Advances in Photosynthesis and Respiration 43
Including Bioenergy and Related Processes

Guillaume Tcherkez
Jaleh Ghashghaie *Editors*

Plant Respiration: Metabolic Fluxes and Carbon Balance

Springer

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Young leaves of beech (*Fagus sylvatica* L.) in the spring (Photo by Jean-Louis Fontaine, Compiègne, France)

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VOLUME 43

This 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, andeven research specialists, acomprehensive, 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 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.

More information about this series at http://www.springer.com/series/5599

Plant Respiration: Metabolic Fluxes and Carbon Balance

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 43: Plant Respiration: Metabolic Fluxes and Carbon Balance

This is Volume 43 "Plant Respiration: Metabolic Fluxes and Carbon Balance" in this series on *Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes*. We note that *respiration in plants* is often ignored by some schools; a common misconception among some secondary school and undergraduate students is that plants do not respire. Animals respire while plants photosynthesize. It is often very difficult to get students to appreciate that plants respire just as animals do. This is obviously essential given non-photosynthetic plant parts (e.g., roots) and the need to survive at night. However, plant respiration is essential even in photosynthesizing cells. A surprisingly large fraction of carbon fixed in photosynthesis is consumed by the plant in respiration in non-photosynthetic plant parts and by leaves at night and to power growth.

In fact, plants exhibit significant flexibility in their respiratory processes. In addition to the canonical glycolysis/tricarboxylic acid cycle/mitochondrial electron transport pathways that provide ATP, plant respiratory processes have many other roles in plant metabolism, many of them unique to plants and other photosynthetic organisms. For example, photorespiration is a metabolic salvage pathway that reduces the damage done when oxygen replaces carbon dioxide at Rubisco. Plants make many compounds essential for life that animals do not make (e.g., the essential amino acids). Respiratory pathways, for example, parts of the tricarboxylic acid cycle, are needed for these anaplerotic processes. Plants have a cyanide-insensitive terminal oxidase that allows them to carry out cyanide-insensitive respiration. The reasons for this respiratory process are not yet completely clear. Mitochondrial processes are important in actively photosynthesizing cells although the linkages to photosynthesis are not yet entirely clear.

Plant respiration has been studied for a long time. Stiles and Leach wrote in 1932 (W. Stiles and W. Leach (1932) **Respiration in Plants**. Methuen's Monographs on Biological Subjects. Methuen & Co. Ltd, London:

> The supreme importance of respiration, being as it one of the most universal and fundamental process of living protoplasm, is recognized by all physiologists. In spite of this, students of botany frequently give respiration little more than a passing consideration. The curious state of affairs is largely due to the fact that most of the existing accounts of respiration in plants are unsatisfactory because they are either insufficiently comprehensive or insufficiently lucid.

The co-series editors believe this new volume is "satisfactory" and "sufficiently comprehensive and lucid" to help students and researchers understand the various processes that are called respiration in plants. In this volume, two experts in respiratory processes invited authors to describe what is known about many of the respiratory processes found in plants. This volume joins five others in this series that cover respiration and mitochondrial processes.

Volume 35 (2012) – Genomics of Chloroplasts and Mitochondria, edited by Ralph Bock and Volker Knoop
Volume 18 (2005) – Plant Respiration: From Cell to Ecosystem, edited by Hans Lambers and Miquel Ribas-Carbo
Volume 17 (2004) – Plant Mitochondria: From Genome to Function, edited by David Day, A. Harvey Millar, and James Whelan
Volume 16 (2004) – Respiration in Archaea and Bacteria: Diversity of Prokaryotic Respiratory Systems, edited by Davide Zannoni
Volume 15 (2004) – Respiration in Archaea and Bacteria: Diversity of Prokaryotic Electron Transport Carriers, edited by Davide Zannoni

Authors of Volume 43

We note with great pride that the current volume is truly an international book; it has authors from the following 12 countries: Australia (10), Austria (1), Belgium (1), Brazil (1), Canada (1), France (7), Germany (2), Italy (1), the Netherlands (1), New Zealand (1), the UK (7), and the USA (7).

We begin by specifically mentioning here two authors, who are also editors of this volume: Guillaume Tcherkez (Australia) and Jaleh Ghashghaie (France). There are 40 authors (including the two editors), who are experts in the field of plant respiration. Alphabetically (by last names), they are Cyril **A**badie, Owen K. Atkin, Doug P. Aubrey, Franz-W. **B**adeck, Nur H.A. Bahar, Margaret M. Barbour, Camille Bathellier, Richard Bligny, Jasper Bloemen, Keith J. Bloomfield, Adam **C**arroll, Antonio C.L. da Costa, Martine **D**ieuaide-Noubhani, Mathias Disney, Jaleh **G**hashghaie, Elisabeth Gout, Kevin L. Griffin, Martin **H**erold, Mary A. Heskel, Chris Huntingford, Christoph A. **L**ehmeier, Anis M. Limami, Jérémy Lothier, Yadvinder **M**alhi, Alberto Martinez de la Torre, Mary Anne McGuire, Patrick Meir, Brendan M. **O**'Leary , Ulrike Ostler, Elisabeth **P**lanchet, William C. Plaxton, Dominique **R**olin, Lucy Rowland, Svetlana Ryazanova, Hans **S**chnyder, Alexander Shenkin, Nicholas G. Smith, Kathy Steppe, Guillaume **T**cherkez, Robert O. Teskey, and Matthew H. Turnbull. We are grateful for their efforts in making this important volume.

Our Books

We list below information on the 42 volumes that have been published thus far (see http://www.springer.com/series/5599 for the series web site). Electronic access to individual chapters depends on subscription (ask your librarian), but Springer provides free downloadable front matter as well as indexes for nearly all volumes. The available web sites of the books in the series are listed below:

- **Volume 42 (2016) – Canopy Photosynthesis: From Basics to Applications**, edited by Kouki Hikosaka from Japan, Ülo Niinemets from Estonia, and Neils P.R. Anten from the Netherlands. Fifteen chapters, 423 pp, hardcover ISBN 978-94-017-7290-7, eBook ISBN 978-94-017-7291-4 [http://www.springer.com/book/9789401772907]
- **Volume 41 (2016) – Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling**, edited by William A. Cramer and Tovio Kallas, from the USA. Thirty-five chapters, 734 pp, hardcover ISBN 978-94-017-7479-6, eBook ISBN 978-94-017-7481-9 [http://www.springer.com/book/9789401774796]

- **Volume 40 (2014) – Non-photochemical Quenching and Energy Dissipation in Plants, Algae, and Cyanobacteria**, edited by Barbara Demmig-Adams, Győző Garab, William W. Adams III, and Govindjee, from the USA and Hungary. Twenty-eight chapters, 649 pp, hardcover ISBN 978-94-017-9031-4, eBook ISBN 978-94-017-9032-1 [http://www.springer.com/life+sciences/plant+sciences/book/978-94-017-9031-4]
- **Volume 39 (2014) – The Structural Basis of Biological Energy Generation**, edited by Martin F. Hohmann-Marriott, from Norway. Twenty-four chapters, 483 pp, hardcover ISBN 978-94-017-8741-3, eBook ISBN 978-94-017-8742-0 [http://www.springer.com/life+sciences/book/978-94-017-8741-3]
- **Volume 38 (2014) – Microbial Bioenergy: Hydrogen Production**, edited by Davide Zannoni and Roberto De Philippis, from Italy. Eighteen chapters, 366 pp, hardcover ISBN 978-94-017-8553-2, eBook ISBN 978- 94-017-8554-9 [http://www.springer.com/life+sciences/plant+sciences/book/978-94-017-8553-2]
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- **Volume 36 (2013) – Plastid Development in Leaves During Growth and Senescence**, edited by Basanti Biswal, Karin Krupinska, and Udaya Biswal, from India and Germany. Twenty-eight chapters, 837 pp, hardcover ISBN 978-94-007-5723-33, eBook ISBN 978-94-007-5724-0 [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-5723-3]
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- **Volume 32 (2011) – C_4 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, softcover ISBN 978-94-007-3381-7, eBook ISBN 978-90-481-9407-0 [http://www.springer.com/life+sciences/plant+sciences/book/978-90-481-9406-3]
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Future Advances in Photosynthesis and Respiration and Other Related Books

The readers of the current series are encouraged to watch for the publication of the forthcoming books (not necessarily arranged in the order of future appearance):

- *Photosynthesis and Climate Change* (working title) (editors: Joy K. Ward, Danielle A. Way, and Katie M. Becklin)

- *Cyanobacteria* (editor: Donald Bryant)
- *Leaf Photosynthesis* (editors: William W. Adams III and Ichiro Terashima)
- *Photosynthesis in Algae* (editors: Anthony Larkum and Arthur Grossman)
- *Our Photosynthetic Planet* (editors: Mike Behrenfeld, Joe Berry, Lianhong Gu, Nancy Jiang, Anastasia Romanou, and Anthony Walker)
- *Modeling Photosynthesis and Growth* (editors: Xin-Guang Zhu and Thomas D. Sharkey)

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

Algae, Cyanobacteria: Biofuel and Bioenergy
Artificial Photosynthesis
ATP Synthase: Structure and Function
Bacterial Respiration
Evolution of Photosynthesis
Green Bacteria and Heliobacteria
Interactions Between Photosynthesis and Other Metabolic Processes
Limits of Photosynthesis: Where Do We Go from Here?
Photosynthesis, Biomass, and Bioenergy
Photosynthesis Under Abiotic and Biotic Stress

If you have any interest in editing/coediting 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 (gov@illinois.edu). In addition, Julian Eaton-Rye will soon be coming on board as our co-series editor. Thus, we recommend that you contact him at julian.eaton-rye @ otago.ac.nz. Suggestions for additional topics are also welcome. Instructions for writing chapters in books in our series are available by sending e-mail requests to any of us; they may also be downloaded from Govindjee's web site http://www.life.illinois.edu/govindjee as the first item under "Announcements" on the main page.

We would like to note that bibliographic tools are expanding to cover chapters in books making it easier to document the importance of research in terms that can be understood by promotion committees and administrators. We believe that chapters in edited volumes remain an important part of scientific understanding. An author can be more expansive in a chapter and can present information in a complete manner that makes it easier for readers to understand nuances. Thus, our book series serves an important educational goal for all concerned.

We take this opportunity to thank and congratulate Guillaume Tcherkez and Jaleh Ghashghaie for their outstanding editorial work in this volume; they have indeed 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 40 authors of this book (see the list given above); without their authoritative chapters, there would be no such volume. We give special thanks to Mrs. Rathika Ramkumar of SPi Global, India, for directing the typesetting of this book; her expertise has been crucial in bringing this book to completion. We owe Jacco Flipsen and Ineke Ravesloot (of Springer) thanks for their friendly working relation with us that led to the production of this book.

August 5, 2017

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Series Editors

A 2017 informal photograph of Govindjee (*right*) and his wife Rajni (*left*) in a suburb of Chicago, Illinois, 2017. Photo by Ashwani Kumar, visiting from Jaipur, India

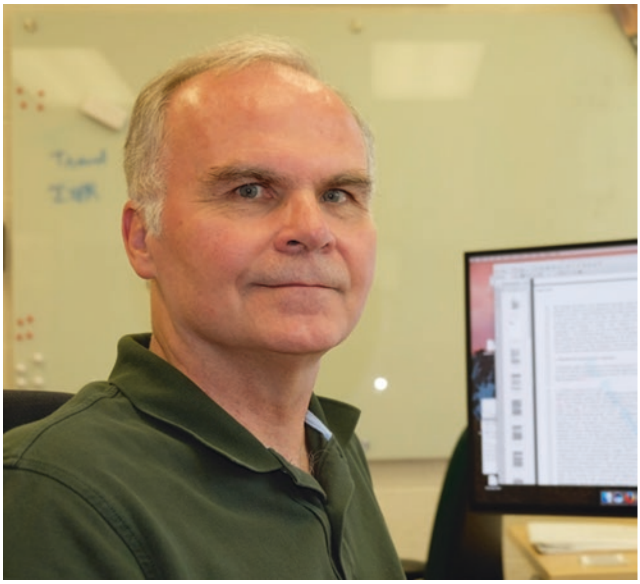
Govindjee who uses one name only, was born on October 24, 1932, in Allahabad, India. Since 1999, he has been professor emeritus of biochemistry, biophysics, and plant biology at the University of Illinois at Urbana-Champaign (UIUC), Urbana, IL, USA, after serving on the faculty there for 40 years. He obtained his BSc (chemistry, botany, and zoology) and MSc (botany, plant physiology) in 1952 and 1954 from the University of Allahabad. He learned his plant physiology from Shri Ranjan, who was a student of Felix Frost Blackman (of Cambridge, UK). Then, Govindjee studied *photosynthesis* at the UIUC, under two giants in the field, Robert Emerson (a student of Otto Warburg) and Eugene Rabinowitch (who had worked with James Franck), obtaining his PhD, in biophysics, in 1960.

Govindjee is best known for his research on excitation energy transfer, light emission (prompt and delayed fluorescence and thermoluminescence), primary photochemistry, and electron transfer in *photosystem II* (PS II, water-plastoquinone oxidoreductase). His research, with many others, includes the discovery of a short-wavelength form of chlorophyll (Chl) *a* functioning in 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 others, include an understanding of the basic relationship 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; 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* and in *photosynthesis education*.

Govindjee's honors include fellow of the American Association for the Advancement of Science (AAAS); distinguished lecturer of the School of Life Sciences, UIUC; fellow and lifetime member of the National Academy of Sciences (India); president of the American Society for Photobiology (1980–1981); Fulbright scholar (1956), Fulbright senior lecturer (1997), and Fulbright specialist (2012); honorary president of the 2004 International Photosynthesis Congress (Montreal, Canada); the first recipient of the Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology (2006); recipient of the Communication Award of the International Society of Photosynthesis Research (2007); and the Liberal Arts and Sciences Lifetime Achievement Award of the UIUC (2008). Further, Govindjee has been honored many times: (1) in 2007, through 2 special volumes of *Photosynthesis Research*, celebrating his 75th birthday and for his 50-year dedicated research in photosynthesis (guest editor: Julian Eaton-Rye); (2) in 2008, through a special International Symposium on "Photosynthesis in a Global Perspective," held in November 2008, at the University of Indore, India (this was followed by a book *Photosynthesis: Basics and Applications* (edited by S. Itoh, P. Mohanty, and K.N. Guruprad)); (3) in 2012, through *Photosynthesis: Plastid Biology, Energy Conversion, and Carbon Assimilation*, edited by Julian Eaton-Rye, Baishnab C. Tripathy, and one of us (TDS); (4) in 2013, through special issues of *Photosynthesis Research* (Volumes 117 and 118), edited by Suleyman Allakhverdiev, Gerald Edwards, and Jian-Ren Shen celebrating his 80th (or rather 81st) birthday; (5) in 2014, through celebration of his 81st birthday in Třeboň, the Czech Republic (O. Prasil [2014] Photosynth Res 122: 113–119); (6) in 2016, through the prestigious Prof. B.M. Johri Memorial Award of the Society of Plant Research, India; (7) in 2017, he was one of the three scientists, honored at the 8th International Conference on Photosynthesis and Sustainability, held at the University of Hyderabad; and (8) again in 2017, a 2-day Symposium on Photosynthesis was held in his honor at M.S. University, Udaipur, India, celebrating his 85th birthday. Currently, *Photosynthetica* is planning to publish, in 2018, a special issue to celebrate his 85th birthday (editor: Julian Eaton-Rye, member of the advisory board of this series).

Govindjee's unique teaching of the Z-scheme of photosynthesis, where students act as different intermediates, has been published in two papers: (1) P.K. Mohapatra and N.R. Singh [2015] Photosynth Res 123:105–114 and (2) S. Jaiswal, M. Bansal, S. Roy, A. Bharati, and B. Padhi [2017] Photosynth Res 131: 351–359. Govindjee is a coauthor of a classic and highly popular book *Photosynthesis* (with E.I. Rabinowitch, 1969) and of a historical book *Maximum Quantum Yield of Photosynthesis: Otto Warburg and the Midwest Gang* (with K. Nickelsen, 2011). He is editor (or coeditor) of many books including *Bioenegetics of Photosynthesis* (1975); *Photosynthesis*, 2 volumes (1982); *Light Emission by Plants and Bacteria* (1986); *Chlorophyll a Fluorescence: A Signature of Photosynthesis* (2004); *Discoveries in Photosynthesis* (2005); and *Non-photochemical Quenching* *and Energy Dissipation in Plants, Algae and Cyanobacteria* (2015).

Since 2007, each year a **Govindjee and Rajni Govindjee Award** is given to graduate students, by the Department of Plant Biology (odd years) and by the Department of Biochemistry (even years), 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.



A 2017 photograph of Thomas D. Sharkey in his office at Michigan State University. Photo by Sean E. Weise

Thomas (Tom) D. 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, USA. After 2 years as a research technician, Tom entered a PhD program in the Department of Energy Plant Research Laboratory at Michigan State University under the mentorship of Klaus Raschke and finished in 1979. Postdoctoral research was carried out with Graham Farquhar at the Australian National University, in Canberra, where he coauthored a landmark review on photosynthesis and stomatal conductance. For 5 years, he worked at the Desert Research Institute, Reno, Nevada. After Reno, Tom spent 20 years as professor of botany at the University of Wisconsin in Madison. In 2008, Tom became professor and chair of the Department of Biochemistry and Molecular Biology at Michigan State University. In 2017, Tom stepped down as department chair and moved to the MSU-DOE Plant Research Laboratory completing a 38-year sojourn back to his beginnings. Tom's research interests center on the exchange of gases between plants and the atmosphere and carbon metabolism of photosynthesis. The biochemistry and biophysics underlying carbon dioxide uptake and isoprene emission from plants form the two major research topics in his laboratory. Among his contributions are measurement of the carbon dioxide concentration inside leaves, an exhaustive study of short-term feedback effects in carbon metabolism, and a significant contribution to elucidation of the pathway by which leaf starch breaks down at night. In the isoprene research field, his laboratory has cloned many of the genes that underlie isoprene synthesis, and he has published many important papers on the biochemical regulation of isoprene synthesis. Tom's work has been cited over 26,000 times according to Google Scholar in 2017. He has been named an outstanding faculty member by Michigan State University, and in 2015, he was named a university distinguished professor. He is a fellow of the American Society of Plant Biologists and of the American Association for the Advancement of Science. Tom has coedited three books, the first on trace gas emissions from plants in 1991 (with Elizabeth Holland and Hal Mooney), Volume 9 of this series (with Richard Leegood and Susanne von Caemmerer) on the *Physiology of Carbon Metabolism of Photosynthesis* in 2000, and Volume 34 (with Julian Eaton-Rye and Baishnab C. Tripathy) entitled *Photosynthesis*: *Plastid Biology*, *Energy Conversion, and Carbon Assimilation*. Tom has been co-series editor of this series since Volume 31.

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Preface

Although respiration represents a minor carbon flux as compared to photosynthesis and photorespiration at the leaf level, it is one of the major components of the carbon balance at different scales. This book is dedicated to current knowledge on respiratory metabolism in plants. Several aspects have been reviewed, from enzymatic/energetic control and metabolic fluxes to impacts on respiratory CO_2 release at the forest and global scale.

In leaf gas exchange, respiration has long been viewed as a simple phenomenon that can be modeled as an invariant CO_2 efflux. However, this representation is too simplistic, because respiratory metabolism is complicated by multiple enzymatic reactions (glycolysis and tricarboxylic acid (TCA) cycle), alternative pathways, as well as ancillary pathways such as the pentose phosphate pathway. In addition, anaplerotic carbon fixation occurs by the enzyme phospho*enol*-pyruvate carboxylase (PEPC) for TCA pathway replenishment (anaplerotic pathway). Metabolic pathways associated with biosynthesis of amino acids and carbon and nitrogen metabolism are tightly interconnected through respiration. Plant respiratory regulation thus relies on a complex metabolic network depending on species/tissues and environmental conditions. Crossroads between carbon, nitrogen, and sulfur metabolism through interactions between day respiration and photorespiration are reviewed in Chap. 1. Energetic aspects of plant respiration are covered in Chap. 2 and further combined to flux assessment and other pathways (such as pentose phosphates) with ^{13}C natural abundance in Chap. 3.

Technological advances have contributed considerably to improving our knowledge of plant respiratory metabolism and regulation during the past decade, and they are also discussed through the corresponding chapters: FACE (free-air CO_2 enrichment) experimental systems to investigate respiratory response to elevated CO_2 (Chap. 4); new methods to measure and model stem respiration (Chap. 5 and also Chap. 9); emerging global datasets, which provide opportunities to improve parameterization of leaf respiration in large-scale models (Chap. 6); high time-resolution isoflux measurements with tunable diode laser (TDL) to study day respiration near the light and CO_2 compensation points (Chap. 7); and dynamic ^{13}C labeling associated with compartmental modeling to characterize the substrate supply system of respiration, including estimations of size and turnover of kinetically distinct pools (Chap. 8).

As will appear in this volume, respiratory metabolic fluxes should be viewed as essential for the response of plants to environmental constraints, in a range of developmental situations. This is typically the case in the adaptive response of plants to low-oxygen stress, which is associated with a considerable orchestration of both carbon and nitrogen metabolism (Chap. 10). In CAM plants, respiration is an important actor of the diurnal carbon budget, because it is directly linked to organic acid metabolism and CO_2 refixation (Chap. 11). During germination, respiration has also a key role in generating intermediates partitioned between catabolism and biosyntheses, from remobilized reserves, and this is extensively discussed using recent results of nonstationary ^{13}C labeling in Chap. 12.

The mechanisms of metabolic control are still incompletely understood, but in the past years, considerable advances have been made in the examination of protein phosphorylation and other posttranslational modifications involved in enzyme activity regulation. Chapter 13 gives an extensive overview of this aspect, which is also discussed in Chap. 1 (focused on day respiration).

The final chapter (Chap. 14) illustrates recent findings on the metabolic interactions between the TCA pathway and other pathways, so as to establish a list of key actors of regulation that should be considered in future investigations.

Despite these tremendous technological and scientific advances in understanding respiratory metabolism and its regulation during the past decade, some key questions are still unanswered. One of the most enduring mysteries is to find means to model plant leaf respiration, that is, most important factors that determine the rate of CO_2 efflux. Intense efforts have been devoted to show that leaf respiration changes with gaseous conditions, temperature, or nutrient availability, but we still do not know how to formally produce an equation that would yield the CO_2 production rate by respiration. In the preface of his book *Plant Respiration* (Oxford Press 1953), W.O. James used the term "chameleon" to describe respiration, because its meaning is rather vague and adapts itself to the context (enzymatic, gas exchange, etc.). Further, James mentions that the "obvious exchange of gases is only the most superficial aspect of respiration." Sixty-five years later, this observation remains correct. In effect, the CO_2 efflux is the result of a complicated, regulated series of metabolic steps, and thus the specific origin of carbon atoms found in respiration is still viewed as a jigsaw puzzle. With no doubt, this book will shed some light on these aspects and will open perspectives for future research.

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About the Editors

Guillaume Tcherkez at the inauguration of the exhibition "The Flora of the Paris Basin" in October 2016 taking place at the Australian National Botanic Gardens, Canberra

Guillaume Tcherkez received an MS (ecology 2001) from the University of Paris-Sud (France), after 4 years at the Ecole Normale Supérieure (Paris). He started his PhD at the University of Paris-Sud (supervised by Jaleh Ghashghaie) and worked on the carbon isotope composition of respired CO_2. Subsequently, he carried out postdoctoral studies on the chemical mechanism and isotope effects of enzymes – including Rubisco – in Australia with Prof. Graham Farquhar (Australian National University, Canberra) and was at the origin of the concept that the mechanism of the first enzyme of photosynthesis, Rubisco, is probably nearly perfectly optimized to prevalent growth conditions of autotrophic organisms. In 2005, he was appointed as assistant professor at the University of Paris-Sud and then head professor of the isotopics and metabolomics facility in 2008. He is now professor at the Australian National University. His research is mostly focused on the control of leaf day respiration and metabolic interactions with major pathways such as photorespiration. He is one of the best experts in isotope effects in metabolism, applied to plant biology but also human health. Within a global initiative, he has shown the usefulness of natural isotope abundance in metabolites for breast cancer biomarkers, a discovery that has been widely covered by Australian and French media in 2016. He has been awarded the Bronze Medal of the CNRS (*Centre National de la Recherche Scientifique*, French National Center for Scientific Research) in 2009 and a Future Fellowship of the Australian Research Council in 2014. He has been an editor of the journal *Plant, Cell and Environment* (editor in chief: Keith Mott) since 2015.

Jaleh Ghashghaie at the "Stable Isotopes and Metabolomics" facility founded by Eliane Deléens and Jean-Louis Prioul in 1996, at the University of Paris-Sud, Orsay. Photo by Yang Xia, PhD student of Jaleh, July 2017

Jaleh Ghashghaie was born on March 20, 1956, in the Azerbaijan province of Iran. After a 4-year study of biology at the Faculty of Science, University of Tabriz, she received a grant from the French government to go to France in 1979. At the University of Paris-Sud in Orsay, she obtained a master's degree (supervised by Gabriel Cornic) in 1982 and a PhD (supervised by Bernard Saugier) in 1986 in plant ecophysiology. In 1991, she was appointed as a lecturer at the same institution. In 2004, she defended her habilitation thesis, and in 2009, she became a full professor. In addition to her full teaching program, she has been doing research at the Laboratory of Ecology, Systematics and Evolution (ESE), of the University of Paris-Sud in Orsay, since 1989.

During the first 10 years at ESE, she, together with Gabriel Cornic, investigated photosynthetic and stomatal responses to environmental constraints (mostly drought). Then, in 1993, she met Eliane Deléens, who had obtained an isotope-ratio mass spectrometer (IRMS) at the Institute of Plant Biology (University of Paris-Sud). Eliane trained Jaleh to the use of stable isotopes, and they coupled, with the technical assistance of Eliane's husband (Marc Berry), the IRMS to the gas exchange system to analyze the carbon isotope composition of CO_2 released by respiration of attached leaves or roots. The carbon isotope discrimination (or fractionation) during dark respiration had not been investigated since the early 1970s. At the same time, Franz-W. Badeck was working at ESE as a postdoc and expressed his interest in this topic. Jaleh's collaboration with Eliane and Franz was the beginning of a great scientific *adventure*. This team, along with Jaleh's PhD students (including two contributors of this volume: Guillaume Tcherkez and Camille Bathellier), demonstrated that, in contrast to what was assumed before, (i) there is carbon isotope fractionation during respiration in leaves (leaf-respired CO_2 being ^{13}C-enriched compared with leaf sugars), that (ii) this fractionation is highly variable depending on species and environmental conditions, and that (iii) respiratory fractionation in roots is opposite to that found in leaves (i.e., root-respired CO_2 is ^{13}C-depleted compared with root sugars). In collaboration with Graham Farquhar, they modeled the intramolecular ^{13}C distribution in glucose of C_3 plants (Tcherkez, Farquhar, Badeck & Ghashghaie, 2004, in *Functional Plant Biology* 31:857–877), which is eventually the metabolic source of all carbon atoms found in respired CO_2. Jaleh Ghashghaie and her coworkers also investigated the metabolic origin of the respiratory fractionation in leaves and roots. They published original and highly cited papers as well as invited reviews, the latest being a Tansley review (Ghashghaie & Badeck 2014, *New Phytologist* 201:751–769).

Jaleh coordinated, together with Howard Griffiths (Cambridge, UK) and Franz-W. Badeck, a European research-training network called NETCARB (Network for Ecophysiology in Closing the Terrestrial Carbon Budget), dealing with the use of stable isotopes in plants at different ecophysiological scales (2000–2004). NETCARB was a successful project including 8 partners from different countries, and funding from the European Commission (EC, HPRN-CT-1999-00059) allowed the appointment of 15 young researchers, the organization of 3 summer schools, and the publication of more than 30 papers.

Jaleh is a member of the French Society of Stable Isotopes and organized, together with Christine Hatté (LSCE, Saclay, France), the 2nd Joint European Stable Isotope Users Meeting (JESIUM) in the south of France (Giens) in 2008 (http://www.jesium2008.eu/). The papers presented at JESIUM-2008 were published in 2009 in special volumes in *Rapid Communications in Mass Spectrometry* and in *Isotopes in Environmental and Health Studies*.

Eliane Deléens, Jaleh's close collaborator, sadly passed away in 2003, but Jaleh continues the work initiated by Eliane in collaboration with Franz Badeck (now at the Council for Agricultural Research and Agricultural Economics Analysis, Italy) and Guillaume Tcherkez (now at the Australian National University, Canberra) and with other colleagues she met at NETCARB and SIBAE-BASIN conferences.

For further information about Jaleh's work, see her webpage (http://www.ese.u-psud.fr/article416.html?lang=en).

Abbreviations

^{11}C	Artificial carbon radioisotope
^{13}C	Minor natural stable carbon isotope
$^{13}CO_2$	^{13}C isotopologue of CO_2
^{14}C	Natural carbon radioisotope
6PGDH	6-Phosphogluconate dehydrogenase (EC 1.1.1.44)
a	Advection of CO_2 through the xylem (mol m s^{-1}) (Chap. 9)
a	Isotope fractionation associated with CO_2 diffusion in air (Chaps. 3 and 7)
A	Leaf net CO_2 assimilation
AAC	ADP/ATP carrier
ABA	Abscisic acid
Acetyl-CoA	Acetyl coenzyme A
Aco	Aconitase (aconitate in Chap. 14)
ADH	NAD-dependent alcohol dehydrogenase (EC 1.1.1.1)
ADP	Adenosine diphosphate
a_e	Isotope fractionation associated with internal CO_2 dissolution and diffusion
AK	Adenylate kinase (EC 2.7.4.3)
AlaAT	Alanine aminotransferase (EC 2.6.1.2)
AOX	Alternative oxidase (EC 1.10.3.11)
ARQ	Apparent respiratory quotient
AS	ATP synthase
ASE	Allometric scaling equation
AspAT	Aspartate aminotransferase (EC 2.6.1.1)
ATP	Adenosine triphosphate
b	Isotope fractionation associated with carboxylation
BTPC	Bacterial-type phospho*enol*pyruvate carboxylase
C	Carbon
CA	Carbonic anhydrase (EC 4.2.1.1.)
c_a	CO_2 mole fraction in the atmosphere
CAM	Crassulacean acid metabolism
c_c	CO_2 mole fraction at the carboxylation sites (chloroplasts)
CDPK	Ca^{2+}-dependent protein kinase
c_i	Leaf intercellular CO_2 mole fraction
Cit	Citrate

CO_2	Carbon dioxide (μmol mol^{-1} or %)
CO_2*	All forms of DIC in xylem sap: carbon dioxide, bicarbonate, and carbonate
COX	Cytochrome c oxidase
cPK	Cytosolic pyruvate kinase
CS	Citrate synthase (EC 2.3.3.1)
CWD	Coarse woody debris
D	CO_2 diffusion coefficient (m^2 s^{-1})
DIC	Dissolved inorganic carbon (mol L^{-1})
Diff	Radial diffusion of CO_2
e	Isotope fractionation associated with respiratory CO_2 evolution in the light, with respect to recently fixed photosynthates
*e**	Apparent isotope fractionation associated with respiratory CO_2 evolution in the light and considering disequilibria between δ^{13}C of growth and measurement CO_2
E_A	Efflux of CO_2 from the trunk to the atmosphere (μmol CO_2 m^{-3} sapwood s^{-1})
e_h	Isotope fractionation associated with respiratory CO_2 evolution in the light from a photosynthetically disconnected pool (heterotrophic cells)
e_{int}	Intrinsic isotope fractionation associated with respiratory CO_2 evolution in the light
ERF	Ethylene response factors
ESM	Earth system model
ETC	Electron transport chain
f	Isotope fractionation associated with photorespiratory CO_2 evolution
F	Unitless scaling factor
F2KP	Fructose-6-phosphate 2-kinase/fructose-2,6-bisphosphatase (EC 3.1.3.46)
f_A	Rate of air flow (mol s^{-1})
FACE	Free-air carbon dioxide enrichment
Fru-2,6-P_2	Fructose-2,6-bisphosphate
f_S	Sap flow (l s^{-1})
Fum	Fumarate
G3PDH	Glyceraldehyde-3-phosphate dehydrogenase (EC 1.2.1.12)
G6PDH	Glucose-6-phosphate dehydrogenase (EC 1.1.1.49)
GABA	γ-Aminobutyric acid
GABA-T	GABA aminotransferase (EC 2.6.1.19)
GAD	Glutamate decarboxylase (EC 4.1.1.15)
GAPN	Non-phosphorylating glyceraldehyde-3-phosphate dehydrogenase (EC 1.2.1.9)
GDC-SHMT	Glycine decarboxylase-serine hydroxymethyl transferase complex
GDH	Glutamate dehydrogenase (NAD/NADP, EC 1.4.1.2/EC 1.4.1.4)
Glc	Glucose
g_m	Leaf internal CO_2 conductance (mol m^{-2} s^{-1})
GOGAT	Glutamine 2-oxoglutarate aminotransferase (ferredoxin-dependent, EC 1.4.7.1)
GPP	Gross primary productivity