Advances in Photosynthesis and Respiration 47
Including Bioenergy and Related Processes

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Photosynthesis: Molecular Approaches to Solar Energy Conversion

Springer

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VOLUME 47

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Photosynthesis: Molecular Approaches to Solar Energy Conversion

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 47: Photosynthesis: Molecular Approaches to Solar Energy Conversion

Photosynthesis represents the central process in nature that has established the diversity of life on Earth. Each year, photosynthesis is responsible for using solar energy to convert about 100 gigatons of carbon dioxide into the energy-rich carbohydrates that ultimately support almost all ecosystems. The key step for the conversion of solar energy into chemical energy takes place in molecular machines known as photosystems. These are found in biological membranes in the chloroplasts of plants and algae and in similar membranes in photosynthetic bacteria. One of these photosystems, known as Photosystem II, uses light-energy to obtain electrons from water that are utilized in the reactions leading to fixing carbon into sugars while at the same time being the source of the oxygen we breathe and the oxygen of the protective ozone layer of our planet.

In volume 47 of the Advances in Photosynthesis and Respiration (AIPH) series, Jian-Ren Shen, Kimiyuki Satoh, and Suleyman Allakverdiev have brought together an impressive team of experts providing a detailed appraisal of current knowledge on the molecular systems that operate in biological solar energy conversion. Inspired by the outstanding career of the late Professor Vyacheslav Vasilevich Klimov, and as a tribute to his many contributions to our understanding of Photosystem II, the chapters focus on photosystems in plants, algae, and cyanobacteria and their light-harvesting systems. The importance of this field for the development of artificial photosynthesis and photosynthetic hydrogen production for clean energy technologies is also emphasized in this book.

Authors of Volume 47

Reflecting the international impact of Professor Klimov's career and the international focus of the AIPH book series, this volume has authors from 14 countries: Australia (6), China (2), Germany (2), Hungary (3), India (2), Iran (1), Israel (2), Japan (17), Russia (10), Slovak Republic (2), Spain (3), Ukraine (1), UK (1), and the USA (2). There are 54 authors (including the 3 editors) who are all recognized experts in their fields. Alphabetically (by last names), they are Parveen **A**khtar, Seiji Akimoto, Fusamichi Akita, Miguel Alfonso, Suleyman I. Allakhverdiev, James **B**arber, Vinzenz Bayro-Kaiser, Marian Brestic, Min **C**hen, Thomas **F**riedrich, Vera **G**rechanik, Győző Garab, Miguel A. **H**ernández-Prieto, Harvey J.M. Hou, Kentaro **I**fuku, Hiroshi Isobe, Takahashi **K**awakami, Andrey A. Khorobrykh, Petar H. **L**ambrev, María A. Luján, Sai Kiran **M**adireddi, Mahir

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- Modeling Photosynthesis and Growth (Editors: Xin-Guang Zhu and Thomas D. Sharkey)

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Algae, Cyanobacteria: Biofuel and Bioenergy
Artificial Photosynthesis

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- Bacterial Respiration 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/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 Julian Eaton-Rye (julian.eaton-rye@otago.ac.nz). 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.

We take this opportunity to thank and congratulate Jian-Ren Shen, Kimiyuki Satoh, and Suleyman Allakhverdiev for their outstanding editorial work; they have collectively done an excellent 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 54 authors of this book (see the list given earlier and on the following pages); without their authoritative chapters, there would be no such volume. We give special thanks to Mr. Prasad Gurunadham at Straive, India, for directing the typesetting of this book; his expertise has been crucial in guiding the final steps that have bought this book to completion. We also thank Zuzana Bernhart, Andre Tournois, and Mariska van der Stigchel (Springer) for their friendly working relation with us that led to the production of this book and for their ongoing organization and assistance with the AIPH series.

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Series Editors

A 2017 informal photograph of Govindjee (right) and his wife Rajni (left) in Champaign-Urbana, Illinois; Photograph by Dilip Chhajed.

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, botany, and zoology) and M.Sc. (botany and plant physiology) in 1952 and 1954, respectively, from the University of Allahabad. He learned plant physiology from Shri Ranjan, who was a student of Felix Frost Blackmann (of Cambridge, UK). Then, Govindjee studied photosynthesis at the UIUC, under two giants in the field, Robert Emerson (a student of Otto Warburg) and Eugene Rabinowitch (who had worked with James Franck), obtaining his Ph.D. in biophysics in 1960.

Govindjee is best known for his research on excitation energy transfer, light emission (prompt and delayed fluorescence, and thermoluminescence), primary photochemistry, and electron transfer in *Photosystem II* (PS II, water-plastoquinone oxidoreductase). His research, with many others, includes the discovery of a short-wavelength form of chlorophyll (Chl) *a* functioning in PS II; of the two-light effect in Chl *a* fluorescence; and, with his wife Rajni Govindjee, of the two-light effect (Emerson Enhancement) in NADP+ reduction in chloroplasts. His major achievements, together with several others, include an understanding of the basic relationship 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; the theory of thermoluminescence in plants; the first picosecond measurements on the primary photochemistry of PS II; and the use of fluorescence lifetime imaging microscopy (FLIM) of Chl *a* fluorescence in understanding photoprotection by plants against excess light. His current focus is on the history of photosynthesis research and in photosynthesis education. He has served on the faculty of the UIUC for approximately forty 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 (1997), 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; recipient of the Communication Award of the International Society of Photosynthesis Research, 2007; and of the Liberal Arts and Sciences Lifetime Achievement Award of the UIUC, (2008). Further, Govindjee has been honored many times: (1) in 2007, through 2 special volumes of Photosynthesis Research, celebrating his 75th birthday and for his 50-year dedicated research in photosynthesis (guest editor: Julian J. Eaton-Rye); (2) in 2008, through a special International Symposium on "Photosynthesis in a Global Perspective", held in November 2008, at the University of Indore, India; this was followed by a book *Photosynthesis: Basics and Applications* (edited by S. Itoh, P. Mohanty and K.N. Guruprad); (3) in 2012, through *Photosynthesis – Plastid Biology, Energy Conversion and Carbon Assimilation*, edited by Julian J. Eaton-Rye, Baishnab C. Tripathy, and Thomas D. Sharkey; (4) in 2013, through special issues of Photosynthesis Research (volumes 117 and 118), edited by Suleyman Allakhverdiev, Gerald Edwards, and Jian-Ren Shen celebrating his 80th (or rather 81st) birthday; (5) in 2014, through celebration of his 81st birthday in Třeboň, the Czech Republic (O. Prasil [2014] Photosynth Res 122: 113–119); and (6) in 2016, through the prestigious Prof. B.M. Johri Memorial Award of the Society of Plant Research, India. In 2018, *Photosynthetica* published a special issue to celebrate his 85th birthday (Editor: Julian J. Eaton-Rye).

Govindjee's unique teaching of the Z-scheme of photosynthesis, where students act as different intermediates, has been published in two papers (1) P.K. Mohapatra and N.R. Singh [2015] Photosynth Res 123:105–114); (2) S. Jaiswal, M. Bansal, S. Roy, A, Bharati, and B, Padhi [2017] Photosynth Res 131: 351—359. Govindjee is a coauthor of a classic and highly popular book *Photosynthesis* (with E.I. Rabinowitch, 1969) and of a historical book *Maximum Quantum Yield of Photosynthesis: Otto Warburg and the Midwest Gang*" (with K. Nickelsen, 2011). He is editor (or coeditor) of many books including: *Bioenergetics of Photosynthesis* (1975); *Photosynthesis*, 2 volumes (1982); *Light Emission by Plants and Bacteria* (1986); *Chlorophyll a Fluorescence: A Signature of Photosynthesis* (2004); *Discoveries in Photosynthesis* (2005); and *Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria* (2015).

Since 2007, each year, a **Govindjee and Rajni Govindjee Award** is given to graduate students, by the Department of Plant Biology (odd years) and by the Department of Biochemistry (even years), at the UIUC, to recognize excellence in biological sciences. For further information on Govindjee, see his website at 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, 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. In 2017, Tom stepped down as department chair and moved to the MSU-DOE Plant Research Laboratory, completing a 38-year sojourn back to his beginnings. 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, 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 26,000 times according to Google Scholar in 2017. He has been named an Outstanding Faculty member by Michigan State University, and in 2015, he was named a University Distinguished Professor. He is a fellow of the American Society of Plant Biologists and of the American Association for the Advancement of Science. Tom has co-edited 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 J. Eaton-Rye and Baishnab C. Tripathy) entitled *Photosynthesis*: *Plastid Biology*, *Energy Conversion and Carbon Assimilation*. Tom has been co-editor of this series since volume 31.

Julian J. Eaton-Rye is a professor in the Department of Biochemistry at the University of Otago, New Zealand. He received his undergraduate degree in botany from the University of Manchester in the UK in 1981 and his Ph.D. from the University of Illinois in 1987, where he worked with Govindjee on the role of bicarbonate in the regulation of electron transfer through Photosystem II. Before joining the Biochemistry Department at Otago University in 1994, he was a postdoctoral researcher focusing on various aspects of Photosystem II protein biochemistry with Professor Norio Murata at the National Institute of Basic Biology in Okazaki, Japan, with Professor Wim Vermaas at Arizona State University, and with Dr. Geoffrey Hind at Brookhaven National Laboratory. His current research interests include structure-function relationships of Photosystem II proteins both in biogenesis and electron transport as well as the role of additional protein factors in the assembly of Photosystem II. Julian has been a consulting editor for the Advances in Photosynthesis and Respiration series since 2005, and edited volume 34 (with Baishnab C. Tripathy and Thomas D. Sharkey) entitled *Photosynthesis*: *Plastid Biology*, *Energy Conversion and Carbon Assimilation*. He is also an associate editor for the *New Zealand Journal of Botany* and an associate editor for the Plant Cell Biology part of *Frontiers in Plant Science*. He edited a Frontiers Research Topic titled *Assembly of the Photosystem II Membrane-Protein Complex of Oxygenic Photosynthesis* (with Roman Sobotka) in 2016 and this is available as an eBook [ISBN 978-2-88945-233-0]. Julian has served as president of the New Zealand Society of Plant Biologists (2006–2008) and as president of the New Zealand Institute of Chemistry (2012). He has been a member of the International Scientific Committee of the Triennial International Symposium on Phototrophic Prokaryotes (2009–2018) and is currently the secretary of the International Society of Photosynthesis Research.

Foreword

What a wonderful collection of chapters dedicated to the memory of Slava Klimov. The editors are to be congratulated, and particularly Suleyman Allakhverdiev for drawing together chapters covering a wide spectrum of aspects of the light reactions of photosynthesis. Suleyman studied under the direction of Slava for his PhD and is one of his most successful students.

Slava Klimov contributed greatly to photosynthesis research but perhaps his most important and lasting contribution was the discovery that pheophytin is the primary electron acceptor in the Photosystem Two (PS II) reaction center (1). In fact it was the study of PS II which dominated his research focus as recorded in the memorial paper published in Photosynthesis Research in 2017 soon after he passed away (2). What could be more important than unravelling the molecular mechanisms of one of the most important enzymes on our planet which has been the "Engine of Life" for the past three billion years?

In fact life on our planet occurred about four billion years ago following half a billion years of geological and chemical evolution. It took the form of single-cell prokaryotic chemotrophs obtaining their energy from chemicals which could act as electron donors. After 1.5 billion years there were a wide variety of anaerobic prokaryotes which fell into two groups, archaea and bacteria. Darwinian principles had allowed these prokaryotes to be widely distributed in many different types of environments and evolve complex systems to capture and utilize energy for the reductive process of cellular biochemistry. Sooner or later, however, the energy sources (oxidizable substrates) available to these chemotrophic prokaryotes became limiting and some developed the capacity to supplement their metabolic energy requirements by absorbing solar radiation. This heralded the "Big Bang of Evolution" since this strategy gave rise to phototrophic organisms which could use sunlight to totally drive their bioenergetics. This was achieved by using solar energy to extract "hydrogen" (in the form of high energy electrons and protons) from water and release oxygen into the atmosphere. From then on life prospered and diversified on an enormous scale driven by Darwinian evolution. It was from this success that humans evolved as a very special species with abilities far beyond any other animals that have ever lived on planet Earth. Yet we are on a very dangerous course which some believe could result in the elimination of our species in a matter of a few hundred years if we carry on the way we do today, that is, continue to use fossil fuel as a major energy source. Biology solved its energy problem by using sunlight to split water and extract the stored energy by recombining "hydrogen" with oxygen via respiration. We must do the same by using energy from the sun captured directly via photovoltaic cells and indirectly by hydro-, wind-, and wave-power to give electricity and hydrogen as the two main energy carriers. The latter complements batteries for renewable energy storage and must come from the electrolysis of water. There is an urgent need to progress by expanding and developing the appropriate technologies and putting in place the infrastructure, particularly for the generation of hydrogen and its storage, transport, and use. The studies of Slava Klimov and the many other contributions represented in this book serve as a blue print for tackling the most urgent problem facing organized humankind, namely, anthropogenic climate change.

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Professor James Barber passed away on January 5, 2020 at the age of 79. He kindly wrote this forward for us while he was alive. The editors would like to acknowlege his great contributions in the field of photosynthesis research and pray for the repose of his soul.

Preface

Photosynthesis has been the subject of extensive research for several decades involving a number of scientists in different fields, in order to elucidate and understand the mechanisms underlying the solar energy conversion reactions and to utilize them artificially to obtain renewable energy for the realization of a sustainable society. In recent years, photosynthesis research has increasingly developed into a deeper understanding of the molecular and atomic level of the components involved. The present book, *Photosynthesis: Molecular Approaches to Solar Energy Conversion*, focuses on such aspects as solar energy harvesting, utilization, and novel pigments absorbing and utilizing far-red light, from a molecular to an atomic level. Owing to the rapid development of X-ray crystallography and cryo-electron microscopy, the structures of photosystem I (PS I), photosystem II (PS II), and their complexes with various light-harvesting complexes (LHCs), have been solved, and they are the subject of this book.

Chapter 1 describes the structure of the PS II core, its conservation and differences, from various organisms, and the mechanism of water oxidization achieved by recent pump-probe X-ray free electron laser experiments. This experimental result is followed by two theoretical chapters (Chaps. 2 and 3) describing the theoretical calculations of the Mn_4CaO_5 cluster and the mechanism of water oxidation. Chapter 2 favors the high oxidation scenario, whereas Chap. 3 favors the low oxidation scenario, of the Mn ions within the Mn_4CaO_5 cluster. Chapter 4 deals with the artificial utilization of solar energy by modeling natural water oxidization. A molecular mechanism for asymmetric electron transfer on the donor side of PS II is described in Chap. 12.

Due to the low energy density that solar energy has on the surface of the earth, light energy has to be collected and transferred to the reaction center of PS II and PS I to initiate the charge separation and a series of electron transfer reactions. The pigments involved in light-energy harvesting and transfer are reviewed in Chap. 5, with the emphasis on two recently characterized, far-red light absorbing pigments, chlorophyll *d* and *f*. Subsequently, the light-harvesting complexes II and I from various oxygenic photosynthetic organisms are described in Chaps. 6 and 7. These Chapters describe the structure and function of LHCII and LHCI from various organisms from red algae to diatoms and higher plants, and give a consensus overview of the LHC proteins and their associated pigments. In particular, the functions of chlorophyll *d* and *f*, absorbing light energy in the far-red region that was thought of little use before, have been "hot spots" of recent extensive studies, and their functions and energy transfer properties are considered further in Chaps. 8 and 9. The light energy absorbed will need to be distributed over the two PSs differently based on the light intensity, and there are a number of mechanisms to regulate the energy balance between the two PSs. Two major mechanisms for energy balancing, spill-over and state transitions, are described in Chaps. 10 and 11.

Photosynthetic light-dependent reactions occur in the thylakoid membranes of cyanobacteria, various algae and higher plants, and the properties of membrane structure and organization will have great effects on the photosynthetic performance. There are a number of chapters dealing with the membrane dynamics and regulation, which include temperature-dependent regulation of photosynthesis studied by EPR (Chap. 13), plasticity of PS II (Chap. 14), role of lipids and fatty acids in the assembly and maintenance of photosynthetic complexes during PS II turnover (Chap. 15). Evolution and function of extrinsic proteins in water oxidization is described in Chap. 16, and effects of trehalose on the functional properties of PS II is reviewed in Chap. 17. Dynamic processes of the thylakoid membranes are discussed in Chap. 18, and its specific thermodynamic information detected by photoacoustics is described in Chap. 19. Accumulation of metabolites in plants under different light quality is reviewed in Chap. 20.

Finally, artificial utilization of photosynthesis research is reviewed in Chaps. 21 and 22. Chapter 21 considers hydrogen production by natural PSs in an economic background, whereas Chap. 22 compares the ways to produce hydrogen by different approaches.

By bringing a number of scientists working on the molecular to atomic levels of photosynthetic systems from various fields, the book provides an important overview on the current status of photosynthesis research.

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Kimiyuki Satoh
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A Tribute to Vyacheslav (Slava) Vasilyevich Klimov (1945–2017)

Vyacheslav Vasilyevich (V.V.) Klimov (or Slava, as most of us called him) was born on January 12, 1945, and passed away on May 9, 2017. He began his scientific career at the Bach Institute of Biochemistry of the USSR Academy of Sciences, Moscow, Russia, and then he became associated with the Institute of Photosynthesis, Pushchino, Moscow Region, for about 50 years. He worked in the field of biochemistry and biophysics of photosynthesis. He is known for his studies on the molecular organization of photosystem II (PS II). He was an eminent scientist in the field of photobiology, a well-respected professor, and, above all, an outstanding researcher. Furthermore, he was one of the founding members of the Institute of Photosynthesis in Pushchino, Russia. To most, Slava Klimov was a great human being. He was one of the pioneers of research on the understanding of the mechanism of light energy conversion and of water oxidation in photosynthesis. Slava had many collaborations all over the world, and he is (and will be) very much missed by the scientific community and friends in Russia as well as around the world. We present here a brief biography and some comments on his research in photosynthesis. We remember him as a friendly and enthusiastic person who had an unflagging curiosity and energy to conduct outstanding research in many aspects of photosynthesis, especially that related to PS II.*

*For more details see: Allakhverdiev SI, Zharmukhamedov SK, Rodionova MV, Shuvalov VA, Dismukes GC, Shen JR, Barber J, Samuelsson S, Govindjee (2018) Vyacheslav (Slava) Klimov (1945-2017): A scientist par excellence, a great human being, a friend, and a Renaissance man. Photosynth Res, v. 136, p. 1-16. The text below is an edited excerpt from this article.

Vyacheslav (Slava) Vasilyevich Klimov was born on January 12, 1945, in the village of Karavainka, Stalingrad (later Volgograd) in the Union of Soviet Socialist Republics (USSR). His parents were teachers: his father (Vasiliy Alexandrovich Klimov) was a history teacher and his mother (Elizaveta Ivanovna Klimova) was a primary school teacher. In 1963, after graduating from Gorno-Balykley secondary school, also in the Volgograd region, Slava Klimov entered the Department of Biology and Soil Science of M.V. Lomonosov Moscow State University. In 1968, after graduating cum laude, he did postgraduate work on "Photoinduced Changes of Chlorophyll *a* Fluorescence Yield during Photosynthesis" in the same department. This research was done under the mentorship of Academician (Prof.) Alexander A. Krasnovsky, a world-recognized leader in photobiochemistry, and (Prof.) Navasard V. Karapetyan. Later, after Slava Klimov obtained the Candidate degree (equivalent to a PhD), he joined research group(s) led by A.A. Krasnovsky and Vladimir (Vlad) A. Shuvalov and worked first as a junior, and later as a senior, research investigator at the Institute of Photosynthesis of AN SSSR in Pushchino, Moscow Region. Then, in 1982, Slava Klimov was appointed as the head of the research laboratory for "Photosynthetic Water Oxidation and Oxygen Evolution" at the Institute of Basic Biological Problems (formerly Institute of Photosynthesis), Russian Academy of Science, RAS, where he worked until the last days of his life. In 1986, Slava Klimov obtained his Doctor of Science (specialization: Biochemistry) from the A.N. Bach Institute of Biochemistry, RAS, for his work on "Light Reactions of Electron Transfer in Photosystem II of Plants and Algae." Slava Klimov was not only a brilliant scientist in the field of photosynthesis, but he was equally involved in educating young scientists. He became Professor of Biochemistry, teaching initially at the Pushchino State University and then at the Pushchino Branch of Moscow State University (MSU). In 1991, he became one of the laureates of the USSR State Prize for Science, awarded to the school of Academician Krasnovsky (A.A. Krasnovsky, Yu.E. Erokhin, V.B. Evstigneev [posthumously], N.V. Karapetyan, A.V. Klevanik, V.V. Klimov and V.A. Shuvalov) for studies on the *Photobiochemistry of Chlorophylls*. In addition, Slava Klimov was named to the prestigious Soros Professorship several times.

As mentioned, Slava Klimov's research centered on the molecular mechanism of light energy conversion and water oxidation during photosynthesis. He formulated and experimentally proved fundamentally new ideas about the mechanism of light energy conversion in oxygen-evolving PS II (Klimov and Krasnovsky 1981) that were widely accepted and included in contemporary reviews, monographs, and university courses on photosynthesis and advanced plant physiology. During his scientific career, Slava Klimov pioneered, along with his coworkers, the investigation of pheophytin participation in primary charge separation at the reaction center of PS II (see Klevanik et al. 1977; Klimov et al. 1977, 1978, 1979a, b, 1980a, b, c, 1986). Furthermore, he and his collaborators revealed the quantitative composition and heterogeneity of the manganese cluster of WOC, the water-oxidizing complex (Klimov et al. 1982, 1985, 1990; Allakhverdiev et al. 1983, 1989a).

Under Slava Klimov's guidance, the concept of water photooxidation through a two-electron mechanism with the production of peroxide as an intermediary product was experimentally justified (Ananyev et al. 1992; Klimov et al. 1993b). In addition, the role of bicarbonate as a significant component for the formation and functioning of the WOC was revealed (Klimov et al. 1995a, b, 1997a, b; Wincencjusz et al. 1996; Allakhverdiev et al. 1997b; Hulsebosch et al. 1998; Yruela et al. 1998). Slava Klimov, together with others, put forward and experimentally proved the hypothesis regarding the crucial role of Mn-bicarbonate complexes in the evolutionary origin of oxygenic photosynthesis (Klimov et al. 1995a, b; Dismukes et al. 2001). For discoveries on the unique role of bicarbonate bound to non-heme-iron involved in electron transport (between the platoquinone electron acceptors Q_A and Q_B) and plastoquinone protonation, see Shevela et al. (2012).

Furthermore, Slava was involved in the discovery of a new class of photosynthesis inhibitors (see Allakhverdiev et al. 1989b, 1997a; Klimov et al. 1992, 1993a, 1995c, for details). In contrast to the known inhibitors, the action of this class of chemicals was shown to be based on the formation of a short electron cycle around the PS II reaction center. Being a powerful tool for the investigation of charge separation and recombination in PS II, such inhibitors can also be considered as potential eco-friendly herbicides since they inhibit reactions specific to plants (but not animals). In the laboratory headed by Slava Klimov, PS II associated carbonic anhydrase, important for both WOC functioning and stability, was also revealed (Villarejo et al. 2002; Shutova et al. 2008; Shitov et al. 2009, 2011; Karacan et al. 2012, 2014, 2016; also see Rodionova et al. 2017). Furthermore, upon the removal of a Mn-cluster from the WOC, an increase in photoinhibition was described by Klimov et al. (1990).

On the chlorophyll (Chl) *a* fluorescence front, a new hypothesis for the origin of PS II variable Chl *a* fluorescence, as a recombination luminescence, was put forward (Klimov et al. 1978; Allakhverdiev et al. 1994a), and the redox potential values of the PS II primary electron donors and acceptors were first determined in his lab (Klimov et al. 1979a, b; Allakhverdiev et al. 2010, 2011). Slava Klimov had collaborations at many universities and research centers in the Netherlands, USA, United Kingdom, Canada, Japan, Sweden, and Spain. His colleagues and friends remember him as a kind-hearted, cheerful person, a wise leader, and trusted comrade ready to help in any situation. We note that he had worked with a large number of scientists including Robert Carpentier (Canada), Norio Murata (Japan), James Barber (UK), Charles Dismukes (USA), Bacon Ke (USA), Göran Samuelsson (Sweden), Hans van Gorkom (the Netherlands), Arnold Hoff (the Netherlands), Gernot Renger (Germany), Rafael Picorel (Spain).

Reminiscences

Jian-Ren Shen

It was really a sad news to hear that Prof. Slava Klimov passed away suddenly in May 2017. I met and talked with him many times at international conferences, and knew his great work along with his colleagues on the discovery of pheophytin in PS II, when I was a graduate student. I followed his numerous studies on the structure and function of PS II since then. He was a great person, and I have a wonderful memory of meeting him when I was in Pushchino to attend the "Photosynthesis Research for Sustainability" conference in 2014. His passing away is a great loss to the photosynthesis community, and I will miss him very much.

Suleyman I. Allakhverdiev

It is obvious that the contribution of the laboratory headed by Slava Klimov had a great impact on the investigation of photosynthetic water oxidation and the mechanism of light energy conversion. Among Slava Klimov's students, there were 18 Candidates of Science (PhD) and 2 Doctors of Science (Dr. Sci.), *and I (SIA) was his first PhD student*; Slava was not only my teacher, but a good friend. On October 2, 1977, I came from Baku (Azerbaijan) to Pushchino (Moscow Region, USSR) for my PhD thesis, and I joined the same group led by A.A. Krasnovsky and Vladimir A. Shuvalov. I worked on the investigation of pheophytin in photosynthetic reaction centers (RCs) under Slava Klimov and academician A.A. Krasnovsky as my supervisors. At that time two papers on pheophytin were published (Klevanik et al. 1977; Klimov et al. 1977). But this work was criticized by other researchers, who stated that it was an artifact. These were really very exciting times! Together, we tried to show that the participation of pheophytin in reaction centers of PS II is not an artifact. At that time, we published several papers in Russian (see Klimov et al. 1978, 1979a, b, 1980a), and then Slava visited Bacon Ke's lab in the USA (see Klimov et al. 1980b, c) where he performed additional experiments. The experimental evidence for pheophytin participation, and the energetics and kinetics of electron transport in PS II in the presence of pheophytin, was summarized in my PhD thesis. In 1984, I defended my thesis (in Physics and Mathematics [specialties-Biophysics]): "Photoreduction of Pheophytin in Reaction Centers of Photosystem II in Higher Plants and Algae" at the Institute of Biophysics, USSR Academy of Sciences, Pushchino, Moscow region, Russia. Then, in 2002, I obtained my Doctor of Science (highest/top degree in science) in Plant Physiology and Photobiochemistry from the Institute of Plant Physiology, RAS, Moscow, on "Functional Organization and Inactivation of Photosystem II."

During 1977–1986, together with Slava Klimov, Sasha Klevanik, Vlad Shuvalov, and Professor Likhtenshtein's group (at the branch of the Institute of Chemical Physics of the USSR Academy of Sciences in Chernogolovka, Moscow Region), we determined the number of manganese (Mn) atoms acting in the WOC of PS II. It had been shown that the WOC on the PS II donor side contains four atoms of Mn. Reconstitution of the Mn-cluster after a complete removal of Mn from PS II preparations had been shown using Mn(II) as well as various artificial Mn-organic complexes (binuclear and/or tetranuclear). We studied the magnetic interaction of Mn with pheophytin and P680, and evaluated the distance between the main components of PS II. The immersion depths of the main components of PS II reaction center in thylakoid membranes were also analyzed (Klimov et al. 1982, 1985, 1990; Allakhverdiev et al. 1983, 1986, 1989a, b, 1994b; Kulikov et al. 1983).

The effect of enhancement of PS II photoinhibition, upon the removal of Mn-cluster from the WOC, had been described by Klimov et al. (1990). In our joint work with Ivan Setlik's group in Třeboň, we showed that under anaerobic and reducing conditions, photoinhibition occurs on the acceptor side of PS II at the level of Q_A and Q_B , whereas under aerobic conditions, it occurs on the acceptor and/or donor side of PS II; at the same time, separation and stabilization of charges in PS II RC remain unchanged (Allakhverdiev et al. 1987, 1993; Klimov et al. 1990; Setlik et al. 1990).

From 1988 to 1995, together with Slava Klimov, we spent more time on the bicarbonate effect on the electron donor side of PS II. Previously bicarbonate has been considered only as an important component for electron transfer between the plastoquinone electron acceptors, Q_A and Q_B; however, we found that while bound to the nonheme Fe (Shevela et al. 2012), removal of bicarbonate affects the PS II donor side reactions (see Klimov et al. 1995a, b, 1997a, b).

Bicarbonate availability for the PS II donor side is especially significant for reactivation of the Mn-containing WOC after its removal by different treatments. It was suggested that bicarbonate may serve as a ligand to Mn, convert the aqua-ions of Mn (nonoxidized by PS II) into an easily oxidizable form Mn(HCO_3), or act as a structural component important for the formation of a functionally active Mn cluster, or function in proton transfer (from water to the lumen). We didn't risk publishing our results until 1995, and then investigations in the Netherlands (in the research groups of Arnold Hoff and Hans van Gorkom), in Spain (in the research group of Rafael Picorel), and in Sweden (in the research group of Göran Samuelsson) contributed to the shaping of our studies (see Klimov et al. 1995a, b, 1997a, b; 2003; Wincencjusz et al. 1996; Allakhverdiev et al. 1997a; Hulsebosch et al. 1998; Yruela et al. 1998; Shutova et al. 2008).

Once again, I would like to emphasize that, for me, Slava was a teacher, a senior colleague, but also a good friend, serving as an adviser in both science and life in general. It is true to say that he was my very close friend and a dear teacher. I very much miss Slava Klimov for his stimulating attitude.

Slava Klimov was a brilliant scientist. We are particularly impressed with his, and his colleague's discovery of "pheophytin" and fundamental works about the functioning of PS II, including functioning of four atoms of Mn and the role of bicarbonate on the electron donor side of PS II. He was a wonderful human being and his whole life was devoted to *science*.

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