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 Polívka (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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