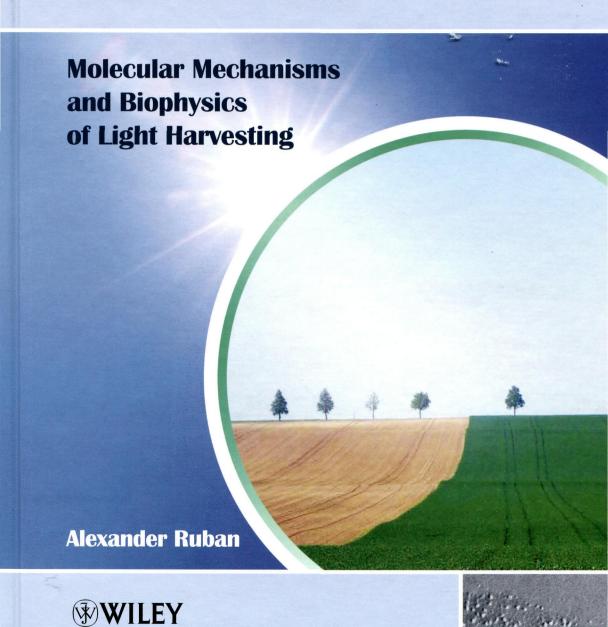
The Photosynthetic Membrane



The Photosynthetic Membrane

Molecular Mechanisms and Biophysics of Light Harvesting

ALEXANDER RUBAN

School of Biological and Chemical Sciences, Queen Mary, University of London, UK



This edition first published 2013 © 2013 John Wiley & Sons, Ltd.

Registered Office

John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, United Kingdom

For details of our global editorial offices, for customer services and for information about how to apply for permission to reuse the copyright material in this book please see our website at www.wiley.com.

The right of the author to be identified as the author of this work has been asserted in accordance with the Copyright, Designs and Patents Act 1988.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by the UK Copyright, Designs and Patents Act 1988, without the prior permission of the publisher.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Designations used by companies to distinguish their products are often claimed as trademarks. All brand names and product names used in this book are trade names, service marks, trademarks or registered trademarks of their respective owners. The publisher is not associated with any product or vendor mentioned in this book. This publication is designed to provide accurate and authoritative information in regard to the subject matter covered. It is sold on the understanding that the publisher is not engaged in rendering professional services. If professional advice or other expert assistance is required, the services of a competent professional should be sought.

The publisher and the author make no representations or warranties with respect to the accuracy or completeness of the contents of this work and specifically disclaim all warranties, including without limitation any implied warranties of fitness for a particular purpose. This work is sold with the understanding that the publisher is not engaged in rendering professional services. The advice and strategies contained herein may not be suitable for every situation. In view of ongoing research, equipment modifications, changes in governmental regulations, and the constant flow of information relating to the use of experimental reagents, equipment, and devices, the reader is urged to review and evaluate the information provided in the package insert or instructions for each chemical, piece of equipment, reagent, or device for, among other things, any changes in the instructions or indication of usage and for added warnings and precautions. The fact that an organization or Website is referred to in this work as a citation and/or a potential source of further information does not mean that the author or the publisher endorses the information the organization or Website may provide or recommendations it may make. Further, readers should be aware that Internet Websites listed in this work may have changed or disappeared between when this work was written and when it is read. No warranty may be created or extended by any promotional statements for this work. Neither the publisher nor the author shall be liable for any damages arising herefrom.

Library of Congress Cataloguing-in-Publication Data

Ruban, Alexander (Alexander V.)

The photosynthetic membrane : molecular mechanisms and biophysics of light harvesting / Alexander Ruban. p. cm.

Includes index.

ISBN 978-1-119-96054-6 (cloth) – ISBN 978-1-119-96053-9 (pbk.)

Photosynthesis. 2. Photosynthetic pigments. 3. Light absorption. I. Title. QK882.R83 2013
572',46-dc23

2012025765

A catalogue record for this book is available from the British Library.

Set in 10/12pt Times by SPi Publisher Services, Pondicherry, India Printed and bound in Singapore by Markono Print Media Pte Ltd

Contents

Preface Acknowledgements			xí xiii	
1	Life, Energy and Light			1
	1.1	The D	efinition of Life	1
	1.2	The E	nergy of Matter	2 3
		1.2.1	The Source of Life's Energy	
			y for the Future	3
	1.4	Photos	synthesis by Life	4
		1.4.1	Photon Energy Transformations	5
		erence		6
	Bibl	iograp)	hy	6
2	The Space of the Cell			
	2.1	The C	ell Concept: Fundamental Nature of Life	7
	2.2	Comp	artmentalization: The Cult of the Membrane	9
	2.3 Membrane Components: Fundamentals of Proteins			
	2.4 Functional Classification of Membrane Proteins			
	Reference			
	Bibl	iograp)	hy	16
3	The Photosynthetic Membrane: Outlook			
	3.1 Knowledge of the Pre-Atomic Structure Era: Organization			
		of the	Photosynthetic Membrane System	17
	3.2	Comp	osition of the Photosynthetic Membrane	21
		3.2.1	Lipids	21
		3.2.2	Lipid-Related Compounds of the Photosynthetic Membrane	22
		3.2.3	Proteins and Protein Complexes	25
	3.3	Oligo	merization, Interactions and Mobility of the Photosynthetic	
	Proteins: Enabling Functions and Adaptations			28
		3.3.1	Oligomerization and Clustering of Photosynthetic	
			Membrane Proteins	28
		3.3.2	Protein Mobility	30
	Reference			32
	Ribl	iogran	hx/	32

4	Popular Methods and Approaches to Study Composition,				
	Stru	cture and Fun	ctions of the Photosynthetic Membrane	33	
	4.1	Biochemistry	and Molecular Biology Approaches	33	
		4.1.1 Isolatie	on of Chloroplasts and Subchloroplast Particles	33	
		4.1.2 Isolatic	on of Membrane Protein Complexes	35	
		4.1.3 Analys	is of Lipids and Pigments	37	
		4.1.4 Protein	n Expression and Reconstitution In Vitro	38	
		4.1.5 Recons	stitution of Membrane Proteins in Liposomes	39	
		4.1.6 Mutag	enesis and Transgenic Manipulations	40	
	4.2				
		4.2.1 Optical Microscopy		41	
		4.2.2 Electro	on Microscopy (EM)	42	
		4.2.3 Atomic	c Force Microscopy (AFM)	45	
		4.2.4 Crysta	llography Methods	45	
	4.3	Function Prob	ing Methods	48	
		4.3.1 Absorp	otion-Based Approaches	49	
		4.3.2 Raman	Spectroscopy	54	
		4.3.3 Fluore	scence-Based Approaches	55	
	Ref	References			
	Bib	iography		65	
5	Prir	nary Processes	of the Light Phase of Photosynthesis:		
	Principles of Light Harvesting in Antennae				
	5.1	· · · · · · · · · · · · · · · · · · ·			
	5.2	Absorption of	Light by Molecules	71	
	5.3	Fate of Absorb	oed Light Energy	73	
	5.4	The Need for	the Photosynthetic Antenna and the Fifth		
		Fate of Excita	tion Energy	75	
	5.5	Photosynthetic	c Antenna Pigments	81	
		5.5.1 Chloro	phylls	82	
		5.5.2 Xantho	pphylls	87	
	5.6	Variety and Cl	lassification of Photosynthetic Antennae	91	
	5.7	Principles of I	Light Harvesting: Summary	93	
	5.8	Connecting Li	ght Harvesting Antenna to the Photosystems:		
		Red Energy Ti	raps	96	
	References			99	
	Bibliography			99	
6	Tow	ards the Atom	ic Resolution Structure of Light Harvesting		
	Antennae: On the Path of Discoveries				
	6.1				
		Plant Antenna	· · · · · · · · · · · · · · · · · · ·	102	
	6.2		of Isolation Methods: Intactness,		
		Purity and Qu		104	

	6.3	LHCII Crystallography: The Beginnings	107
	6.4	Revealing the Atomic Resolution Structure of LHCII	
		Antenna Complexes	111
		6.4.1 Key Biochemical and Spectroscopic Advances that Aided	
		the Emergence of the Current Atomic LHCIIb Structure	111
		6.4.2 The New Structure of LHCIIb	115
	6.5	Structure of a Minor LHCII Complex CP29	126
	6.6	Comparison of LHCII Structure with the Structure of a Simpler	
		Light Harvesting Complex from Purple Bacteria, LH2	129
	Ref	erences	133
	Bibl	iography	134
7	Stru	ictural Integration of Antennae within Photosystems	135
	7.1	Light Harvesting Complexes Gene Family	136
	7.2	Toward the Structure of a Complete Photosystem II Unit:	
		Supercomplexes	137
	7.3	Supramolecular Structure of Photosystem I: LHCI	145
	7.4	Photosynthetic Membrane Protein Landscapes	147
	7.5	Robustness of the Light Harvesting Antenna Design: Resurrecting	
		the Structure to Preserve the Function	150
	Ref	erences	156
	Bibl	iography	157
8	Dyn	amics of Light Harvesting Antenna: Spectroscopic Insights	159
	8.1	Steady-State Optical Spectroscopy of LHCII:	
		Composition and Order	160
	8.2	Time-Resolved Spectroscopy of LHCII: Energy Migration	165
		8.2.1 Time-Resolved Fluorescence Spectroscopy	165
		8.2.2 Time-Resolved Absorption Spectroscopy	167
	8.3	Spectral and Structural Identity of LHCII Xanthophylls	170
	8.4	Plasticity of Light Harvesting Antenna Design: Tailoring the	
		Structure to Optimize the Function	176
	8.5	LHCII Oligomerization: Dynamics of the 'Programmed Solvent'	179
		8.5.1 Alterations in the Spectral Properties of LHCII	179
		8.5.2 Structural Changes within LHCII	183
	8.6	Kinetics of the Collective LHCII Transition into the Dissipative	
		State: Exploring 'The Switch' Control	189
		erences	194
	Bib	iography	195
9	Ada	ptations of the Photosynthetic Membrane to Light	197
	9.1	The Need for Light Adaptations and their Various Strategies	198
	9.2	Long-Term Regulation of the Photosystem Ratio and their	
		Antenna Size: Acclimation	201

	9.3	Short-	Term Adaptations to Light Quality: State Transitions	202
		9.3.1	The Phenomenology of State Transitions	202
		9.3.2	The Molecular Mechanism of State Transitions	205
		9.3.3	Chromatic Adaptations in Plants Lacking the Polypeptides	
			of the Major LHC II Complex	209
		9.3.4	Future of State Transitions Research	212
	9.4 Short-Term Adaptations to Light Quantity		Term Adaptations to Light Quantity	214
		9.4.1	Control of Excess Light Energy in Photosystem II –	
			The Phenomenon of Nonphotochemical Chlorophyll	
			Fluorescence Quenching (NPQ)	214
		9.4.2	The Molecular Components and Processes Involved in NPQ	217
		9.4.3	Future of qE Research	238
	Refe	rences	•	238
	Bibli	ograph	y	239
10	Wha	t is in it	for Plant, Biosphere and Mankind?	241
	10.1		e and Society	241
	10.2		y Balance of Photosynthesis: A Wasteful Process?	242
	10.3		and Light Harvesting	247
	10.4	•	Harvesting Principles for Future Applications: Liberation	
		_	Saturation Constraints	249
	10.5	Effect	s of Changing Climate – The Onset of Disorder	253
	Bibli	ograph		254
11	Conc	clusions		257
Ind	ex			261