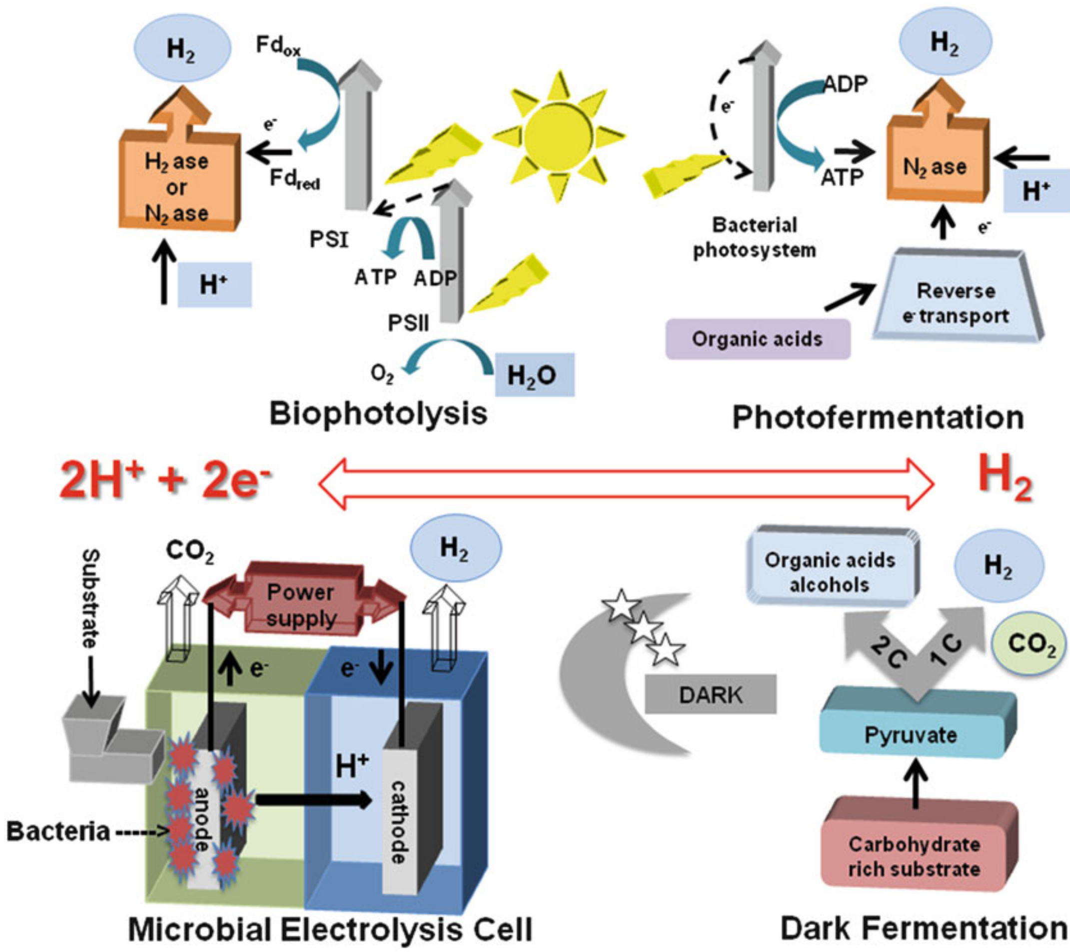
Microbial BioEnergy: Hydrogen Production



Different Ways for BioHydrogen Production The four possible ways for producing H_2, by exploiting microbial activities, are shown here. *Biophotolysis*: H_2 production by microalgae (through H_2-ase) or Cyanobacteria (through H_2-ase or N_2-ase) by using low potential reductants derived from either water or stored sugars *via* the photosynthetic machinery. *Photofermentation*: H_2 production by anoxygenic photosynthetic bacteria (through N_2-ase) by using reductants obtained from the oxidation of organic compounds as well as solar energy used through photosynthesis. *Dark fermentation*: H_2 production by mesophilic or thermophilic chemoheterotrophic bacteria (through H_2-ase) by using reductants and energy obtained from the oxidation of organic compounds. *Microbial Electrolysis Cell (MEC):* H_2 production by means of cathodic proton reduction with applied potential exploiting the low redox potential produced by exoelectrogenic bacteria at the anode. This figure is adapted from Fig. 1.3 in Chap. 1 of this book.

Advances in Photosynthesis and Respiration
Including Bioenergy and Related Processes

VOLUME 38

The book series Advances in Photosynthesis and Respiration *Including Bioenergy and Related Processes* provides a comprehensive and state-of-the-art account of research in photosynthesis, respiration and related processes. Virtually all life on our planet Earth ultimately depends on photosynthetic energy capture and conversion to energy-rich organic molecules. These are used for food, fuel, and fiber. Photosynthesis is the source of almost all bioenergy on Earth. The fuel and energy uses of photosynthesized products and processes have become an important area of study, and competition between food and fuel has led to resurgence in photosynthesis research. This series of books spans topics from physics to agronomy and medicine; from femtosecond processes through season-long production to evolutionary changes over the course of the history of the Earth; from the photophysics of light absorption, excitation energy transfer in the antenna to the reaction centers, where the highly-efficient primary conversion of light energy to charge separation occurs, through the electrochemistry of intermediate electron transfer, to the physiology of whole organisms and ecosystems; and from X-ray crystallography of proteins to the morphology of organelles and intact organisms. In addition to photosynthesis in natural systems, genetic engineering of photosynthesis and artificial photosynthesis is included in this series. The goal of the series is to offer beginning researchers, advanced undergraduate students, graduate students, and even research specialists, a comprehensive, up-to-date picture of the remarkable advances across the full scope of research on photosynthesis and related energy processes. The purpose of this series is to improve understanding of photosynthesis and respiration at many levels both to improve basic understanding of these important processes and to enhance our ability to use photosynthesis for the improvement of the human condition.

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Microbial BioEnergy: Hydrogen Production

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This book is dedicated to the memory of

Hans Gaffron (1902–1979) and **Howard Gest (1921–2012)**

pioneers of the microbial based hydrogen gas production

From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 38: Microbial BioEnergy: Hydrogen Production

We are delighted to announce the publication of volume 38 in this series. The title of our series *Advances in Photosynthesis and Respiration* was already updated in volume 35 to include the subtitle*: Including Bioenergy and Related Processes*. Earlier, the front cover of each volume had a distinctive white background and color palette; from volume 35, it has been changed to a web-friendly green background; and each volume begins with a unique figure, representing the book. Further, the publisher, Springer, makes the front matter of all of the volumes freely available online. Links to each volume are given under "Our Books: Published Volumes." Readers may also notice that this volume and the past few volumes have had color figures integrated into the chapters, instead of being collected in one section of the book. This improvement was possible because of changes in how the books are produced. Another change is that references to chapters in books are now being tracked by bibliographic services. This will help authors provide evidence of the importance of their work. We hope that these updates will maintain the importance of these edited volumes in the dissemination of the science of photosynthesis and bioenergy.

We are delighted to announce that volume 38 is the first one to deal with the new direction "*Including Bioenergy and Related Processes.*" We are indeed fortunate to have two distinguished authorities with us as editors of this new volume 38: Davide Zannoni, and Roberto De Philippis. Zannoni is a Professor of General Microbiology, at the University of Bologna, Italy; he is an authority on the structure and the function of membrane redox-complexes in microbes, and a pioneer of bioenergetics and genomics of microbial remediation of metals in many systems. More importantly, his present focus is on the production of hydrogen by thermophilic bacteria and electricity from microbial systems. De Philippis is an Associate Professor of Microbial Biotechnology at the University of Florence, Italy. He is an authority on exopolysaccharide-producing cyanobacteria and their biotechnological exploitation and, more importantly, in the last 15 years he has been deeply involved in studies on the photofermentative production of hydrogen indoors and outdoors and on the efficient conversion of light energy into hydrogen energy.

This Book: Volume 38

Microbial BioEnergy: Hydrogen Production is a comprehensive book covering most of the processes important for the microbial hydrogen production. It provides a broad coverage of this emerging research field and, in our opinion, it should be accessible to advanced undergraduates, graduate students, and researchers needing to broaden their knowledge on the photosynthetic and fermentation processes applied to hydrogen gas generation. For biologists, biochemists, biophysicists and microbiologists, this volume provides a solid and quick starting base to get into biotechnological problems of "microbial bioenergy." We believe that this volume will also be of interest to teachers of advanced undergraduate and graduate students in chemical engineering and biotechnology needing a single reference book on the latest understanding of the critical aspects of microbial bioenergy production.

The *Preface* of this book appropriately states "Solar energy is the source of most of the living organisms on Earth so that the overall efficiency of oxygenic and/or non-oxygenic photosynthesis, when used to generate biomass, bioenergy and biofuels, is a critical point to be considered." This volume in our series, however, not only provides a comprehensive view of the current understanding of the photosynthetic mechanisms linked to bio-hydrogen production but also extends this view to the anaerobic-dark processes involved in transforming the solar-generated biomass into bio-hydrogen along with an in-depth coverage of both structural and functional aspects of the main enzymes involved, such as *nitrogenases* and *hydrogenases*.

In our opinion, this book has been appropriately dedicated to Hans Gaffron (1902–1979) and Howard Gest (1921–2012), founders of the microbial based hydrogen gas production technologies. One of us (Govindjee) is fortunate to have known personally both these giants of photosynthesis research. Among the various other discoveries, Gaffron was the first to observe, in 1942, hydrogen production by green algae under sulfur starvation, while Gest was the first to describe, in 1949, hydrogen-production by purple non-sulfur phototrophic bacteria (See below for information on "Discoveries in Photosynthesis" volume 20, in our series, where these discoveries are described).

Authors

The current book contains 15 chapters written by 42 international authors from 10 different countries (Australia, Canada, France, Germany, Italy, Portugal, Russia, Spain, Turkey, USA). We give special thanks to each and every author for their valuable contribution to the successful production of this unique book:

Francisco Gabriel **A**cién-Fernández (Spain; Chap. 13); Alessandra Adessi (Italy; Chap. 12); Giacomo Antonioni (Italy; Chap. 15); Sara E. **B**lumer-Schuette (USA; Chap. 8); Hermann Bothe (Germany; Chap. 6); Martina **C**appelletti (Italy; Chap. 9); Jonathan M. Conway (USA; Chap. 8); Roberto **D**e Philippis (Italy; Chap. 12); Alexandra Dubini (USA; Chap. 5); Carrie **E**ckert (USA; Chap. 5); Ela Eroglu (Australia; Chap. 11); Inci Eroglu (Turkey; Chap. 11); José M. **F**ernández-Sevilla (Spain; Chap. 13); Juan C. Fontecilla-Camps (France; Chap. 2); Dario Frascari (Italy; Chap. 15); Maria L. **G**hirardi (USA; Chap. 5); Ufuk Gündüz (Turkey; Chap. 11); Patrick C. **H**allenbeck (Canada; Chap. 1); Robert M. **K**elly (USA; Chap. 8); Paul W. King (USA; Chap. 5); Sergey Kosourov (Russia; Chap. 14); Pierre-Pol **L**iebgott (France; Chap. 3); Pin-Ching **M**aness (USA; Chap. 5); James B. McKinlay (USA; Chap. 7); Emilio Molina-Grima (Spain; Chap. 13); David W. Mulder (USA; Chap. 5); William E. **N**ewton (USA; Chap. 6); Paulo **O**liveira (Portugal; Chap. 4); Bernard Ollivier (France; Chap. 9); Ebru Özgür (Turkey; Chap. 11); Catarina C. **P**acheco (Portugal; Chap. 4); Anne Postec (France; Chap. 9); John M. **R**egan (USA; Chap. 10); Marc Rousset (France; Chap. 3); Paula **T**amagnini (Portugal; Chap. 4); Anatoly Tsygankov (Russia; Chap. 14); Anne **V**olbeda (France; Chap. 2); Hengjing **Y**an (USA; Chap. 10); Jianping Yu (USA; Chap. 5); Meral Yücel (Turkey; Chap. 11); Davide **Z**annoni (Italy; Chap. 9); Jeffrey V. Zurawski (USA; Chap. 8).

Our Books: Published Volumes

We list below information on all the 37 volumes that have been published thus far (see http://www.springer.com/series/5599 for the web site of the series). Electronic access to individual chapters depends on subscription (ask your librarian) but Springer provides free downloadable front matter as well as indexes at the above site. As of July, 2011, Tables of Contents have been available for all the volumes. The available web sites of the books in the Series are listed below.

- **Volume 37 (2014)** Photosynthesis in Bryophytes and Early Land Plants, edited by David T. Hanson and Steven K. Rice, from USA. Eighteen chapters, approx. 500 pp, Hardcover, ISBN: 978-94-007-6987-8 (HB) ISBN 978-94-007-6988-5 (e-book) [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-6987-8]
- **Volume 36 (2013) Plastid Development in Leaves During Growth and Senescence**, edited by Basanti Biswal, Karin Krupinska and Udaya Biswal, from India and Germany. Twenty-eight chapters, 837 pp, Hardcover, ISBN: 978-94-007-5723-3 (HB) ISBN 978-94-XXXXX (e-book) [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-5723-3]
- **Volume 35 (2012) Genomics of Chloroplasts and Mitochondria**, edited by Ralph Bock and Volker Knoop, from Germany. Nineteen chapters, 475 pp, Hardcover, ISBN: 978-94-007-2919-3 (HB) ISBN 978-94-007-2920-9 (e-book) [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-2919-3]
- **Volume 34 (2012) Photosynthesis – Plastid Biology, Energy Conversion and Carbon Assimilation**, edited by Julian Eaton-Rye, Baishnab C. Tripathy, and Thomas D. Sharkey, from New Zealand, India, and USA. Thirty-three chapters, 854 pp, Hardcover, ISBN: 978-94-007-1578-3 (HB) ISBN 978-94-007-1579-0 (e-book) [http://www.springer.com/life+sciences/plant+sciences/book/978-94-007-1578-3]
- **Volume 33 (2012): Functional Genomics and Evolution of Photosynthetic Systems**, edited by Robert L. Burnap and Willem F. J. Vermaas, from USA. Fifteen chapters, 428 pp, ISBN: 978-94-007- 1532–5 [http://www.springer.com/life+sciences/book/978-94-007-1532-5]
- **Volume 32 (2011): C_4 Photosynthesis and Related CO_2 Concentrating Mechanisms**, edited by Agepati S. Raghavendra and Rowan Sage, from India and Canada. Nineteen chapters, 425 pp, Hardcover, ISBN: 978-90-481-9406-3 [http://www.springer.com/life+sciences/plant+sciences/book/978-90-481-9406-3]
- **Volume 31 (2010): The Chloroplast: Basics and Applications**, edited by Constantin Rebeiz (USA), Christoph Benning (USA), Hans J. Bohnert (USA), Henry Daniell (USA), J. Kenneth Hoober (USA), Hartmut K. Lichtenthaler (Germany), Archie R. Portis (USA), and Baishnab C. Tripathy (India). Twenty-five chapters, 451 pp, Hardcover, ISBN: 978-90-481-8530-6 [http://www.springer.com/life+sciences/plant+sciences/book/978-90-481-8530-6]
- **Volume 30 (2009): Lipids in Photosynthesis: Essential and Regulatory Functions**, edited by Hajime Wada and Norio Murata, both from Japan. Twenty chapters, 506 pp, Hardcover, ISBN: 978-90-481-2862-4; e-book, ISBN: 978-90-481-2863-1 [http://www.springer.com/life+sciences/plant+sciences/book/978-90-481-2862-4]
- **Volume 29 (2009): Photosynthesis in Silico: Understanding Complexity from Molecules**, edited by Agu Laisk, Ladislav Nedbal, and Govindjee, from Estonia, The Czech Republic, and USA. Twenty chapters, 525 pp, Hardcover, ISBN: 978-1-4020-9236-7 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-9236-7]
- **Volume 28 (2009): The Purple Phototrophic Bacteria**, edited by C. Neil Hunter, Fevzi Daldal, Marion C. Thurnauer and J. Thomas Beatty, from UK, USA and Canada. Forty-eight chapters, 1053 pp, Hardcover, ISBN: 978-1-4020-8814-8 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-8814-8]
- **Volume 27 (2008): Sulfur Metabolism in Phototrophic Organisms**, edited by Christiane Dahl, Rüdiger Hell, David Knaff and Thomas Leustek, from Germany and USA.

Twenty-four chapters, 551 pp, Hardcover, ISBN: 978-4020-6862-1 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-6862-1]

- **Volume 26 (2008): Biophysical Techniques Photosynthesis**, Volume II, edited by Thijs Aartsma and Jörg Matysik, both from The Netherlands. Twenty-four chapters, 548 pp, Hardcover, ISBN: 978-1-4020-8249-8 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-8249-8]
- **Volume 25 (2006): Chlorophylls and Bacteriochlorophylls: Biochemistry, Biophysics, Functions and Applications**, edited by Bernhard Grimm, Robert J. Porra, Wolfhart Rüdiger, and Hugo Scheer, from Germany and Australia. Thirty-seven chapters, 603 pp, Hardcover, ISBN: 978-1-40204515-8 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-4515-8]
- **Volume 24 (2006): Photosystem I: The Light-Driven Plastocyanin: Ferredoxin Oxidoreductase**, edited by John H. Golbeck, from USA. Forty chapters, 716 pp, Hardcover, ISBN: 978-1-40204255-3 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-4255-3]
- **Volume 23 (2006): The Structure and Function of Plastids**, edited by Robert R. Wise and J. Kenneth Hoober, from USA. Twenty-seven chapters, 575 pp, Softcover, ISBN: 978-1-4020-6570–6; Hardcover, ISBN: 978-1-4020-4060-3 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-4060-3]
- **Volume 22 (2005): Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase**, edited by Thomas J. Wydrzynski and Kimiyuki Satoh, from Australia and Japan. Thirty-four chapters, 786 pp, Hardcover, ISBN: 978-1-4020-4249-2 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-4249-2]
- **Volume 21 (2005): Photoprotection, Photoinhibition, Gene Regulation, and Environment**, edited by Barbara Demmig-Adams, William W. Adams III and Autar K. Mattoo, from USA. Twenty-one chapters, 380 pp, Hardcover, ISBN: 978-14020-3564-7 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-3564-7]
- **Volume 20 (2006): Discoveries in Photosynthesis**, edited by Govindjee, J. Thomas Beatty, Howard Gest and John F. Allen, from USA, Canada and UK. One hundred and eleven chapters, 1304 pp, Hardcover, ISBN: 978-1-4020-3323-0 [http://www.springer.com/life+sciences/plant+sciences/book/978-1-4020-3323-0]
- **Volume 19 (2004): Chlorophyll *a* Fluorescence: A Signature of Photosynthesis**, edited by George C. Papageorgiou and Govindjee, from Greece and USA. Thirty-one chapters, 820 pp, Hardcover, ISBN: 978-1-4020-3217-2 [http://www.springer.com/life+sciences/biochemistry+%26+biophysics/book/978-1-4020-3217-2]
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- **Volume 14 (2004): Photosynthesis in Algae**, edited by Anthony W. Larkum, Susan Douglas and John A. Raven, from Australia, Canada and UK. Nineteen chapters, 500 pp, Hardcover, ISBN: 978-0-7923-6333-0 [http://link.springer.com/book/10.1007/978-94-007-1038-2/page/1]
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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):

- The Structural Basis of Biological Energy Generation (Editor: Martin Hohmann-Marriott) [This book is almost ready to go to the typesetters]
- Canopy Photosynthesis: From Basics to Applications (Editors: Kouki Hikosaka, Ülo Niinemets and Niels P. R. Anten)
- Non-Photochemical Quenching (NPQ) and Energy Dissipation in Plants, Algae and Cyanobacteria (Editors: Barbara Demmig-Adams, Győző Garab and Govindjee)
- Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling (Editors: William Cramer and Toivo Kallas)
- Photosynthesis for Bioenergy (Editors: Elizabeth A. Ainsworth and Stephen P. Long)

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

- Algae, Cyanobacteria: Biofuel and Bioenergy
- Artificial Photosynthesis
- ATP Synthase
- Bacterial Respiration II
- Carotenoids II
- Cyanobacteria II
- Ecophysiology
- Evolution of Photosynthesis
- Global Aspects 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
- Plant Respiration II

If you have any interest in editing/co-editing 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 at gov@illinois.edu. Suggestions for additional topics are also welcome.

In view of the interdisciplinary character of research in photosynthesis and respiration, it is our 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, Chemical Biology, Biological Physics, and Biophysics, but also in Bioengineering, Chemistry, and Physics.

Acknowledgments

We take this opportunity to thank and congratulate Davide Zannoni and Roberto De Philippis 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 42 authors of this book (see the list above); without their authoritative chapters, there would be no such volume. We give special thanks to A. Lakshmi Praba, 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.

October 24, 2013 **Govindjee**

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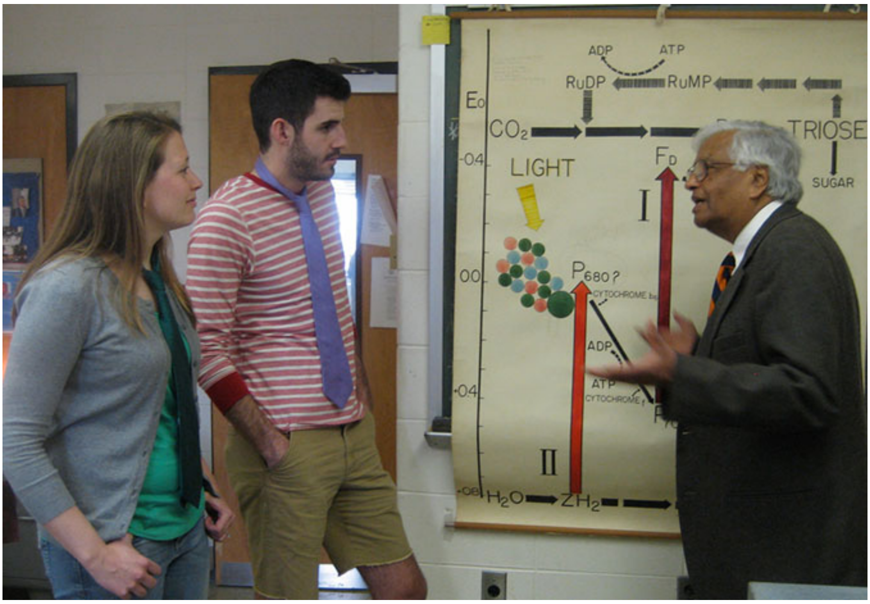
Series Editors



The above photograph shows the 1965 Z-Scheme that Govindjee had made when he, with Eugene Rabinowitch, had coined the term P680 for the reaction center of Photosystem II. From left to right: Rebecca Slattery (a graduate student of Donald R. Ort), Robert Koester (a graduate student of Lisa Ainsworth), and Govindjee. Photo by Joan Huber taken in May, 2013.

Govindjee, who uses one name only, was born on October 24, 1932, in Allahabad, India. Since 1999, he has been Professor Emeritus of Biochemistry, Biophysics, and Plant Biology at the University of Illinois at Urbana-Champaign (UIUC), Urbana, IL, USA. He obtained his B.Sc. (Chemistry and Biology) and M.Sc. (Botany: Plant Physiology) in 1952 and 1954 from the University of Allahabad. Govindjee studied "Photosynthesis" at the UIUC under two pioneers of photosynthesis, Robert Emerson and Eugene Rabinowitch, obtaining his Ph.D. in 1960, in Biophysics. He is best known for his research on excitation energy transfer, light emission, primary photochemistry, and electron transfer in "Photosystem II" (PS II, water-plastoquinone oxidoreductase). His early research included the discovery of a short-wavelength form of chlorophyll (Chl) *a* functioning in the Chl *b*-containing system, now called PS II; of the two-light effect in Chl *a* fluorescence; and, with his wife Rajni, of the two-light effect (Emerson enhancement) in NADP reduction in chloroplasts. His major achievements, with many collaborators, include an understanding of the basic relationships between Chl *a* fluorescence and photosynthetic reactions; a unique role of bicarbonate/carbonate on the electron acceptor side of PS II, particularly in the protonation events involving the Q_B binding region in PSII; molecular understanding of thermoluminescence in plants, algae and cyanobacteria; the first picosecond measurements on the primary photochemistry of PS II; and the first use of Chl *a* fluorescence lifetime measurements in understanding photoprotection, by plants and algae, against excess light. His current focus is on the "History of Photosynthesis Research," on "Photosynthesis Education," and on "What to Learn from Natural Photosynthesis to do Artificial Photosynthesis." He has served on the faculty of the UIUC for approximately 40 years. Govindjee's honors include: Fellow of the American Association of Advancement of Science (AAAS); Distinguished Lecturer of the School of Life Sciences, UIUC; Fellow and Lifetime Member of the National Academy of Sciences (India); President of the American Society for Photobiology (1980–1981); Fulbright Scholar (1956), Fulbright Senior Lecturer (1998) and Fulbright Specialist (2012); Honorary President of the 2004 International Photosynthesis Congress (Montréal, Canada); the first recipient of the Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology, 2006; 2007 recipient of the Communication Award of the International Society of Photosynthesis Research (ISPR); 2008 recipient of the Liberal Arts & Sciences (LAS) Lifetime Achievement Award of the UIUC. Further, Govindjee was honored **(1)** in 2007, through two special volumes of *Photosynthesis Research*, celebrating his 75th birthday and for his 50-year dedicated research in "Photosynthesis" (Guest Editor: Julian Eaton-Rye); **(2)** in 2008, through a special International Symposium on "Photosynthesis in a Global Perspective," at the University of Indore, India; **(3)** in 2012, through dedication to him of volume 34 of this series, celebrating his 80th year; **(4)** in 2012, through another book *Photosynthesis: Overviews on Recent Progress and Future Perspectives*, honoring him for *his outstanding research and teaching of photosynthesis and for being a global leader for stimulating photosynthesis research throughout the world*; and **(5)** in 2013, through two special volumes of *Photosynthesis Research*, on "Photosynthesis Education", which also celebrates his 80th birthday (Guest Editors: Suleyman Allakhverdiev; Jian-Ren Shen and Gerald Edwards). Govindjee is coauthor of *Photosynthesis* (John Wiley, 1969) and editor of many books, published by several publishers including Academic Press and Springer. Since 2007, each year Govindjee and Rajni Govindjee Award for Excellence in Biological Sciences is being given to graduate students by the Department of Plant Biology at the UIUC. Starting in 2014, these awards will alternate between Department of Biochemistry (even years) and Department of Plant Biology (odd years). For further information on Govindjee, see his website http://www.life.illinois.edu/govindjee.

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 in the federally funded Plant Research Laboratory at Michigan State University under the mentorship of Prof. Klaus Raschke, Tom entered the Ph.D. program in the same lab, and graduated in 1980. Postdoctoral research was carried out with Prof. Graham Farquhar at the Australian National University, in Canberra, where he co-authored a landmark review on photosynthesis and stomatal conductance that continues to receive much attention 30 years after its publication. For 5 years, Tom worked at the Desert Research Institute together with Prof. Barry Osmond, followed by 20 years as a 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 biochemistry and biophysics of gas exchange between plants and the atmosphere. Photosynthetic gas exchange, especially carbon dioxide uptake and use, and isoprene emission from plants, are the two major research topics in his laboratory. Among his contributions are measurements of the carbon dioxide concentration inside leaves, studies of the resistance to diffusion of carbon dioxide within the mesophyll of leaves of C_3 plants, and an exhaustive study of short-term feedback effects on carbon metabolism. As part of the study of short-term feedback effects, Tom's research group demonstrated that maltose is the major form of carbon export from chloroplasts at night, and made significant contributions to the elucidation of the pathway by which leaf starch is converted to sucrose 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 papers on the biochemical regulation of isoprene synthesis. Tom has coedited three books: T.D. Sharkey, E.A. Holland and H.A. Mooney (Eds.) *Trace Gas Emissions from Plants*, Academic, San Diego, CA, 1991; R.C. Leegood, T.D. Sharkey, and S. von Caemmerer (Eds.) *Physiology and Metabolism*, Advances in Photosynthesis (and Respiration), Volume 9 of this Series, Kluwer (now Springer), Dordrecht, 2000; and Volume 34 of this series *Photosynthesis: Plastid Biology, Energy Conversion and Carbon Assimilation*, Advances in Photosynthesis and Respiration *Including Bioenergy and Related Processes,* Julian J. Eaton-Rye, Baishnab C. Tripathy and Thomas D. Sharkey (Eds.) Springer. Tom joined the series founder Govindjee as Series Co-editor from Volume 31 of this series. Tom is currently the Chairperson of the Department of Biochemistry and Molecular Biology, Michigan State University, East Lansing, Michigan. For further information see his web page at: <http://www.bmb.msu.edu/faculty/sharkey/Sharkey/index.html>

Contents

Part II: Applied Aspects in Biohydrogen Production

Preface

There is a general consensus in considering the use of fossil fuels (petroleum, natural gas and coal) as the cause of serious environmental problems. Because the amount of energy derived from these fossil reserves is close to 80 % of the entire World's energy consumption, there is a pressing need of new, non-polluting and renewable energy sources (Report of the International Energy Agency, 2010). Although hydrogen (H_2) is not a primary energy source, it has been considered a promising alternative to fossil fuels. By definition, an energy source is such only if useful energy can be directly extracted or recovered from it; in this respect, H_2 is an "energy carrier" as it is derived from an energy reservoir and it can be used, like electricity, for the "transport" of energy from the production site to the sites of its use. The main consequence of this feature is that hydrogen can be produced only by consuming primary energy sources, which at the moment are mainly fossil fuels. However, there are at least two properties making the use of hydrogen quite attractive, namely: its large presence in nature, even if usually linked with other atoms, e.g. with oxygen in water or with oxygen, carbon and other elements in organic compounds, and the possibility to use it without releasing pollutants or greenhouse gases (GHGs) in the atmosphere. Interestingly, hydrogen can also be produced by exploiting the metabolic features of several microorganisms in a carbon neutral process that has been called "biological hydrogen production". Bio-hydrogen production is also characterized by important advantages over the thermochemical and electrochemical techniques currently utilized or under study. Indeed, microbiological processes can produce hydrogen using renewable resources, in carbon neutral processes operating at room temperature and pressure, and with low environmental impact. A negative aspect of the microbial hydrogen production in natural habitats is the fact that although a large number of bacteria, belonging to different taxonomic groups, possess the capability to produce hydrogen, free hydrogen of biological origin can hardly be captured in nature because hydrogen-producing and hydrogen-consuming microorganisms live in the same natural environments.

Bio-hydrogen production has been known for almost a century and research directed at applying this process to a practical means of hydrogen fuel production has been carried out for over a quarter of a century. A milestone in bio-hydrogen research was the observation by Hans Gaffron, while working at the University of Chicago in 1939, that algae can generate hydrogen by both fermentation and photochemistry (H. Gaffron (1939) Reduction of CO_2 with H_2 in green plants. *Nature* 143:204–205). Ten years later, Gest and Kamen (H. Gest and M.D. Kamen (1949) Photoproduction of molecular hydrogen by *Rhodospirillum rubrum. Science* 109: 558–559) discovered the light-dependent production of hydrogen in parallel to nitrogen fixation by the facultative photosynthetic bacterium *Rhodospirillum rubrum*. Notably, in "*Memoir of a 1949 railway journey with photosynthetic bacteria*" (Photosynthesis Res 61: 91–96), H. Gest (1999) commented on this discovery as "*A serendipic observation at the Hopkins Marine Station of Stanford University in 1948 led to the discovery that anoxygenic photosynthetic bacteria can fix molecular nitrogen … and generate hydrogen*". One of us (Zannoni D), while working as an associate researcher at the St. Louis University Medical School in 1978, was fortunate enough to have known personally H. Gest, Professor of Microbiology at the University of Bloomington (Indiana). He remembers that they had a long discussion on the way to define what it is now recognized as the "accessory oxidant-dependent fermentation in photosynthetic bacteria" (See: *The Phototrophic Bacteria: Anaerobic Life in the Light*, J.G. Ormerod Ed., 1983, vol 4, University of California Press, Blackwell Sc. Pub.). Enormous advances have been made since then on genetics, biochemistry, and biotechnological applications of photosynthetic bacteria and the present book, entitled *Microbial BioEnergy: Hydrogen Production* is a compendium overviewing most of the processes important for the microbial hydrogen production including bacterial hydrogen photo-generation.

The book begins with a chapter on bioenergy from microorganisms describing some of the challenges in meeting future energy needs in order to address climate changes through the development of bioenergy (Chap. 1). Critical factors in mature technologies and future directions in nascent technologies are also reviewed. The volume includes a section (Chaps. 2, 3, 4, and 5) covering structural, molecular, and functional aspects of hydrogenases as efficient biological catalysts for the production of molecular hydrogen and, consequently, its oxidation a way to get rid of the excess reducing power in cyanobacteria and green algae. As cyanobacteria are unique organisms that accommodate both oxygenic photosynthesis and nitrogen fixation, they are extensively covered in Chap. 6 with respect to their production of ammonium concomitantly with hydrogen formation. Solar energy is also used by photosynthetic purple non-sulfur bacteria to generate hydrogen gas from organic sources via the enzyme nitrogenase. Chapter 7 focuses on the advances that have been made in hydrogen generation through the use of systems biology approaches such as genomics, transcriptomics and ^{13}C-fluxomics in *Rhodopseudomonas palustris* CGA009. Chapters 8 and 9 cover two emerging research fields in hydrogen production: the use of thermophilic and hyperthermophilic microorganisms of the genera *Caldicellulosiruptor* and *Thermotoga*. As these genera utilize an extraordinary array of substrates that are converted by dark-fermentation to hydrogen at efficiencies approaching the "Thauer limit" of 4 mol H_2/mol glucose, the availability of several genome sequences and their metabolic features open new perspectives for biohydrogen generation. Bioelectrochemical systems coupled to indirect hydrogen production are reviewed in Chap. 8. These systems are not subjected to the hydrogen yield constraints and have been proven to work with any biodegradable organic substrate. Chapters 11, 12, 13, and 14 are mostly dedicated to photobioreactors using purple non-sulfur bacteria and microalgae. This section of the book examines in detail how hydrogen production depends on various kinds of organic wastes, on the photosynthetic efficiency and light distribution. The basic principles for designing photobioreactors in mass culture for biofuel are also examined along with the advantages and limitations of immobilized cell-systems for hydrogen photoproduction. The volume ends with a chapter (Chap. 15) dealing with the unconventional concept that if hydrogen is used as an energy carrier, there are consistent benefits to be expected, depending on how hydrogen is generated. The existing technical problems lying ahead for the creation of an apparent "Hydrogen Based Society" are examined and it is concluded that they will be solved within a reasonable period of time.

Following the suggestion of the Series editors, Govindjee and Tom Sharkey, we are deeply honored to dedicate this book to Hans Gaffron (1902–1979) and Howard Gest (1921–2012).

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The Editors

Davide Zannoni, Professor of General Microbiology, received the doctoral degree in Biological Sciences, in 1973, from the University of Bologna, Italy; his thesis was on the Bioenergetics of the facultative photosynthetic bacterium *Rhodobacter (Rb.) capsulatus*. During 1977–1978, he was a research fellow of the North Atlantic Treaty Organization (NATO) at the St. Louis Medical School, Department of Biochemistry, St. Louis MO, USA, under the supervision of Prof. Barry L. Marrs. In 1979, he was appointed Lecturer in Plant Biochemistry, and in 1981, he was promoted to become Associate Professor of Plant Biochemistry, at the Faculty of Sciences, University of Bologna. As a research fellow of the European Molecular Biology Organization (EMBO) in 1981, 1983 and 1991, he visited several European laboratories, namely: Department of Biochemistry and Microbiology, St. Andrews University, St. Andrews Scotland U.K.; Département de Biologie Cellulaire et Moléculaire, Centre National Recherche Scientifique (CNRS), Commissariat à l'Energie Atomique (CEA) Saclay Gif-sur-Yvette, France; Department of Microbiology, University of Göttingen, Göttingen, Germany, to investigate both the structure and the function of membrane redox-complexes in a variety of microbial genera. Zannoni's scientific interests now include bioenergetics and genomics of microbial remediation of metals and metalloids in planktonic cells and biofilms of *Rb. capsulatus* and *Pseudomonas pseudoalcaligenes*, molecular mechanisms of bacterial movement (chemo- and photo-taxis) and biofilm formation, alkane and naphthenic acid degradation by *Rhodococcus* spp., the use of microbial biofilms as electricity-producing systems, and, finally, bio-hydrogen anaerobic production by *Thermotoga*. Zannoni's pioneering work on hydrogen metabolism in *Rb. capsulatus* began in 1981 (European Community Solar Energy Research & Development). He is author and/or co-author of more than 130 publications in international research journals, and he has published several research as well as text-books for students. From 2004 to 2010, Prof. Zannoni has been the Head of the Department of Biology of the University of Bologna. He is presently acting as a Coordinator of the Master's degree in Molecular & Industrial Biotechnology at the Department of Pharmacy & Bio-Technology, University of Bologna – Alma Mater Studiorum, Italy. See his website <http://www.unibo.it/docenti/davide.zannoni> for further information.

Roberto De Philippis, Associate Professor of Microbial Biotechnology, received his Laurea degree in Chemistry from the University of Florence, Italy, in 1978; his thesis was on the chemical interactions between nucleic acids and amino acids, as studied by means of NMR and EPR techniques. During 1978–1981, he was a research scientist at the Research Center on Plastic Polymers at "Montedison" SpA, Milan, Italy; during 1981–1983 he was responsible for the scientific and technical aspects of Baker's yeast production at a Food Industry in Florence. During 1984–1990, he was a Research Fellow at the Institute of Agricultural and Technical Microbiology, University of Florence. During 1990–2001, he served as a Lecturer at the Department of Food and Microbiological Science and Technology, University of Florence. From 2001, he has been an Associate Professor of Microbial Biotechnology at the University of Florence, Department of Agrifood Production and Environmental Sciences. He is, at the same time, an Associate Researcher at the Institute of Chemistry of Organometallic Compounds, Italian National Research Council (ICCOM-CNR), Florence. His research activity is mainly concerned with the physiology and biochemistry of photosynthetic bacteria. In particular, Roberto is studying the physiology and the possible biotechnological exploitation of phototrophic microorganisms in the production of biopolymers of industrial interest or in processes related to the production of energy from renewable resources or for the treatment of polluted waters. He is also involved in studies on the formation of phototrophic biofilms on monuments or in the stabilization of desert soils by the use of phototrophic microorganisms. He has been hosted for his research by several Institutions in China, India, Israel, Mexico, Portugal and USA. He has published more than 80 scientific papers in international peer-reviewed journals, ten chapters in books, and has participated in more than 90 international and national Congresses. During 1999–2001, Roberto was Secretary/Treasurer, and currently, he is President-elect of the International Society for Applied Phycology. He is an Assistant Editor of the *Journal of Applied Phycology*. From 2010, he has been a Delegate for Italy in the IEA-HIA (International Energy Agency-Hydrogen Implementing Agreement) New Annex 21 "Bio-inspired and Biological Hydrogen". See the following website for further information: http://www.unifi.it/p-doc-2012-200001-D-3f2a3d29392930.html

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