

Light-Harvesting Antennas in Photosynthesis

Edited by

Beverley R. Green

*University of British Columbia,
Vancouver, Canada*

and

William W. Parson

*University of Washington,
Seattle, U.S.A.*



KLUWER ACADEMIC PUBLISHERS

DORDRECHT / BOSTON / LONDON

Contents

Editorial	vii
Contents	xi
Preface	xvii
Color Plates	CP-1

Part I. Introduction to Light-Harvesting

1	Photosynthetic Membranes and Their Light-Harvesting Antennas	1–28
	<i>Beverley R. Green, Jan M. Anderson and William W. Parson</i>	
	Summary	2
	I. Introduction	2
	II. Photosynthetic Prokaryotes	6
	III. Chloroplasts of Photosynthetic Eukaryotes	14
	To be Continued...	23
	Acknowledgments	23
	References	23
2	The Pigments	29–81
	<i>Hugo Scheer</i>	
	Summary	29
	I. Introduction	30
	II. Functions: A Short Overview	30
	III. The Pigments	34
	IV. Analytics	67
	V. Pigment Substitution Methods	69
	References	71
3	Optical Spectroscopy in Photosynthetic Antennas	83–127
	<i>William W. Parson and V. Nagarajan</i>	
	Summary	84
	I. Introduction	84
	II. Absorption Coefficient	85
	III. Charge-Transfer Transitions	86
	IV. Circular Dichroism	86
	V. Configuration Interactions	90
	VI. Dipole Strength	92
	VII. Electromagnetic Radiation	92
	VIII. Excitons	95
	IX. Fluorescence Yield and Lifetime	100

X.	Infrared Spectroscopy	101
XI.	Internal Conversion	103
XII.	Linear Dichroism and Fluorescence Anisotropy	103
XIII.	Mathematical Tools	106
XIV.	Raman Scattering	107
XV.	Resonance Energy Transfer	108
XVI.	Singlet and Triplet States	111
XVII.	Spectral Bandshapes and Dynamics	113
XVIII.	Spontaneous Fluorescence	116
XIX.	Time-Resolved Spectroscopy	118
XX.	Transition Dipoles	120
XXI.	Wavefunctions	123
	Acknowledgement	125
	References	125

4 The Evolution of Light-harvesting Antennas **129–168** *Beverley R. Green*

	Summary	130
I.	Introduction	130
II.	Origins	131
III.	How Proteins and Their Genes Evolve	136
IV.	Pigment Biosynthesis Genes	142
V.	Photosynthetic Reaction Centers and the Core Antenna Family	145
VI.	Phycobiliproteins	148
VII.	LHC Superfamily	150
VIII.	Single Membrane Helix Antennas of Purple and Green Filamentous Bacteria	155
IX.	Antenna Proteins Unique to Certain Groups	156
X.	The Big Picture: The Five Divisions of Photosynthetic Bacteria	157
	References	160

Part II. Structure and Function in Light-Harvesting

5 The Light-Harvesting System of Purple Bacteria **169–194** *Bruno Robert, Richard J. Cogdell and Rienk van Grondelle*

	Summary	170
I.	Introduction	170
II.	Components of the Light-Harvesting System of Purple Bacteria	171
III.	Structure-Function Relationships in Bacterial Antennas	176
IV.	Energy Transfer in Light-Harvesting Proteins from Purple Bacteria	181
V.	Conclusion	188
	Acknowledgments	188
	References	188

6 Antenna Complexes from Green Photosynthetic Bacteria **195–217** *Robert E. Blankenship and Katsumi Matsuura*

	Summary	195
--	---------	-----

I.	Introduction	196
II.	Chlorosome Structure, Pigment Stoichiometry and Protein Content	201
III.	Redox-Dependent Regulation of Energy Transfer in Chlorosomes	204
IV.	Fenna-Matthews-Olson Protein	207
V.	Kinetics and Pathways of Energy Transfer in Chlorosomes and Membranes of Green Bacteria	209
VI.	Conclusions and Future Work	210
	Acknowledgment	211
	References	211
7	Light-Harvesting in Photosystem II	219–251
	<i>Herbert van Amerongen and Jan P. Dekker</i>	
	Summary	220
I.	Introduction	220
II.	The Photosystem II Genes and Proteins	221
III.	Individual Photosystem II Antenna Complexes	222
IV.	Reaction Center Containing Photosystem II Complexes	235
V.	Overall Trapping of Excitation Energy	242
	References	245
8	Structure and Function of the Antenna System in Photosystem I	253–279
	<i>Petra Fromme, Eberhard Schlodder and Stefan Jansson</i>	
	Summary	254
I.	Introduction	254
II.	The Architecture of Cyanobacterial Photosystem I	255
III.	Structural Organization of the Core Antenna System	261
IV.	Plant Photosystem I	266
V.	Excitation Energy Transfer and Trapping in PS I	270
	Acknowledgment	275
	References	275
9	Antenna Systems and Energy Transfer in Cyanophyta and Rhodophyta	281–306
	<i>Mamoru Mimuro and Hiroto Kikuchi</i>	
	Summary	282
I.	Introduction	282
II.	Molecular Architecture of Antenna Systems in Cyanobacteria and Red Algae	282
III.	Energy Flow in Antenna Systems of Cyanobacteria	291
IV.	Three-Dimensional Structures of Phycobiliproteins	292
V.	Electronic States of Chromophores in Phycobiliproteins	298
VI.	Energy Transfer	301
VII.	Concluding Remarks	302
	Acknowledgments	302
	References	302

10 Antenna Systems of Red Algae: Phycobilisomes with Photosystem II and Chlorophyll Complexes with Photosystem I **307–322**
Elisabeth Gantt, Beatrice Grabowski and Francis X. Cunningham, Jr.

Summary	307
I. Introduction	308
II. Structure and Composition of the Antenna Systems	308
III. Phylogenetic Implications of LHC Structure and Function	315
IV. Light Acclimation Responses	315
V. Energy Distribution	318
VI. Future Problems to be Addressed	319
Acknowledgments	319
References	319

11 Light-Harvesting Systems in Chlorophyll *c*-Containing Algae **323–352**
Alisdair N. Macpherson and Roger G. Hiller

Summary	324
I. Introduction	324
II. Groups Having One Main Light Harvesting System	328
III. Groups Having Two Distinct Light Harvesting Systems	333
IV. Concluding Remarks	347
Acknowledgments	348
References	348

Part III. Biogenesis, Regulation and Adaptation

12 Biogenesis of Green Plant Thylakoid Membranes **353–372**
Kenneth Cline

Summary	353
I. Introduction	354
II. Methodologies for Higher Plant Chloroplasts	354
III. Overview of Localization Processes	356
IV. Different Mechanisms Address Different Translocation Problems	359
V. The In Vivo Site of Thylakoid Protein Transport and Insertion	364
VI. Chlorophyll Synthesis And The Insertion Of Antenna Proteins	364
VII. Future Prospects	367
References	368

13 Pulse Amplitude Modulated Chlorophyll Fluorometry and its Application in Plant Science **373–399**
G. Heinrich Krause and Peter Jahns

Summary	373
I. Introduction	374
II. The Measuring Principle of the Pulse Amplitude Modulation Fluorometer	374
III. Initial and Variable Fluorescence	375
IV. Ratio of Maximum Variable to Maximum Total Fluorescence, F_V/F_M	378
V. Fluorescence Quenching	379

VI. Photosynthetic Yield and Rate of Linear Electron Transport Determined by Fluorescence Analysis	388
VII. Application of Chlorophyll Fluorescence in the Study of Mutants	391
VIII. Conclusion and Perspectives	392
Acknowledgment	393
References	393
14 Photostasis in Plants, Green Algae and Cyanobacteria: The Role of Light Harvesting Antenna Complexes	401–421
<i>Norman P. A. Huner, Gunnar Öquist and Anastasios Melis</i>	
Summary	402
I. Introduction	402
II. Stress and Photostasis	404
III. Acclimation And Photostasis	409
IV. Chloroplast Biogenesis and Photostasis	415
V. Sensing Mechanisms Involved in Photostasis	416
Acknowledgments	416
References	417
15 Photoacclimation of Light Harvesting Systems in Eukaryotic Algae	423–447
<i>Paul G. Falkowski and Yi-Bu Chen</i>	
Summary	424
I. Introduction	424
II. Photoacclimation	425
III. Light in aquatic environments	425
IV. Physiological Responses to Changes in Spectral Irradiance	429
V. Light Harvesting Systems and the Effective Absorption Cross Section of Photosystem II	432
VII. Light Harvesting Complexes	438
VIII. The 'Nested Signal' Hypothesis	442
Acknowledgments	443
References	443
16 Multi-level Regulation of Purple Bacterial Light-harvesting Complexes	449–470
<i>Conan S. Young and J. Thomas Beatty</i>	
Summary	450
I. Introduction	450
II. Gene Organization and Expression	452
III. Assembly of LH Complexes	459
IV. Other genes and proteins relevant to LH complex assembly or structure	462
V. Concluding Remarks and Future Prospects	464
Acknowledgments	465
References	465

17 Environmental Regulation of Phycobilisome Biosynthesis 471–495
Arthur R. Grossman, Lorraine G. van Waasbergen and David Kehoe

Summary	471
I. Introduction	472
II. Phycobilisome Structure	472
III. Complementary Chromatic Adaptation	473
IV. Model for the Control of Complementary Chromatic Adaptation	481
V. Control of Phycobilisome Biosynthesis During Nutrient Limitation	482
VI. Concluding Remarks	488
Acknowledgments	488
References	488

Index 495