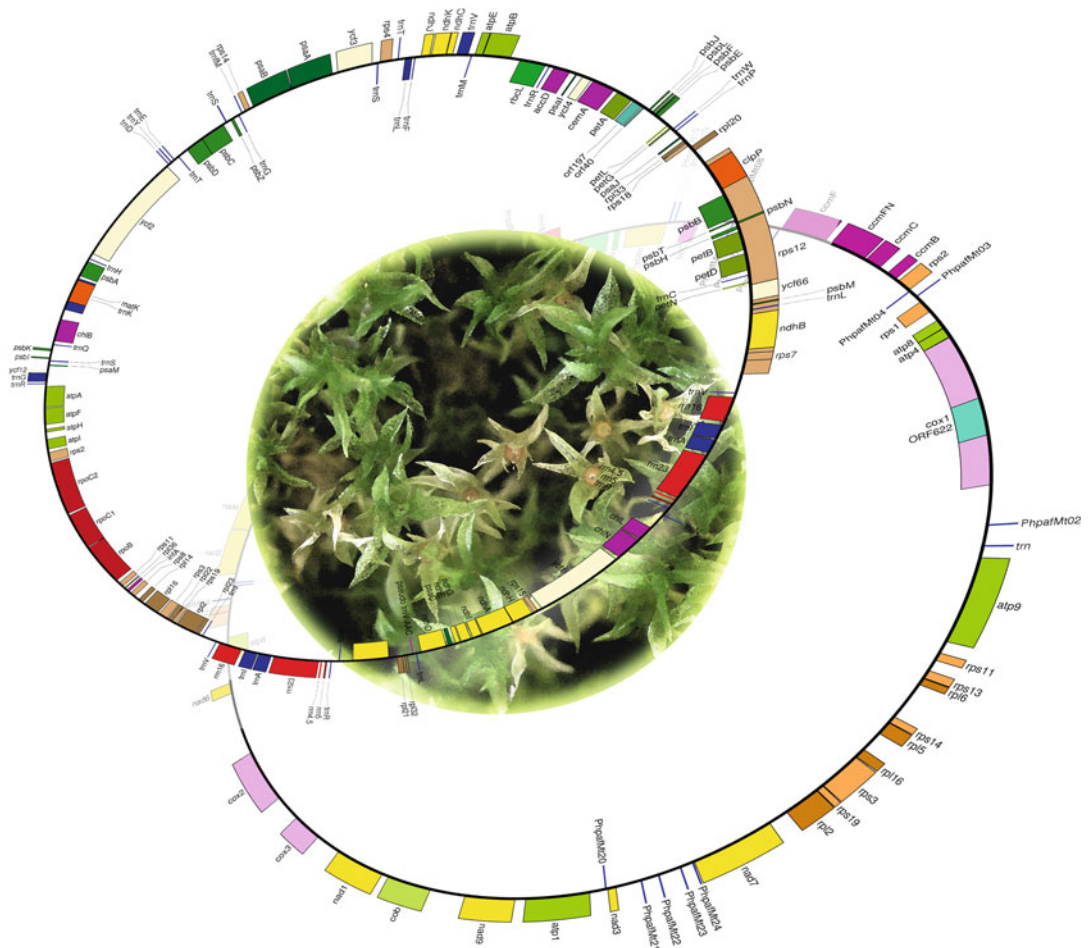


Genomics of Chloroplasts and Mitochondria



This illustration is a collage of a photograph of the model moss *Physcomitrella patens* and the graphic maps of its plastid (top/front) and mitochondrial (bottom/back) genomes. The *Physcomitrella* photograph (kindly provided by Anika Nicolaudius, Bonn and modified with Adobe Photoshop Elements including the water color style filter option) shows plantlets with developing light-brown spherical sporophytes. The organelle genome maps (modified with the Adobe tilting and shifting options) were constructed from the retrieved sequence files for the plastid genome (GenBank accession number AP005672) and the mitochondrial genome (GenBank accession number AB251495) using the freely available drawing tool for organellar genomes OGDRAW (<http://ogdraw.mpimp-golm.mpg.de/>). For details on nomenclature and color coding of gene classes, see: Lohse M, Drechsel O and Bock R (2007) OrganellarGenomeDRAW (OGDRAW) - a tool for the easy generation of high-quality custom graphical maps of plastid and mitochondrial genomes. *Curr Genet* 52: 267–274.

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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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Genomics of Chloroplasts and Mitochondria

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 35: Genomics of Chloroplasts and Mitochondria

We are delighted to announce the publication of Volume 35 in this series. With this volume we are making some changes to keep the books a leading source of information on photosynthesis and related energy processes. The series title is now updated to *Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes*. The front cover, which had a distinctive white background and color palette has been changed to a web-friendly green background. The series publisher, Springer, now makes the table of contents of all of the volumes freely available online. Links to each volume are given below. Readers may also see that this volume and the past few volumes have had significantly more color and the color figures are now better integrated into the chapters, instead of being collected in one section of the book. This improvement was possible because of changes in how the books are produced. Another change is that references to chapters in books 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

This volume, *Genomics of Chloroplasts and Mitochondria* was conceived and edited by Ralph Bock (Director and Scientific Member

at the Max Planck Institute for Molecular Plant Physiology, Postdam-Golm, Germany) and Volker Knoop (Head of the Department of Molecular Evolution at Bonn University, Germany). Professors Bock and Knoop are leading experts on the genomics of plant organelles. Mitochondria and chloroplasts are the energy organelles of plant cells and have their own genomes, reflecting their evolutionary origins as once free-living bacteria. While mitochondria are a hallmark of all eukaryotes, chloroplasts define plants and related photosynthetic organisms. This volume consists of 19 chapters of up-to-date information on the genomics of these fascinating organelles. Both organelles exchange genetic information with the host nucleus and at the same time retain some genes critical for the bioenergetics in these organelles. Further, both organelles have unique roles in photosynthesis and in plants more generally. Both organelles exhibit very interesting genomic behaviors. Perhaps most puzzling and worth learning about is RNA editing, in which plant organelles literally change the RNA sequence after transcription such that the protein sequence is different from that coded by the DNA. Changes in the mitochondrial genome over the course of evolution of plants and algae is also a fascinating theme woven through the book. We hope the readers will find this volume enlightening and fascinating. We are grateful to the editors for their timely submission of the book and to all the 52 authors who contributed to this look at the genomics of the energy organelles that underlie life on Earth.

Authors

The current book contains 19 chapters written by 52 authors from 8 countries (Australia (5); Belgium (2); Canada (6); France (4); Germany (13); Italy (2); UK (1); and USA (19)). We thank all the authors for their valuable contribution to this book; their names (arranged alphabetically) are:

John M. Archibald (Canada; Chap. 1); Michael A. Ayliffe (Australia; Chap. 9); Sidonie Bellot (Germany; Chap. 10); Debashish Bhattacharya (USA; Chap. 2); Alexandra-Viola Bohne (Germany; Chap. 16); Nathalie Bonnefoy (France; Chap. 19); Hans-Peter Braun (Germany; Chap. 15); Gertraud Burger (Canada; Chap. 6); Teodoro Cardi (Italy; Chap. 14); Anil Day (UK; Chap. 18); Holger Eubel (Australia; Chap. 15); Sabrina Finster (Germany; Chap. 13); Susan Gabay-Laughnan (USA; Chap. 12); Philippe Giegé (France; Chap. 14); Michael W. Gray (Canada; Chap. 1); Stephan Greiner (Germany; Chap. 11); Jeferson Gross (USA; Chap. 2); Patrice Hamel (USA; Chap. 19); Robert K. Jansen (USA; Chap. 5); Sabine Kahlau (Germany; Chap. 14); Kenneth G. Karol (USA; Chap. 4); Frank Kempken (Germany; Chap. 19); Volker Knoop (Germany; Chap. 8); B. Franz Lang (Canada; Chap. 3); Veronique Larosa (Belgium; Chap. 19); Julia Legen (Germany; Chap. 13); Libo Li (USA; Chap. 7); Yang Liu (USA; Chap. 7); Andrew H. Lloyd (Australia; Chap. 9); Pal Maliga (USA; Chap. 17); Aurora M. Nedelcu (Canada; Chaps. 3 and 6); Kathleen J. Newton (USA; Chap. 12); Jörg Nickelsen (Germany; Chap. 16); Karen N. Pelletreau (USA; Chap. 2); Yin-Long Qiu (USA; Chap. 7); Yujiao Qu (Germany; Chap. 13); Claire Remacle (Belgium; Chap. 19); Susanne S. Renner (Germany; Chap. 10); Adrian Reyes-Prieto (USA; Chap. 2); Mathieu Rousseau-Gueutin (France; Chap. 9); Tracey A. Ruhlman (USA; Chap. 5); Mary E. Rumpho (USA; Chap. 2); Thalia Salinas (France; Chap. 19); Christian Schmitz-Linneweber (Germany; Chap. 13); Nunzia Scotti (Italy; Chap. 14); Anna E. Sheppard (Australia; Chap. 9); Nitya Subramanian (USA; Chap. 19); Jeremy N. Timmis (Australia; Chap. 9);

Bin Wang (USA; Chap. 7); Paul G. Wolf (USA; Chap. 4); Jiayu Xue (USA; Chap. 7).

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We list below information on all the 35 volumes that have been published thus far (see <http://www.springer.com/series/5599> for the series web site). We are pleased to note that Springer, our publisher, is now producing complete *Tables of Contents* of these books. Electronic access to individual chapters depends on subscription (ask your librarian) but Springer provides free downloadable front matter as well as indexes. As of July, 2011, Tables of Contents are available for all volumes. The available web sites of the books in the Series are listed below.

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- **Volume 32 (2011): C4 Photosynthesis and Related CO₂ Concentrating Mechanisms**, edited by Agepati S. Raghavendra and Rowan Sage, from India and Canada. Nineteen chapters, 425 pp., Hardcover, ISBN: 978-90-481-9406-3 [<http://www.springerlink.com/content/978-90-481-9406-3/>]
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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):

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- 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)
- Saga of Non-Photochemical Quenching (NPQ) and Thermal Energy Dissipation In Plants, Algae and Cyanobacteria (Editors: Barbara Demmig-Adams, Gyözö Garab, William W. Adams III, and Govindjee)

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- Interactions between Photosynthesis and other Metabolic Processes
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- Photosynthesis, Biomass and Bioenergy
- Photosynthesis under Abiotic and Biotic Stress
- Plant Respiration II

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

In view of the interdisciplinary character of research in photosynthesis and respiration, it is our earnest hope that this series of books will be used in educating students and researchers not only in Plant Sciences, Molecular and Cell Biology, Integrative Biology, Biotechnology, Agricultural Sciences, Microbiology, Biochemistry, Chemical Biology, Biological Physics, and Biophysics, but also in Bio-engineering, Chemistry, and Physics.

We take this opportunity to thank and congratulate Ralph Bock and Volker Knoop for their outstanding editorial work; they have done a fantastic job not only in editing, but also in organizing this book for all of us, and for their highly professional dealing with the reviewing process. We thank all the 52 authors of this book (see the list above): without their authoritative chapters, there would be no such volume. We give special thanks to Saravanan Purushothaman, SPi Global, India for directing the typesetting of this book; his expertise has been crucial in bringing this book to completion. We owe Jacco Flipsen, Ineke Ravesloot and André Tournois (of Springer) thanks for their friendly working relation with us that led to the production of this book.

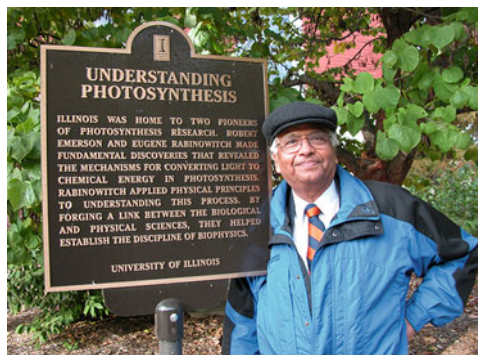
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Series Editors



Govindjee, who uses one name only, was born on October 24, 1932, in Allahabad, India. Since 1999, he has been Professor Emeritus of Biochemistry, Biophysics and Plant Biology at the University of Illinois at Urbana-Champaign (UIUC), Urbana, IL, USA. He obtained his B.Sc. (Chemistry and Biology) and M.Sc. (Botany; Plant Physiology) in 1952 and 1954, from the University of Allahabad. He studied 'Photosynthesis' at the UIUC, under two pioneers of photosynthesis Robert Emerson, and Eugene Rabinowitch, obtaining his Ph.D. in 1960, in Biophysics. He is best known for his research on 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, 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; an unique role of bicarbonate/carbonate on the electron acceptor side of PS II, particularly in the protonation events involving the Q_B binding region; the theory of thermoluminescence in plants; the first picosecond measurements on the primary photochemistry of PS II; and the use of Fluorescence Lifetime Imaging Microscopy (FLIM) of Chl *a* fluorescence in understanding photoprotection, by plants, against excess light. His current focus is on the 'History of Photosynthesis Research', 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 & 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; and (3) Volume 34 of this Series "*Photosynthesis – Plastid Biology, Energy*

Conversion and Carbon Assimilation", edited by Julian Eaton-Rye, Baishnab C. Tripathy, and Thomas D. Sharkey, was dedicated to him, celebrating his 80th year. Govindjee is coauthor of 'Photosynthesis' (John Wiley, 1969); and editor of many books, published by several publishers including Academic Press and Kluwer Academic Publishers (now Springer). Since 2007, each year a Govindjee and Rajni Govindjee Award is given to graduate students, by the Department of Plant Biology, at the UIUC, to recognize Excellence in Biological Sciences. For further information on Govindjee, see his web site at <http://www.life.illinois.edu/govindjee>.



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Among his contributions are measurement of the carbon dioxide concentration inside leaves, an exhaustive study of short-term feedback effects in carbon metabolism, and a significant contribution to elucidation of the pathway by which leaf starch breaks down at night. In the isoprene research field, Tom is recognized as the leading advocate for thermotolerance of photosynthesis as the explanation for why plants emit isoprene. In addition, his laboratory has cloned many of the genes that underlie isoprene synthesis and published many papers on the biochemical regulation of isoprene synthesis. Tom has co-edited three books, the first on trace gas emissions from plants in 1991 (with Elizabeth Holland and Hal Mooney) and then volume 9 of this series (with Richard Leegood and Susanne von Caemmerer) on the physiology of carbon metabolism of photosynthesis in 2000 and volume 34 (with Julian Eaton-Rye and Baishnab C. Tripathy) entitled *Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*. Tom is listed in Who's Who and is a "Highly Cited Researcher" according to the Thomson Reuters Institute for Scientific Information.

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Preface

The genomics era for plant cell organelles started in 1979, when Hans Kössel at the University of Freiburg, Germany, sequenced the first piece of chloroplast DNA: the 3'-terminal part of the 16S ribosomal RNA gene from maize (*Zea mays*). This was a remarkable feat, because, in addition to obtaining the very first DNA sequence from a plant, the study also provided strong molecular evidence for the endosymbiotic origin of plastids (which, at that time, was still hotly debated). By showing that the chloroplast 16S ribosomal RNA sequence displayed strong similarity to the (previously sequenced) 16S ribosomal RNA gene from the bacterium *Escherichia coli*, Hans and his post-doc Zsuzsanna Schwarz-Sommer provided compelling evidence for the plastid DNA stemming from a prokaryotic ancestor. In the following years, many more plastid genes were sequenced from many different plant species. At the same time, with the advent of new molecular tools, such as restriction enzymes and hybridization techniques, insights into the overall structure and organization of the chloroplast genome were obtained. Numerous restriction maps and physical maps were constructed and integrated with the growing amount of sequence information. In 1986, the mapping, cloning and sequencing efforts culminated in the determination of two complete chloroplast genome sequences: from a bryophyte, the liverwort *Marchantia polymorpha* (sequenced by Kanji Ohyama's group), and from a seed plant, the cultivated tobacco *Nicotiana tabacum* (sequenced by Masahiro Sugiura's group).

Due to its more complex genome structure and smaller copy number per cell, research on plant mitochondrial genomes followed suit with some delay. In 1992, it was again Kanji Ohyama's group who determined the first complete genome sequence of a plant mitochondrial genome, again from their

favorite model plant, the liverwort *Marchantia polymorpha*. Five years later, the first genome sequence from a seed plant, the brassicaceous weed *Arabidopsis thaliana*, followed (sequenced by Axel Brennicke's laboratory).

The past decade has seen an explosion of completed organellar genome projects and the list of fully sequenced plastid and mitochondrial genomes (<http://www.ncbi.nlm.nih.gov/genomes/GenomesHome.cgi?taxid=2759&hopt=html>) is now growing almost every day. Importantly, this development has been accompanied by a steadily improving coverage of diverse taxonomic groups and, in this way, organellar genomics continues to contribute greatly to resolving unclear evolutionary links and phylogenetic relationships. Over the last few years, next-generation sequencing techniques have revolutionized the genomics field and, foreseeably, their ever increasing power will keep accelerating also genome research on plant organelles. At the same time, technologies for the genome-wide analysis of gene expression at the RNA and protein levels become more and more powerful and, while currently mainly applied in a handful of model plants, will likely become routine tools for monitoring the dynamic changes of organellar transcriptomes and proteomes in response to environmental stimuli and developmental cues in many more species. With that, plant organelles can potentially be at the forefront of future efforts to model gene expression networks and metabolite networks, which represents one of the cornerstones of the nowadays much-talked-about field of systems biology.

This volume of *Advances in Photosynthesis and Respiration* attempts to summarize the state of the art in genomics research on plant mitochondria and plastids. Its first two chapters are dedicated to the evolution of organelles by primary, secondary and higher-order

endosymbioses. Both chapters illustrate Nature's amazing fondness of experimenting with endosymbiotic associations and pinpoint important principles involved in the successful establishment of enduring endosymbiotic relationships. The following six chapters (Chaps. 3, 4, 5, 6, 7, 8) give an account of genomics research in the various taxonomic groups of algae and embryophyte plants. They describe the characteristic features of plastid and mitochondrial genomes in each taxonomic group, highlight recurring evolutionary patterns that underlie changes in genome structure and gene content and emphasize the enormous contributions of organellar genomics to constructing phylogenetic trees and resolving uncertain evolutionary relationships. Chapters 9 and 10 are dedicated to the gene transfer processes involving organellar DNA. While the intracellular transfer of plastid and mitochondrial DNA to the nucleus represents the initiating event in endosymbiotic gene transfer and, in its presumably non-functional form, generates so-called promiscuous DNA (Chap. 9), the transfer of organellar DNA between cells can result in marvelous examples of horizontal gene transfer between plants, but also between plants and other organisms (Chap. 10). Chapters 11 and 12 deal with mutants in plant organellar genomes, their isolation and experimental induction. In both plastids and mitochondria, the study of mutants has contributed greatly to our understanding of organelle physiology and the mechanisms of organellar gene expression. In addition, mutations in organellar genomes are responsible for important agronomic traits, such as cytoplasmic male sterility and resistances to herbicides. Chapters 13, 14 and 15 illuminate general aspects of the expression of plant organellar genomes. Chapter 13 summarizes our current knowledge about RNA editing, a still largely enigmatic RNA processing step that post-transcriptionally alters the identity of individual nucleotide positions in organellar transcripts and may represent a mechanism

to correct DNA mutations at the RNA level (Chap. 13). The two following chapters address the expression of plastid and mitochondrial genomes at the RNA (Chap. 14) and protein (Chap. 15) levels. The authors describe methods for expression profiling (transcriptomics) and proteomics and the exciting insights that these studies have provided into the dynamic changes in organellar gene expression in response to environmental cues, developmental stimuli and genetic perturbations of the organellar genetic system. The final four chapters (Chaps. 16, 17, 18, 19) are dedicated to the genetic transformation of organellar genomes. The current status in transformation methods for plastid genomes of algae (Chap. 16) and higher plants (Chap. 17) as well as methods for mitochondrial transformation and transfection of isolated organelles (Chap. 19) are reviewed and the various applications that organelle transformation technologies have in basic research and biotechnology are discussed. A special chapter (Chap. 18) is devoted to reverse genetics in plastids, which has not only been instrumental in elucidating gene functions and structure-function relationships in chloroplast proteins, but also has provided fundamental insights in principles of organelle transformation, recombination and genome sorting and, moreover, led to the development of novel tools for plastid transformation that are widely applicable.

This volume of *Advances in Photosynthesis and Respiration* is written primarily for researchers working in the fields of organelle genetics, gene expression and biotechnology as well as plant systematics and evolutionary biology. In addition to providing a comprehensive overview of their topic, the authors of the individual chapters have tried to discuss concepts, appraise current hypotheses and emphasize general principles. Inevitably, there is some overlap between the contributions, which, however, has been largely limited to the extent needed to ensure that the individual chapters can be read in isolation.

Authors and editors hope that this book will also serve as a stepping stone for students becoming interested in organelle biology, genomics and evolution and for new researchers entering these fields.

Last but not least, we wish to express our sincere thanks to the authors of each chapter. We have been very fortunate to win pre-eminent experts for all chapters – their thoroughness and commitment made this book possible. We are also grateful to the Series Editor Tom Sharkey and the staff at Springer Publishers for their valuable help in editing

and formatting this volume of *Advances in Photosynthesis and Respiration*.

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Ralph Bock

Ralph Bock was born on October 8, 1967 in Wolfen, Germany. He is a Director at the Max Planck Institute of Molecular Plant Physiology (MPI-MP) in Potsdam-Golm, Germany, and a Professor of Plant Biology at the University of Potsdam. Ralph received an M.Sc. (Diplom) degree in Genetics in 1993 from the University of Halle, Germany, under the supervision of Professor Rudolf Hagemann. He did his Ph.D. work at the Waksman Institute, Rutgers, The State University of New Jersey (with Professor Pal Maliga), and at the University of Freiburg, Germany (with Professor Hans Kössel), and received his Ph.D. in 1996 from the University of Freiburg. He was an Assistant Professor at the Institute of Biology III, University of Freiburg from 1996 to 2001, and a Full Professor at the University of Münster, Germany, from 2001 to 2004, before joining the Max Planck Society as a Director at MPI-MP in 2004. Ralph is distinguished for his manifold contributions to chloroplast genetics, biochemistry and biotechnology. His early work was focused on chloroplast RNA processing and, especially, on the study of RNA editing, a curious transcript maturation step by which individual

nucleotides in the messenger RNA are post-transcriptionally altered. Later, he broadened his research interests to include the study of the mechanisms and regulation of other transcriptional and post-transcriptional processes in plastid gene expression, with the ultimate goal to obtain a systems-level understanding of organellar function in the context of the genetic and biochemical networks operating in the plant cell. He has also made seminal contributions to the development of tools for the genetic engineering of higher plant chloroplast genomes and their application in functional genomics, photosynthesis research and biotechnology. Using experimental evolution approaches, Ralph's research team successfully reconstructed endosymbiotic gene transfer processes in laboratory experiments and, recently, also discovered a path for horizontal gene transfer between plants. Among many other community activities, Ralph currently serves on the editorial boards of *Current Genetics*, *Transgenic Research* and *Eukaryotic Cell*. His pioneering research contributions were recognized, inter alia, by his election as a Member of the National Academy of Science (Leopoldina).



Volker Knoop

Volker Knoop was born on July 13, 1963 in Dortmund, Germany. He is Professor of Botany at the University of Bonn, Germany and head of the Molecular Evolution group at the IZMB (Institute for Cellular and Molecular Botany). Volker received his Diplom (M.Sc. equivalent) in Biochemistry from the Free University Berlin (West-Berlin at that time) in 1989 under the supervision of Professor Lothar Willmitzer at the Institut für Genbiologische Forschung GmbH (IGF) in Berlin-Dahlem in the independent research group of Dr. Ulla Bonas (now Professor at the University of Halle). He did his Ph.D. work on trans-splicing and RNA editing in plant mitochondria at the IGF under the supervision of Prof. Axel Brennicke and received his Ph.D. (Dr. rer. nat.) in 1992. He continued his work on molecular evolution of plant mitochondrial DNA as an independent group leader in the department of Axel Brennicke, first at the IGF in Berlin and, from 1996 to 2002, at the University of Ulm. In 2002, Volker was appointed as a professor at the Institute of Botany at the University of Bonn and, in 2003, he became the founding director of the newly established IZMB. Volker is best known for his work on the

“deep green” molecular evolution of mitochondrial DNA in early land plants, with a strong focus on peculiarities in RNA processing, such as the origin of RNA editing and the evolutionary history of trans-splicing introns. More recently, his group also investigated the particularly unique mitochondrial DNAs of lycophytes. Volker received the Merckle research prize in 2000. Aside from his evolutionary interests, his group investigates a gene family of membrane transport proteins for magnesium in the model plants *Arabidopsis thaliana* and *Physcomitrella patens*. Volker was in charge of masterminding the Plant Sciences master course program at the University of Bonn – the first study program exclusively dedicated to plant sciences in Germany, which is now starting into its fourth year. Volker currently serves on the editorial board of *Journal of Systematics and Evolution*. Together with Kai Müller (now Professor at the University of Münster), he has authored the textbook “Gene und Stammbäume” (Genes and Phylogenetic Trees) on phylogenetic analyses, the second edition of which was published in 2009. Volker is married and has four children.

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