
981-8555, Japan
wada@biochem.tohoku.ac.jp

Peter Westhoff

Department of Developmental and
Molecular Biology of Plants,
Heinrich-Heine-University of Düsseldorf,
Universitätsstr. 1, 40225 Düsseldorf,
Germany
west@uni-duesseldorf.de

Astrid Wingler

Research Department of Genetics,
Evolution and Environment, University
College London, Gower Street, London
WC1E 6BT, United Kingdom
a.wingler@ucl.ac.uk

Mercedes Wrisher

Ruder Bošković Institute, Laboratory
for Electron Microscopy,
Division of Molecular Biology,
Bijenička Cesta 54,
HR-10 000 Zagreb, Croatia

Michela Zottini

Department of Biology, University
of Padua, Via U. Bassi, 58/B, 35131 Padua,
Italy
michela.zottini@unipd.it

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