

4 ***Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase,***
5 ***edited by Thomas J. Wydrzynski and Kimiyuki Satoh, Volume 22, Advances***
6 ***in Photosynthesis and Respiration, Springer, Dordrecht, The Netherlands***

9 I am delighted to announce the publication, in
10 *Advances in Photosynthesis and Respiration*
11 (AIPH) Series, of *Photosystem II: The Light-Dri-*
12 *ven Water: Plastoquinone Oxidoreductase*, a book
13 covering the central role of the oxygen-evolving
14 system for life on earth; it deals with both the
15 structure and the function of this unique process.
16 Two distinguished authorities have edited this
17 volume: Thomas J. Wydrzynski of Australia and
18 Kimiyuki Satoh of Japan. Some of the earlier
19 volumes have included descriptions of Photosys-
20 tem II: Volume 4 (*Oxygenic Photosynthesis: The*
21 *Light Reactions*, edited by Donald R. Ort and
22 Charles F. Yocum); Volume 10 (*Photosynthesis:*
23 *Photobiochemistry and Photobiophysics*, authored
24 by Bacon Ke); and Volume 19 (*Chlorophyll a*
25 *Fluorescence: A Signature of Photosynthesis*, edited
26 by George C. Papageorgiou and Govindjee). The
27 current volume follows the 21 volumes listed
28 below.

29 **Published Volumes (1994–2005)**

30 *Volume 1: Molecular Biology of Cyanobacteria* (28
31 Chapters; 881 pages; 1994; edited by Donald A.
32 Bryant, from USA; ISBN: 0-7923-3222-9);

33 *Volume 2: Anoxygenic Photosynthetic Bacteria*
34 (62 Chapters; 1331 pages; 1995; edited by Robert
35 E. Blankenship, Michael T. Madigan and Carl E.
36 Bauer, from USA; ISBN: 0-7923-3682-8);

37 *Volume 3: Biophysical Techniques in Photosyn-*
38 *thesis* (24 Chapters; 411 pages; 1996; edited by the
39 late Jan Amesz and the late Arnold J. Hoff, from
40 The Netherlands; ISBN: 0-7923-3642-9);

41 *Volume 4: Oxygenic Photosynthesis: The Light*
42 *Reactions* (34 Chapters; 682 pages; 1996; edited by
43 Donald R. Ort and Charles F. Yocum, from USA;
44 ISBN: 0-7923-3683-6);

45 *Volume 5: Photosynthesis and the Environment*
46 (20 Chapters; 491 pages; 1996; edited by Neil R.
47 Baker, from UK; ISBN: 0-7923-4316-6);

Volume 6: Lipids in Photosynthesis: Structure, 48
Function and Genetics (15 Chapters; 321 pages; 49
1998; edited by Paul-André Siegenthaler and 50
Norio Murata, from Switzerland and Japan; 51
ISBN: 0-7923-5173-8); 52

Volume 7: The Molecular Biology of Chlorop- 53
lasts and Mitochondria in Chlamydomonas (36 54
Chapters; 733 pages; 1998; edited by Jean David 55
Rochaix, Michel Goldschmidt-Clermont and 56
Sabeeha Merchant, from Switzerland and USA; 57
ISBN: 0-7923-5174-6); 58

Volume 8: The Photochemistry of Carotenoids 59
(20 Chapters; 399 pages; 1999; edited by Harry A. 60
Frank, Andrew J. Young, George Britton and 61
Richard J. Cogdell, from USA and UK; ISBN: 62
0-7923-5942-9); 63

Volume 9: Photosynthesis: Physiology and 64
Metabolism (24 Chapters; 624 pages; 2000; edited 65
by Richard C. Leegood, Thomas D. Sharkey and 66
Susanne von Caemmerer, from UK, USA and 67
Australia; ISBN: 0-7923-6143-1); 68

Volume 10: Photosynthesis: Photobiochemistry 69
and Photobiophysics (36 Chapters; 763 pages; 2001; 70
authored by Bacon Ke, from USA; ISBN: 0-7923- 71
6334-5); 72

Volume 11: Regulation of Photosynthesis (32 73
Chapters; 613 pages; 2001; edited by Eva-Mari 74
Aro and Bertil Andersson, from Finland and 75
Sweden; ISBN: 0-7923-6332-9); 76

Volume 12: Photosynthetic Nitrogen Assimila- 77
tion and Associated Carbon and Respiratory 78
Metabolism (16 Chapters; 284 pages; 2002; edited 79
by Christine Foyer and Graham Noctor, from UK 80
and France; ISBN: 0-7923-6336-1); 81

Volume 13: Light Harvesting Antennas (17 82
Chapters; 513 pages; 2003; edited by Beverley 83
Green and William Parson, from Canada and 84
USA; ISBN: 0-7923-6335-3); 85

Volume 14: Photosynthesis in Algae (19 Chap- 86
ters; 479 pages; 2003; edited by Anthony Larkum, 87
Susan Douglas and John Raven, from Australia, 88
Canada and UK; ISBN: 0-7923-6333-7); 89

90 *Volume 15: Respiration in Archaea and Bacteria:*
91 *Diversity of Prokaryotic Electron Transport Carriers*
92 (13 Chapters; 326 pages; 2004; edited by Davide
93 Zannoni, from Italy; ISBN: 1-4020-2001-5);

94 *Volume 16: Respiration in Archaea and Bacteria*
95 *2: Diversity of Prokaryotic Respiratory Systems* (13
96 chapters; 310 pages; 2004; edited by Davide Zan-
97 noni, from Italy; ISBN: 1-4020-2002-3);

98 *Volume 17: Plant Mitochondria: From Genome*
99 *to Function* (14 Chapters; 325 pages; 2004; edited
100 by David A. Day, A. Harvey Millar and James
101 Whelan, from Australia; ISBN: 1-4020-2339-5);

102 *Volume 18: Plant Respiration: From Cell to*
103 *Ecosystem* (13 Chapters; 250 pages; 2005; edited
104 by Hans Lambers, and Miquel Ribas-Carbo from
105 Australia and Spain; ISBN: 1-4020-3588-8);

106 *Volume 19: Chlorophyll a Fluorescence: A Sig-*
107 *nature of Photosynthesis* (31 Chapters; 817 pages;
108 2004; edited by George C. Papageorgiou and
109 Govindjee, from Greece and USA; ISBN: 1-4020-
110 3217-X);

111 *Volume 20: Discoveries in Photosynthesis* (111
112 Chapters; 1262+xxx pages; 2005; edited by Gov-
113 indjee, J. Thomas Beatty, Howard Gest and John
114 F. Allen, from USA, Canada and Sweden (& UK);
115 ISBN: 1-4020-3323-0); and

116 *Volume 21: Photoprotection, Photoinhibition,*
117 *Gene Regulation and Environment* (21 Chapters;
118 ~500 pages; 2005; edited by Barbara Demmig-
119 Adams, William W. Adams III and Autar K.
120 Mattoo, all from USA; ISBN: 1-4020-3564-0).

121 For a description of the scope of the AIPH
122 Series, see the back cover of this book. Further
123 information on these books and ordering instruc-
124 tions can be found at <<http://www.springeron->
125 [line.com](http://www.springeronline.com)> under the Book Series 'Advances in
126 Photosynthesis and Respiration.' Special discounts
127 are available for members of the International
128 Society of Photosynthesis Research, ISPR
129 (<<http://www.photosynthesisresearch.org>>).

130 **Photosystem II: The Light-Driven Water:** 131 **Plastoquinone Oxidoreductase**

132 Photosystem II is truly an unprecedented
133 discovery of evolution; one couldn't have modeled
134 it 30-40 years ago despite all the advances in
135 chemistry, physics and biology. It consists of a
136 light-harvesting unit (antenna) and a reaction
137 center unit that operates at an unusually high

redox potential; it is this latter unique character- 138
istic that allows it to oxidize water to oxygen at its 139
'oxygen-evolving complex.' A book on this unique 140
system has been edited by two outstanding 141
authorities in the area of the structure and the 142
function of the oxygen-evolving Photosystem II: 143
Thomas J. Wydrzynski (of the Research School of 144
Biological Sciences, The Australian National 145
University, Canberra, Australia) and Kimiyuki 146
Sato (of the Department of Biology, Okayama 147
University, Okayama, Japan). 148

Respiring organisms, including humans, on this 149
planet depend on the oxygen that green plants, 150
algae, and cyanobacteria generate through 151
Photosystem II. Thus, this book is a very impor- 152
tant addition to the already published books in the 153
AIPH Series. It essentially addresses water first as 154
a source of the electrons that are necessary for the 155
reductive syntheses of organic matter, and then as 156
a source of molecular oxygen that is necessary for 157
the energy producing catabolic oxidations, 158
including respiration. 159

During the last decade or so, dramatic advan- 160
ces have been made in elucidating the structure of 161
Photosystem II to near atomic scale through X-ray 162
crystallography, and in relating it to its biophys- 163
ical, biochemical and molecular biological proper- 164
ties. Thirty-four chapters, authored by 75 165
internationally acknowledged experts, summarize 166
this extraordinary scientific progress, covering 167
areas that range from the capture of fleeting 168
photons, their conversion into chemical energy 169
(oxidation-reduction), to the dynamic regulatory 170
processes that sustain and optimize the photo- 171
synthetic oxidation of water. A discussion is also 172
provided on the beginnings of Photosystem II and 173
photosynthesis more than 3 billion years ago (in 174
the Archaean Era) and on its eventful evolution to 175
the present day diversity of microbial and higher 176
plants. Lastly, the design of artificial (biomimetic) 177
Photosystems II is also discussed. Who knows, one 178
day these systems may serve the needs of humanity 179
either on Earth, or on some distant outpost in 180
Space. 181

The book is designed to be used by graduate 182
students, beginning researchers and advanced 183
undergraduate students in the areas of plant 184
sciences, microbiology, cell and molecular biology, 185
biochemistry, biophysics, bioenergetics and 186
chemistry, as well as those in agriculture and 187
biotechnology. 188

189 This book is appropriately dedicated to a
 190 pioneer in the field Gerald T. Babcock (the dedi-
 191 cation is authored by Charles F. Yocum, Robert
 192 Blankenship and Shelagh Ferguson-Miller, all of
 193 USA). Kimiyuki Satoh (Japan), Thomas J.
 194 Wydrzynski (Australia) and Govindjee (USA)
 195 provide an *Introduction* to Photosystem II and the
 196 chapters in this volume (*Chapter 1*). It is followed
 197 by five chapters that deal with the *Protein*
 198 *Constituents of Photosystem II*: Beverley Green
 199 (Canada) and Elisabeth Gantt (USA) discuss the
 200 distal and extrinsic antenna (*Chapter 2*); Julian
 201 Eaton-Rye (New Zealand) and Cindy Putnam-
 202 Evans (USA) summarize our understanding of the
 203 CP 47 and CP 43 core antenna components
 204 (*Chapter 3*); Peter Nixon (UK), Mary Sarcina
 205 (UK) and Bruce Diner (USA) provide an account
 206 of the D1 and D2 core proteins (*Chapter 4*). This is
 207 followed by *Chapter 5*, by Terry Bricker (USA)
 208 and Robert Burnap (USA) on the oxygen
 209 enhancing extrinsic proteins, and *Chapter 6*, by
 210 Leeann Thornton (USA), Johnna Roose (USA),
 211 Himadri Pakrasi (USA) and Masahiko Ikeuchi
 212 (Japan) on the low molecular weight components.

213 The next nine chapters focus on the *Organiza-*
 214 *tion of the Functional Sites in Photosystem II*:
 215 Gernot Renger and Alfred Holzwarth (both of
 216 Germany) discuss the primary electron transfer
 217 (*Chapter 7*); Vasili Petrouleas (Greece) and
 218 Anthony Crofts (USA) summarize information on
 219 the quinone-iron acceptor complex (*Chapter 8*);
 220 Bruce Diner and David Britt (both of USA)
 221 discuss the redox active tyrosines Y_Z and Y_D
 222 (*Chapter 9*); Vittal Yachandra (USA) summarizes
 223 the current understanding about the organization
 224 of the manganese ions of the manganese cluster of
 225 the O_2 -evolving complex (*Chapter 10*); Richard
 226 Debus (USA) summarizes what is known about
 227 protein ligands of the manganese cluster (*Chapter*
 228 *11*); Karin Åhrling (Australia), Ronald Pace
 229 (Australia) and Michael Evans (UK) provide
 230 information on spectroscopic observations and
 231 their implications on structural and functional
 232 details of catalytic manganese cluster (*Chapter 12*);
 233 Hans van Gorkom (The Netherlands) and Charles
 234 Yocum (USA) discuss the roles of Calcium and
 235 Chloride ions (*Chapter 13*); Jack van Rensen (The
 236 Netherlands) and Vyacheslav Klimov (Russia)
 237 address the unique role of bicarbonate on the
 238 acceptor side and the donor side of Photosystem II
 239 reaction center (*Chapter 14*); and Peter Faller,

240 Christian Fufezan and William Rutherford (all of
 241 France) examine the secondary electron transfer
 242 pathways around the Photosystem II reaction
 243 center (*Chapter 15*).

244 Subsequently, in the next six chapters, the focus
 245 shifts to the *Structural Basis for Photosystem II*:
 246 Takumi Noguchi (Japan) and Catherine Bertho-
 247 mieu (France) analyze the molecular structure of
 248 the intermediates of the system, using information
 249 obtained from vibrational spectroscopy (*Chapter*
 250 *16*); Robert Bittl (Germany) and Asako Kawamori
 251 (Japan) summarize the configuration of the elec-
 252 tron transport intermediates of Photosystem II, as
 253 obtained by electron paramagnetic resonance
 254 spectroscopy (*Chapter 17*); Ben Hankamer
 255 (Australia), James Barber (UK) and Jon Nield
 256 (UK) describe the structure of the core/antenna
 257 holocomplex as visualized by electron microscopy
 258 (*Chapter 18*); Horst Witt (Germany) discusses the
 259 first three-dimensional structure of Photosystem II
 260 obtained by X-ray crystallography and other bio-
 261 physical methods (*Chapter 19*); Jian-Ren Shen and
 262 Nobuo Kamiya (both of Japan) discuss this
 263 structure, using also X-ray crystallography
 264 (*Chapter 20*); and James Barber and So Iwata
 265 (both of UK) discuss a somewhat refined
 266 structure, and its implications to the function of
 267 Photosystem II (*Chapter 21*).

268 These chapters on the structure are followed by
 269 four chapters on *Molecular Dynamics of Photo-*
 270 *system II*: Laura Barter (UK), David Klug (UK)
 271 and Rienk van Grondelle (The Netherlands)
 272 summarize our understanding about excitation
 273 energy trapping and its equilibration (*Chapter 22*);
 274 Barry Pogson (Australia), Heather Rissler
 275 (Australia) and Harry Frank (USA) elaborate the
 276 role of carotenoids in energy quenching (*Chapter*
 277 *23*); Vladimir Shinkarev (USA) discusses the pat-
 278 tern and the analyses of the O_2 evolution in a train
 279 of light flashes (*Chapter 24*); and Warwick Hillier
 280 (Australia) and Johannes Messinger (Germany)
 281 present an overview on the mechanism of water
 282 oxidation (*Chapter 25*).

283 This is followed by a discussion of *Assembly*
 284 *and Biodynamics of Photosystem II* in four chap-
 285 ters: Charles Dismukes, Gennady Ananyev and
 286 Richard Watt (all of USA) discuss the photoas-
 287 sembly of the catalytic manganese cluster (*Chapter*
 288 *26*); Wah Soon Chow (Australia) and Eva-Mari
 289 Aro (Finland) summarize our understanding of
 290 photoinactivation and mechanisms of recovery

291 (*Chapter 27*); Kenichi Yamaguchi (USA), Stephen
292 Mayfield (USA) and Mamoru Sugita (Japan)
293 present a current picture of transcriptional and
294 translational regulation of gene expression
295 (*Chapter 28*); and Steven Theg and Lan-Xin Shi
296 (both of USA) discuss transport and post-trans-
297 lational processing in biosynthesis and homeo-
298 stasis (*Chapter 29*).

299 This is followed by a discussion of the
300 *Comparison of Photosystem II with Other Natural/*
301 *Artificial Systems* in four chapters: Charles
302 Dismukes and Robert Blankenship (both of USA)
303 describe the origins and the evolution of oxygenic
304 photosynthesis (*Chapter 30*); Gary Brudvig (USA)
305 and Mårten Wikström present mechanistic com-
306 parisons between Photosystem II and Cytochrome
307 *c* oxidase (*Chapter 31*); Lázló Kálmán (Hungary),
308 JoAnn Williams (USA) and James Allen (USA)
309 summarize research on mimicking the properties
310 of Photosystem II in purple bacterial reaction
311 centers (*Chapter 32*); Brian Gibney (USA) and
312 Cecilia Tommos (Sweden) discuss *de novo* protein
313 design in respiration and photosynthesis (*Chapter*
314 *33*); and Ann Magnuson, Stenbjörn Styring and
315 Leif Hammarström (all of Sweden) end this book
316 with an understanding of Photosystem II through
317 artificial photosynthesis.

318 The ISBN number of this volume is 1-4020-
319 4249-3; it has 16 color plates; and xxvii + 786 pages
320 (including a 10-page index).

321 **A Bit of History: First Clear Evidence of the Series**
322 **Scheme, and the Naming of System 2 (Now**
323 **Photosystem II) by Louis N.M. Duysens,**
324 **Jan Amesz and B.M. Kamp in 1961**

325 A recently published time-line on oxygenic pho-
326 tosynthesis covers many aspects of the history of
327 'Photosystem II' (see Govindjee and D. Krogmann
328 (2004) Discoveries in oxygenic photosynthesis
329 (1727–2003): A perspective. *Photosynth Res* 80:
330 15–57). Chapter 1 of this book by K. Satoh, T.J.
331 Wydrzynski and Govindjee includes a historical
332 account of Photosystem II (for references, see this
333 chapter). In a paper, published on May 6, 1961,
334 Louis N.M. Duysens, Jan Amesz and B.M. Kamp
335 (Two photochemical systems in photosynthesis.
336 *Nature* 190: 510–511) used for the first time the
337 name 'System 2' for the photosystem responsible
338 for the action spectrum of chlorophyll *a* fluores-

339 cence; it was the system that was suggested to
340 oxidize water to oxygen, and reduce cytochrome.
341 'System 1', on the other hand, oxidized cyto-
342 chrome, and reduced pyridine nucleotide. Duysens
343 and colleagues added first red light (680 nm light;
344 absorbed mainly by chlorophyll) and observed
345 oxidation of a cytochrome in a red alga *Por-*
346 *phyridium cruentum*, and then they added green
347 light (562 nm; absorbed mainly in phycoerythrin)
348 and observed reduction of this oxidized
349 cytochrome. Addition of the herbicide DCMU
350 eliminated the reduction of cytochrome by green
351 light, but not its oxidation by red light. This
352 antagonistic effect of light 1 and 2 on cytochrome
353 provided not only the evidence for the series
354 scheme of photosynthesis, but was the first paper
355 to call the system that oxidized water and
356 reduced cytochrome as 'System 2' (currently,
357 Photosystem II), whereas the other system that
358 oxidized cytochrome as 'System 1' (currently,
359 Photosystem I). In this seminal paper, Duysens
360 and colleagues had recognized not only their
361 own work, but that of Robert Emerson (with
362 Marcia Brody), Eugene Rabinowitch (with
363 Emerson, and with Rajni Govindjee and Jan B.
364 Thomas), C. Stacy French (with V.K. Young,
365 and with Jack Myers), Norman Bishop, and Leo
366 Vernon (with L.P. Zaugg). Since in sunlight both
367 systems are excited simultaneously and begin to
368 function almost simultaneously, it is not a
369 question of which starts first. The naming of the
370 system is thus arbitrary.

Future AIPH books 371

The readers of the current series are encouraged to
372 watch for the publication of the forthcoming
373 books (not necessarily arranged in the order of
374 future appearance):
375

The Structure and Function of Plastids (Editors:
376 Robert Wise and J. Kenneth Hooper; expected to
377 contain 27 Chapters and ~775 pages; ISBN:
378 1-4020-4060-1);
379

Chlorophylls and Bacteriochlorophylls: Bio-
380 *chemistry, Biophysics, Functions and Applications*
381 (Editors: Bernhard Grimm, Robert J. Porra,
382 Wolfhart Rüdiger and Hugo Scheer);
383

Photosystem I: The Light-Driven Plastocyanin:
384 *Ferredoxin Oxidoreductase* (Editor: John Gol-
385 beck);
386

387	<i>Biophysical Techniques II</i> (Editors: Thijs J. Aartsma and Jörg Matysik);	<i>Readers are encouraged to send their suggestions for future volumes (topics, names of future editors, and of future authors) to me by E-mail (gov@uiuc.edu) or fax (1-217-244-7246).</i>	417
388			418
389	<i>Photosynthesis: A Comprehensive Treatise: Physiology, Biochemistry, Biophysics and Molecular Biology, Part 1</i> (Editors: Julian Eaton-Rye and Baishnab Tripathy); and		419
390			420
391		I take this opportunity to thank Thomas J. Wydrzynski and Kimiyuki Satoh for their outstanding and painstaking editorial work. We are grateful to them for (personally) subsidizing 8 of the 16 color plates in this volume. I thank all the 75 authors of volume 22: without their authoritative chapters, there would be no such volume. I thank Jacco Flipsen and Noeline Gibson (both of Springer) for their friendly working relationship with us that led to the production of this book.	421
392			422
393	<i>Photosynthesis: A Comprehensive Treatise: Physiology, Biochemistry, Biophysics and Molecular Biology, Part 2</i> (Editors: Baishnab Tripathy and Julian Eaton-Rye).		423
394			424
395			425
396			426
397	In addition to these contracted books, we are already in touch with prospective Editors for the following books:		427
398			428
399			429
400	Molecular Biology of Cyanobacteria II		430
401	Protonation and ATP Synthases		431
402	Genomics and Proteomics	Special thanks go to Larry Orr for his wonderful work in typesetting this book. His constant advise to the editors and his outstanding interactions with all those involved in this book are a source of inspiration to all of us.	432
403	Sulfur Metabolism in Photosynthetic Systems		433
404	Molecular Biology of Stress in Plants		434
405	Global Aspects of Photosynthesis and Respiration		435
406	(2 volumes)		436
407	Artificial Photosynthesis.		
408	In view of the interdisciplinary character of research in photosynthesis and respiration, it is my earnest hope that this series of books will be used in educating students and researchers not only in Plant Sciences, Molecular and Cell Biology, Integrative Biology, Biotechnology, Agricultural Sciences, Microbiology, Biochemistry, and Biophysics, but also in Bioengineering, Chemistry, and Physics.		
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		Govindjee	437
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