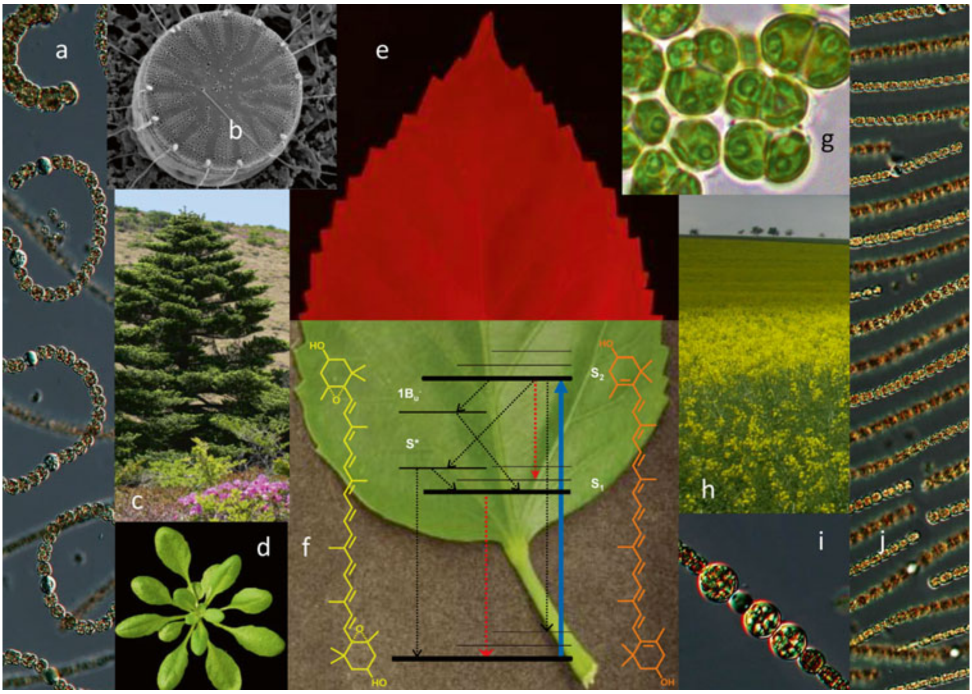
Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria



Figures showing species and properties relevant to non-photochemical quenching studies. (**a**) Filamentous planktonic cyanobacteria *Dolichospermum crassum* and *D. flos-aquae* by Petr Znachor; (**b**) SEM image of the diatom *Cyclotella meneghiniana* by Claudia Büchel; (**c**) *Abies koreana* (Korean fir) on Mount Halla, Korea, by Seok Chan Koh; (**d**) *Arabidopsis* Col-0 by Jared Stewart; (**e**) Combination of two photographs, by Wolfgang Bilger and Hartmut Kaiser, of a *Hibiscus rosa-sinensis* leaf in room light (*lower part*), and of the leaf's chlorophyll fluorescence (*upper part*). Fluorescence was excited by *blue* LED of an Imaging-PAM fluorometer (IMAG-MAX/L, Walz, Effeltrich, Germany) at 350 μmol photons m^{-2} s^{-1}, and the objective had a far-red filter to collect chlorophyll fluorescence; (**f**) energy-level scheme and relaxation dynamics of carotenoids and molecular structure of violaxanthin (*yellow*) and zeaxanthin (*orange*) by Tomas Polivka; (**g**) green alga *Scenedesmus* by Nicoletta La Rocca and Tomas Morosinotto; (**h**) canola field in Germany by Melanie Adams; (**i**) Spheroid akinets and a heterocyst of cyanobacterium *Anabaena aphanizomenoide* by Petr Znachor; (**j**) Straight filaments of cyanobacterium *Dolichospermum planctonicum* by Petr Znachor.

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Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 40: Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria

We are delighted to announce the publication of Volume 40 in this series. The series publisher, Springer, now makes the table of contents of all of the volumes freely available online. Links to each volume are given below. The increased color and web presence of these books since Volume 35 makes the books more accessible and allows bibliographic tracking. We hope that these updates will maintain the importance of these edited volumes in the dissemination of the science of photosynthesis and bioenergy. 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.

This Book: Volume 40

Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria was conceived and edited by Barbara Demmig-Adams, Győző Garab, William W. Adams III, and Govindjee. Govindjee, in his role as both Series Editor and Editor, and Tom Sharkey are grateful to the editors and the authors who have contributed to this important volume.

The overall topic of this book is the regulation of solar-energy collection (i.e., light harvesting) by plants, algae and cyanobacteria via processes functioning to (i) optimize the efficiency of light collection and (ii) safely deal with excess absorbed light when the rate of excitation energy use for productive photochemistry falls behind the rate of light absorption. The major focus of the book is the safe disposal of excess excitation energy via thermal dissipation as conveniently monitored through the decrease (or quenching) of chlorophyll a fluorescence by processes other than photochemistry (i.e., non-photochemical quenching, NPQ).

Several chapters include cautions against some assumptions about the meaning of NPQ. Normally, chlorophyll fluorescence decreases due to an increase in photochemistry (via photochemical fluorescence quenching) since energy used in photochemistry is energy not available for fluorescence. However, what is described in this volume is the discovery that restrictions in the rate of photochemistry actually result in less chlorophyll fluorescence emission (hence termed non-photochemical quenching of chlorophyll fluorescence), opposite to what would be observed in a simpler system. This realization had a profound effect on studies of photosynthesis. In hindsight, it makes sense to dissipate the flow of energy as close to its absorption as possible whenever the downstream reactions are unable to use all of the incoming energy.

The discovery of the role of the xanthophyll cycle is described in an engaging way, especially in Chap. 2. Barbara Demmig-Adams' singular role in making the connection between the xanthophyll cycle (specifically the VAZ, i.e., violaxanthin antheraxanthin zeaxanthin, cycle) and NPQ should be highlighted and for this reason it is especially relevant that she is lead Editor of this volume. It is important to distinguish between the essential nature of the cycling of the xanthophylls and the mechanism of NPQ. Further, the cycling between violaxanthin and zeaxanthin is not the mechanism by which excess light is dissipated.

Among the authors are many of the scientists who have made seminal discoveries that led to new insights. The book is a comprehensive – and in many cases personal – look at NPQ. At the same time, the book has educational aspects, with clear recommendations for strict use of terms and methods. This guidance can be invaluable to help a field speak the same language. A case in point is NPQ itself. It originally meant, and the book recommends should continue to mean, quenching of fluorescence. The actual quenching (or dissipation) of incoming photons is a distinct phenomenon even if closely linked.

Nearly everyone who studies photosynthesis needs to understand NPQ. This book provides a single source to learn the history of important discoveries, the role and relevance of NPQ today and how to use the concepts of NPQ in developing explanations of the phenomena we observe. This volume is a must-read for photosynthesis researchers.

Authors

The book contains 28 chapters written by 54 authors from 15 countries [Canada (3); The Czech Republic (3); France (4); Germany (7); Greece (1); Hungary (1); Italy (3); Japan (1); Korea (1); The Netherlands (5); South Africa (1); Spain (5); Sweden (1); UK (5); and USA (13)]. We thank all the authors for their valuable contribution to this book; their names (arranged alphabetically) are:

Anunciación **A**badía (Spain; Chap. 27); Javier Abadía (Spain; Chap. 27); William W. Adams III (USA; Chaps. 2, 7, 23, 24 and 28); Maxime Alexandre (The Netherlands; Chap. 6); Roberto **B**assi (Italy; Chap. 14); Wolfgang Bilger (Germany; Chaps. 7 and 19); Matthew D. Brooks (USA; Chap. 13); Claudia Büchel (Germany; Chap. 11); Christopher M. **C**ohu (USA; Chaps. 23 and 24); Barbara **D**emmig-Adams (USA; Chaps. 2, 7, 23, 24 and 28); Raquel **E**steban (Spain; Chap. 12); Giovanni **F**inazzi (Italy; Chap. 21); Graham R. Fleming (USA; Chap. 9); Harry A. Frank (USA; Chap. 8); Győző **G**arab (Hungary; Chap. 16); José I. García-Plazaola (Spain; Chaps. 12 and 26); Reimund Goss (Germany; Chap. 20); Govindjee (USA; Chaps. 1 and 4); Jeremy **H**arbinson (The Netherlands; Chap. 25); Michel Havaux (France; Chap. 26); Christoph-Peter Holleboom (Germany; Chap. 9); Alfred R. Holzwarth (Germany; Chap. 5); Peter Horton (UK; Chaps. 3 and 6); Cristian **I**lioaia (The Netherlands; Chap. 6); Peter **J**ahns (Germany; Chap. 5); Stefan Jansson (Sweden; Chap. 13); Radek **K**aňa (The Czech Republic; Chap. 22); Yaser R. Khan (Canada; Chap. 4); Diana Kirilovsky (France; Chap. 22); Seok-Chan Koh (Korea; Chap. 24); David M. Kramer (USA; Chap. 18); Tjaart Krüger (South Africa and The Netherlands; Chap. 6); Johann Lavaud (France; Chap. 20); Barry Logan (USA; Chap. 7); Jun **M**inagawa (Japan; Chap. 21); Fermín Morales (Spain; Chap. 27); Tomas Morosinotto (Italy; Chap. 14); Onno Muller (USA; Chaps. 23 and 24); Conrad W. Mullineaux (UK; Chap. 17); Erik H. Murchie (UK; Chap. 25); Krishna K. **N**iyogi (USA; Chap. 13); Evgeny E. **O**stroumov (Canada; Chap. 4); George **P**apageorgiou (Greece; Chap. 1); Andrew K. Pascal (UK; Chap. 10); Tomáš Polivka (The Czech Republic; Chap. 8); Ondřej Prášil (The Czech Republic; Chap. 22); Bruno **R**obert (France; Chap. 10); Alexander Ruban (UK; Chaps. 10 and 17); Greg **S**choles (Canada; Chap. 4); Jared J. Stewart (USA; Chaps. 24 and 28); Deserah D. Strand (USA; Chap. 18); Herbert **v**an Amerongen (The Netherlands; Chap. 15); Rienk van Grondelle (The Netherlands; Chap. 6); Peter J. **W**alla (Germany; Chap. 9).

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

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

We take this opportunity to thank and congratulate Barbara Demmig-Adams and her co-editors Győző Garab, William W. Adams III, and Govindjee 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 54 authors of this book (see the contributor list); without their authoritative chapters, there would be no such volume. We give special thanks to Srinath Raju of SPi Global, India, for directing the typesetting of this book; his expertise has been crucial in bringing this book to completion. We owe Jacco Flipsen, 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 2012 photo of Govindjee with Neelam Sodha, of the School of LifeSciences, Jawaharlal Nehru University, New Delhi, India. Photo Credit: Ashwani Pareek.

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 pioneers of photosynthesis, Robert Emerson and Eugene Rabinowitch, obtaining his Ph.D. in 1960 in Biophysics. He is best known for his research on excitation energy transfer, light emission (prompt and delayed fluorescence, and thermoluminescence), primary photochemistry and electron transfer in "Photosystem II" (PS II, water-plastoquinone oxido-reductase).

His research, with many collaborators, has included the discovery of a short-wavelength form of chlorophyll (Chl) *a* functioning in what is now called PS II; of the two-light effect in Chl *a* fluorescence; and, with his wife Rajni Govindjee, of the two-light effect (Emerson Enhancement) in NADP reduction in chloroplasts. His major achievements, together with several other researchers, include an understanding of the basic 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.

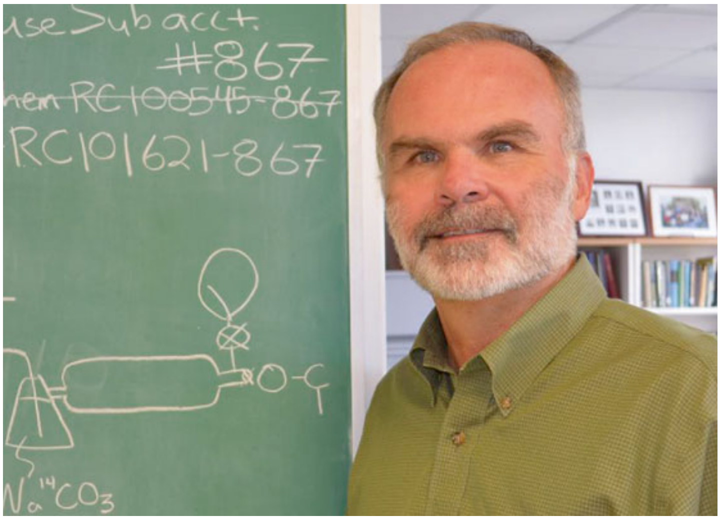
His current focus is on the "History of Photosynthesis Research", in "Photosynthesis Education", as well as in the "Possible Existence of Extraterrestrial Life". He has served on the faculty of the UIUC for ~40 years.

Govindjee's honors include: Fellow of the American Association of Advancement of Science (AAAS); Distinguished Lecturer of the School of Life Sciences, UIUC; Fellow and Lifetime member of the National Academy of Sciences (India); President of the American Society for Photobiology (1980–1981); Fulbright Scholar (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 the Liberal Arts & Sciences Lifetime Achievement Award of the UIUC, 2008.

Further, Govindjee was honored (**1**) in 2007, through two special volumes of Photosynthesis Research, celebrating his 75th birthday and for his 50-year dedicated research in "Photosynthesis" (Guest Editor: Julian Eaton-Rye); (**2**) in 2008, through a special International Symposium on "Photosynthesis in a Global Perspective", held in November, 2008, at the University of Indore, India; (**3**) 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), was dedicated to Govindjee, celebrating his academic career; and (**4**) in 2013, through a special issue 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 (during October 23–25, 2013) in Trebon, The Czech Republic (see O. Prasil [2014] Govindjee, an institution, at his 80th [or rather 81st] birthday in Trebon in October, 2013: A pictorial essay. *Photosynth Res*. doi:10.1007/s11120-014-9972-0).

Govindjee is coauthor of *Photosynthesis* (John Wiley, 1969) and editor of many books, published by several publishers including Academic Press and Kluwer Academic Publishers (now Springer).

Since 2007, each year a Govindjee and Rajni Govindjee Award (http://sib.illinois.edu/grants_Govindjee.htm) 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 web site at http://www.life.illinois.edu/govindjee.



Thomas D. (Tom) Sharkey obtained his Bachelor's degree in Biology in 1974 from Lyman Briggs College, a residential science college at Michigan State University, East Lansing, Michigan. After 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. Post-doctoral 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. 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 papers on the biochemical regulation of isoprene synthesis. Tom has co-edited three books, the first on trace gas emissions from plants in 1991 (with Elizabeth Holland and Hal Mooney) and then volume 9 of this series (with Richard Leegood and Susanne von Caemmerer) on the physiology of carbon metabolism of photosynthesis in 2000 and volume 34 (with Julian Eaton-Rye and Baishnab C. Tripathy) entitled *Photosynthesis*: *Plastid Biology*, *Energy Conversion and Carbon Assimilation*. Tom has been co-series editor of this series since volume 31.

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Preface

While few would disagree that interdisciplinary studies are important, bringing together researchers from vastly different fields remains quite a challenge. All authors and editors contributing to the present book have made a genuine effort to integrate different views, and we are proud of the remarkable outcome. This book brings together viewpoints from disciplines as diverse as photo-physics, chemistry/biochemistry, physiology, molecular genetics, and comparative ecophysiology (covering much of the diversity of photosynthetic life that evolved to inhabit many environments). Authors and editors have endeavored to contribute the best each discipline had to offer towards presenting an updated view of the current understanding of our field and to outline a vision of what is needed next.

This book focuses on the harvesting of solar energy by plants and photosynthetic microbes like algae and cyanobacteria, and the regulation of light harvesting via the photoprotective removal of excess absorbed light. Why is studying the regulation of light harvesting important? Natural photosynthesis provides virtually all food and fuel (fossil fuels from past photosynthesis and "biofuels" from current photosynthesis), as well as many materials (from, e.g., fiber and building materials to vitamins and medicines). While sunlight harnessed in photosynthesis is the basis of virtually all food chains on this planet, too much of a good thing – more light being absorbed than can be utilized in photosynthesis – presents a potentially deadly threat. An excess of excitation energy can lead to the formation of potentially damaging oxidants, which is why photosynthetic organisms universally employ powerful mechanisms to safely remove excess excitation energy in a process (thermal energy dissipation) that can be monitored by its impact on chlorophyll fluorescence (quantified as non-photochemical quenching of chlorophyll *a* fluorescence, NPQ), the topic of this book.

Future opportunities to manipulate photosynthesis by engineering will depend on an improved understanding of all processes involved in its operation and regulation. The ability to mimic natural photosynthesis, and potentially increase the portion of sunlight that goes to the accumulation of energy carriers as opposed to supporting the photosynthetic organisms' own growth and reproduction – via synthetic systems or "biohybrids" – will depend on further improvements in the mechanistic understanding of *how* natural light harvesting works. This understanding of *how* it works depends critically on contributions from, e.g., photophysical and molecular genetic studies, as outlined in this book. In turn, an improved understanding is needed of *why* all known photosynthetic organisms fall behind in the utilization of absorbed light under full sun exposure, a question to which integrative studies can contribute, as also outlined in this book.

Furthermore, it is becoming increasingly clear that the photosynthetic light-harvesting system provides essential input into the signaling networks that control the photosynthetic organism's rate of growth, cell division, reproduction, and, eventually, an organism's demise via aging (senescence; see Volume 36 [2013] Plastid Development in Leaves during Growth and Senescence, edited by Basanti Biswal, Karin Krupinska and Udaya Biswal). Any excitation energy that is not utilized for energy-carrier production or safely diverted via thermal energy dissipation produces potentially destructive oxidants that shift the cellular redox state (balance of oxidants and anti-oxidants; see Volume 21 [2006] Photoprotection, Photoinhibition, Gene Regulation, and Environment, edited by Barbara Demmig-

Adams, William W. Adams III and Autar K. Mattoo). Cellular redox state, in turn, orchestrates growth, development, and multiple defenses of the organism. The state of the light-harvesting system (see Volume 13 [2003] Light-Harvesting Antennas in Photosynthesis, edited by Beverley R. Green and William W. Parson) thus exerts far-reaching control over virtually all aspects of the structure and the function of the organism. In plants, signals derived from the leaf's light-harvesting system are integrated with signals carrying information about the leaf's carbon-export capacity and whole-plant demand for the products of photosynthesis. An understanding of the impact of light harvesting on whole-organism function in particular environments thus requires integrating studies of whole organisms in different environments. Doing so will help to understand, and predict, the responses of different species in communities to the impacts of climate change. Moreover, such an understanding is needed to allow applications in agriculture to improve crop productivity and defenses against physical (e.g., unfavorable temperature or water shortage) and/or biological factors (pathogens and pests) that currently cause staggering losses in crop yields. This book brings together studies addressing all of these aspects.

In addition to addressing the mechanisms underlying photoprotective thermal dissipation, and placing these into the context of the whole organism, this book identifies challenges in the measurement, interpretation, and nomenclature of non-photochemical fluorescence quenching and remaining unresolved questions. For example, while much agreement exists that non-photochemical quenching involves xanthophylls and proteins, the roles of specific xanthophylls and proteins continues to be debated. Another area of debate is the nature of the relationship between plant productivity and non-photochemical quenching.

This volume on *Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria* includes 28 chapters and is authored by 54 researchers from 15 countries. The book begins with three chapters that provide personal perspectives on the history of contributions to this research field: George Papageorgiou (Greece) and Govindjee (USA) present definitions, timelines, viewpoints, and open questions surrounding the non-photochemical quenching of the excited state of chlorophyll a in plants (Chap. 1); William W. Adams III (USA) and Barbara Demmig-Adams (USA) provide their personal perspective on lessons from nature as obtained via comparative ecophysiology, involving fieldwork in many different habitats and controlled environment studies (Chap. 2); Peter Horton (UK) discusses the history of developments in NPQ research, especially the emergence of key ideas, theories and experimental approaches (Chap. 3).

These three historical perspectives are followed by 25 additional chapters. In Chap. 4, Evgeny E. Ostroumov, Yaser R. Khan, Gregory Scholes (all from Canada) and Govindjee describe the photophysics of photosynthetic pigment-protein complexes. Alfred R. Holzwarth and Peter Jahns (both from Germany) address how ultrafast-fluorescence-kinetics measurements have been used to study mechanisms of NPQ in intact organisms in Chap. 5. Tjaart Krüger (South Africa), Cristian Ilioaia (The Netherlands), Maxime Alexandre (The Netherlands), Peter Horton (UK) and Rienk van Grondelle (The Netherlands) discuss how inherent protein disorder in light-harvesting complexes controls NPQ (Chap. 6). In Chap. 7, Barry Logan (USA), Wolfgang Bilger (Germany), William W. Adams III (USA), and Barbara Demmig-Adams (USA) place NPQ into the context of other photoprotective mechanisms, and provide a guide for the measurement and quantification of NPQ. Tomáš Polivka (The Czech Republic) and Harry A. Frank (USA) summarize spectroscopic investigations of carotenoids involved in NPQ in Chap. 8. In Chap. 9, Peter Jomo Walla (Germany), Christoph-Peter Holleboom (Germany), and Graham Richard Fleming (USA) present a summary of electronic carotenoid-chlorophyll interactions regulating photosynthetic light harvesting of higher plants and green algae. Andrew

A. Pascal (France), Alexander Ruban (UK), and Bruno Robert (France) present how resonance Raman spectroscopy can reveal conformational changes in antenna proteins (Chap. 10). In Chap. 11, Claudia Büchel (Germany) provides an overview of fucoxanthin-chlorophyll-proteins and NPQ of diatoms. In Chap. 12, Raquel Esteban and José I. García-Plazaola (both from Spain) discuss an involvement in NPQ of the lutein epoxide cycle, as a second xanthophyll cycle in plants. In Chap. 13, Matthew D. Brooks (USA), Stefan Jansson (Sweden), and Krishna K. Niyogi (USA) review PsbS-dependent NPQ. Tomas Morosinotto and Roberto Bassi (both from Italy) discuss molecular mechanisms for the activation of NPQ in organisms from unicellular algae to mosses and higher plants in Chap. 14.

The question of whether chlorophyll-carotenoid interactions are responsible for rapidly reversible NPQ is discussed by Herbert van Amerongen (The Netherlands) in Chap. 15. Győző Garab (Hungary) describes structural changes and NPQ in oxygenic photosynthetic organisms in Chap. 16. In Chap. 17, Alexander V. Ruban and Conrad W. Mullineaux (both from UK) discuss NPQ and the dynamics of photosystem II structure. Deserah Strand and David Kramer (both from USA) describe how the proton circuit of photosynthesis controls non-photochemical quenching (Chap. 18). In Chap. 19, Wolfgang Bilger (Germany) summarizes what is known about the desiccation-induced quenching of chlorophyll fluorescence in cryptogams, such as lichens and mosses. Johann Lavaud (France) and Reimund Goss (Germany) describe the features of NPQ in diatoms and brown algae in Chap. 20. A review by Giovanni Finazzi (Italy) and Jun Minagawa (Japan) on the high-light acclimation of green microalgae is available in Chap. 21. Diana Kirilovsky (France), Radek Kaňa and Ondřej Prášil (both from The Czech Republic) review mechanisms that modulate energy arriving at the reaction centers in cyanobacteria in Chap. 22. In Chap. 23, William W. Adams III, Onno Muller, Christopher M. Cohu, and Barbara Demmig-Adams (all from USA) discuss links among whole-plant demand for the products of photosynthesis, leaf carbohydrate status, photosystem II efficiency and photoinhibition, and NPQ. Chap. 24, by Barbara Demmig-Adams (USA), Seok-Chan Koh (Korea), Christopher M. Cohu (USA), Onno Muller (Germany), Jared J. Stewart (USA), and William W. Adams III (USA), provides an overview of differences in the capacity for NPQ as dependent on plant species and the environment. Erik H. Murchie (UK) and Jeremy Harbinson (The Netherlands) discuss measurements and the diverse manifestations of NPQ across scales in Chap. 25. In Chap. 26, Michel Havaux (France) and José I. García-Plazaola (Spain) discuss the overlapping antioxidant functions of zeaxanthin and tocopherols ("vitamin E"). Fermín Morales, Javier Abadía, and Anunciación Abadía (all from Spain) summarize findings about thermal energy dissipation in plants growing under unfavorable soil conditions in Chap. 27. The final Chap. 28, by Barbara Demmig-Adams, Jared J. Stewart, and William W. Adams III (all from USA), places chloroplast photoprotection into the context of the control of cellular redox state, and outlines possible trade-offs between the abiotic and biotic defenses of plants.

By bringing together chapters describing approaches from different disciplines, such as physics/chemistry and biology, this book also offers directions for future progress via an even closer integration of these disciplines. For example, while physics/chemistry offers powerful, highly exact spectroscopic measurements, biology offers rigorously defined contrasting states of the plant/algal system for analysis. Moreover, mutant analysis has contributed to the important conclusion that elimination of one of the steps in the cascade of photoprotective processes leads to augmentation of others. One promising future direction is thus to complement existing studies with the employment of spectroscopic approaches to the analysis of biological wildtype systems carefully defined as having high versus low electron transport capacities (photochemical quenching capacities) in all possible combinations with high versus low thermal dissipation capacities (non-photochemical quenching capacities).

We are grateful for the dedication and patience of the authors in making this volume possible. We, the editors, learned much from our communication with the authors and hope that the authors and readers of this volume share this sentiment and the sense of excitement and inspiration that surrounded much of the work on this book. We are also most grateful to series editor Tom Sharkey with his sure sense of direction and great insight. Furthermore, three of us (B.D-A., G.G. and W.W.A.III) thank the indomitable Govindjee who wore multiple hats as series editor, editor of this volume, and co-author of two chapters.

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The Editors

Barbara Demmig-Adams (*second from left*) and William W. Adams III (*far right*) with their children Robert Adams (*first from left*) and Melanie Adams (*third from left*)

Barbara Demmig-Adams and **William W. Adams III** are Professors in the Department of Ecology and Evolutionary Biology at the University of Colorado at Boulder, USA. **Barbara Demmig** received her undergraduate degree (1979) in biology and chemistry and her graduate degree (1984) in plant physiology (with the late Prof. Hartmut Gimmler) from the Universität Würzburg. She subsequently spent two eventful years (1984–1986) as a postdoctoral fellow in the laboratory of Prof. Olle Björkman (Department of Plant Biology, Carnegie Institution of Washington) in Stanford, California. Barbara and Olle characterized the photoprotective thermal energy dissipation that occurs in the antenna pigments of photosystem II, including the fact that this process can become sustained in leaves of evergreens thereby lowering the photon yield of photosystem II for prolonged periods.

William attended the University of Kansas, receiving degrees in biology (1981) and atmospheric sciences (1983) as well as a Master's degree (1984) in botany (investigating adaptations of epiphytic bromeliads from Mexico under the guidance of Prof. Craig E. Martin). This was followed by 18 months (1984–1985) of research in Reno, Nevada and Death Valley, California, for the first half of his Ph.D. work.

During this time, William and Barbara began to collaborate personally and professionally across the Sierra Nevada divide that separated Reno and Stanford. Barbara returned to Würzburg in 1986 and provided the first evidence that the xanthophyll zeaxanthin, formed from violaxanthin under excess light, is involved in thermal energy dissipation. While Barbara was in Germany pursuing the role of zeaxanthin, William completed another 17 months of research in Canberra and at three field sites in Australia, resulting in a Ph.D. (1987) from the Australian National University under Prof. C. Barry Osmond's mentorship. This work centered on photoinhibition in crasulacean acid metabolism (CAM) plants, and included the first reports of photoinhibition and photoprotection under natural conditions in the field. With the support of a North Atlantic Treaty Organization (NATO) postdoctoral fellowship and a fellowship from the Alexander von Humboldt Foundation, William then spent 2 years at the Universität Würzburg, where the personal and professional collaboration with Barbara became more firmly established. In the spring of 1988, Barbara completed her habilitation in plant biology (at the Lehrstuhl II of Prof. Otto L. Lange in Würzburg) and Barbara and William made their union official. They moved to the University of Colorado in 1989, saw their personal collaboration come to fruition with two children (Robert and Melanie), and continued their collaborative scientific efforts on various aspects of the ecology and physiology of zeaxanthin-dependent thermal dissipation.

One focus of their work has been the study of unique modifications to photoprotective energy dissipation in evergreen species. They have used tropical evergreens as models for the role of sustained thermal dissipation during shade-sun acclimation, and conifers and other evergreen species to study its importance in acclimation during Colorado winters. These studies have included ecological, comparative, and mechanistic approaches to integrate photoprotective energy dissipation and photoinhibition into whole plant functioning. This has also led them to evaluate the influence of foliar carbon-export pathways on the acclimation of photosynthesis. In addition, Barbara has had a long-standing interest in the role of zeaxanthin and other plant protective compounds in human health. Their research has been cited frequently by colleagues, leading to their recognition as highly cited researchers in the Plant & Animal Science category by the Institute for Scientific Information (http://isihighlycited.com/). Furthermore, William has been honored for his efforts in teaching by University of Colorado students (Mortar Board Certificate of Recognition for Exceptional Teaching, 2000), and both have been recognized for their teaching by faculty peers (Boulder Faculty Assembly Excellence in Teaching Award, to William in 2004 and to Barbara in 2010). Barbara was elected to *Leopoldina* (National Academy of Sciences of Germany, Austria, and Switzerland) in 2011, and appointed Professor of Distinction at the University of Colorado in 2013.

Győző Garab, born in 1948, is the Head of the Laboratory for Photosynthetic Membranes (since 1987), at the Institute of Plant Biology, Biological Research Center, Hungarian Academy of Sciences, Szeged. After obtaining his *Diplom* (equivalent to M.Sc. degree) in Physics in 1971 from the University of Szeged, he switched from solid-state physics to biology, and joined the newly formed Photosynthesis Group led by Ágnes Faludi-Dániel (1929-1986) in the Biological Research Center (BRC), a modern basic biology institute that is now a Center of Excellence of the European Union. His Ph.D, in 1974, was on the "*Band-structure of the 77K fluorescence of thylakoid membranes*", which he showed to originate from six different chlorophyll forms. During his Ph.D. studies and as a young postdoc, he had several 2–4 month-long fellowships to foreign laboratories. In the Service de Biophysique, Commissariat à l'Ènergie Atomique (CEA) Saclay (France), hosted by Jacques Breton, he received an excellent introduction to pioneering research on the orientation of pigment molecules.

Systematic studies in the 1970s and 1980s in several laboratories, including the BRC, led to the recognition of what is known today as a universal property, i.e., that the pigment molecules in all mature photosynthetic membranes and pigment-protein complexes are non-randomly oriented with respect to the membrane plane and the protein axes. In other visits to Saclay, he worked with Jack Farineau on the slow (ms) rise of the electrochromic absorbance transients related to proton pumping. In the Institut de Biologie Physico-Chimique, working with Pierre Joliot and also in collaboration with Guy Paillotin (CEA, Saclay), he provided an understanding of the nature of light-induced fast and slow light scattering transients in intact algal cells. Also in the 1970s, he visited the Moscow State University, where, in the laboratory of Andrey B. Rubin and Vladimir Z. Paschenko, he performed picosecond fluorescence spectroscopy experiments. Later, in Szeged, his attention turned to the interaction between the respiratory and the photosynthetic electron transport chains, and to chlororespiration. His studies provided the first experimental evidence for the existence of chlororespiration in higher plants – a subject that was later explored more systematically in collaboration with Claudia Büchel.

During his visits to USA, between 1985 and 1990, his circular dichroism spectroscopy and microscopy experiments revealed what has been termed the macrodomain (long-range order) organization of the complexes in the thylakoid membranes – ideas stemming from the Szeged laboratory with key experiments performed at the Brookhaven National Laboratory, in the laboratory of Geoffrey Hind, and in Albuquerque, with Carlos Bustmante. These highly organized macroassemblies, extended ordered arrays of light-harvesting and core complexes of photosystem II (LHCII:PS II), have turned out to be most interesting for their ability to undergo light-induced reversible structural reorganizations that are also observed in lamellar aggregates of isolated LHCII and are largely independent of the photochemical activity of thylakoid membranes.

These experiments, conducted in Szeged together with his Ph.D. student, Virginijus Barzda (now at the University of Toronto Mississauga), led to the discovery of what they termed the thermo-optic mechanism in photosynthesis, i.e., elementary structural changes induced by ultrafast thermal transients due to the dissipation of excess excitation energy in light harvesting antenna complexes. The mechanisms and effects of excess-excitation energy dissipation remains the focus of his research group. The formation of LHCII:PS II macrodomains has also offerred a mechanism to sort the two photosystems between the stacked and unstacked thylakoid membrane regions, and thus aimed at the understanding of the self-assembly and 3D ultrastructure of granal thylakoid membranes, which he studied together with László Mustárdy, using electron tomography in the laboratory of Carmen Mannella (Wadsworth Center, Albany, NY). In order to monitor the structural-functional plasticity of these and other highly organized multilamellar systems, he turned to small-angle neutron scattering. This non-invasive technique revealed a much greater-than-expected structural flexibility in isolated thylakoid membranes as well as in intact cyanobacteria, algal cells and higher plant leaves. Another form of structural plasticity of high interest to his group is the (enigmatic) role of non-bilayer lipids in the bilayer thylakoid membranes. Phosphorus-31 NMR experiments, conducted in collaboration with Herbert van Amerongen, have shown the presence of non-bilayer lipid phases in functional thylakoid membranes.

Győző has served as secretary general of the XI International Biophysics Congress (Budapest, 1993), chairman of the XI International Congress on Photosynthesis (Budapest, 1998), and has organized several international schools, conferences and workshops on photosynthesis and biophysics. He has also served(s) in different international and Hungarian committees and societies, including the Biophysics of Photosynthesis Programme of the European Science Foundation, the International Society for Photosynthesis Research, the Hungarian Biophysical Society, and the Photosynthesis – Life from Light – Foundation (Hungary). He is co-owner and manager of the spin-off company Biofotonika R&D Ltd. He has been awarded the Straub medal (from the BRC), the Ernst Jenő medal (from the Hungarian Biophysical Society), the Farkas Gábor medal (from Scientia Amabilis Foundation for the Hungarian Plant Biology), the title of Knight (from the International Order of Inventors) and the Széchenyi Professor fellowship (from the Ministry of Education of Hungary).

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