


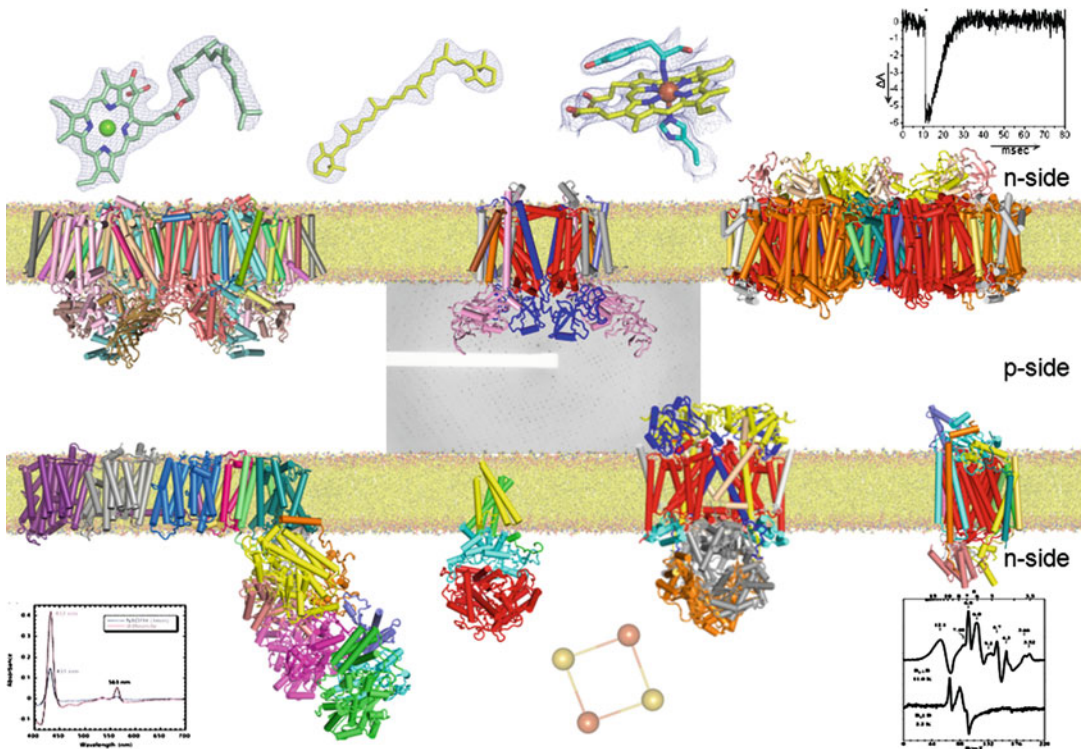
Advances in Photosynthesis and Respiration 41
Including Bioenergy and Related Processes

William A. Cramer
Toivo Kallas *Editors*



Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling

Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling



Experimental Information Important for Understanding Properties of Photosynthetic Cytochromes. Along the top are stick diagrams and electron density of pigments involved in light-harvesting – Chl-*a*, β -carotene, and heme of cytochrome *f* with unusual Tyr–His axial ligation (pdb, protein data base code, 4OGQ). This is followed by a flash kinetic trace of cytochrome oxidation-reduction. Along the bottom is a redox difference spectrum of the cytochrome *b₆f* complex, the [2Fe-2S] cluster in the Rieske iron-sulfur protein (pdb 4OGQ), and electron spin resonance spectra showing the unique $g = 12$ signal for the heme b_n – c_n couple in the cytochrome *b₆f* complex. In the center is an X-ray diffraction pattern of cytochrome *b₆f* crystals (pdb 4OGQ). **Protein structures** (left to right); **upper bilayer:** Photosynthetic electron transfer chain – Photosystem II (pdb 2WU2), cytochrome *b₆f* complex (pdb 4OGQ), Photosystem I (pdb 1JB0); **lower bilayer:** Mitochondrial electron transport chain – NDH complex (pdb 4HEA), succinate dehydrogenase (pdb 1NEN), cytochrome *bc₁* complex (pdb 3CX5), cytochrome *c* oxidase (pdb 1V54). The lipid bilayer is a homogeneous DOPC bilayer generated with the CHARMM program. *Abbreviations:* p, n-side, electrochemically positive and negative side of the membrane (drawing by S. Saif Hasan)

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Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling

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ISSN 1572-0233 ISSN 2215-0102 (electronic)
Advances in Photosynthesis and Respiration
ISBN 978-94-017-7479-6 ISBN 978-94-017-7481-9 (eBook)
DOI 10.1007/978-94-017-7481-9

Library of Congress Control Number: 2016934058

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 41: Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling

We are delighted to announce the publication of Volume 41 in this series on *Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes*. Oxygenic photosynthesis begins with conversion of light energy into chemical energy at two photochemical reaction centers in two separate photosystems (PS) I and II; this is followed by oxidation of water to molecular oxygen, reduction of pyridine nucleotide NADP⁺ (nicotinamide adenine dinucleotide phosphate) to NADPH, and synthesis of ATP from ADP and inorganic phosphate by ATP synthase, the latter using the proton motive force produced across the thylakoid membrane during electron transport from water to NADP⁺. Four protein complexes are essential for the completion of the entire process that leads to the formation of O₂, NADPH, and ATP: (1) Photosystem II (PSII); (2) Photosystem I (PSI); (3) Cytochrome (Cyt) *b₆f* complex; and (4) ATP synthase. Volume 22 in our Series, edited by T. Wydrzynski and K. Satoh and published in 2005, covered in great depth structure and function of PSII (Water-Plastoquinone Oxidoreductase); and volume 24, edited by J.H. Golbeck and published in 2006, did the same for PSI (Plastocyanin-ferredoxin oxidoreductase). Now, in 2016, we are fortunate to be able to present a complete structure-function description of not only Cyt *b₆f* complex but related complexes from mitochondria as well as from anoxygenic photosynthesis. This book (volume 41), *Cytochrome Complexes: Evo-*

lution, Structures, Energy Transduction, and Signaling, was edited by two international authorities in biology, biochemistry, and biophysics: William A. Cramer and Toivo Kallas. In oxygenic photosynthesis, Cyt *b₆f* provides the link between PSII and PSI; it takes plastoquinol (PQH₂) made by PSII and reduces plastocyanin, which, in turn, is the source of electrons to reduce ferredoxin (and, thus, NADP⁺) by PSI. In addition, the cytochrome complex functions in the so-called Q cycle that is essential in generating an electrochemical proton gradient sufficient to generate the necessary ATP.

This book starts, appropriately, with a chapter by the late Derek S. Bendall, where he described the historical background of the field as well as the cytochrome notation. The book includes a discussion of the evolution of cytochromes and their functions. Students will benefit by an extensive exposure to both the experiments and the theory underlying electron transfer in proteins, as well as that of the molecular structures of cytochromes and even supercomplexes from both eukaryotes and prokaryotes. Essentially, one has, for the first time, as one would say, “*All we wanted to know about cytochromes, but could not bring ourselves to ask.*” Yes, the book includes authoritative information even on macromolecular assembly, regulation, and signaling via the Cyt *b₆f* complex.

Because volume 41 covers an extensive subset of the cytochrome complexes that are involved not only in oxygenic photosynthesis

but also in anoxygenic photosynthesis, as well as in respiration, one is confident that this book will be used in educating undergraduate and graduate students and researchers not only in plant and agricultural sciences but animal sciences as well as in microbiology. And since the book covers in depth the structure and function, the molecular biology, and the biochemistry as well as the biophysics of these cytochrome complexes (see Preface as well as Table of Contents of this book for further details), it can be used by students in molecular & cell biology, biochemistry, chemical biology, and biophysics. Further, one can see its significance in areas of agricultural and chemical engineering and in biotechnology, all of which should contribute to the significance of this book.

Authors of Volume 41

We note with great pride that the current volume is truly an international book; it has authors from 13 countries: Finland (1); France (6); Germany (10); Italy (3); Ireland (3); Israel (2); Japan (8); Lithuania (2); Poland (6); Russia (10); Switzerland (1); UK (8); and USA (25).

We begin by specifically mentioning here two authors, who are also editors of this volume: William A. Cramer of Purdue University, Indiana, USA, and Toivo Kallas of University of Wisconsin Oshkosh, Wisconsin, USA (see their biographies in this volume). Cramer's theme of research is the structure and function of membrane proteins, with a major focus on photosynthetic energy transduction via the cytochrome b_6f protein complex. We recommend that you visit his websites since they provide information on him as well as on his research: <https://www.bio.purdue.edu/lab/cramer/>; https://www.bio.purdue.edu/People/faculty_dm/directory.php?refID=12 Kallas's theme of research is overall photosynthesis, but in particular, electron transport through the cytochrome b_6f complex. His work has often focused on cyanobacteria; his web page is at <http://www.uwosh.edu/facstaff/kallas>.

There are 80 authors (including the two editors), who are experts in the field of their research, especially cytochromes. Alphabetically (by last names), they are Jean Alric, Eva-Mari Aro, Danas Baniulis, Adrian C. Barbrook, Carl E. Bauer, the late Derek S Bendall, Gabor Bernat, Edward Berry, Wojciech Bialek, Robert E. Blankenship, Elisa Bombarda, Martin Caffrey, William A. Cramer, Fevzi Daldal, Miguel A. De la Rosa, Irene Díaz-Moreno, Antonio Díaz-Quintana, Timothy J. Donohue, Anne-Lise Ducluzeau, Seda Ekici, Robert Ekiert, Lothar Esser, Giovanni Finazzi, Maria Luisa Genova, Patrice Hamel, Shigeharu Harada, S. Saif Hasan, Florian Hilbers, Christopher J. Howe, Li-shar Huang, Saheed Imam, Daniel Ken Inaoka, Giles N. Johnson, Toivo Kallas, Bahia Khalfaoui-Hassani, Kiyoshi Kita, Hans-Georg Koch, Piotr Kolesinski, David Kramer, Lev I. Krishtalik, Genji Kurisu, Giorgio Lenaz, Joseph A. Lyons, Erica L.W. Majumder, Alizée Malnoë, Benjamin May, Yuval Mazor, I. Miliute, Jun Minagawa, Anthony L. Moore, Frank Müh, Lars Mueller, Nathan Nelson, Robert H. Nimmo, Wolfgang Nitschke, Daniel R. Noguera, Artur Osyczka, Jean-David Rochaix, Matthias Rögner, Marcin Sarewicz, Georg Schmetterer, Dirk Schneider, Tomoo Shiba, Toshiharu Shikanai, Namita Shroff, Melanie A. Spero, Andrzej Szczepaniak, Petru-Iulian Trasnea, G. Matthias Ullmann, Marcel Utz, Andreia F. Verissimo, Di Xia, Shinya Yoshikawa, Luke Young, Chang-An Yu, Sébastien Zappa, Fei Zhou, Francesca Zito, and Athina Zouni.

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- Further information on these books and ordering instructions is available at <http://www.springer.com/series/5599>. Contents of volumes 1–28 can also be found at < <http://www.life.uiuc.edu/govindjee/photosynSeries/ttocs.html>>.
- Special 25 % discounts are available to members of the International Society of Photosynthesis Research, ISPR <http://www.photosynthesisresearch.org/>. See <http://www.springer.com/ispr>.

Future Advances in Photosynthesis and Respiration and Other Related Books

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

- *Canopy Photosynthesis: From Basics to Applications* (Editors: Kouki Hikosaka, Ülo Niinemets and Niels P.R. Anten); it is already available; see < <http://www.springer.com/us/book/9789401772907>>
- *Photosynthesis and Climate Change* (working title) (Editor: Joy K. Ward)

- *Cyanobacteria* (Editor: Donald Bryant)
- *Leaf Photosynthesis* (Editors: William W. Adams III and Ichiro Terashima)
- *Photosynthesis in Algae* (Editors: Anthony Larkum and Arthur Grossman)
- *Plant Respiration* (Editor: Guillaume Tcherkez)

In addition to the above contracted books, the following topics are under consideration:

- Algae, Cyanobacteria: Biofuel and Bioenergy
- Artificial Photosynthesis
- ATP Synthase: Structure and Function
- Bacterial Respiration II
- Carotenoids II
- Evolution of Photosynthesis
- Green Bacteria and Heliobacteria
- Interactions between Photosynthesis and other Metabolic Processes
- Limits of Photosynthesis: Where do we go from here?
- Photosynthesis, Biomass and Bioenergy
- Photosynthesis under Abiotic and Biotic Stress

If you have any interest in editing/coediting any of the above listed books, or being an author, please send an e-mail to Tom Sharkey (tsharkey@msu.edu) and/or to Govindjee (gov@illinois.edu). Suggestions for additional topics are also welcome.

Instructions for writing chapters in books in our series are available by sending e-mail requests to one or both of us; they may also be downloaded from Govindjee's website <http://www.life.illinois.edu/govindjee> as the fourth item under "Announcements" on the main page.

Acknowledgments

We take this opportunity to thank and congratulate William A. Cramer and Toivo Kallas for their outstanding editorial work; they have indeed done a fantastic job, not only in editing but also in organizing this book for all of us, and for their highly professional dealing with the reviewing process. We thank all the 81 authors of this book (see the list given earlier); without their authoritative chapters, there would be no such volume. We give special thanks to S. Koperundevi of SPi Global, India, for directing the typesetting of this book; her expertise has been crucial in bringing this book to completion. We owe Jacco Flipsen, Andre Tournois, and Ineke Ravesloot (of Springer) thanks for their friendly working relation with us that led to the production of this book.

March 15, 2016

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Series Editors



Govindjee is the founding series editor of *Advances in Photosynthesis*, as it was called then, with volume 1 (*The Molecular Biology of Cyanobacteria*, 1994). In addition to being co-series editor (with Tom Sharkey) since volume 31 (*The Chloroplast: Basics and Applications*, 2010), he has coedited (1) Volume 19 (*Chlorophyll a Fluorescence: A Signature of Photosynthesis*, 2004); (2) Volume 20 (*Discoveries in Photosynthesis*, 2006); (3) Volume 29 (*Photosynthesis In Silico: Understanding Complexity from Molecules to Ecosystems*, 2009); and (4) Volume 40 (*Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria*, 2014).

Govindjee, who uses one name only, has been Professor Emeritus of Biochemistry, Biophysics, and Plant Biology at the University of Illinois at Urbana-Champaign (UIUC), since 1999. His short evolving biography can be found in each volume of *Advances in Photosynthesis and Respiration*, and other information on him and his activities is available at his website <http://www.life.illinois.edu/govindjee>. An interview for Annual Reviews Inc., by

Don Ort, is available at <https://www.youtube.com/watch?v=cOzuL0vxEi0>. His recent publications are listed at http://www.life.illinois.edu/govindjee/recent_papers.html, and earlier publications since 1955 are at <http://www.life.illinois.edu/govindjee/pubschron.html>.

Govindjee was trained in Plant Physiology (1952–1956) by Shri Ranjan (a student of Felix Frost Blackman of UK), in Biology and Biochemistry of Photosynthesis (1956–1958) by Robert Emerson (a student of the Nobel laureate Otto Warburg), and in Biophysics of Photosynthesis (1958–1961) by Eugene Rabinowitch (a postdoc student of the Nobel laureate James Franck). After his Ph.D. in Biophysics in 1960 from the UIUC, he has learned many concepts and techniques from many others including Louis N.M. Duysens (Leiden, The Netherlands); C. Stacy French (Stanford, California, USA); Herbert S. Gutowsky (Urbana, Illinois, USA); Bessel Kok (Baltimore, Maryland, USA); Jean Lavorel (Gif-sur-Yvette, France); Gregorio Weber (Urbana, Illinois); and Horst Witt (Berlin, Germany).

Govindjee's discoveries, with his coworkers and graduate students, include the participation of chlorophyll (Chl) *a* (in what we now call Photosystem (PS) II); proof of the existence of two light reactions in NADP reduction, and in Chl *a* fluorescence; temperature dependence of excitation energy transfer down to 4° K in algae and cyanobacteria; molecular understanding of both the fast and slow Chl *a* fluorescence (both prompt and delayed) changes—that includes participation of membrane potential, pH gradient, “traffic jam” in PSI, and the so-called state changes; first picosecond measurements on the primary photochemistry of PSI and PSII; unique role of bicarbonate in electron transfer and protonation events at the Q_B binding site; first comprehensive theory of thermoluminescence in plants; and the first use of lifetime of Chl *a* fluorescence measurements in understanding photoprotection in plants.

Govindjee's activities include, besides research on “Light Reactions of Photosynthesis,” honoring others (Robert Blankenship; Bob Buchanan; Andre Jagendorf; Wolfgang Junge; Hartmut Lichtenthaler; George Papageorgiou; William Ogren; Vladimir Shuvalov; and Diter Von Wettstein; see Govindjee's website) in the field, as well as participating in writing and editing obituaries and tributes (Lou Duysens; Colin Wraight; Al Bassham; Rene Marcelle; V.S.R. Rama Das; Prasanna Mohanty; Jalal Aliyev; Al Frenkel; and Andy Benson). In addition, he enjoys lecturing on the

history of photosynthesis research and in teaching photosynthesis by having students act as molecules and demonstrating the path of electrons in photosynthesis by having them enact a drama. He has had many honors, but he cherishes five of them dearly: 2006 Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology; 2007 Communication Award of the International Society of Photosynthesis Research; 2008 Liberal Arts & Sciences Lifetime Achievement Award of UIUC; 2015 Dr. B.M. Johri Memorial Award for Excellence in Plant Biology, from the Society of Plant Research, India; and a 2016 Distinguished Alumnus Award from his High School (Colonelganj Inter College) in Allahabad. In addition, he has enjoyed what others have written on him at his 75th and 80th birthdays (see *Photosynth Res* **93**:1–5 (2007); **94**: 153–178 (2007); **100**: 49–55 (2009); **116**: 107–110; 111–144 (2013); **122**: 113–119); also see <<https://www.linkedin.com/pulse/govindjee-living-legend-i-met-dr-ravi-sharma>>. (To see this site, click on “living-legend”.) A rather useful effort in teaching others is through the article “Photosynthesis Web Resources” <<http://www.life.illinois.edu/govindjee/photoweb/>>. Also see a collection of education books at <http://www.life.illinois.edu/govindjee/g/Books.html>. He is always delighted to respond to questions on both photosynthesis research and education (e-mail: gov@illinois.edu).



Thomas D. (Tom) Sharkey obtained his Bachelor's degree in Biology in 1974 from Lyman Briggs College, a residential science college at Michigan State University, East Lansing, Michigan, USA. After 2 years as a research technician, Tom entered a Ph.D. program in the Department of Energy Plant Research Laboratory at Michigan State University under the mentorship of Klaus Raschke and finished in 1979. Postdoctoral research was carried out with Graham Farquhar at the Australian National University, in Canberra, where he coauthored a landmark review on photosynthesis and stomatal conductance. For 5 years he worked at the Desert Research Institute, Reno, Nevada. After Reno, Tom spent 20 years as Professor of Botany at the University of Wisconsin in Madison. In 2008, Tom became Professor and Chair of the Department of Biochemistry and Molecular Biology at Michigan State University. Tom's research interests center on the exchange of gases between plants and the atmosphere and carbon metabolism of photosynthesis. The biochemistry and biophysics underlying carbon dioxide uptake and isoprene emission from plants form the two major research topics in his laboratory. Among his contributions are measurement of the carbon dioxide concentration inside leaves, an

exhaustive study of short-term feedback effects in carbon metabolism, and a significant contribution to elucidation of the pathway by which leaf starch breaks down at night. In the isoprene research field, Tom is recognized as the leading advocate for thermotolerance of photosynthesis as the explanation for why plants emit isoprene. In addition, his laboratory has cloned many of the genes that underlie isoprene synthesis and he has published many important papers on the biochemical regulation of isoprene synthesis. Tom's work has been cited over 21,000 times according to Google Scholar in 2015. He has been named an Outstanding Faculty member by Michigan State University and in 2015, he was honored, and named as a University Distinguished Professor. Tom has coedited three books, the first on trace gas emissions from plants in 1991 (with Elizabeth Holland and Hal Mooney), volume 9 of this series (with Richard Leegood and Susanne von Caemmerer) on the *Physiology of Carbon Metabolism of Photosynthesis* in 2000, and volume 34 (with Julian Eaton-Rye and Baishnab C. Tripathy) entitled *Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*. Tom has been co-series editor of this series since volume 31.

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Preface

Why study cytochrome complexes? An answer is provided by the range of subtopics in the book, “evolution, structures, energy, and signaling,” which are described in the book title. Studies on the cytochrome family of proteins encompass a uniquely wide area of basic and applied research. Research in this field utilizes a range of theoretical and computational approaches, as well as a broad cross section of experimental techniques. Understanding obtained on the structure and function of the cytochromes and cytochrome complexes utilizes an extraordinary range of experimental approaches, including computational biology, genetics, macromolecular biochemistry, molecular biology, physics of charge transfer reactions, structure analysis using x-ray and electron diffraction, and ultrafast spectroscopy.

As reflected in the book title, the information and understanding gained in the field has an influence on a wide range of subjects, including evolution, mechanisms of membrane-based respiratory and photosynthetic energy transduction, theory of charge transfer in proteins, structure-function of large hetero-oligomeric membrane proteins, including lipid-protein interactions, and transmembrane signaling.

A special aspect of cytochromes, cytochrome complexes, as well as other proteins involved in bioenergetics and charge transfer is that they allow function to be quantitatively analyzed. Thus, in this group of proteins, it is possible to determine that a protein or protein complex is functional before committing a large amount of time to crystallization and analysis of structure. Dating back to the 1988 Nobel Prize in Chemistry, given to J. Deisenhofer, H. Michel, and R. Huber for determination of the crystal structure of the bacterial photosynthetic reaction center, the majesty of the crystal structures of hetero-

oligomeric membrane proteins obtained in the subsequent 10 years were of energy-transducing proteins. Of these, a substantial fraction involved cytochrome complexes.

The Logic of the Collection The book starts with an Introduction by Derek Bendall describing cytochrome notation, which is connected to the history of the field, focusing on research in England in the pre-World War II era. An *ab initio* “start with the beginning” logic then leads to a discussion of the evolution of cytochromes and hemes. Before presentation of the many individual cytochrome systems, the fundamentals of the theory of electron transfer in proteins are presented, followed by an extensive description of the molecular structures of cytochromes and cytochrome complexes from eukaryotic and prokaryotic sources, including those derived from photosynthetic reaction centers. The presentation of atomic structure information has a major role in these discussions, including the relatively new subject of “supercomplexes.” This structure information has a major niche in the broad field of membrane structure-function. Expanding the perspective beyond structure-function applied to charge transfer and energy storage, the problems of protein and macromolecule assembly, regulation, and signaling, including transmembrane signaling, which have conceptual connections to central areas of biochemistry, biophysics, and cell biology, are considered. Regarding subjects related to cutting-edge areas of biology and plant biology, the up-to-date presentation of the topics of *Regulation* and *Signaling* is noted here.

The broad extent of fundamental intellectual and research areas that are represented in this book makes it a useful resource for teaching of academic courses and presentation of seminars on fundamental and