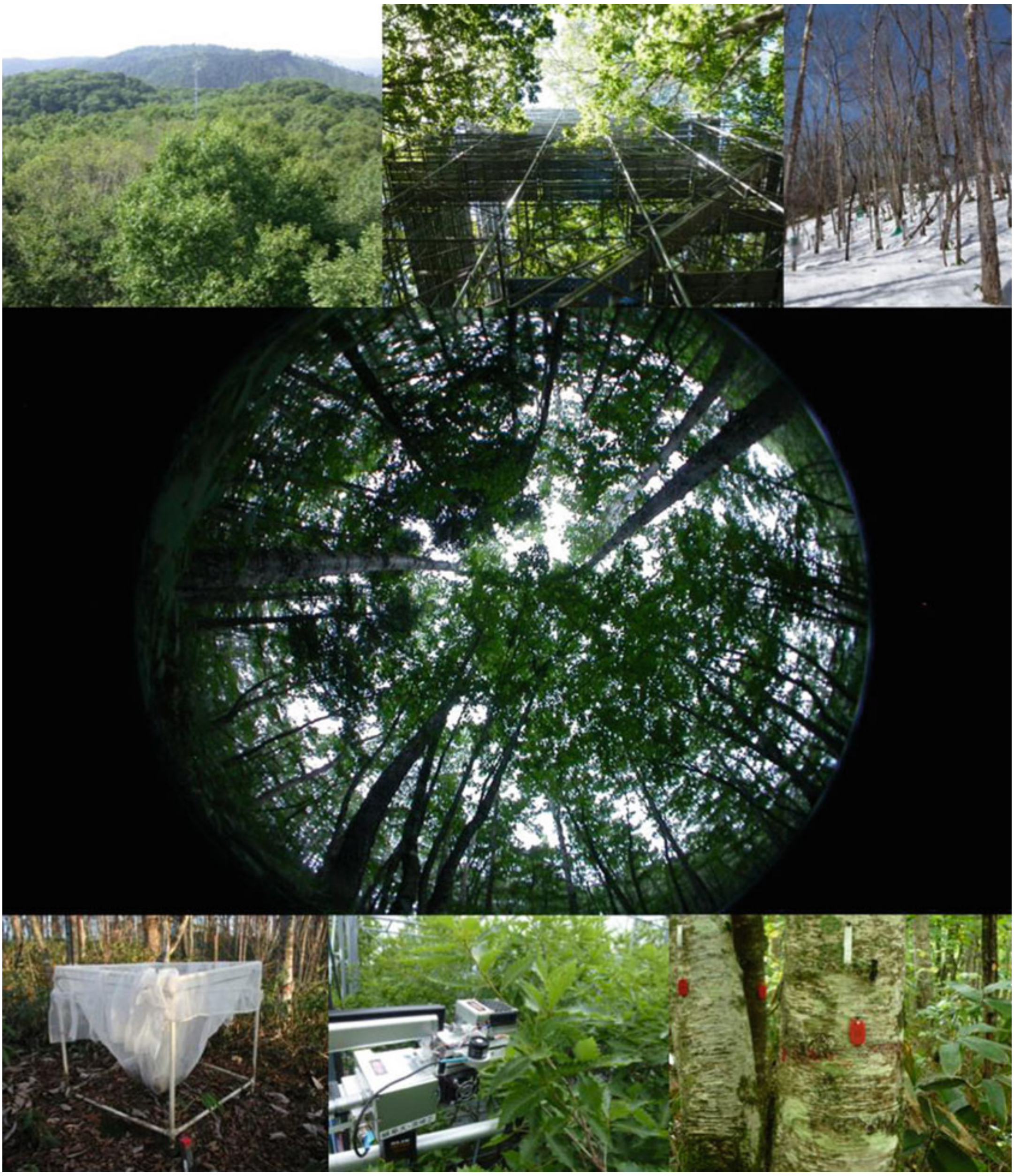
Advances in Photosynthesis and Respiration 42
Including Bioenergy and Related Processes

Kouki Hikosaka
Ülo Niinemets
Niels P.R. Anten *Editors*

# Canopy Photosynthesis: From Basics to Applications

Springer

# Canopy Photosynthesis: From Basics to Applications



Measurements of carbon cycle in the Takayama Experimental Forest, Japan. Meteorological $CO_2$ flux observation tower (*left-top*; National Institute of Advanced Science and Technology), canopy tower (*center-top*), forest in winter time (*right-top*), canopy hemispherical photograph from the understory (*center*), litter trap (*left-bottom*), leaf gas exchange measurements on canopy tower (*center-bottom*), and tree biomass survey (*right-bottom*). Photographs were taken by Hiroyuki Muraoka. See Chap. 12

# Advances in Photosynthesis and Respiration
## *Including Bioenergy and Related Processes*

---

### VOLUME 42

---



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, 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 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.

For other titles published in this series, go to http://www.springer.com/series/5599

# Canopy Photosynthesis: From Basics to Applications

*Edited by*

**Kouki Hikosaka**
*Graduate School of Life Sciences*
*Tohoku University*
*Sendai*
*Japan*

**Ülo Niinemets**
*Environmental Sciences*
*Estonian University of Life Sciences*
*Tartu*
*Estonia*

and

**Niels P.R. Anten**
*Crop and Weed Ecology*
*Centre for Crop Systems Analysis*
*Wageningen University*
*Wageningen*
*The Netherlands*

Springer

*Editors*
Kouki Hikosaka
Graduate School of Life Sciences
Tohoku University
Sendai, Japan

Ülo Niinemets
Environmental Sciences
Estonian University of Life Sciences
Tartu, Estonia

Niels P.R. Anten
Crop and Weed Ecology
Centre for Crop Systems Analysis
Wageningen University
Wageningen, The Netherlands

ISSN 1572-0233 ISSN 2215-0102 (electronic)
Advances in Photosynthesis and Respiration
ISBN 978-94-017-7290-7 ISBN 978-94-017-7291-4 (eBook)
DOI 10.1007/978-94-017-7291-4

Library of Congress Control Number: 2015957424

Springer Dordrecht Heidelberg New York London


Printed on acid-free paper

Springer Science+Business Media B.V. Dordrecht is part of Springer Science+Business Media (www.springer.com)

# From the Series Editors

## Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

### *Volume 42: Canopy Photosynthesis: From Basics to Applications*

We are delighted to announce the publication of Volume 42 in this series. We believe these books provide a forum for discussion of important developments in the field in a more in-depth and complete way than can be achieved in individual papers or even in extended reviews. The publisher has taken steps to ensure that these books and individual chapters are easily found. A large number of university libraries buy electronic access. Downloaded PDFs are of high quality. Data can be downloaded for easy import into reference management programs. Because most distribution is now digital, there are no longer significant constraints on the use of color or placement of figures within the text. 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.

### This Book: Volume 42

*Canopy Photosynthesis: From Basics to Applications* addresses how the display of photosynthetic structures affects photosynthesis. Photosynthesis provides the energy and basic substrates for life on earth. Knowledge of photosynthetic functioning at the physiological and molecular level is advancing rapidly, but its relevance for food production, ecosystem carbon cycling, and climate feedback acts at the level of vegetation stands such as forests, grasslands, or agricultural crops. The canopies of these vegetation types are highly complex and varied, presenting a wide range of plant architectures and leaf displays. Understanding the complex relationships between leaf display and photosynthesis requires a quantitative approach to understanding light distribution, leaf heating, and optimal distribution of resources such as nitrogen among the leaves experiencing different environmental conditions through their life. These quantitative approaches are often thought of in terms of forest canopies but these concepts are important when studying any canopy, including a canopy of the standard lab plant *Arabidopsis*. Simulating canopy processes involves the application of rigorous physical concepts such as energy balance equations that can predict leaf temperature from its radiation environment and evaporation rate. In some cases, energy balance estimates are more representative of leaf temperature than direct measurement because of the difficulties of measuring leaf temperature without changing it. Another area of study important in canopy photosynthesis is called micrometeorology. Wind field structure, including 3D frictional velocity distribution, turbulence characteristics, and water content of the air are some of the fundamental issues that must be understood in sufficient detail to study canopy photosynthesis.

We, the series editors, are indeed delighted that three scientists who have made major contributions to the understanding of canopy photosynthesis agreed to edit this volume. Kouki Hikosaka (from Japan), Ülo Niinemets (from Estonia), and Niels P. R. Anten (from the Netherlands) have conceived a book in five parts with three to four chapters per section. The sections progress from leaf-specific issues like temperature and light distribution among leaves in Part 1 through successively larger scales to ecological and evolutionary processes in Part 5. Twenty-five authors (see list of contributors) from seven countries (UK, USA, Canada, Estonia, Japan, Netherlands, and Switzerland) have contributed to this volume.

With the knowledge gained from reading this book it will be easier to understand two interesting "counter-intuitive" observations: (*1*) Under humid conditions, increasing wind speed can reduce evaporation, and (*2*) sometimes when volcanoes inject dust into the atmosphere, reducing the intensity of sunlight by increased light scattering, global photosynthesis increases. In the first case energy balance equations show that the cooling by increased wind speed of sun-warmed leaves reduces the potential for evaporation more than it increases conductance for water loss. The second case happens if scattered light penetrates deeper into the canopy, striking more leaves than what the direct beam of the sun can reach.

Many of our readers will want to have a good reference for the equations and their applications, and they will be found in this book. Further, for those who study photosynthesis in leaves, chapters in this volume will help them understand the steps involved in measuring how leaves gather light and how we obtain leaf temperature.

## Our Books: Now 42 Volumes

We list below information on the 41 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 41 (2015) Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling**, Edited by William A. Cramer and Tovio Kallas from the USA. Thirty five chapters – In press
- **Volume 40 (2015) 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 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 Phillipis, 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]
- **Volume 37 (2014) Photosynthesis in Bryophytes and Early Land Plants**, edited by David T. Hanson and Steven K. Rice, from USA. Eighteen chapters, approx. 342 pp, Hardcover ISBN 978-94-007-6987-8, eBook ISBN 978-94-007-6988-5 [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-6987-8]
- **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]

- **Volume 35 (2012) Genomics of Chloroplasts and Mitochondria**, edited by Ralph Bock and Volker Knoop, from Germany. Nineteen chapters, 475 pp, Hardcover ISBN 978-94-007-2919-3 eBook ISBN 978-94-007-2920-9 [http://www.springer.com/life+sciences/plant+sciences/book/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. Thirty-three chapters, 854 pp, Hardcover, ISBN 978-94-007-1578-3, eBook ISBN 978-94-007-1579-0 [http://www.springer.com/life+sciences/plant+sciences/book/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, Hardcover ISBN 978-94-007-1532-5, Softcover ISBN 978-94-007-3832-4, eBook ISBN 978-94-007-1533-2 [http://www.springer.com/life+sciences/book/978-94-007-1532-5]
- **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]
- **Volume 31 (2010): The Chloroplast: Basics and Applications,** edited by Constantin Rebeiz (USA), Christoph Benning (USA), Hans J. Bohnert (USA), Henry Daniell (USA), J. Kenneth Hoober (USA), Hartmut K. Lichtenthaler (Germany), Archie R. Portis (USA), and Baishnab C. Tripathy (India). Twenty-five chapters, 451 pp, Hardcover ISBN 978-90-481-8530-6, Softcover ISBN 978-94-007-3287-2, eBook ISBN 978-90-481-8531-3 [http://www.springer.com/life+sciences/plant+sciences/book/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, Softcover ISBN 978-94-007-3073-1 eBook ISBN 978-90-481-2863-1 [http://www.springer.com/life+sciences/plant+sciences/book/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, Softcover ISBN 978-94-007-1533-2, eBook ISBN 978-1-4020-9237-4 [http://www.springer.com/life+sciences/plant+sciences/book/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, eBook ISBN 978-1-4020-8815-5 [http://www.springer.com/life+sciences/plant+sciences/book/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, Softcover ISBN 978-90-481-7742-4, eBook ISBN 978-1-4020-6863-8 [http://www.springer.com/life+sciences/plant+sciences/book/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, Softcover ISBN 978-90-481-7820-9, eBook ISBN 978-1-4020-8250-4 [http://www.springer.com/life+sciences/plant+sciences/book/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, Softcover ISBN 978-90-481-7140-8, eBook ISBN 978-1-4020-4516-5 [http://www.springer.com/life+sciences/plant+sciences/book/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, Softcover ISBN 978-90-481-7088-3, eBook ISBN 978-1-4020-4256-0 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-4255-3]
- **Volume 23 (2006): The Structure and Function of Plastids**, edited by Robert R. Wise and J. Kenneth Hoober, from USA. Twenty-seven chapters, 575 pp, Softcover, ISBN: 978-1-4020-6570–6; Hardcover ISBN 978-1-4020-4060-3, Softcover ISBN 978-1-4020-6570-5, eBook ISBN 978-1-4020-4061-0 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-4060-3]
- **Volume 22 (2005): Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase**, edited by Thomas J. Wydrzynski and Kimiyuki Satoh, from Australia and Japan. Thirty-four chapters, 786 pp, Hardcover ISBN 978-1-4020-4249-2, eBook ISBN 978-1-4020-4254-6 [http://www.springer.com/life+sciences/plant+sciences/book/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, Softcover ISBN 978-1-4020-9281-7, eBook ISBN 978-1-4020-3579-1 [http://www.springer.com/life+sciences/plant+sciences/book/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, eBook ISBN 978-1-4020-3324-7 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-3323-0]
- **Volume 19 (2004): Chlorophyll *a* Fluorescence: A Signature of Photosynthesis**, edited by George C. Papageorgiou and Govindjee, from Greece and USA. Thirty-one chapters, 820 pp, Hardcover, ISBN 978-1-4020-3217-2, Softcover ISBN 978-90-481-3882-1, eBook ISBN 978-1-4020-3218-9 [http://www.springer.com/life+sciences/biochemistry+%26+biophysics/book/978-1-4020-3217-2]
- **Volume 18 (2005): Plant Respiration: From Cell to Ecosystem,** edited by Hans Lambers and Miquel Ribas-Carbo, from Australia and Spain. Thirteen chapters, 250 pp, Hardcover ISBN 978-14020-3588-3, Softcover ISBN 978-90-481-6903-0, eBook ISBN 978-1-4020-3589-0 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-3588-3]
- **Volume 17 (2004): Plant Mitochondria: From Genome to Function**, edited by David Day, A. Harvey Millar and James Whelan, from Australia. Fourteen chapters, 325 pp, Hardcover, ISBN: 978-1-4020-2399-6, Softcover ISBN 978-90-481-6651-0, eBook ISBN 978-1-4020-2400-9 [http://www.springer.com/life+sciences/cell+biology/book/978-1-4020-2399-6]
- **Volume 16 (2004): Respiration in Archaea and Bacteria: Diversity of Prokaryotic Respiratory Systems,** edited by Davide

Zannoni, from Italy. Thirteen chapters, 310 pp, Hardcover ISBN 978-14020-2002-5, Softcover ISBN 978-90-481-6571-1, eBook ISBN 978-1-4020-3163-2 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-2002-5]

- **Volume 15 (2004): Respiration in Archaea and Bacteria: Diversity of Prokaryotic Electron Transport Carriers**, edited by Davide Zannoni, from Italy. Thirteen chapters, 350 pp, Hardcover ISBN 978-1-4020-2001-8, Softcover ISBN 978-90-481-6570-4 (no eBook at this time) [http://www.springer.com/life+sciences/biochemistry+%26+biophysics/book/978-1-4020-2001-8]
- **Volume 14 (2004): Photosynthesis in Algae**, edited by Anthony W. Larkum, Susan Douglas and John A. Raven, from Australia, Canada and UK. Nineteen chapters, 500 pp, Hardcover ISBN 978-0-7923-6333-0, Softcover ISBN 978-94-010-3772-3, eBook ISBN 978-94-007-1038-2 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-6333-0]
- **Volume 13 (2003): Light-Harvesting Antennas in Photosynthesis**, edited by Beverley R. Green and William W. Parson, from Canada and USA. Seventeen chapters, 544 pp, Hardcover ISBN 978-07923-6335-4, Softcover ISBN 978-90-481-5468-5, eBook ISBN 978-94-017-2087-8 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-6335-4]
- **Volume 12 (2003): Photosynthetic Nitrogen Assimilation and Associated Carbon and Respiratory Metabolism,** edited by Christine H. Foyer and Graham Noctor, from UK and France. Sixteen chapters, 304 pp, Hardcover ISBN 978-07923-6336-1, Softcover ISBN 978-90-481-5469-2, eBook ISBN 978-0-306-48138-3 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-6336-1]
- **Volume 11 (2001): Regulation of Photosynthesis,** edited by Eva-Mari Aro and Bertil Andersson, from Finland and Sweden. Thirty-two chapters, 640 pp, Hardcover ISBN 978-0-7923-6332-3, Softcover ISBN 978-94-017-4146-0, eBook ISBN 978-0-306-48148-2 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-6332-3]
- **Volume 10 (2001): Photosynthesis: Photobiochemistry and Photobiophysics,** authored by Bacon Ke, from USA. Thirty-six chapters, 792 pp, Hardcover ISBN 978-0-7923-6334-7, Softcover ISBN 978-0-7923-6791-8, eBook ISBN 978-0-306-48136-9 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-6334-7]
- **Volume 9 (2000): Photosynthesis: Physiology and Metabolism,** edited by Richard C. Leegood, Thomas D. Sharkey and Susanne von Caemmerer, from UK, USA and Australia. Twenty-four chapters, 644 pp, Hardcover ISBN 978-07923-6143-5, Softcover ISBN 978-90-481-5386-2, eBook ISBN 978-0-306-48137-6 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-6143-5]
- **Volume 8 (1999): The Photochemistry of Carotenoids,** edited by Harry A. Frank, Andrew J. Young, George Britton and Richard J. Cogdell, from USA and UK. Twenty chapters, 420 pp, Hardcover ISBN 978-0-7923-5942-5, Softcover ISBN 978-90-481-5310-7, eBook ISBN 978-0-306-48209-0 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-5942-5]
- **Volume 7 (1998): The Molecular Biology of Chloroplasts and Mitochondria in *Chlamydomonas***, edited by Jean David Rochaix, Michel Goldschmidt-Clermont and Sabeeha Merchant, from Switzerland and USA. Thirty-six chapters, 760 pp, Hardcover ISBN 978-0-7923-5174-0, Softcover ISBN 978-94-017-4187-3, eBook ISBN 978-0-306-48204-5 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-5174-0]
- **Volume 6 (1998): Lipids in Photosynthesis: Structure, Function and Genetics**, edited by

Paul-André Siegenthaler and Norio Murata, from Switzerland and Japan. Fifteen chapters, 332 pp. Hardcover ISBN 978-0-7923-5173-3, Softcover ISBN 978-90-481-5068-7, eBook ISBN 978-0-306-48087-4 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-5173-3]

- **Volume 5 (1997): Photosynthesis and the Environment,** edited by Neil R. Baker, from UK. Twenty chapters, 508 pp, Hardcover ISBN 978-07923-4316-5, Softcover ISBN 978-90-481-4768-7, eBook ISBN 978-0-306-48135-2 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-4316-5]
- **Volume 4 (1996): Oxygenic Photosynthesis: The Light Reactions**, edited by Donald R. Ort and Charles F. Yocum, from USA. Thirty-four chapters, 696 pp, Hardcover ISBN 978-0-7923-3683-9, Softcover ISBN 978-0-7923- 3684–6, eBook ISBN 978-0-306-48127-7 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-3683-9]
- **Volume 3 (1996): Biophysical Techniques in Photosynthesis**, edited by Jan Amesz and Arnold J. Hoff, from The Netherlands. Twenty-four chapters, 426 pp, Hardcover ISBN 978-0-7923-3642-6, Softcover ISBN 978-90-481-4596-6, eBook ISBN 978-0-306-47960-1 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-3642-6]
- **Volume 2 (1995): Anoxygenic Photosynthetic Bacteria**, edited by Robert E. Blankenship, Michael T. Madigan and Carl E. Bauer, from USA. Sixty-two chapters, 1331 pp, Hardcover ISBN 978-0-7923-3682-8, Softcover ISBN 978-0-7923-3682-2, eBook ISBN 978-0-306-47954-0 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-3681-5]
- **Volume 1 (1994): The Molecular Biology of Cyanobacteria**, edited by Donald R. Bryant, from USA. Twenty-eight chapters, 916 pp, Hardcover, ISBN 978-0-7923-3222-0, Softcover ISBN 978-0-7923-3273-2, eBook ISBN 978-94-011-0227-8 [http://www.springer.com/life+sciences/plant+sciences/book/978-0-7923-3222-0]

Further information on these books and ordering instructions are available at http://www.springer.com/series/5599. Front matter of volumes 1–25 can also be found at <http://www.life.uiuc.edu/govindjee/photosynSeries/ttocs.html>.

Special 25 % discounts are available to members of the International Society of Photosynthesis Research, ISPR http://www.photosynthesisresearch.org/. See http://www.springer.com/ispr.

## Future Advances in Photosynthesis and Respiration and Other Related Books

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

- *Photosynthesis and Climate Change* (working title) (Editor Joy K. Ward)
- *Cyanobacteria* (Editor Donald Bryant)
- *Leaf Photosynthesis* (Editors William W. Adams III, Ichiro Terashima)
- *Photosynthesis in Algae* (Editors Anthony Larkum and Arthur Grossman)
- *Global Photosynthesis* (Editors Lianhong Gu et al.)
- *Plant Respiration: Metabolic Fluxes and Carbon Balance* (Editors Guillaume Tcherkez, Jaleh Ghashghaie)

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

Algae, Cyanobacteria: Biofuel and Bioenergy
Artificial Photosynthesis
ATP Synthase: Structure and Function
Bacterial Respiration II
Carotenoids II
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
Plant Respiration II

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

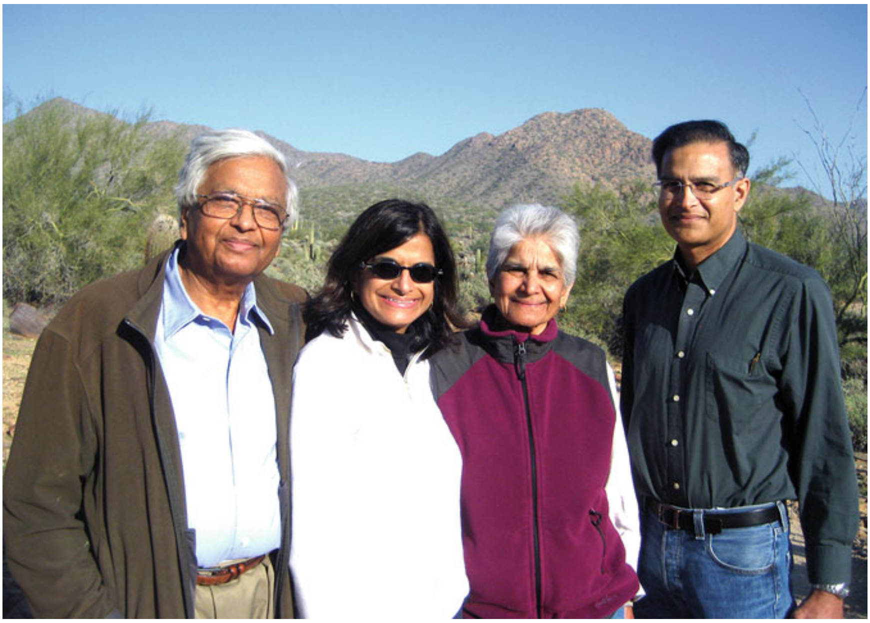
We take this opportunity to thank and congratulate Kouki Hikosaka and his coeditors Ülo Niinemets and Niels Anten for their outstanding editorial work; they have done a fantastic job, not only in editing but also in organizing this book for all of us and for their highly professional dealing with the reviewing process. We thank all 25 authors of this book (see the contributor list); without their authoritative chapters, there would be no such volume. We give special thanks to Manjusha Nalamolu and S. Bhuvanalakshmi of SPi Global, India, for directing the typesetting of this book; their expertise have been crucial in bringing this book to completion. We owe thanks to Jacco Flipsen, Andre Tournois, Corina VanderGiessen and Ineke Ravesloot (of Springer) for their friendly working relation with us that led to the production of this book.

**January 1, 2016**

**Thomas D. Sharkey**
Department of Biochemistry
and Molecular Biology
Michigan State University
East Lansing, MI 48824, USA
tsharkey@msu.edu

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

# Series Editors



*Left to right*: Govindjee, Anita, Rajni, and Sanjay. Photo was taken in December 2014 in Arizona

**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, botany and zoology) and M.Sc. (botany, plant physiology) in 1952 and 1954, from the University of Allahabad. He studied "Photosynthesis" at the UIUC, under two giants in the field, 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 (prompt and delayed fluorescence and thermoluminescence), 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 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 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." 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 (1956), Fulbright senior lecturer (1997), and Fulbright specialist (2012); 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; and recipient of the Communication Award of the International Society of Photosynthesis Research, 2007; and of the Liberal Arts and Sciences Lifetime Achievement Award of the UIUC, (2008). Further, Govindjee has been honored **(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; **(3)** in 2012, through Volume 34 of this series *Photosynthesis - Plastid Biology, Energy Conversion and Carbon Assimilation*, edited by Julian Eaton-Rye, Baishnab C. Tripathy, and one of us (TDS); it was dedicated to him, celebrating his academic career; and (**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. An additional honor was the celebration of his birthday in Třeboň, the Czech Republic (O. Prasil [2014] Govindjee, an institution, at his 80th [or rather 81st] birthday in Třeboň in October, 2013: A pictorial essay. Photosynth Res **122**: 113–119). His unique teaching of the Z-scheme of photosynthesis, where students act as different intermediates, was recently published (P.K. Mohapatra and N.R. Singh [2015] Teaching the Z-Scheme of electron transport in photosynthesis: a perspective. Photosynth Res **123**:105–114).

Govindjee is coauthor of a classic and popular book *Photosynthesis* (John Wiley, 1969; available free on his web site); he is editor (or coeditor) 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 being 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 website at http://www.life.illinois.edu/govindjee.

Tom Sharkey, October 2012 in Taiwan

**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, USA. After 2 years as a research technician, Tom entered a Ph.D. program in the Department of Energy Plant Research Laboratory at Michigan State University under the mentorship of Klaus Raschke and finished in 1979. His 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. 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, 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 important papers on the biochemical regulation of isoprene synthesis. Tom has coedited 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 has been co-series editor of this series since Volume 31.

# Contents

## Part II: Physiological Processes from Leaves to Canopies

## Part III: Whole-plant Processes in Leaf Canopies



## Part IV: Assessments of Vegetation Functioning

## Part V: Application to Ecological and Evolutionary Processes

# Preface

A plant canopy, a collection of leaves, is an ecosystem-level unit of photosynthesis that assimilates carbon dioxide and exchanges other gases and energy with the atmosphere in a manner highly sensitive to ambient conditions including atmospheric carbon dioxide and water vapor concentrations, light and temperature, and soil resource availability. In addition to providing carbon skeletons and chemical energy for most of the living organisms, these key canopy functions affect global climate through modification of atmospheric carbon dioxide concentration and through altering surface albedo. This interaction, the climate-carbon cycle feedback, is one of the most uncertain processes for projection of future global climate.

Rapid increase in human population in combination with global change poses major challenges for human life on Earth. The population increase drives the need for enhanced food and (renewable) energy supply, while global change potentially entails negative impacts on plant productivity. Carbon dioxide assimilation by plant canopies is one of the most important determinants of food and energy crop yields. Thus, understanding canopy functioning is indispensable for establishing sustainable agricultural practices and for breeding of crops that would have higher productivity under future climate.

Canopy photosynthesis is an integration of various physical, chemical, and biological processes extending from molecular, cellular, and organ-level processes to turbulent transport. About a hundred years ago, Peter Boysen Jensen first determined canopy photosynthesis of a plant stand – though it was a tiny stand established in a small pot and demonstrated that the canopy photosynthetic rate is not simply a product of the leaf photosynthetic rate and the number of the leaves. He correctly argued that canopy photosynthesis is influenced not only by conditions above the canopy but also by canopy structure and by heterogeneity of the microclimate and of leaf traits within the canopy. Masami Monsi, Toshiro Saeki, Cornelis T. de Wit, John L. Monteith, William G. Duncan, and other early researchers have succeeded in integrating these complex processes into mathematical models capable of simulating canopy photosynthetic rate under changing environmental conditions. Advances in photosynthesis physiology and modeling studies improved our understanding and prediction of environmental responses of leaf-level gas exchange rates. In particular, modeling of Rubisco and electron transport processes (Graham D. Farquhar, Susanne von Caemmerer, and Joseph A. Berry) and linking photosynthesis and stomatal processes (J. Timothy Ball, Ian E. Woodrow, and Joseph A. Berry) were the key milestones that made it possible to simulate carbon dioxide responses of photosynthesis. These models are now essential parts of larger models for prediction and simulation of crop production, climate change, and regional and global carbon dynamics.

Advances in molecular techniques have helped clarify molecular mechanisms of morphogenesis and regulation in leaf canopies, though there still remain many uncertainties. On the other hand, meteorological studies have permitted estimates of gas and energy exchange in vegetation at a landscape scale. Remote sensing techniques have enabled us to evaluate vegetative functions at a global scale. One of the main challenges lies in quantitatively scaling between these levels of organization. Systems biology is evolving to address this but tends to regard the cellular level as the upper limit. There is a need to further develop this well beyond the current levels.

The development of leaf canopy studies has contributed to deeper understanding of other ecological phenomena. Photosynthesis provides both the energy and the carbon for growth, reproduction and other plant functions, while regulation of transpiration plays an important role in the water and temperature balance of plants. Plant gas exchange traits and their response to different growth conditions therefore have important adaptive values. Modeling of canopy gas exchange, thus, plays an increasingly important role in evolutionary ecological research. A particular issue of interest here has been competition for light between individuals as well as between species as this is one of the most important constraints influencing population density, stand biomass, species composition, and, in turn, biodiversity in plant communities. Canopy photosynthesis models have been a good tool to analyze light interception by individuals or by species in plant communities.

This book describes our current knowledge of canopy photosynthesis that has accumulated over the last hundred years since the pioneering study of P. Boysen Jensen. The book provides a comprehensive analysis of plant canopy physiology, ecology, and physics with emphasis on predictive modeling techniques. The book is divided into five parts covering the hierarchy of canopy processes in time and space. Two chapters in Part I discuss the basic physical processes on light attenuation and energy transfer in plant canopies, while three chapters in Part II deal with the principle mechanisms of leaf gas-exchange regulation and the patterns and mechanisms of variations in leaf traits. Three chapters in Part III focus on whole-plant processes in plant canopies. Part IV (in four chapters) describes how vegetation functions are assessed by modeling, eddy-covariance techniques, and remote sensing and forest inventory. Finally, three chapters in Part V discuss the relationships between canopy photosynthesis and other vegetation processes in plant stands.

The book is designed primarily for graduate students and beginning scientists interested in measuring and modeling vegetation performance, and we hope that it will help in raising a new generation of scientists who are fascinated by the challenge of understanding the varied functions of the canopy of plants. Thus, each chapter of the book describes the basic background of the specific topic and provides equations that are indispensable for its quantitative understanding. In fact, we believe that readers would even be able to construct their own canopy model based on the equations provided in this book. On the other hand, we hope that this synthesis is also beneficial to the mentors of these students and ecologists, foresters, crop physiologists, and agronomists broadly interested in improving crop productivity and simulating vegetation-climate feedbacks. We are of the opinion that being involved in canopy research is a highly stimulating, perspective-widening, and often an exciting experience.

All the chapters were peer reviewed by the editors, authors and/or ad hoc reviewers. We, the editors, especially thank all the reviewers and acknowledge by name the reviewers: Kohei Koyama, Martijn Slot, Kaoru Kitajima, Hisae Nagashima, and Yusuke Onoda. We also thank Govindjee and Tom Sharkey, series editors of *Advances in Photosynthesis and Respiration*, for their continuous advice and support through the preparation of this book.

We hope that this book will be useful not only to beginning scientists, in the field of canopy photosynthesis, but to teachers and researchers alike who are interested in solving the problem of plant productivity in the world for the benefit of all.

**Kouki Hikosaka**
Sendai, Japan

**Ülo Niinemets**
Tartu, Estonia

**Niels P.R. Anten**
Wageningen, The Netherlands

# The Editors

Kouki Hikosaka (*center*) with his wife Hisae Nagashima (*left*), who is a plant ecologist and a reviewer, and their daughter Romi (*right*)

**Kouki Hikosaka** was born on January 25, 1968, in Odate, Akita, Japan. He was a high jumper when he was a student and the best record was 2m13cm in 1989. He received his bachelor of science degree in 1990 for nitrogen allocation between leaves in a plant canopy under the guidance of Professor Tadaki Hirose in the Department of Biology, Faculty of Science, Tohoku University, Japan. Subsequently, he studied nitrogen allocation not only between but also within leaves as a Ph.D. student under the guidance of Dr. Ichiro Terashima (a contributor to this volume) and Professor Sakae Katoh in the Department of Botany, Graduate School of Science, the University of Tokyo, Japan. He used a vine grown horizontally and manipulated the light environment of each leaf to assess effects of leaf age and light environment on leaf nitrogen content and photosynthetic characteristics separately. He constructed a mathematical model of optimal nitrogen partitioning in the photosynthetic apparatus and tested the optimality in actual plants. In addition, he studied photosynthetic nitrogen use efficiency, which is a key physiological trait for leaf economics spectrum, in species belonging to different functional groups and found that nitrogen allocation to Rubisco and Rubisco use efficiency vary among species. After receiving his Ph.D. in 1995, he returned to Tohoku University as an assistant professor in the laboratory of Professor Tadaki Hirose. Currently he is professor in the Graduate School of Life Sciences, Tohoku University.

His interests are diverse in scales from molecules to the globe, but always related to ecological significance of plant functions. For biochemical levels, he has investigated how parameters of photosynthesis models respond to environmental change and how such changes are related to the improvement of resource use efficiency in biomass production under changing environment. For example, he has found that leaves alter the balance between carboxylation and regeneration of RuBP depending on growth temperature, which contributes to optimization of nitrogen use. He has also found that leaves, including canopy leaves in a deciduous forest, change temperature dependence of RuBP carboxylation rate depending on growth temperature, which causes a shift of optimal temperature of photosynthesis. For canopy levels, he has extended the optimal nitrogen allocation theory to leaf dynamics and has studied leaf dynamics in actual plants. He has also incorporated the game theory to canopy photosynthesis model to understand the role of light competition with neighbors in canopy productivity. Recently these two theories were combined in collaboration with Professor Niels Anten (coeditor of this volume). For population and community levels, he has analyzed photosynthetic production of an individual or species as the product of resource acquisition efficiency and resource use efficiency and is attempting to understand the roles of plant functional traits in competition and coexistence in a plant community. For global issues, he is attempting to improve the accuracy of the canopy photosynthesis scheme in global carbon flux simulations. He studies environmental response (including elevated $CO_2$ concentrations) and interspecific variation in parameters in canopy photosynthesis models with Dr. Akihiko Ito (a contributor in this volume) and other collaborators.

Ülo Niinemets after giving the inaugural lecture (Oratie) on the occasion of his appointment to F. C. Donders Chair at the Utrecht University in Autumn 2007

**Ülo Niinemets** was born on March 19, 1970, in Tartu, Estonia. In 1996, he was awarded a Ph.D. in plant ecophysiology from the University of Tartu, Estonia (adviser: Prof. Olevi Kull). At the time of his Ph.D., in the newly independent Estonia, the availability of research equipment was extremely limited, and his Ph.D. was focused on structural factors on shade tolerance of forest trees, a work that did not require much equipment. One of the main conclusions from this work was that foliage structure was a key controlling factor in determining species shade tolerance. As a broader message from this work, guiding his future studies was that structural factors are often as significant in affecting leaf photosynthetic capacity as photosynthetic potential of single cells. With all the new sophisticated equipment becoming available, researchers increasingly tend to forget structure, although it is central in understanding plant performance under stressful environment in the field.

As the research environment improved in independent Estonia, his research focus gradually shifted to more physiologically oriented work, especially on tree acclimation to within-canopy gradients. He initiated the Estonian forest tree acclimation project in 1994. Within this project, tall scaffoldings of 27 m were erected in a mixed deciduous forest in south-eastern Estonia, and acclimation of tree foliage photosynthetic characteristics, morphology, anatomy and chemistry to within-canopy light gradients were extensively investigated by him and his coworkers over several years. This work has resulted in detailed understanding of the overall extent of photosynthetic acclimation, structural, chemical, and physiological controls of acclimation and acclimation time constants. He is currently chair of the Department of Plant Physiology at the Estonian University of Life Sciences where his team focuses on quantification and predictive modeling of plant carbon gain and trace gas exchange from genes to leaves and from leaves to ecosystem, landscape, and biome scales under globally changing climates.

Apart from the work in Estonia, he has been very active internationally. He has conducted postdoctoral work at the University of Bayreuth, Germany, where he initiated the development of process-based isoprenoid emission models; at the University of Antwerp, Belgium, where he studied physiological controls of species invasions; and at the Centro di Ecologia Alpina, Trento, Italy, where he investigated structural controls of mesophyll diffusion conductance. His international faculty appointments include: Erskine Fellow (2002, Canterbury

University, New Zealand), annual G. P. Wilder Chair (2006–2007, University of Hawaii, U.S.A.), and F. C. Donders Chair (Utrecht University, the Netherlands). He has collaborated with more than 550 scientists from 44 countries and has (co-)authored more than 250 international articles and book chapters. He currently serves the community as an editor or as editorial board member of international plant science journals such as *Tree Physiology, Oecologia, Frontiers in Plant Science, AoB Plants, Journal of Plant Research,* and *Plant, Cell and Environment and* Springer *Tree Physiology* book series as well as a board member of several international research programs and science policy committees such as the Scientific Committee for Life, Environmental and Geo Sciences (LEGS) of Science Europe.

Niels Anten enjoying a cold autumn morning in Limburg in the south of The Netherlands

**Niels P.R. Anten** was born on May 14, 1966, in Bukumbi, Tanzania. He spent a large part of his childhood in Tanzania and Nepal and enjoyed the spectacular nature of those countries, but also became acquainted with their challenges in sustainably producing food. Probably not surprisingly he then spent a career zigzagging between crop science and ecology of natural plant systems. Niels completed his masters, in 1990, in Tropical Crop Science at Wageningen University, the Netherlands, where among other things he had the privilege to do his thesis on modeling cocoa growth with Prof. Jan Goudriaan (author of Chap. 1) and Prof. Marius Wessel. He then went on to do a Ph.D. in plant ecology at Utrecht University under the guidance of Prof. Marinus J.A. Werger and Prof. Ernesto Medina (IVIC, Venezuela) studying nitrogen use at the canopy level of $C_3$ and $C_4$ plants in Venezuela. In 1995, he obtained his Ph.D. with honors. He then went on to do a postdoc with Prof. Tadaki Hirose at Tohoku University in Japan, studying competition and species coexistence in Japanese grasslands. Here he also started a close collaboration with Prof. Kouki Hikosaka (coeditor of this book). After Japan, Prof. David Ackerly invited Niels to do a postdoc with him at Stanford University, USA, studying the sustainable harvesting of non-timber forest products in Mexico. After another stay at Tohoku University, in 2002, he obtained a tenured position at Utrecht University, where he stayed until 2012, when he took his current position as professor in Crop and Weed Ecology at the Centre of Crop Systems Analysis, Wageningen University.

Niels' main research line is the analysis of how emerging properties at the level of natural or agricultural plant communities, e.g., vegetation structure, productivity and species diversity, arise from basic physiological processes and plant functional traits. He pursues this scaling question through a combination of computer modeling, experiments and field observations and builds this work from basic optimization and game theories, as well as from disciplines of engineering. He uses this approach not only to understand the ecological interaction that drives the functioning of natural plant communities but increasingly also to see how this, in turn, can be applied to (semi-)agricultural systems. Based on game theory, he has worked with the idea that natural selection tends to lead to plant communities that are non-optimal in the sense of maximum per unit land area production, a so-called tragedy of the commons. This in turn, he hopes, would provide ideas for crop breeding or crop management. Similarly, newer concepts about diversity effects on plant community functioning in natural systems may provide ideas for highly productive diverse cropping