The Leaf: A Platform for Performing Photosynthesis

Medal (note the leaf scroll at the top) received by W. Adams at the Missouri State Science Fair. The backdrop of leaves includes those from (beginning in the upper left, moving clockwise) Gambel oak (*Quercus gambelii*), yellow twig dogwood (*Cornus sericea*), Virginia creeper (*Parthenocissus quinquefolia*), honey locust (*Gleditsia triacanthos*), Oregon grape holly (*Mahonia aquifolium*), and mullein (*Verbascum thapsus*). (Photograph by Melanie S. Adams)

Advances in Photosynthesis and Respiration
Including Bioenergy and Related Processes

VOLUME 44

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 these areas. Virtually all life on our planet Earth ultimately depends on photosynthetic energy capture and conversion to energy-rich organic molecules that are then used through respiration for fueling metabolism, growth, and reproduction. Photosynthesis is also an energy source for food, fuel, and fiber. Photosynthesis is ultimately the source of almost all Bioenergy on Earth, including fossil fuels. The fuel and energy uses of photosynthesized products and processes have become an important area of study, with competition between food and fuel leading to a 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, respiration, and related energy processes. The purpose of this series is to explore 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. Beginning in 2018, Govindjee has become emeritus, though still very interested in the success of the series. Julian Eaton-Rye has joined as co-series editor, welcome Julian.

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

The Leaf: A Platform for Performing Photosynthesis

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 44: The Leaf: A Platform for Performing Photosynthesis

After 43 volumes in this series, our good friend and colleague Govindjee has stepped away from his duties as series editor. This is the first volume since his retirement, but even so, volumes in this series will continue to be shaped by Govindjee's enthusiasm for all things photosynthesis and his care and dedication to this series. Julian J. Eaton-Rye will be co-series editor beginning with this volume. It is hoped that our new team of series editors will continue to identify new topics that would benefit from an edited volume and editors that will take on the task of coordinating a volume that will serve the photosynthesis community.

Our understanding of photosynthesis can be organized in many different ways. The topics of books in this series reflect this variety of approaches. Some books are focused on a type of organism, others on specific processes. In this volume, the focus is on understanding relationships between photosynthesis and leaves, the primary site of photosynthesis in most land plants. The leaf is a particularly convenient level of organization because leaves are critical for light capture, carbon uptake, carbon processing, and carbon export from the photosynthetic bacterial endosymbiont (chloroplast) to other parts of the plant used for food, fuel, and fiber. The understanding of leaf-level photosynthesis is a critical part of models that look to understand regional- and global-scale photosynthesis.

The plant leaf is like a solar panel. The ability to intercept light is dependent on only two dimensions; leaf depth plays little role in light capture. Within this two-dimensional structure, large amounts of water must be distributed throughout, and at the same time, sugars and other end products must be collected from all parts of the leaf and provided to the rest of the plant. The challenges of this plumbing have been under intensive study lately making this an opportune time for a book that tackles this important area of research.

Leaf shape and display are important for how leaves cope with their environment. Internal architecture is critical for maximizing light collection and carbon dioxide uptake. Several chapters in this book describe important leaf architecture considerations and mechanisms by which leaf architecture is determined.

This volume joins volume 42 (*Canopy Photosynthesis: From Basics to Applications*, editors Kouki Hikosaka, Ülo Niinemets, and Niels P.R. Anten) in describing the study of photosynthesis at a particular organizational scale. Together, these books provide a solid foundation for understanding how the physical environment can affect how plants develop and display their resources to maximize photosynthesis.

Authors of Volume 44

We note with great pride that the current volume is truly an international book; it has authors from the following 12 countries: Australia (4), Austria (1), Brazil (1), Canada (1), Chile (1), China (1), Czech Republic (1), France (1), Japan (19), Spain (6), UK (5), and USA (22).

There are 61 authors (including the 3 editors) who are experts in the field of leaf-level photosynthesis. Alphabetically (by last names), they are Anunción **A**badía, Javier Abadía, William W. Adams III, Evgenios Agathokleous, Fransisca C. Anozie, Brian Ayre, Anne M. **B**orland, Federica Brandizzi, Timothy J. Brodribb, Thomas N. Buckley, Marcelo L. **C**ampos, Francisco Javier Cano, Marc Carriquí, Rafael E. Coopman, Asaph B. Cousins, Barbara **D**emmig-Adams, Norikazu **E**guchi, Jaume **F**lexas, Irwin N. Forseth, Jr., Takashi Fujita, Ryo Funada, Brigitte **G**ontero, Kouki **H**ikosaka, Tadashi Hirasawa, Gregg A. Howe, Rongbin Hu, Natalia Hurtado-Castano, Kihachiro **K**ikuzawa, Sang-Jin Kim, Yong-Sig Kim, Mitsutoshi Kitao, Takayoshi Koike, Tracy **L**awson, Martin J. Lechowicz, Alistair Leverett, Stephen C. **M**aberly, Ian T. Major, Yusuke Mizokami, Fermín Morales, Erik T. **N**ilsen, Riichi **O**guchi, Yusuke Onoda, Andrej **P**avlovič, Stephanie K. Polutchko, Luciana **R**enna, Thomas D. **S**harkey, Jared J. Stewart, Mitsutaka **T**aniguchi, Ichiro Terashima, Danny Tholen, Michael F. Thomashow, Hirokazu Tsukaya, Robert Turgeon, Yin **W**ang, Makoto Watanabe, Yoko Watanabe, Sarathi M. Weraduwage, Ian J. Wright, Dongliang **X**iong, Xiaohan **Y**ang, and Yuki Yoshida. We are grateful for their efforts in making this important volume.

Our Books

We list below information on the 43 volumes that have been published thus far (see http://www.springer.com/series/5599 for the series website). Electronic access to individual chapters depends on subscription (ask your librarian), but Springer provides free downloadable front matter as well as indexes for all volumes. The available websites of the books in the series are listed below.

- **Volume 43 (2018)** ***Plant Respiration: Metabolic Fluxes and Carbon Balance***, Edited by Guillaume Tcherkez from Australia and Jaleh Ghashghaie from France. Fourteen chapters, 302 pp, Hardcover ISBN 978-3-319-68701-8, eBook ISBN 978-3-319-68703-2 [http:// http://www.springer.com/us/book/9783319687018]
- **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 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]

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- **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]
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- **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]
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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: Katie M. Becklin, Joy K. Ward, and Danielle A. Way)
- *Cyanobacteria* (Editor: Donald Bryant)
- *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 and cyanobacteria: biofuel and bioenergy
Artificial photosynthesis
ATP synthase: structure and function
Bacterial respiration 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

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 Julian Eaton-Rye (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 one or both of us.

We take this opportunity to thank and congratulate William Adams and Ichiro Terashima for their outstanding editorial work and for their highly professional dealing with the reviewing process; they have indeed done a fantastic job, not only in editing but also in organizing this book for all of us. We thank all 61 authors of this book (see the list given earlier and on the following pages); without their authoritative chapters, there would be no such volume. We give special thanks to Mr. Joseph Daniel and Mrs. Rathika Ramkumar of SPi Global, India, for directing the typesetting of this book; their expertise has been crucial in bringing this book to completion. We owe Jacco Flipsen, Andre Tournois, and Ineke Ravesloot (of Springer) thanks for their friendly working relation with us that led to the production of this book.

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Series Editors

A 2017 informal photograph of Govindjee (right) and his wife Rajni (left) in Champaign-Urbana, Illinois. (Photograph by Dilip Chhajed)

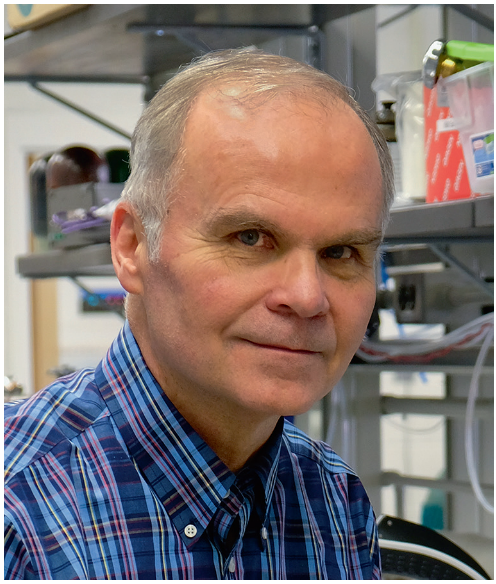
The founding series editor **Govindjee**, who uses one name only, was born on October 24, 1932, in Allahabad, India. Since 1999, he has been professor emeritus of biochemistry, biophysics, and plant biology at the University of Illinois at Urbana-Champaign (UIUC), Urbana, IL, USA. He obtained his B.Sc. (chemistry, botany. and zoology) and M.Sc. (botany, plant physiology) in 1952 and 1954, from the University of Allahabad. He learned his plant physiology from Shri Ranjan, who was a student of Felix Frost Blackmann (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 Ph.D., 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*. 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; 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 many times: (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 J. 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, which was followed by the 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 J. 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 award of the prestigious Prof. B.M. Johri Memorial Award of the Society of Plant Research, India. In 2018, *Photosynthetica* published a special issue to celebrate his 85th birthday (editor, Julian J. Eaton-Rye; now co-series editor for this book 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 the classic and highly popular book *Photosynthesis* (with E.I. Rabinowitch, 1969) and of the historical book *Maximum Quantum Yield of Photosynthesis: Otto Warburg and the Midwest Gang* (with K. Nickelsen, 2011). He is editor (or co-editor) of many books including *Bioenergetics of Photosynthesis* (1975); *Photosynthesis*, two 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 website at http://www.life.illinois.edu/govindjee.



Photograph by Sean E. Weise, 2017

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. 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 co-edited 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 J. Eaton-Rye and Baishnab C. Tripathy) entitled *Photosynthesis*: *Plastid Biology*, *Energy Conversion and Carbon Assimilation*. Tom has been co-editor of this series since volume 31.

Julian J. Eaton-Rye is a professor in the Department of Biochemistry at the University of Otago, New Zealand. He received his undergraduate degree in botany from the University of Manchester in the UK in 1981 and his Ph.D. from the University of Illinois in 1987, where he worked with Govindjee on the role of bicarbonate in the regulation of electron transfer through photosystem II. Before joining the Biochemistry Department at Otago University in 1994, he was a postdoctoral researcher focusing on various aspects of photosystem II protein biochemistry with Professor Norio Murata at the National Institute of Basic Biology in Okazaki, Japan, with Professor Wim Vermaas at Arizona State University, and with Dr. Geoffrey Hind at Brookhaven National Laboratory. His current research interests include structure-function relationships of photosystem II proteins both in biogenesis and electron transport as well as the role of additional protein factors in the assembly of photosystem II. Julian has been a consulting editor for the *Advances in Photosynthesis and Respiration* series since 2005, and he edited volume 34 (with Baishnab C. Tripathy and Thomas D. Sharkey) entitled *Photosynthesis*: *Plastid Biology*, *Energy Conversion and Carbon Assimilation*. He is also an associate editor for the *New Zealand Journal of Botany* and an associate editor for the Plant Cell Biology section of *Frontiers in Plant Science*. He edited a Frontiers Research Topic on the *Assembly of the Photosystem II Membrane-Protein Complex of Oxygenic Photosynthesis* (with Roman Sobotka) in 2016, and this is available as an eBook [ISBN 978-2-88945-233-0]. Julian has served as the president of the New Zealand Society of Plant Biologists (2006–2008) and as president of the New Zealand Institute of Chemistry (2012). He has been a member of the International Scientific Committee of the Triennial International Symposium on Phototrophic Prokaryotes (2009–2018) and is currently the secretary of the International Society of Photosynthesis Research.

Contents

Preface: The Importance of Leaves to Life and Humanity

Whether looking down on our planet from space or up at the sky from its surface, blue is the dominant color in the absence of condensed water vapor. The primary color of life on Earth, however, is green due to the ubiquitous presence of leaves as the drivers of primary productivity on land and in shallow aquatic habitats. Given the order of magnitude loss of energy through each transformation as it makes its way through a food web, the overwhelming prevalence of primary producers is inevitable. As Richard Dawkins (2009) pointed out, "It is no accident that we see green almost wherever we look … Without green plants to outnumber us at least ten to one there would be no energy to power us."

Following the emergence of leaves between 380 and 360 million years ago (Kenrick and Crane 1997; Boyce and Knoll 2002; Osborne et al. 2004a, b), there was an explosion in diversity of leaf shape and size as plants evolved to fill virtually every available niche. At the heart of that variation in leaf form is its functionality as an organ optimized for (1) intercepting and harvesting photons from sunlight to fuel the energization of electrons in photosynthetic light harvesting and electron transport, (2) allowing the inward diffusion of carbon dioxide from the atmosphere in order to convert the energized electrons into a relatively stable chemical form (reduced sugars), (3) passive and active movement of photosynthate (primarily sugars) into foliar pipelines (sieve elements of the phloem) that provide for the distribution of these energy-rich, reduced carbon compounds throughout the plant, (4) distribution of water and nutrients through pipelines (tracheary elements of the xylem) within the leaf, and (5) exercising considerable control over the transpirational loss of water molecules to the atmosphere. Three key features that allowed these specialized organs to arise and proliferate include the ability to deposit a waxy cuticle on the outside surface of the epidermis virtually impenetrable to water loss from the water-laden tissue, a vascular system capable of transporting fluids into and out of the leaf, and stomatal pores with guard cells responsive to internal and external cues permitting regulation of water efflux and carbon dioxide influx. The mere presence of stomata, however, was insufficient to permit evolution of broad lamina for intercepting sunlight; only with development of sufficient stomatal numbers that could facilitate a rate of transpirational cooling capable of preventing overheating and death did large, flat leaves become abundant concomitant with declining atmospheric CO_2 concentrations (Beerling et al. 2001; Beerling 2005).

As the key to mitigation of the second law of thermodynamics, thereby permitting the majority of life on earth to persist, the creation of chemically stored energy through the process of photosynthesis has supplied the energy, molecular building blocks, and oxygen necessary for the evolution and proliferation of millions of species. Interestingly, leaves also comprise some of the most flammable components of the ecosystems in which these species coexist (e.g., grasslands, needles of conifer-dominated forests, leaves of *Eucalyptus*-dominated habitats, chaparral vegetation, etc.), with fire constituting a major driver responsible for the maintenance and even rejuvenation of such habitats (Bond and Keeley 2005; Keane et al. 2008; Bowman et al. 2009, 2014; de Groot et al. 2013). While leaves, as the organs that provide the platform for most of terrestrial photosynthesis, underpin the major land-based biomes (Field et al. 1998), their essential role in humanity's progression is no less remarkable.

Leaves provide the food, either directly through fruits, nuts, roots, grains, leaves, or other plant parts or secondarily through animals, saprophytes, microbes, etc. whose functioning depends on the solar energy harvested by plants, without which we could not survive. The rise of human civilization depended to a large extent on the development of domesticated crop plants (Chrispeels and Sadava 2003). The agricultural products of many of these crops are major sinks for the products of photosynthesis, but humans consume the leaves of quite a few species as well (cultivars of *Lactuca sativa* [lettuces], *Brassica* [cabbages, Brussels sprouts, kale, rapini, collard, turnip, and mustard greens], *Beta vulgaris* [chards], *Spinacia oleracea* [spinach], *Cichorium* [endive, radicchio], a variety of ferns, grape leaves, and a number of others) and use just as great a variety of leafy herbs to enhance the flavor, nutrition, and even aesthetic value of our cuisine (basil, bay laurel, chives, cilantro, dill, fennel, garlic, lavender, lemon grass, marjoram, a number of mints, onion, oregano, parsley, rosemary, tarragon, thyme, etc.). Moreover, the leaves of many grasses and other species serve as forage for our domesticated animals.

As important as leaves are in generating the food upon which we (and our fellow heterotrophs) rely to fuel our bodies, they have played an equally important role in providing the energy for civilization's development. The cellulose-infused, and thus energy-rich, products of photosynthesis (wood, peat, etc.) constituted a fuel source for fire used in cooking food (increasing the accessibility of energy and nutrients for uptake by our digestive system; Wrangham and Carmody 2010; Carmody et al. 2016), making fire-strengthened and ultimately glazed pottery, heating of habitations that could also bring light to the night, smelting of metal ores and the formation of metal-alloy implements, and melting of silica to form useful glass products (Hough 1932). The industrial revolution, fueled by fossil biofuels (and particularly the converted remains of plants in the form of coal that was laid down during the carboniferous era; Lee 2017), spurred technological innovation at an increasing rate (Fernihough and O'Rourke 2014; Nelsen et al. 2016). This led to generation of electricity, the lighting and heating of our businesses and dwellings, and the invention of electricity-powered machines and devices for any number of purposes. The tapping of the buried reserves of compact energy derived from photosynthetic products also yielded unprecedented changes in transportation, from steam-powered ships and trains to automobiles and, airplanes. Although the shift from renewable to fossil fuels transformed much of the developed world, between two and three billion people still rely on wood, charcoal, leftover biomass from agriculture, and plant biomass processed by livestock (dung) as a source of fuel for cooking and heating (Ekouevi and Tuntivate 2012; Zuzhang 2017). The use of such renewable biofuels may be laudable, but it can nonetheless have negative consequences for the environment (Draper 2011; Sawe 2012) and health of those who are exposed to excessive levels of indoor pollution (Fullerton et al. 2008; Nijhuis 2017).

Leaves also fuel the generation of many products that have proved useful to humans and contributed to the advancement of civilization. Wood has been and is fashioned into various useful implements (e.g., utensils, tools and handles for tools, pencils, and even jewelry); used to build houses, boats, furniture, railroads, fences, etc.; and pulped to make paper, cardboard, and paperboard for packaging, toilet paper and facial tissues, etc. Natural plant fibers (e.g., cotton, linen) are woven into clothing, blankets, etc. A number of leaves have been and are used directly, including those of a number of species that serve as thatching material for the protection of shelters from inclement weather or intense sunlight. The leaves of Spanish moss (*Tillandsia usneoides*), and especially their resilient, vascular strands, were used to stuff pillows, mattresses, and the upholstery of furniture (a sofa in the childhood home of the author was filled with this material). Leaves have also been woven into baskets, mats, boats, ropes (especially cordage made from the parallel veins of long monocotyledonous leaves), and other useful devices, fashioned into articles of clothing, and used in the preparation and serving of food. Where available, palm leaves have played a prominent role in many of these functions, and more specifically for the generation of manuscripts in India and southeast Asia.

The cultural importance of leaves has been immense. The leaves of the laurel tree (*Laurus nobilis*) held special significance to the ancient Greeks (the mythical god Apollo bore a crown of laurel leaves), branches of which were woven into wreaths and worn around the head as a symbol of achievement or ranking in society (e.g., for those athletes who triumphed in Olympic contests). Wreaths from other species (oak, olive, myrtle, grapevine, some herbaceous species) served as well in Greek, Roman, and some Native American groups. Laurel wreaths were often invoked to fete the founders of the USA (Chernow 2004, 2010) and, upon his death in early 1919, laurel wreaths were dropped from airplanes circling Theodore Roosevelt's residence and laurel branches lined his gravesite (Morris 2010). The use of honorific wreaths has persisted into some modern-day athletic competitions (e.g., Olympic Games, Boston Marathon), and the term laurel and its derivatives has continued to connote great accomplishment in the English language. For instance, as a noun, laurels refer to the achievements earned or accomplished for which one is recognized (it can also be used as a verb). Perhaps most notably, those who are honored for exceptional achievements are bestowed the title of laureate (e.g., Nobel Laureate, poet laureate). While it may be quite acceptable to rest on one's laurels at the end of a long and distinguished career, the phrase can take on a less than positive tenor should one cease to make contributions to an area at an earlier age!

The palm leaf has served as an important symbol to Christians. Furthermore, the use of a fig leaf to cover those things that some might find to be objectionable or embarrassing originated with the opening story of the Bible. The lotus (*Nelumbo nucifera*) leaf (not to be confused with water lily leaves) plays a prominent role in Indian culture and Hinduism (Kintaert 2010, 2011), while mango and banana leaves are made into garlands that adorn entryways to Hindu houses and used in Hindu religious rituals. Likely originating in the British Isles, the belief that a clover leaf with four leaflets (the leaves of which normally consist of only three) imbues the individual who finds or possesses such a leaf with good luck is widespread.

Leaves have played a major role in art and architecture. *Acanthus* leaves were depicted in friezes and other architectural accents on buildings erected by ancient Greeks and Romans. Likewise, leaf scroll is often used as a border or decorative accent (see frontispiece image). Leaf motifs also appear in and on artworks (e.g., paintings, statuary, pottery) or recurring on clothing (see the shirt worn by W. Adams in the photograph that accompanies his biography on p. XXXV), curtains, bedding, towels, wallpaper, etc. Even jewelry is fashioned in the shape of leaves or leaves in the abstract.

Some leaves have been important sources and drivers of commerce while also contributing to human suffering, social strife, political upheaval, and revolution. Tobacco (genus *Nicotiana*), used by native Americans for thousands of years, became a major trade commodity following European colonization of America. During the 1600s and 1700s, large quantities of tobacco leaves were exported to England, playing no small part in the economic development of the American colonies (Chernow 2010). This boon to the colonies, however, came at the horrendous cost of immeasurable suffering and death to the many enslaved Africans working the fields of this labor-intensive crop. Much suffering has also, of course, befallen those who use(d) tobacco for smoking, chewing, or snuffing. Such use is at the root of numerous diseases and deaths that affect not only the users but also society as a whole. It is estimated that the negative economic impact of tobacco exceeds US$500 billion per annum (Ekpu and Brown 2015).

The leaves of *Camellia sinensis*, an evergreen shrub from Asia, have been used by the Chinese to make tea for thousands of years. Tea also has a rich, although more recent, history in Korea, Japan, and other Asian countries. It became an important trading commodity following its introduction to Europe in the early 1600s, after which the forerunner of the East India Company was established to facilitate global trade in tea and many other products. Although this company's monopoly on tea trade with the American colonies, and the taxes imposed on the American colonies for this desired leaf, instigated a pivotal party in the harbor of Boston that contributed to the start of the Revolutionary War and founding of the USA (Chernow 2004, 2010), the East India Company's activities in other parts of the world were no less profound. The desire to control not only the trade in tea but also its production led to arrangements between the East India Company and Great Britain that brought the planting of tea to major regions of colonial India (and later Africa), contributing to the domination of these areas by the British Empire and the latter's control of global trade.

Leaves from several species have been, and are used, for the psychoactive impact that they impart to the individuals who chew or brew them into teas (or in some cases concentrate the active ingredients for administration through other means). These include coca, khat (qat, chat, or several other terms), betel, etc. Moreover, various pharmaceuticals and medicines are, or at least were originally, derived from plant parts including the leaves of a number of species (e.g., menthol, digitalis [digoxin], caffeine, atropine, cocaine, eucalyptus oil, artemisinin). The use of the leaves (buds and flowers) of the marijuana plant *Cannabis sativa* (and its pharmacological derivatives tetrahydrocannabinol and cannabidiol) for alleviation of nausea (e.g., associated with chemotherapy), pain, depression, anxiety, and symptoms of many medical conditions including Parkinson's, Alzheimer's, HIV/AIDS, glaucoma, etc. has led to its legalization for medical purposes in more than half of the USA and some countries (although growth of the plant and sale of its products may be restricted). Legalization of marijuana for recreational use has even occurred in a number of US states and a few countries, opening new entrepreneurial opportunities and additional sources of revenue for various levels of government.

Leaves have also played a role in the affairs of government and corporate entities. The maple leaf is widely employed as a symbol of Canada, appearing on its currency and the national flag, and is used as a logo by the airline Air Canada, professional ice hockey (Toronto Maple Leafs, Toronto Marlies, and Winnipeg Jets) and lacrosse (Toronto Rock) teams, and national teams (e.g., ice hockey, soccer, basketball, softball, ice skating, swimming, skiing). The shamrock leaf is likewise a symbol associated with Ireland and many things Irish, as well as with several companies (Shamrock Foods, Shamrock Oil and Gas - Diamond Shamrock, etc.). In addition, leaves of various species have been featured on the currency of a number of other countries, including France, Germany, Japan, Poland, Australia, and the USA (van Wie 1999), and have been utilized in military service medals (Elder et al. 2003; Zabecki 2014). Recognizing the unique patterns that leaf veins display, Benjamin Franklin duplicated such designs on the currency of some colonial states and the first US currency in order to make it difficult for individuals to print counterfeit money (Isaacson 2003). In order to tout their "green" and sustainable approach to business, a number of corporations have the word leaf as part of their name and/or utilize a leaf as their logo. One such example is the LEAF electric car, Nissan's "zero emission" vehicle.

For all of their importance to life, the development of human civilization, and pervasiveness in culture, the scientific study of leaf function was slow to arise but accelerated swiftly once an understanding of the nature of gases and their exchange between atmosphere and organism became established. Theophrastus undertook a cataloging of the variety of leaf shapes in ancient Greece (Hort 1916), while Caroli Linnæi took it to a definitive level with the publication of *Species Plantarum* in 1753, founding modern taxonomy and instituting the binomial nomenclature of genus and species. However, such descriptions lacked any recognition of leaf function. The following (two paragraph) short history of research into leaf function has been compiled from several sources (Walker 1992; Govindjee and Krogmann 2004; Lee 2017). Jan Baptist Van Helmont performed an experiment (published in 1648, 4 years after his death) in which a 5-pound willow shoot was planted in 200 pounds of soil. After growing for 5 years, the willow weighed 169 pounds, but the soil had only lost 0.13 pounds (Hershey 1991). Although the weight gain by the tree was not yet attributed to carbon dioxide acquired from the air (only water added to the soil was implicated at the time), the stage was set for elucidating leaf function during the following century. In 1727, Stephen Hales published a volume describing his observations of leaves interacting with the atmosphere, including their loss of water vapor to the surrounding air (i.e., transpiration; he surmised that plants were able to move water through their tissues and that leaves were involved) and their ability to reduce the volume of surrounding air in a closed container (an impact for which he was unable to provide an adequate explanation). Although Hales speculated that leaves were important for provision of something from the air that was essential to the plant and that light might also be important in that provisioning, he did not have the wherewithal to put everything together in a meaningful way.

In 1754, Charles Bonnet suggested that leaves absorb gas (after observing bubbles exuded by illuminated leaves underwater), and Joseph Priestley, using a device previously employed by Hales, subsequently demonstrated that plants could produce a gaseous substance (later identified as oxygen) that permitted a mouse to live or a candle to burn in a sealed enclosure. Antoine Lavoisier, after learning of these results (as well as those of Carl Wilhelm Scheele), realized that air was comprised of at least two different gases (oxygen and nitrogen). Following on all of these findings, the Dutch scientist Jan Ingen-Housz conducted many experiments showing that those parts of a plant that are green produce oxygen (as it would later be called) when they are illuminated with light and produce much smaller amounts of a different gas (later identified as carbon dioxide) in darkness. By the end of the eighteenth century, Ingen-Housz had clarified not only the role of light in photosynthesis but also suggested that carbon accumulated in plants comes from absorbed CO_2 (the concomitant absorption of CO_2 and production of O_2 by leaves during photosynthesis were demonstrated by Jean Senebier during the 1780s). Shortly thereafter, Nicolas Theodore de Saussure conducted experiments leading him to surmise that water was a direct participant in the process of photosynthesis; he also experimented with cactus cladodes, revealing the essential gas exchange features of what would come to be known as Crassulacean acid metabolism (see Chapter 10) a century and a half later.

Following earlier characterizations of plant anatomy by Marcello Malpighi (1675) and Nehemiah Grew (1682), a structure-function view of the leaf was put on a firm footing by Gottlieb Haberlandt (1884; and subsequent revisions drawing also upon Schimper 1898). Ten years later, Dixon and Joly (1894) put forth the hypothesis that water in leaf cell walls transitioning from liquid into vapor followed by its transpirational loss via stomata at the leaf-atmosphere boundary resulted in the drawing of water up through the xylem portion of a plant's vascular tissue (due to the cohesion of water molecules for one another). Whereas this cohesion-tension mechanism of water movement through the tracheary elements of the xylem involves a pressure potential gradient that becomes increasingly more negative from soil through the leaves and into the atmosphere, movement of sugars (the product of photosynthesis) from the leaves to distant sinks in the plant involves a positive pressure potential gradient. As proposed by Ernst Münch (1930), sugars in high concentration near the site of synthesis accumulate in the phloem of the leaf and water, moving from higher concentration in neighboring cells (e.g., the xylem) to lower concentration in the phloem (filled with sugars), increase the pressure potential in the phloem. Sugars are simultaneously being removed from the phloem of distant sinks (e.g., fruits, roots), as well as along the intervening route, and water follows those sugars moving from the phloem into the surrounding tissues, thereby lowering the pressure potential of the phloem at those sites. The sugar-laden sap in the sieve tubes (sieve elements aligned end to end) thus moves under positive pressure from sites of sugar loading (where the phloem sap is under higher pressure) to sites of sugar unloading (where the phloem sap is under lower pressure).

In summary, the leaf is an organ optimized for capturing sunlight and safely using that energy through the process of photosynthesis to drive the productivity of the plant and, through plants' position as primary producers, that of Earth's biosphere. It is an exquisite organ composed of multiple tissues, each with unique functions, working synergistically to (1) deliver water, nutrients, signals, and sometimes energy-rich carbon compounds throughout the leaf (xylem), (2) deliver energy-rich carbon molecules and signals to the leaf during its development and then from the leaf to the plant once the leaf has matured (phloem), (3) regulate exchange of gasses between the leaf and the atmosphere (epidermis and stomata), (4) modulate the radiation that penetrates into the leaf tissues (trichomes, the cuticle, and its underlying epidermis), (5) harvest the energy of visible sunlight to transform water and carbon dioxide into energy-rich sugars or sugar alcohols for export to the rest of the plant (palisade and spongy mesophyll), and (6) store sugars and/or starch during the day to feed the plant during the night and/or acids during the night to support light-driven photosynthesis during the day (palisade and spongy mesophyll). Various regulatory controls that have been acted upon through the evolutionary history of each plant species result in an incredible diversity of leaf form across the plant kingdom. Genetic programming is also flexible in allowing acclimatory phenotypic adjustments that optimize leaf functioning in response to a particular set of environmental conditions and biotic influences experienced by the plant. Moreover, leaves and the primary processes carried out by the leaf respond to changes in their environment, and the status of the plant, through multiple regulatory networks over time scales ranging from seconds to seasons. This book brings together the findings from laboratories at the forefront of research into various aspects of leaf function and particularly in relationship to photosynthesis.

The editors are grateful for the dedication and patience of the authors in making this volume possible. They also wish to express their gratitude to the series editors Tom Sharkey and Julian Eaton-Rye and the indomitable Govindjee, who immediately endorsed the pursuit of this volume following the submission of a prospectus.

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The Editors

William W. Adams III (*far right*; note the pattern of leaves on his shirt) **with his wife and colleague Barbara Demmig-Adams** (*second from left*) **and their children Robert** (*far left*) **and Melanie** (*second from right*) **Adams.** (Photograph by Markus Demmig)

A Fascination with Leaves

William W. Adams III is a professor in the Department of Ecology and Evolutionary Biology at the University of Colorado in Boulder, Colorado, USA. The initiation of his interest in leaves began in late summer 1975. He had collected a moss growing in Trimble Wildlife Area (now underwater following the completion of Smithville Dam in 1977 and subsequent flooding to create Smithville Lake, north of Kansas City, Missouri), with an eye toward using it for his project in an advanced biology high school course. Before the start of the school day, William used a mirror to reflect direct light from the rising sun up through a microscope stage and was mesmerized by the brilliant green of the moss' simple leaves, setting the stage for a lifelong focus on plants and investigation of leaves.

During his junior year at the University of Kansas, William became the first student to join the laboratory of a recent hire, Prof. Christopher H. Haufler, who suggested a project on the fern *Gleichenia bifida*. After collecting *G. bifida* fronds on a trip to Costa Rica, William conducted a study of gametophyte development that culminated in an honors thesis, half of which was published (Haufler and Adams 1982, William's least-cited publication). A rigorous course on plant physiological ecology (taught by Prof. Rolf Borchert; see http://www.kuonlinedirectory.org/endacott/data/OralHistoryTranscripts/Borchert.wpd.pdf and, e.g., Borchert et al. 2015) proved pivotal in generating a desire to work in the area of plant ecophysiology. The course also featured presentations by finalists for a plant ecophysiologist position in the Department of Botany. William subsequently became the first student to join the laboratory of the individual chosen for that position, Prof. Craig E. Martin. For his master's thesis, William suggested a comparative ecophysiological study of a pair of *Tillandsia* species (see Martin and Adams 1987 for one of them) he had encountered during trips to Mexico, but the two proved to be too similar in their adaptations to the epiphytic habitat. As an alternative, Craig suggested a study of the juvenile (with trichome-covered atmospheric leaves; see Figs. 1.4 and 5.9i) and adult (with relatively glabrous, overlapping leaves that create a tank for impoundment of water and detritus) forms of the epiphyte *Tillandsia deppeana*, resulting in a successful characterization of the structure and function of its heterophyllous leaves (Adams and Martin 1986a,b,c).

Prof. C. Barry Osmond generously served as William's Ph.D. mentor, providing resources for multiple studies on the potential role of high CO_2 levels (produced by diurnal malic acid decarboxylation in leaves and cladodes of Crassulacean acid metabolism plants) in mitigating photoinhibition (e.g., Adams and Osmond 1988). During the first half of his Ph.D. tenure (undertaken at the Biological Sciences Center of the Desert Research Institute, Reno, Nevada), William was also fortunate to have both Prof. Stanley D. Smith (Adams et al. 1987a) and one of the editors of this book series, Prof. Thomas D. Sharkey (Adams et al. 1987b), as mentors. During the second half of his Ph.D., William joined the other editor of this book (Prof. Ichiro Terashima, then a postdoctoral research associate) in Barry's laboratory at the Australian National University's Research School of Biological Sciences. William solicited Ichiro's assistance with field work, with which his future wife and colleague (Prof. Barbara Demmig-Adams) also became involved (Adams et al. 1988). Almost a decade later, and in conjunction with a Robertson Symposium on Chlorophyll Fluorescence (Adams et al. 1995; Demmig-Adams et al. 1995), Barry was again instrumental in providing financial and logistical support for a 3-month research visit by William, Barbara, their two children, and two of their Ph.D. students to characterize photosynthesis, photoprotection, and photoinhibition of leaves and cactus cladodes in multiple species in three distinctive Australian habitats with varying light and climatic conditions (Logan et al. 1996, 1997; Barker et al. 1998; Adams et al. 1999).

Following the completion of his Ph.D., William pursued various aspects of leaf function including responses to sulfur dioxide (Adams et al. 1989), autumnal senescence (Adams et al. 1990a), and zeaxanthin-associated photoprotection (e.g., Demmig-Adams et al. 1989, 1990; Adams et al. 1990b) with the support of NATO and Alexander von Humboldt fellowships in the laboratory of Prof. Dr. Klaus Winter. This 2-year period in Würzburg solidified the personal and professional collaboration between William and Barbara, yielding two children (see photograph above) and a couple of decades of research on photoprotection (and its sustained variant photoinhibition) under physiologically relevant conditions (for reviews, see Demmig-Adams et al. 1999; Demmig-Adams and Adams 2006; Demmig-Adams et al. 2006, 2012, 2014; Adams et al. 2006, 2013, 2014a,b). The recognition that photoinhibition involved sustained engagement of zeaxanthin in photoprotective energy dissipation accompanied by increased levels of foliar carbohydrates led William to contemplate the role of foliar carbon export in contributing to the response of the photosynthetic apparatus to excess light. In addition, his growing awareness of the different mechanisms through which sugars are loaded into the phloem (through the classes he was teaching) prompted him to initiate a collaboration with one of the preeminent phloem loading experts, Prof. Robert Turgeon (Amiard et al. 2005, 2007; Adams et al. 2007; see Ayre and Turgeon 2018 Chapter 3).

This collaboration catalyzed an evaluation of the relationship between foliar minor vein features (of both phloem and xylem) and photosynthetic capacity (and transpiration) involving multiple summer annual species, winter annual species, biennial species, and both apoplastic and symplastic phloem loaders. These characterizations revealed that anatomical and ultrastructural features of the phloem that serve as proxies for the capacity to load and export sugars vary among species, exhibit acclimatory adjustment to different growth light and temperature regimes, and are consistently and significantly correlated with photosynthetic capacity (Adams et al. 2018 Chapter 2 and multiple references therein). Features of the tracheary elements that serve as proxies for the water flux capacity of the xylem were consistently correlated with transpiration rate among all species across all growth conditions and typically (but not exclusively) with photosynthetic capacity as well. The latter association was not present for winter annuals that exhibited an increased capacity for sugar loading/export and photosynthesis in response to growth under low temperature, a condition under which evaporative demand and the flux capacity for water were both diminished (Adams et al. 2018 Chapter 2). Moreover, the level of foliar vascular and photosynthetic phenotypic plasticity exhibited by *Arabidopsis thaliana* in response to different growth conditions during plant development varied depending on the climatic conditions prevailing in the habitats from which different ecotypes were obtained (i.e., the extent of acclimatory adjustment was dependent on the evolutionary history of each; Adams et al. 2016, 2018 Chapter 2).

As a professor at a public state university, William's energy has also been directed toward the education and training of students, including thousands that have participated in his introductory general biology class over more than a decade. He has been honored for his efforts in this realm by students (Mortar Board Certificate of Recognition for Exceptional Teaching in 2000), faculty peers (Boulder Faculty Assembly Excellence in Teaching Award in 2004), and administration (Chancellor's Award for Excellence in STEM Education 2013–2014). In the laboratory, he has mentored and co-mentored (with Barbara) over 40 undergraduate students and volunteer workers, 22 graduate students, and 10 postdoctoral research associates and collaborated with 4 colleagues as their host during periods of sabbatical leave.

William has co-edited three books, the first resulting from the inaugural Robertson Symposium on the Ecology of Photosynthesis in Sun and Shade (held in 1987, published in 1988) with John R. Evans and Susanne von Caemmerer. The other two have been books in this series, including volume 21 on photoprotection and photoinhibition (with Barbara Demmig-Adams and Autar K. Matoo) in 2006 and volume 40 on non-photochemical chlorophyll fluorescence quenching and energy dissipation (with Barbara Demmig-Adams, Györzö Garab, and Govindjee) in 2014.

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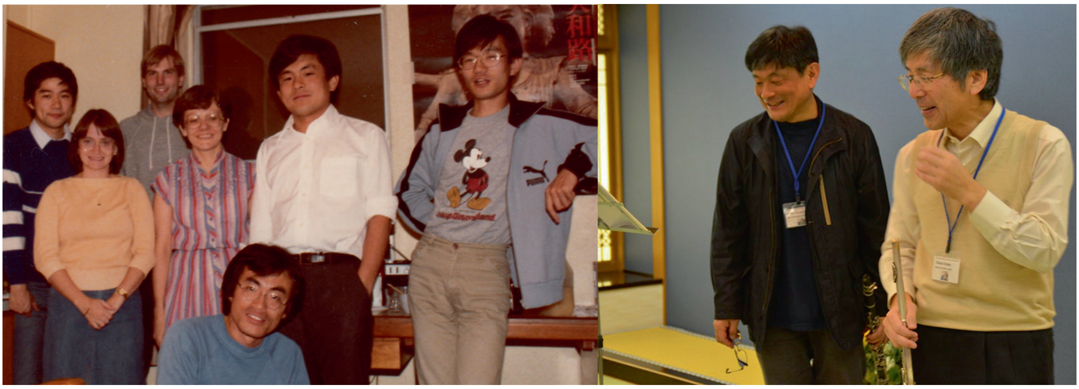

Left: A 1986 photograph taken in Terashima's room at the Australian National University's Bruce Hall. Top row from left to right, Takao Fujikawa (historian), Melodye A. Rooney (stable isotope chemist), William Adams, Catherine M. Brennan (sociologist), Ichiro Terashima, and Takashi Saito (Japan Business Federation). First row, Masashi Hirosue (historian). Right, a recent photo of Terashima (left) after playing a duet piece (clarinet and flute) with Tatsuo Omata (right) on the occasion of a Japan-Germany binational seminar on photosynthesis (March 2016, held at the Atami hot spa, Japan).

Ichiro Terashima entered the University of Tokyo in 1976 and started his studies on the light environment within leaves and its effect on leaf photosynthesis under the supervision of Toshiro Saeki, culminating in a Doctor of Science degree in 1985. He miniaturized his supervisor's study on the light environment and photosynthesis of leaf canopies (Monsi and Saeki 1953, 2005) to the individual leaf scale. He conducted his first postdoctoral study in the laboratory of Noboru Hara, an anatomist specialized in the early phases of leaf development, to study effects of light direction on differentiation of palisade and spongy tissues in bifacial leaves. He then moved to the Australian National University and studied effects of light and nitrogen nutrition on leaf photosynthesis with John R. Evans, patchy leaf photosynthesis in abscisic acid-treated leaves with Graham D. Farquhar, and photoinhibition at chilling temperatures with C. Barry Osmond. He shared an office room with William W. Adams III (see left photograph above), another editor of this volume, and participated in William's field studies. In 1988, he got a position as an assistant professor in the laboratory of Sakae Katoh at the University of Tokyo and studied with Kintake Sonoike. They found that photoinhibition of photosystem I and uncoupling of H^+-ATPase occur in chilling sensitive plants subjected to chilling temperatures in moderate light. He moved to Tsukuba University as an associate professor in 1994 and to Osaka University as a full professor in 1997. With his students and Ko Noguchi, he revealed that CO_2 conducting aquaporins (cooporins) facilitate CO_2 diffusion across the plasma membrane. He also studied systemic regulation of leaf photosynthetic properties, delayed greening of evergreen tree species, roles of alternative oxidase, and extrinsic proteins in photosystem II. In 2006, he moved back to the University of Tokyo and studied the influences of (1) green light in leaf photosynthesis; (2) mesophyll tissue in stomatal responses to environmental conditions; (3) soil dryness, high CO_2, and ABA application on mesophyll conductance; and (4) fluctuating light on photoinhibition of photosystem I. His students who have been studying in the field of photosynthesis and respiration include Kouki Hikosaka, Kiyomi Ono, Momoe Ishibashi, Ko Noguchi, Sachiko Funayama-Noguchi, Shin-ichi Miyazawa, Satoshi Yano, Youshi Tazoe, Wataru Yamori, Takao Araya, Keisuke Yoshida, Takushi Hachiya, Chihiro Watanabe, Yin Wang, Masaru Kono, Yuki Okajima, Kazunori

Miyata, Yusuke Mizokami, and Takashi Fujita. Yuko Hanba, Haruhiko Taneda, Danny Tholen, Riichi Oguchi, and Daisuke Sugiura studied in his laboratory as postdoctoral fellows. W.S. Chow, Poonam Vyas, Ala Druta, Narayan Misra, and Detelin Stefanov spent periods of time in his laboratory as visiting fellows. He stayed in Agu Laisk's laboratory as a visiting fellow in 2003. Light and CO_2 environments within leaves, the role of green light in photosynthesis, photoinhibition of photosystems I and II, and the effects of elevated CO_2 on photosynthesis have been his favorite research subjects. He is an amateur clarinet player (see right photograph above) and is practicing Bach's cello suits and various pieces by Weber, Brahms, Beethoven, Schubert, and, of course, Mozart! He also loves sake and rakugo (Japanese vaudevillian one-man play).

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The Life of a Leaf
by *William W. Adams III*

Throughout the winter leaves remain
Quiescent in seed and bud 'til rain
Emerging with positive pressure potential
Cells burst forth from every axil

Seamlessly shifting from import to export
Sugars through phloem continuously transport
As chloroplasts reach their competency
The leaf attains full maturity

Water from soil to root is drawn
Passing through strip Casparian
Entering xylem to travel on
Held one to another by strong cohesion
Almost breaking with increasing tension
Reaching the leaf for distribution
Through a network of fine venation
Fluxing out stomates via diffusion
In the process of transpiration
As CO_2 enters assimilation
Fueled by solar illumination

Light of wavelengths from blue to red photons
In chlorophyll absorbed, exciting electrons
Splitting water to oxygen/protons
Electron transport ATP spawns
NADPH for use within
The chemical cycle of Calvin
Let's not fail to also mention
The intrepid pair of Bassham and Benson

The C_3 cycle ubiquitous is
Among all leaves with photosynthesis
A C_4 cycle yields increased fitness
Where heat and drought contribute to stress
For C_4 plants between cells spatial
Whereas for CAM a divide temporal

CAM also found in pools vernal
As CO_2 falls each day diurnal
And rises again each night nocturnal
Revealing CAM as thoroughly versatile

Chloroplasts move from dawn to twilight
Fully exposed when low is the light
Self-shaded at midday, whenever too bright
Leaves too may shift, with the sunlight
Horizontal in morning, at noon quite upright
The reactive oxygen not to incite
Others may track from morning to night
Returning to east by predawn starlight

Thermal dissipation also steps up
When high light leads to proton backup
As protons gather in thylakoid lumen
Begetting formation of zeaxanthin
For strong engagement in photoprotection
Through increased levels of dissipation

Chemical energy in sugars stored
Used by the leaf or transferred to gourd
Fuel for the plant or herbivore
Microbe, fungus, or omnivore
Even passed on to carnivore
After death to detritivore

From little fern to sycamore
Springing from seed or tiny spore
From mountain top to far seashore
Across the land, we so adore

Some even manage the life aquatic
Others, in treetop, on branch, epiphytic
Many herbaceous, short-lived, mesophytic
Found on ephemeral, annual, biennial
Others much tougher, long-lived, sclerophytic
Among those evergreen, some perennial
From forest near equator, of the tropic
To those circumpolar, the boreal
Few are so touchy, oh so, thigmonastic
Others get sleepy, at night, nyctinastic

Though some remain green regardless of season
Others transform, such as oak, maple, aspen
Draining resources with great abandon
As leaves turn yellow or start to redden

Some blaze brightly with orange or crimson
Still others more subtle, akin to salmon
In petiole develops the zone of abscission
The bond between leaf and plant to weaken
Until the whole leaf from branch is riven
In its wake leaving cellulose, pectin, and lignin
A bud scale endures drought or vernalization
A woody plant's wondrous adaptation
Awaiting its future full activation

During its life, be it weeks, months, or years
Each leaf serves, through adversity, perseveres
Though some may go while others appear
All play a role through every tier
Removing CO_2 from atmosphere
Supporting life in the biosphere

To all life's relief
Whether long or brief
The life of a leaf
Is nature's motif

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