

# Photosynthesis in Algae

*Edited by*

**Anthony W.D. Larkum**

*School of Biological Sciences,  
University of Sydney, Australia*

**Susan E. Douglas**

*National Research Council,  
Institute for Marine Biosciences, Canada*

and

**John A. Raven**

*Department of Biological Sciences,  
University of Dundee, U.K.*



KLUWER ACADEMIC PUBLISHERS  
DORDRECHT / BOSTON / LONDON

# Contents

<b>Editorial</b>	v
<b>Contents</b>	ix
<b>Preface</b>	xvi
<b>Color Plates</b>	CP-1

## *Introductory Chapters*

---

<b>1 The Algae and their General Characteristics</b>	1–10
<i>Susan E. Douglas, John A. Raven and Anthony W. D. Larkum</i>	
Summary	1
I. Introduction	2
II. The Algae: Their Origins and Diversity	2
III. The Green, Red and Brown Algae	4
IV. The Chromophytes	4
V. The Chlorarachniophytes	7
VI. The Euglenophytes	7
VII. Algal Genomes	7
VIII. Algae as Sources of Natural Products	8
IX. Concluding Remarks	8
Acknowledgements	9
References	9
<b>2 Algal Plastids: Their Fine Structure and Properties</b>	11–28
<i>Anthony W. D. Larkum and Maret Vesk</i>	
Summary	11
I. Introduction	12
II. Origin of Plastids	12
III. Chlorophyte Plastids	13
IV. Rhodophyte Plastids	16
V. Cyanellae (Glaucocystophyte Plastids)	18
VI. Cryptophyte Plastids	18
VII. Chlorarachniophyte Plastids	20
VIII. Euglenophyte Plastids	20
IX. Dinoflagellate Plastids	20
X. Chrysophyte (Ochrophyte) Plastids	22
XI. Phaeophyte, Bacillariophyte, Eustigmatophyte, Raphidophyte, Synurophyte, Pelagophyte, Silicoflagellate, Pedinellid and Xanthophyte Plastids	23
XII. Haptophyte Plastids	23

XIII. Apicomplexan Plastids	24
XIV. Kleptoplastids	24
XV. Microstructure of the Thylakoid Membrane	24
Acknowledgments	26
References	26
<b>3 The Photosynthetic Apparatus of Chlorophyll <i>b</i>- and <i>d</i>-Containing Oxyphotobacteria</b>	<b>29–62</b>
<i>Frédéric Partensky and Laurence Garczarek</i>	
Summary	29
I. Introduction	30
II. Advances in Photosynthesis in Chlorophyll <i>b</i> - and <i>d</i> -Containing Oxyphotobacteria	32
III. Green Oxyphotobacteria and the Endosymbiotic Theory of Green Plastids Evolution	51
IV. Concluding Remarks	55
Acknowledgments	56
References	56
<b>Molecular Genetics of Algae</b>	
<b>4 Structure and Regulation of Algal Light-Harvesting Complex Genes</b>	<b>63–82</b>
<i>Dion G. Durnford</i>	
Summary	63
I. Introduction	64
II. Higher Plant Light-Harvesting Complexes	64
III. Algal Light-Harvesting Complexes	67
IV. Origin and Evolution of the Light-Harvesting Antennae	76
V. Concluding Remarks	77
Acknowledgments	77
References	77
<b>5 Functional Analysis of Plastid Genes through Chloroplast Reverse Genetics in Chlamydomonas</b>	<b>83–94</b>
<i>Jean-David Rochaix</i>	
Summary	83
I. Introduction	84
II. Algal Chloroplast Transformation	84
III. Reverse Chloroplast Genetics of Photosynthesis	85
IV. Several <i>ycfs</i> Encode Novel Proteins Involved in Photosynthesis	87
V. Chloroplast Reverse Genetics of Essential Genes of <i>Chlamydomonas</i>	89
VI. Conclusions and Prospects	92
Acknowledgments	92
References	92

<b>6 Biochemistry and Regulation of Chlorophyll Biosynthesis</b>	<b>95–131</b>
<i>A. Bruce Cahoon and Michael P. Timko</i>	
Summary	96
I. Introduction	96
II. An Overview of Tetrapterrols and Their Derivatives	96
III. Chlorophyll Forms and Their Distribution in Algal Species	98
IV. Early Steps in Chlorophyll Biosynthesis	98
V. The Pathway from ALA to Protoporphyrin IX	102
VI. The Iron Branch	107
VII. The Magnesium Branch—Chlorophyll <i>a</i> Formation	108
VIII. Biosynthesis of Chlorophyll <i>b</i> and Other Algal Chlorophylls	119
Acknowledgments	122
References	122
Summary	133
<b>Biochemistry and Physiology of Algae</b>	
<b>7 Oxygenic Photosynthesis in Algae and Cyanobacteria: Electron Transfer in Photosystems I and II</b>	<b>133–156</b>
<i>Jonathan H. A. Nugent, Saul Purton and Michael C. W. Evans</i>	
Summary	133
I. Introduction	134
II. Overview of Photosystems I and II	134
III. Mutagenesis and Genetic Engineering of the Photosystems	135
IV. Photosystem II Function	139
V. Photosystem II Structure	143
VI. Photosystem I	146
VII. Conclusions	151
Acknowledgment	151
References	151
<b>8 Oxygen Consumption: Photorespiration and Chlororespiration</b>	<b>157–181</b>
<i>John Beardall, Antonietta Quigg and John A. Raven</i>	
Summary	158
I. Introduction	158
II. Photorespiration	159
III. Chlororespiration: A Mechanism to Maintain Thylakoid Membrane Energization in the Dark?	168
Acknowledgments	178
References	179
<b>9 The Water-Water Cycle in Algae</b>	<b>183–204</b>
<i>Chikahiro Miyake and Kozi Asada</i>	
Summary	184
I. Introduction	184
II. The Water-Water Cycle in Plant Chloroplasts	185

III. Operation of the Water-Water Cycle in Cyanobacteria and Eukaryotic Algae	189
IV. Scavenging System of O <sub>2</sub> – and H <sub>2</sub> O <sub>2</sub> in the Algal Water-Water Cycle	190
V. Physiological Functions of the Water-Water Cycle in Cyanobacteria and Eukaryotic Algae	196
VI. Concluding Remarks	197
Acknowledgment	198
References	198

## **10 Carbohydrate Metabolism and Respiration in Algae 205–224**

*John A Raven and John Beardall*

Summary	205
I. Introduction	206
II. Carbohydrate Metabolism: Low M, Compounds	207
III. Carbohydrate Metabolism: Storage Polysaccharides	208
IV. Carbohydrate Metabolism: Structural Polysaccharides	209
V. Respiration: Carbon Pathways	211
VI. Respiration: Redox Reactions and Energy Conservation	213
VII. Respiration: Spatial and Temporal Aspects	218
VIII. Quantifying Carbohydrate Metabolism and Respiration in Relation to Growth and Maintenance	220
Acknowledgments	221
References	221

## **11 Carbon Acquisition Mechanisms of Algae: Carbon Dioxide Diffusion and Carbon Dioxide Concentrating Mechanisms 225–244**

*John A Raven and John Beardall*

Summary	226
I. Introduction	226
II. Rubisco Kinetic Properties in Relation to the CO <sub>2</sub> and O <sub>2</sub> Concentrations in Cyanobacterial and Algal Habitats	226
III. Lines of Evidence Used in Distinguishing Organisms Relying on Diffusive CO <sub>2</sub> Entry from Those Using Carbon Concentrating Mechanisms (CCMs)	229
IV. Occurrence and Mechanism of CCMs	230
V. Evolution of CCMs	240
VI. Conclusions and Prospects	240
Acknowledgments	241
References	241

## ***Light-Harvesting Systems in Algae***

---

## **12 Modeling the Excitation Energy Capture in Thylakoid Membranes 245–276**

*Hans-Wilhelm Trissl*

Summary	246
I. Introduction	246
II. Structural Composition of the Thylakoid Membrane	247
III. Experimental Approaches	253
IV. Kinetic Modeling of the Thylakoid Membrane	256

V. Concluding Remarks	271
Acknowledgments	271
References	272
<b>13 Light-Harvesting Systems in Algae</b>	<b>277–304</b>
<i>Anthony W. D. Larkum</i>	
Summary	278
I. Introduction	278
II. Chlorophylls	279
III. Light-Harvesting Proteins	283
IV. Optimizing Light-Harvesting Architecture	285
V. Problems with Photosystem II	287
VI. Off-Loading Excess Light Energy: Xanthophyll Cycle and Reaction Center Sinks	288
VII. Control of Light Harvesting	291
Acknowledgments	299
References	299
<b>14 Red, Cryptomonad and Glaucocystophyte Algal Phycobiliproteins</b>	<b>305–334</b>
<i>Colleen Mary Toole and F. C. Thomas Allnutt</i>	
Summary	306
I. Introduction	306
II. Structure and Components of Phycobilisomes	307
III. Molecular Biology of Red Algal, Glaucocystophyte and Cryptomonad Phycobiliproteins	310
IV. Phycobiliprotein Structure	311
V. Phycobiliprotein Types	315
VI. Phycobiliprotein Crystal Structure	319
VII. Bilin Chromophores	322
VIII. Energy Transfer	326
IX. Applications/Industrial Uses	328
References	329
<b>15 Carotenoids of Light Harvesting Systems: Energy Transfer Processes from Fucoxanthin and Peridinin to Chlorophyll</b>	<b>335–349</b>
<i>Mamoru Mimuro and Seiji Akimoto</i>	
Summary	335
I. Introduction	336
II. Distribution of Carotenoids in Algae	336
III. Optical Properties of Carotenoids in Relation to Functions	337
IV. Functions	343
V. Antenna Function of Carotenoids in Algae	344
VI. Electronic States and Dynamic Properties of Molecules	345
VII. Energy Transfer Processes and Mechanism	346
References	348

## **General Aspects of Photosynthesis in Algae**

---

<b>16 Photoinhibition, UV-B and Algal Photosynthesis</b>	<b>351–384</b>
<i>Linda A. Franklin, C. Barry Osmond and Anthony W. D. Larkum</i>	
Summary	352
I. Introduction	352
II. The Algal Light Climate	354
III. Photoinhibition by PAR	357
IV. Effects of UV Radiation	364
V. Photoinhibition and UV Stress in the Field	371
VI. Scope for Further Research	373
Acknowledgment	375
References	375
<b>17 Adaptation, Acclimation and Regulation in Algal Photosynthesis</b>	<b>385–412</b>
<i>John A. Raven and Richard J. Geider</i>	
Summary	386
I. Introduction	386
II. The Range of Resource Availabilities and Other Environmental Factors within Which Algae Can Photosynthesize	389
III. Adaptation of the Photosynthetic Apparatus	390
V. Adaptation of Algal Photosynthesis to Environmental Extremes	396
VI. Acclimation of Algal Photosynthesis	400
VII. Regulation of Algal Photosynthesis	406
VIII. Rates of Regulation and Acclimation	407
IX. Conclusions	408
Acknowledgments	409
References	409
<b>18 Photosynthesis in Marine Macroalgae</b>	<b>413–435</b>
<i>D. Hanelt, C. Wiencke and K. Bischof</i>	
Summary	413
I. Introduction	414
II. Radiation Conditions in Coastal Waters	415
III. Light Absorption by Macroalgae	417
IV. Determination of Photosynthetic Rates	418
V. Effects of Excessive Light on Photosynthesis	423
VI. Algal Photosynthesis Under Low Light Conditions	427
VII. Seasonal Photosynthetic Performance of Macroalgae	427
VIII. Adaptation and Acclimation of Photosynthesis and Respiration to Temperature and Salinity	428
References	429
<b>19 Photosynthesis in Symbiotic Algae</b>	<b>437–455</b>
<i>David Yellowlees and Mark Warner</i>	
Summary	437

I.	Introduction	438
II.	Algal Symbiotic Associations	439
III.	The Host-Algal Interface	439
IV.	Carbon Acquisition, Fixation and Secretion	440
V.	Photoacclimation and Photoadaptation	446
VI.	Coral Bleaching and Photoinhibition	447
	References	450

<b>Index</b>	<b>457</b>
--------------	------------