Photosynthesis

Photobiochemistry and Photobiophysics

Bacon Ke Walnut Creek, CA, U.S.A.

KLUWER ACADEMIC PUBLISHERS

DORDRECHT/BOSTON/LONDON

Contents

Ed	itorial: Advances in Photosynthesis Series	vii
Сс	Contents	
Pr	eface	xix
Сс	olor Plates	xxi
<u>0</u>	verview	
1.	Photosynthesis: An Overview I. Solar Energy and Photosynthesis II. Absorption of Light Energy and the Fate of the Electronically Excited States III. Light-Harvesting Pigment Molecules IV. Development of Some Modern Concepts of Photosynthesis V. The Thylakoid Membrane of Chloroplasts VI. The Emerson Enhancement Effect and Evidence for Two Photosystems VII. Freeze-Fracture Electron Microscopy of Thylakoid Membranes VIII. Composition of Thylakoid Membranes – Lipids, Proteins and Electron Carriers IX. Lateral and Transverse Asymmetry of Thylakoid Membranes X. Evolution of Photosynthetic Reaction Centers	1-46 1 4 6 13 19 22 26 30 38 41
<u>B</u>	acterial Photosynthesis	
2.	The Bacterial Photosynthetic Reaction Center: Chemical Composition	
۷.	and Crystal Structure	47-64
	Structure of the Reaction Centers of Photosynthetic Bacteria	48
	 II. Three-Dimensional Structure of Bacterial Photosynthetic Reaction Centers III. Summary – Reaction-Center Structure and Photochemical Reactions 	54 62
3.	Light-Harvesting Pigment-Protein Complexes of Photosynthetic Bacteria I. The Light-Harvesting Pigment-Protein Complexes II. An Early Model for the Light-Harvesting Pigment-Protein Complex	65-85 66 69
	III. Crystal Structure of the Light-Harvesting Complexes of Purple Photosynthetic Bacteria IV. Structure and Function of the Bacterial Photosynthetic Apparatus	71 81
4.	The Primary Electron Donor (P) of Photosynthetic Bacteria I. Spectral Properties II. Other Physical Properties –The Oxidation-Reduction Potential and the	87-99 90
	Differential Molar Extinction Coefficient III. Bacteriochlorophyll Epimer being a Constituent of the Primary Electron Donor of Heliobacteria	96 97
5.	The "Stable" Primary Electron Acceptor (Q_A) of Photosynthetic Bacteria I. Early Spectroscopic Studies of the "Stable" Primary Electron Acceptor II. Functional Role of Ubiquinone and Iron in Photosynthetic Bacteria III. The Oxidation-Reduction Potential of the Stable Primary Electron Acceptor Q_A	101-110 102 105 107

6.	The Secondary Electron Acceptor (Q _B) of Photosynthetic Bacteria I. Structure of the Binding Domain and Functional Properties of Q _A and Q _B II. Evidence for a Secondary Quinone Electron Acceptor III. Electron Transfer between the Two Quinones – Binary Oscillations IV. Protonation of the Secondary Electron Acceptor Q _B V. Transmembrane Proton Pump and ATP Synthesis – A Preliminary Overview	111-128 112 113 114 117 127
7.	The Early Electron Acceptors of Photosynthetic Bacteria – Bacteriochlorophyll and Bacteriopheophytin I. Discovery of the Involvement of 8Φ in Photochemical Charge Separation II. Photochemical Accumulation of the Reduced BΦ (ΒΦ⁻ or I⁻) III. Involvement of the Monomeric BChl in Photochemical Charge Separation	129-146 130 133 137
8.	The Green Bacteria. I. The Light-Harvesting Complex, the Chlorosomes I. Models for the Reaction Center-Antenna Complex of Green Bacteria II. Organization of Bacteriochlorophyll-c Molecules in the Rod Elements of Chlorosomes III. Organization of Chlorophyll Molecules in the Reaction Center-Antenna Complex IV. Pathway and Kinetics of Excitation Energy Transfer in Chlorosomes V. The BChl a-Protein Complex (the "FMO Protein") in the Reaction Center-Antenna Complex	147-158 149 150 152 153
9.	The Green Bacteria. II. The Reaction Center – Photochemistry and Electron Transport I. The Green Sulfur Bacteria III. The Green Filamentous Bacteria IIII. The Newly Discovered Photosynthetic Bacteria – the Heliobacteria IV. Summary	159-178 160 168 173
10	The Secondary Electron Donor of Photosynthetic Bacteria — the Cytochromes I. Reduction of Photooxidized Primary Electron Donor by Cytochromes II. Cytochrome Electron Transfers in the Photosynthetic Bacteria can be Temperature Insensitiviti. Tetraheme Arrangement in the Reaction-Center Complex of Rhodopseudomonas vindis IV. A Reaction Center-Cytochrome c Model System	179-198 182 ve 184 186 194
P	notosystem II '	
11	Photosystem II – Introduction Photosystem II: Protein Components and their Organization Structure of the Photosystem-II Reaction-Center Complex III. Topics on Photosystem II and Oxygen Evolution	199-214 200 202 211
12	The Light-Harvesting Chlorophyll-Protein Complexes of Photosystem II Photosystem-II Light-Harvesting Chlorophyll-Protein Complexes Crystal Structure of LHC II Regulatory Roles of LHC II in Thylakoids	215-228 216 219 224

13.	Role of Carotenoids in Photosynthesis	229-250
	I. The Light-Harvesting Role of Carotenoids	231
	Chlorophyll-Carotenoid-Protein Supramolecular Assemblies – Xanthosomes Singlet-Singlet Energy Transfer Dynamics involving Carotenoids in Light-Harvesting	233 240
	IV. The Photoprotective Role of Carotenoids – Triplet-Triplet Energy Transfer	245
14	Phycobiliproteins and Phycobilisomes	251-269
	I. Phycobiliproteins	253
	II. Phycobilisomes	260
15.	The Primary Electron Donor of Photosystem II, P680, and Photoinhibition	on
		271-288
	I. The Primary Electron Donor of Photosystem II, P680	272
	II. Photoinhibition in Photosystem II – Consequence of the Strong Oxidizing Power of P680*	277
	III. Possible Protective Function of Cytochrome b559 against Photoinhibition	282
16.	The Stable Primary Electron Acceptor Q _A and the Secondary Electron	
	Acceptor Q _B	289-304
	The Stable Primary Electron Acceptor Q _A of Photosystem II	290
	II. Absorption-Spectrum Change accompanying the Reduction of Q _A	291
	III. Redox Properties of Q _A determined by Fluorescence Titration IV. The Two-Electron Gate	294 295
	V. The Plastoquinone-Nonheme Iron Complex	297
	VI. The Binding Sites of Q _A , Q _B and Fe	299
	VII. The Herbicide-Binding Protein D1	300
17.	The Transient Intermediate Electron Acceptor of Photosystem II, Pheop	hytin (Φ)
		305-322
	 Photoaccumulation of Reduced Pheophytin (Φ⁻) in Photosystem II – Discovery of 	
	the Intermediary Electron Acceptor	305
	II. Additional Demonstration of Pheophytin being the Primary Electron Acceptor of Photosyst	
	III. The EPR Spectrum of Φ⁻ – Interaction between Φ⁻ and PQ˙ •Fe²⁺ IV. Midpoint Potential of the Intermediary Electron Acceptor Φ	311 313
	V. Picosecond Kinetics of Photochemical Charge Separation and Electron Transport	313
	in Photosystem II	316
\bigcirc	xygen Evolution	
<u> </u>	kygen Evolution	
18.	Oxygen Evolution – Introduction	323-336
	I. Kinetics of Oxygen Evolution	324
	II. Proton Release accompanying S-State Transitions	331
19.	Oxygen Evolution – The Role of Manganese	337-354
	l. Methods for Extracting Manganese from Photosynthetic Organelles	338
	II. Monitoring Manganese by EPR Spectroscopy	339
	III. Manganese Stoichiometry	340
	 IV. EPR Spectra of the Manganese Complex in the S₂-State V. A Manganese-Cluster Model based on EPR and X-Ray Absorption Spectroscopy 	342 344

20.	Oxygen Evolution – UV Absorbance Changes associated with S-State Transitions I. Absorbance Changes produced by the $S_1 \rightarrow S_2$ Transition II. Absorbance Changes produced by the S-State Transition Cycle	355-364 355 357
21.	Oxygen Evolution – Extrinsic Polypeptides and Inorganic Ionic Cofactors I. The Three Extrinsic Polypeptides: Properties and Functions II. Functional Role of the Inorganic Cofactors in Oxygen Evolution	365-375 366 369
22.	The Electron Donor to P680 ⁺ – EPR Spectroscopy I. The Secondary Electron Donor of Photosystem II – EPR Spectroscopy II. Chemical Identity of the SII Signals III. A New Model of Oxygen Evolution Involving Hydrogen-Atom Abstraction by Yz during the S-State Cycle	377-396 378 384 391
23.	The Electron Donor to P680 ⁺ – Optical Spectroscopy I. Electron Donation from Y _z to P680 ⁺ II. Absorbance Changes and Kinetics due to Y _z Oxidation by P680 ⁺	397- 4 06 398 401
24.	Charge Recombination in Photosystem II and Thermoluminescence I. Energetics of Thermoluminescence II. Some Commonly Observed Thermoluminescence Bands and their Origins III. Concluding Remarks	407-418 407 409 416
<u>Pł</u>	notosystem I	
	Photosystem I — Introduction I. Pigment Molecules, Cofactors, and Protein Subunits of the Photosystem-I Reaction Center II. Protein Subunits of the Photosystem-I Reaction Center III. Protein Subunits of the Photosystem-I Reaction Center	419-430 er 420 422 423
25.	Photosystem I – Introduction I. Pigment Molecules, Cofactors, and Protein Subunits of the Photosystem-I Reaction Center II. Three-dimensional Structure of the Photosystem-I Reaction Center	er 420 422
25. 26.	Photosystem I — Introduction I. Pigment Molecules, Cofactors, and Protein Subunits of the Photosystem-I Reaction Center III. Three-dimensional Structure of the Photosystem-I Reaction Center III. Protein Subunits of the Photosystem-I Reaction Center Photosystem-I Membrane, Complexes and Crystals I. Early Work on Fractionation and Characterization of the Thylakoid Membrane II. Simplified Photosystem-I Reaction-Center Complexes	420 422 423 431-443 432 437

29.	The Membrane-Bound Iron-Sulfur Proteins (FeS-A and FeS-B):	
	Secondary Electron Acceptors of Photosystem I	479-504
	I. Discovery of the Membrane-Bound Iron-Sulfur Proteins FeS-A and FeS-B	
	and their EPR Properties	480
	II. Redox Potentials of the Membrane-Bound Iron-Sulfur Proteins FeS-A and FeS-B	482
	III. Structure and Properties of FeS-A/FeS-B (PsaC)	483
	VI. Electron-Transfer Sequence in the Reduction of FeS-A and FeS-B	494
30.	P430: The Spectral Species Representing the Terminal Electron	
	Acceptor of Photosystem I	505-526
	A Brief Chronicle of the Investigation of the Photosystem-I Primary Electron Acceptor	505
	II. The Speciral Species P430: Its Discovery and Properties	507
	III. Five Possible Fates of the Photooxidized Primary Donor P700* and the Photoreduced	
	"Primary" Acceptor P430	509
	IV. Some Properties of P430 and P700	512
21	The Iron-Sulfur Center FeS-X of Photosystem I, the Photosystem-I Co	ro
J 1.	· · · · · · · · · · · · · · · · · · ·	
	Complex, and Interaction of the FeS-X Domain with FeS-A/FeS-B	527-554
	FeS-X and its Spectral Properties Redox Potential of FeS-X	528 533
	III. Isolation and Characterization of the PS-I Core Complex [P700·A₀·A₄·FeS-X]	536
	IV. Structure and Environment of the FeS-X Cluster in the PS-I Reaction Center	540
	V. Establishment of the Position of FeS-X in the Electron-Transfer Sequence	548
22	The Primary Floatron Assentar A. of Photogratem I	EEE E70
3Z.	The Primary Electron Acceptor A ₀ of Photosystem I	555-578
	 Early Spectroscopic and EPR Studies of A₀ Spectra and Reaction Kinetics of A₀ by Rapid-Spectroscopic Measurements 	556
	ii. Spectra and Reaction Rinetics of A ₀ by Rapid-Spectroscopic Measurements	561
33.	The Intermediate Electron Acceptor A, of Photosystem I	
	- Phylloquinone (Vitamin K ₁)	579-604
	Occurrence of Phylloquinone in Higher Plants, Algae, and Cyanobacteria	580
	II. Spectroscopic Identification of a Quinone Acceptor in Photosystem I	581
	III. Forward Electron Transfer from A ₁ ⁻ to FeS-X	591
	IV. Phylloquinone Extraction, Reconstitution, and Replacement	597
34.	Mobile Electron Carriers Plastocyanin and Ferredoxin,	
	and Ferredoxin·NADP⁺-Reductase	605-634
	Plastocyanin (PC) – Structure and Properties	606
	II. Ferredoxin (Fd)	621
	III. Ferredoxin·NADP*-Reductase (FNR)	628

Proton Transport and Photophosphorylation

35.	The Interphotosystem Cytochrome-b _e f Complex and the Related	
	Cytochrome-bc, Complex	635-664
	I. Topology of Cytochrome $b_{\rm s}f$ and Structure of its Subunits	636
	II. Spectroscopic Characterization of the Subunits of Cytochrome-b _s f Complex	648
	III. Electron Transport and Proton Translocation in Cytochrome b _s f	651
	•	
36.	Proton Translocation and ATP Synthesis	665-737
	I. Introduction	666
	II. Composition and Structure of Chloroplast ATP Synthase (CF ₀ ·F ₁)	668
	III. The Chemiosmotic Theory and ATP Synthesis	676
	IV. Mechanism of ATP Synthesis	707
Δnn	endix: How to View the Stereograms	739
	_	700
Abb	previations	741
Inde	ex	747