

Advances in Photosynthesis and Respiration 45
Including Bioenergy and Related Processes

Anthony W. D. Larkum
Arthur R. Grossman
John A. Raven *Editors*



Photosynthesis in Algae: Biochemical and Physiological Mechanisms

Photosynthesis in Algae: Biochemical and Physiological Mechanisms



Living stromatolites in intertidal region of Carbla in Hamelin Pool, Shark Bay, Western Australia. These biologically-generated structures are basically small limestone rocks with a superficial mat of many kinds of eubacteria including many cyanobacteria and several kinds of anoxygenic photosynthetic bacteria and sulfur bacteria. They are thought to be similar to fossil structures, which were the first known living structures on the Earth more than 3.5 billion years ago, and which were also the site of the precursors to cyanobacteria and anoxygenic photosynthetic bacteria. Photo by Warwick Hillier, Research School of Biological Sciences, Australian National University, Canberra, Australia

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

VOLUME 45

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 45: Photosynthesis in Algae: Biochemical and Physiological Mechanisms

Collectively, algae are a diverse group of eukaryotes including large multicellular organisms such as kelps and many unicellular species. The number of algal species on the planet is not known, but estimates suggest tens of thousands. Their diversity ensures the algae are represented in many, if not all, ecosystems, and as such, they are of major importance as primary producers: they also represent an important group of organisms that benefit mankind. Many nations and cultures already utilize algae for food and fertilizer and a wide range of products such as agar and alginates. It is also recognized that algal cells have the potential to produce more biomass per unit area in a year than any other form of biomass: there is thus great potential for the production of biofuels and other high-value organic compounds.

In volume 45 of the *Advances in Photosynthesis and Respiration* (AIPH) series, Anthony Larkum, Arthur Grossman, and John Raven have assembled a team of experts on algal biochemistry, biophysics, and molecular biology to consider the diversity of algal photosynthesis, recognizing that these organisms (including the *Cyanobacteria*) can provide new knowledge for creative ways to apply algal photosynthesis to the many issues facing humanity today, from conservation biology to food and energy security. This volume joins volume 14 (*Photosynthesis in Algae*, edited by Anthony Larkum, Susan

Douglas, and John Raven) in providing an extensive introduction to the molecular mechanisms utilized by the algae and the enormous potential that is stored in the gene pool of this vast group of organisms.

Authors of Volume 45

The current volume exemplifies the tradition of the AIPH book series in being an international book. It has authors from the following 12 countries: Australia (6), Canada (1), the Czech Republic (3), France (4), Germany (1), Italy (4), Hungary (2), Portugal (1), Sweden (1), Switzerland (1), the UK (4), and the USA (9). There are 37 authors (including the three editors) who, as noted above, are experts in the field of algal photosynthesis. Alphabetically (by last names), they are John Beardall, Erica Belgio, Debashish Bhattacharya, Claudia Büchel, Douglas Campbell, Anna Paola Casazza, Paul M.G. Curmi, Geoffry A. Davis, Jeffery A. Davis, Nicholas Fisher, Myriam M.M. Goudet, Howard Griffiths, Arthur R. Grossman, Parisa Heydarizadeh, Radek Kaňa, Atsuko Kanazawa, Diana Kirilovsky, David Kramer, Anthony W.D. Larkum, Justine Marchand, Moritz Meyer, Peter Neofotis, Ondřej Prášil, Dana C. Price, Antonietta Quigg, Harry W. Rathbone, John A. Raven, Jean-David Rochaix, Stefano

Santabarbara, Benoît Schoefs, João Serôdio, Cornelia Spetea, Milan Szabo, Imre Vass, and Robert Willows. We are grateful for their efforts in making this important volume.

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Special 25% discounts are available to members of the International Society of Photosynthesis Research (ISPR, <http://www.photosynthesis-research.org/>). See <http://www.springer.com/ispr>.

Future Advances in Photosynthesis and Respiration and Other Related Books

The readers of the current series are encouraged to watch for the publication of 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: Biofuels and Value-Added Products* (Editors: Anthony Larkum and John Raven)
- *Our Photosynthetic Planet* (Editors: Mike Behrenfeld, Joe Berry, Lianhong Gu, Nancy Jiang, Anastasia Romanou, and Anthony Walker)
- *Modeling Photosynthesis and Growth* (Editors: Xin-Guang Zhu and Thomas D. Sharkey)

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

Algae, Cyanobacteria: Biofuel and Bioenergy
 Artificial Photosynthesis
 ATP Synthase: Structure and Function
 Bacterial Respiration 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/coediting any of the above listed books or being an author, please send an e-mail to Tom Sharkey (tsharkey@msu.edu) and/or to 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 Anthony Larkum, Arthur Grossman, and John Raven for their outstanding editorial work; they have collectively done an excellent 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 37 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 of SPi Global, India, for directing the typesetting of this book. Once again, his expertise has been crucial in guiding the final steps that have brought this book to completion. We also thank Jacco Flipsen

and Ineke Ravesloot (of Springer) for their friendly working relation with us that led to the production of this book and thank Zuzana Bernhart and her team at Springer for their ongoing organization and assistance with the AIPH series.

January 6, 2020

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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)

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. in Chemistry, Botany, and Zoology and his M.Sc. in Botany and Plant Physiology in 1952 and 1954, respectively, from the University of Allahabad. He learned his Plant Physiology from Shri Ranjan, who was a student of Frederick Frost Blackman (of Cambridge, UK). He then 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 on *photosynthesis education*. He has served on the faculty of the UIUC for ~40 years.

Govindjee's honors include Fellow of the American Association for the Advancement of Science (AAAS); Distinguished Lecturer of the School of Life Sciences, UIUC; Fellow and Lifetime Member of the National Academy of Sciences (India); President of the American Society for Photobiology (1980–1981); Fulbright Scholar (1956), Fulbright Senior Lecturer (1997), and Fulbright Specialist (2012); Honorary President of the 2004 International Photosynthesis Congress (Montréal, Canada); First Recipient of the Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology (2006); and Recipient of the Communication Award of the International Society of Photosynthesis Research (2007) and of the Liberal Arts and Sciences Lifetime Achievement Award of the UIUC (2008). Furthermore, he has been honored many times: (1) in 2007, through two special volumes of *Photosynthesis Research*, celebrating his 75th birthday and his 50-year dedicated research in photosynthesis (Julian J. Eaton-Rye, Guest Editor); (2) in 2008, through a special international symposium on “photosynthesis in a global perspective” held in November 2008 at the University of Indore, India, this was followed by a book *Photosynthesis: Basics and Applications* (edited by S. Itoh, P. Mohanty, and K.N. Guruprasad); (3) in 2012, through *Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*, edited by Julian J. Eaton-Rye, Baishnab C. Tripathy, and Thomas D. Sharkey; (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, Czech Republic (O. Prasil [2014] *Photosynth Res* 122: 113–119); and (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 (Julian J. Eaton-Rye, Editor).

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] *Photosynthesis Research* (123:105–114) and (2) S. Jaiswal, M. Bansal, S. Roy, A. Bharati, and B. Padhi [2017] *Photosynthesis Research* (131: 351–359). Govindjee is a Coauthor of a 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 Coeditor) of many books including *Bioenergetics of Photosynthesis* (1975); *Photosynthesis* (two volumes (1982)); *Light Emission by Plants and Bacteria* (1986); *Chlorophylla 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>.



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, he entered a Ph.D. program in the Department of Energy Plant Research Laboratory at Michigan State University under the mentorship of Klaus Raschke and finished in 1979. His postdoctoral research was carried out with Graham Farquhar at the Australian National University, Canberra, where he coauthored a landmark review on photosynthesis and stomatal conductance. For 5 years, he worked in the Desert Research Institute, Reno, Nevada. After Reno, he spent 20 years as Professor of Botany at the University of Wisconsin in Madison. In 2008, he became Professor and Chair of the Department of Biochemistry and Molecular Biology at Michigan State University. In 2017, he stepped down as Department Chair and moved to the MSU-DOE Plant Research Laboratory completing a 38-year sojourn back to his beginnings. His 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. His 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, 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. He has coedited three books, the first on trace gas emissions from plants in 1991 (with Elizabeth Holland and Hal Mooney), volume 9 of this series (with Richard Leegood and Susanne von Caemmerer) on the physiology of carbon metabolism of photosynthesis in 2000, and volume 34 (with Julian J. Eaton-Rye and Baishnab C. Tripathy), *Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*. He has been Coeditor 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 for 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 in both biogenesis and electron transport as well as the role of additional protein factors in the assembly of Photosystem II. He has been a Consulting

Editor for the Advances in Photosynthesis and Respiration series since 2005 and edited volume 34 (with Baishnab C. Tripathy and Thomas D. Sharkey), *Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*. He is also an Associate Editor for the *New Zealand Journal of Botany* and for the Plant Cell Biology section *Frontiers in Plant Science*. He edited *Frontiers Research Topic Assembly of the Photosystem II Membrane-Protein Complex of Oxygenic Photosynthesis* (with Roman Sobotka) in 2016, which is available as an eBook [ISBN 978-2-88945-233-0]. He has served as the President of the New Zealand Society of Plant Biologists (2006–2008) and of the New Zealand Institute of Chemistry (2012) and has been a Member of the International Scientific Committee of the Triennial International Symposium on Phototrophic Prokaryotes (2009–2018). Currently, he is the Secretary of the International Society of Photosynthesis Research.

Contents

From the Series Editors	vii
Series Editors	xv
Preface: A Brief Introduction to the Algae	xxv
About the Editors	xxvii
Contributors	xxxi
Author Index	xxxv

Part I Introductory Chapters

1 Recent Advances in the Photosynthesis of Cyanobacteria and Eukaryotic Algae	3–9
<i>Anthony W. D. Larkum, Arthur R. Grossman, and John A. Raven</i>	
I. Algal Systematics	4
II. Cyanobacteria	4
III. Crystal Structures	4
IV. Light Harvesting	5
V. Photoinhibition	6
VI. Dinoflagellates and Coral Bleaching	6
VII. Carbon Uptake and Metabolism (See Chap. 7 & 8)	6
VIII. Water-Water Cycles (See Chap. 8)	7
References	8
2 The Algal Tree of Life from a Genomics Perspective	11–24
<i>Debashish Bhattacharya and Dana C. Price</i>	
I. Introduction	11
II. Why Inferring the Algal Tree of Life Is Non-trivial	12
III. Examples of Reticulate Behavior Among Algal Genes	14
IV. From Designer Datasets to Whole Genomes	18
V. Conclusions	20
References	22

Part II Molecular Genetics of Algae

3	Chlorophyll-Xanthophyll Antenna Complexes: In Between Light Harvesting and Energy Dissipation	27–55
	<i>Christo Schiphorst and Roberto Bassi</i>	
	I. Introduction	27
	II. Chromophores	28
	III. The Core Complexes of PSII and PSI	31
	IV. Light Harvesting	32
	V. Antenna Complexes of PSI	37
	VI. Fucoxanthin Chlorophyll Binding Proteins	38
	VII. Photoprotection	40
	VIII. Triggers of Quenching Reactions	43
	IX. Conclusions	45
	References	45
4	The Dynamics of the Photosynthetic Apparatus in Algae	57–82
	<i>Jean-David Rochaix</i>	
	I. Introduction	57
	II. Adaptation to Changes in Light Conditions	60
	III. Response of the Photosynthetic Apparatus to Micronutrient Depletion	69
	IV. Long Term Response: Changes in Nuclear and Chloroplast Gene Expression	71
	V. Conclusions and Perspectives	74
	References	75
5	Biosynthesis of Chlorophyll and Bilins in Algae	83–103
	<i>Robert D. Willows</i>	
	I. Introduction	83
	II. Diversity of Chlorophylls in Algae	84
	III. Diversity of Bilins in Algae	86
	IV. Overview of Biosynthesis of Bilins and Chlorophylls	88
	V. Biosynthesis of Protoporphyrin IX	89
	VI. Biosynthesis of Bilins from Protoporphyrin and Function of Bilin Lyases	92
	VII. Biosynthesis of Chlorophylls from Protoporphyrin IX	93
	VIII. Synthesis of Chlorophyll <i>b</i> , <i>d</i> and <i>f</i>	96
	IX. Concluding Remarks	97
	Bibliography	97

Part III Biochemistry and Physiology of Algae

6	Chloroplast Ion and Metabolite Transport in Algae	107–139
	<i>Justine Marchand, Parisa Heydarizadeh, Benoît Schoefs, and Cornelia Spetea</i>	
	I. Introduction	107
	II. Chloroplast Ion Transport	113
	III. Chloroplast Metabolite Transport	119
	IV. Strategies for Identification of Missing Algal Transporters	127
	V. Conclusions and Perspectives	128
	References	129
7	Structural and Biochemical Features of Carbon Acquisition in Algae	141–160
	<i>John Beardall and John A. Raven</i>	
	I. Introduction	141
	II. Carbon Assimilation	142
	III. Occurrence of CCMs	145
	IV. Mechanisms of CCMs Versus Diffusive CO ₂ Fluxes	146
	V. Structural Aspects of CO ₂ Acquisition	151
	References	153
8	Light-Driven Oxygen Consumption in the Water-Water Cycles and Photorespiration, and Light Stimulated Mitochondrial Respiration	161–178
	<i>John A. Raven, John Beardall, and Antonietta Quigg</i>	
	I. Introduction	162
	II. The Evidence of Light-Dependent O ₂ Uptake	162
	III. Possible Mechanisms of Light-Driven O ₂ Uptake	163
	IV. Functions of the Light-Driven O ₂ Uptake Processes	169
	V. Conclusions	171
	References	171
9	The Algal Pyrenoid	179–203
	<i>Moritz T. Meyer, Myriam M. M. Goudet, and Howard Griffiths</i>	
	I. Introduction	179
	II. Pyrenoid Structure & Function: Lessons from <i>Chlamydomonas</i>	188
	III. When, Where, How and Whither: From Paleo-Origins to Future Synthetic Biology	194
	References	196

Part IV Light-Harvesting Systems in Algae

10	Light-Harvesting in Cyanobacteria and Eukaryotic Algae: An Overview	207–260
	<i>Anthony W. D. Larkum</i>	
	I. Introduction	208
	II. The Photosynthetic Pigments of Cyanobacteria and Eukaryotic Algae	210
	III. The Evolution of Protists with Plastids (Algae)	222
	IV. The Need for Light Harvesting Antennas	231
	V. Light-Harvesting Antennas in Cyanobacteria and Eukaryotic Algae	232
	VI. Control of Energy Supply to PSI and PSII: State Transitions, Absorption Cross-Sectional Changes and Spillover	233
	VII. Non-photochemical Quenching	242
	VIII. Reactive Oxygen Species (ROS) and Other Photoprotective Mechanisms	246
	References	251
11	Light Harvesting by Long-Wavelength Chlorophyll Forms (Red Forms) in Algae: Focus on their Presence, Distribution and Function	261–297
	<i>Stefano Santabarbara, Anna Paola Casazza, Erica Belgio, Radek Kaňa, and Ondřej Prášil</i>	
	I. Long Wavelength (“Red”) Chlorophyll a Forms: Historical Perspective on Their Discovery and General Overview	262
	II. Long Wavelength Chlorophyll Forms Associated to Photosystem I	264
	III. Long Wavelength Chlorophyll Forms Associated to Photosystem II	270
	IV. Survey of Cyanobacterial and Algal Species for the Presence of Long-Wavelength Chlorophyll Forms	274
	V. Effect of Long Wavelength Chlorophyll Forms on the Photochemical Quantum Efficiency	278
	VI. Concluding Remarks	289
	References	291
12	Diversity in Photoprotection and Energy Balancing in Terrestrial and Aquatic Phototrophs	299–327
	<i>Atsuko Kanazawa, Peter Neofotis, Geoffry A. Davis, Nicholas Fisher, and David M. Kramer</i>	
	I. Introduction	299
	II. Energy Storage and Regulation in Oxygenic Photosynthesis	300
	III. The pmf Paradigm for Regulation of the Photosynthetic Light Reactions	302
	IV. The Need to Coordinate q_E and Photosynthetic Control	303

V.	The Critical Need to Balance the Chloroplast Energy Budget	303
VI.	Regulation of CEF	306
VII.	Modulation of <i>pmf</i> Feedback Regulation and Its Impact on Energy Balancing	307
VIII.	How Diverse Photoprotective Mechanisms Challenge the <i>pmf</i> Paradigm and Open Up New Questions	311
IX.	Coping with ATP Excess or NADPH Deficit	314
X.	Conclusions and Perspective	317
	References	318
13	Photoinhibition of Photosystem II in Phytoplankton: Processes and Patterns	329–365
	<i>Douglas A. Campbell and João Serôdio</i>	
I.	Introduction: Scope & Terms	329
II.	Mechanisms of Photoinactivation	330
III.	Measurement and Parameterization of PSII Photoinactivation and Counteracting PSII Repair	332
IV.	Patterns of Photoinactivation and Repair Across Phytoplankton	342
V.	Summary	357
	References	359
14	Modulating Energy Transfer from Phycobilisomes to Photosystems: State Transitions and OCP-Related Non-Photochemical Quenching	367–396
	<i>Diana Kirilovsky</i>	
I.	Introduction	367
II.	The Phycobilisome	368
III.	The OCP-Related NPQ Mechanism	370
IV.	Cyanobacterial State Transitions	381
V.	Perspectives and Conclusions	387
	References	388
15	Coherent Processes in Photosynthetic Energy Transport and Transduction	397–439
	<i>Harry W. Rathbone, Paul M. G. Curmi, and Jeffrey A. Davis</i>	
I.	Introduction	398
II.	Quantum Behaviour, Coherence and Spectroscopy	400
III.	Diversity of Biological Light Harvesting	408
IV.	Deeper Exploration of Energy Transport in Biological Systems	414
V.	Summary and Conclusions	432
VI.	New Horizons	434
VII.	The Wrong Question: “Does Evolution Select for Non-trivial Quantum Effects?”	435
	References	435

16	Light-Harvesting Complexes of Diatoms: Fucoxanthin-Chlorophyll Proteins	441–457
	<i>Claudia Büchel</i>	
	I. Introduction	441
	II. Genes Coding for FCP Polypeptides	442
	III. Supramolecular Organisation of FCP Complexes	443
	IV. Arrangement of Photosynthetic Complexes of Diatoms in the Thylakoid Membrane	444
	V. Pigmentation of FCPs and Excitation Energy Transfer	446
	VI. FCPs in Photoprotection	448
	VII. Regulation of FCP Expression	450
	VIII. Open Questions	452
	References	452
17	A Review: The Role of Reactive Oxygen Species in Mass Coral Bleaching	459–488
	<i>Milán Szabó, Anthony W. D. Larkum, and Imre Vass</i>	
	I. Introduction	460
	II. Review of the Experimental Evidence for Reactive Oxygen Species in Corals and <i>Symbiodinium</i> (Symbiodiniaceae)	464
	III. Molecular Physiology and Bioinformatics	468
	IV. The Detection and Role of Singlet Oxygen	469
	V. Symbiosis and Exocytosis in Corals	471
	VI. The Possible Mechanisms of Coral Bleaching	473
	VII. Bleaching in Anemones	479
	VIII. Conclusions	480
	References	482
	Correction to: Photosynthesis in Algae: Biochemical and Physiological Mechanisms	C1
	Subject Index	489–514

Preface: A Brief Introduction to the Algae

This book covers the process and development of photosynthesis in algae. Photosynthesis is the process by which light energy, predominantly from the sun, is converted into the energy of organic compounds. These photosynthetic products underpin almost all life on Earth; previously, with geological processes, they produced petroleum and coal, and in the future, they can contribute to a wide range of ecological and societal needs. As the world is using up its reserves of petroleum and coal at increasing rates, it is becoming important to understand the replenishment processes, with both biological and geological systems involved. At the same time, the alarming increases in greenhouse gases and the harmful effects on global climate make the use of these fossil fuels less and less desirable. The alternative is to develop new technologies for solar energy conversion, and these will undoubtedly involve algal biofuel production on a massive scale. Much work has been done in this area over the last two decades. On the purely mechanical-physical level, it is possible to set up solar farms and convert sunlight into electrical energy. And from there, it is possible to generate hydrogen by splitting water or to drive chemical half cells involving algae or components of algae to generate hydrogen or useful organic products. Alternatively, it is possible to “farm” algae in a variety of ways to generate fuels or value-added products. However, before any of these futuristic developments can be envisaged, it is necessary to know much more about the photosynthetic processes that occur on the Earth today and the role that algae play in the ecosystems of the Earth. Algae are eukaryotic organisms that exist in a multiplicity of forms and carry out oxygenic photosynthesis. In this book,

our definition also includes *Cyanobacteria* (bacteria which nevertheless possess a process of photosynthesis able to split water). About half a billion years ago (BYA), one branch of green algae (see below) finally colonized the land and gave rise to “land plants” (embryophytes), and all these plants inherit to a greater or lesser extent the photosynthetic mechanisms of their algal forebears. So algae can be used directly in the freshwater and marine systems of the world to generate fuels or value-added organic products, or they can be studied to understand how to enhance the photosynthetic systems that developed from a fraction of the gene pool available in algae.

The Evolution of Photosynthesis

Photosynthesis evolved on the Earth at a very early stage, maybe as early as 3.8 billion years ago (BYA). The earliest mechanisms would have used available sources of hydrogen including hydrogen gas itself, which was much more abundant on the early Earth. The organisms were anaerobic bacteria, but as available sources of reductant were depleted, a new form of photosynthesis was evolving by at least 3 BYA, and maybe much earlier in a primitive form, which could split water and use the hydrogen of water as its source. By 2.45 BYA, cyanobacteria had fully evolved and were liberating oxygen into the Earth’s atmosphere. The oxygenation of the atmosphere in the Great Oxidation Event (GOE) was a revolutionary step, which made possible the endosymbiosis of aerobic proteobacteria and photosynthetic cyanobacteria in protists, which, with genetic integration, evolved into mitochondria and plastids.

The Evolution of Algae

Some dozen phyla of eukaryotic protist organisms, from a total of 60 odd phyla, were algae, i.e., they possessed plastids (photosynthetic organelles developed from cyanobacteria by endosymbiosis) and were oxygenically photosynthetic. After about 2 billion years of evolution and massive diversification, the scene was set for the colonization of the land. One phylum, the green algae, gave rise to a multicellular subgroup, the streptophytes. The streptophytes colonized the land, becoming embryophytes and giving rise to mosses, ferns, and cone-bearing and flowering plants. At the same time, a multicellular group of protists evolved which gave rise to the animals, which also colonized the land, leading to all the animal groups with which we are familiar and eventually leading just 2 million years ago, or so, to man.

The Evolution of Eukaryotic Algae

The oldest algae date to at least 1.5 BYA and are red algae. However, some of the algae appear to be much more recent. For example, the diatoms that have a characteristic outer “shell,” the frustule, are only found in sediments which are from 135 MYA. Other algal groups do not have a characteristic skeleton and cannot be dated in this way. Their origins can only be estimated by phylogenetic means, that is, by comparing their DNA with known fossil ages. Such studies reveal a rich and diverse lineage to the algae, where a “primary endo-

symbiosis” that involved the transfer of all the modern algal pigments was followed by a secondary, and in some cases tertiary, endosymbiosis with interesting pigment combinations. On one of these lines, that leading to the Apicomplexans, of which the malarial parasite is an example, all photosynthetic pigments and most of the photosynthetic mechanisms were lost.

The Rainbow of Algal Photosynthetic Mechanisms

With this rich and diverse history, many different patterns of photosynthesis evolved to suit a rainbow of light climates and ecological niches. Today, it is instructive to understand the fundamental differences involved. However, it is just as important that our understanding reveals how to utilize these varying arrays of pigments and photosynthetic approaches in devising technological approaches to harvesting solar energy by algae.

This book is divided into 17 chapters. These deal with all the major aspects of algal photosynthesis. However, the use of algae to produce biofuels and value-added products has been left to a second volume.

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About the Editors



Anthony (Tony) Larkum is Emeritus Professor at the University of Sydney, Australia, where he was a Staff Member in Plant Sciences for 25 years. He has had a distinguished career in plant physiology, marine biology and phylogenetics. In addition, he has published a book on Charles Darwin and his cousin, William Darwin Fox, entitled *A Natural Calling: Life, Letters and Diaries of Charles Darwin and William Darwin Fox* (Springer Verlag). One of the first scientists to apply underwater techniques, he has contributed over a wide range of fields to advancing the study of underwater organisms, including cyanobacteria, marine algae, seagrasses and corals. In addition to this, he has contributed extensively to the field of light-harvesting and photoinhibition in photosynthetic organisms, having published many

papers, a number of reviews and several books on the subject. Overall, he has published 254 papers in scientific journals; and these have an h-index of 65 (35 since 2014). His most cited papers are on coral bleaching in corals (632) and the discovery of fluorescent pigments in corals (590). And his third most cited work is for coediting a book on seagrasses (*Seagrasses: Biology, Ecology and Conservation*, Springer) in 2006. The current book is the culmination of a lifetime of work in the many fields of photosynthesis in cyanobacteria, eukaryotic algae and seagrasses. His contribution to these fields has been acknowledged by awards and election to scientific committees and boards of scientific journals over the years. He is currently on the Editorial Committee of the *Journal of the Royal Society Interface*.



Arthur Robert Grossman has been a Staff Scientist at the [Carnegie Institution for Science](#), Department of Plant Biology, since 1982 and holds a courtesy [appointment](#) as Professor in the Department of Biology at [Stanford University](#). He has performed research across fields ranging from [plant biology](#), [microbiology](#), [marine biology](#), [ecology](#), genomics, engineering and [photosynthesis](#) and initiated large-scale algal genomics by leading the *Chlamydomonas* genome project. In 2002, he received the Darbaker Prize ([Botanical Society of America](#)) for work on microalgae and in 2009 received the [Gilbert Morgan Smith Medal](#) ([National Academy of Sciences](#)) for the quality of his publications on marine and freshwater algae. In 2017, he was Chair of the Gordon Research Conference on Photosynthesis and gave the Arnon endowed lecture on photosynthesis in Berkeley in March 2017. He has given

numerous plenary lectures and received a number of fellowships throughout his career, including the Visiting Scientist Fellowship, Department of Life and Environmental Sciences (DiSVA), Università Politecnica delle Marche (UNIVPM) (Italy, 2014), the Lady Davis Fellowship (Israel, 2011) and most recently the Chaire Edmond de Rothschild (to work at the IBPC in Paris in 2017–2018). He has been Co-Editor-in-Chief of *Journal of Phycology* and has served on the editorial boards of many well-respected biological journals including the *Annual Review of Genetics*, *Plant Physiology*, *Eukaryotic Cell*, *Journal of Biological Chemistry*, *Molecular Plant* and *Current Genetics*. He has also served on scientific advisory boards for both nonprofit and for profit companies including Phoenix Bioinformatics, Exelixis, Martek Biosciences, Solazyme/TerraVia, Checkerspot and Phycoil.



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