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Bioenergetic Processes of Cyanobacteria

From Evolutionary Singularity to Ecological Diversity

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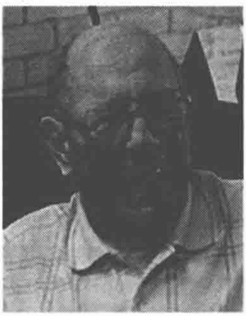
Bioenergetic Processes of Cyanobacteria

Dedication: Jack Edgar Myers (1913–2006)



We dedicate this book on **Cyanobacteria** to Jack Edgar Myers (1913–2006), the most influential algal and cyanobacterial physiologist of the twentieth century. I have known Jack's work since I became a graduate student of Robert Emerson and Eugene Rabinowitch in 1956.

Jack was born in a farmhouse in eastern Pennsylvania to Dr. Gary Cleveland Myers and Mrs. Caroline Clark Myers. Jack was one of the most wonderful and jovial persons I have met in my life. He was highly inquisitive and always asked questions very slowly and clearly, and answered questions in a thoughtful and a detailed manner. He also had a great humor, and was always good natured. He was a social drinker and one enjoyed his company and stories. I can count several such occasions at Conferences that we attended together. Jack was a remarkable family man as he not only took care of his family, but that of his brother when he passed away. He was a great Science educator for children all over the World through his simple descriptions of many aspects of Science through his down-to-earth clear articles in "*Highlights for Children*", a magazine that had been started by his parents.

Jack received his BS in 1934 in Chemistry from Juanita College, Huntington, Pennsylvania, his MS from Montana State (Bozeman), and his PhD (in Botany), in 1939, from the University of Minnesota under George Burr. Jack did his postdoctoral work with E.D. MacAlister before his appointment on the faculty of University of Texas in Austin, in 1941. Jack had been recognized with the Charles F. Kettering Award for Excellence in Photosynthesis Research, a Guggenheim Fellowship and an honorary Doctor of Science degree from Juniata College. Jack was a member of the U.S. National Academy of Sciences.

The best way to understand Jack's thinking about *Photosynthesis Research* is to read his thoughtful essays on the conceptual developments in photosynthesis (Myers 1974). His insight into the work and understanding of the *Photosynthetic Unit* concept is seen in his article on the 1932 experiments of Robert Emerson and William Arnold (Myers 1994). In his autobiographical article (Myers 1996), we obtain a deep understanding of Jack as a young man and his scientific pursuits leading to his work up to 1949, some of which I will highlight below. Jack's last article on the evolution of his thoughts in photosynthesis research titled '*In one era and out the other*' (Myers 2002) contains his views on the work of his favorite scientists (William Arnold, Bessel Kok and C. Stacy French).

A detailed tribute of Jack by Brand et al. (2008) must be consulted for understanding the full impact of Jack on the field of photosynthesis research. Here, I focus on some aspects of Jack's work, rather chronologically. Jack's PhD thesis had dealt with effects of high light on the green alga Chlorella (Myers and Burr 1940) and on pigments produced by some green algae grown in darkness (Myers 1940), both were unique discoveries. During his postdoctoral work, he obtained data on wheat showing antiparallel relationship, up to 4-minute illumination, between chlorophyll *a* fluorescence intensity and CO_2 fixation rate (McAlister and Myers 1940). In the 1940s, when Jack was in Texas, detailed and thorough work on the growth and cultivation of algae began: an apparatus for the continuous culture of algae was invented (see Myers and Clark 1944); and carbon and nitrogen balance of algae was investigated (Myers and Johnston 1949). Research on cyanobacteria was in full swing in the 1950s. The paper of Kratz and Myers (1955) on nutrition and growth of cyanobacteria was used by all who were working on cyanobacteria at that time. Myers and Kratz (1955) described thoroughly the pigments and photosynthetic characteristics of cyanobacteria. When I started working on cyanobacteria in late 1950s and early 1960s, these were the first papers I read before growing what was then known as *Anacystis nidulans*. Jack's work on the mass cultivation of algae and cyanobacteria was done with his long-time associate J.R. Graham (see e.g., Myers and Graham 1959).

After the discovery of the Emerson Enhancement Effect in photosynthesis at the University of Illinois at Urbana (in 1957), Jack went to Stacy French's laboratory and, using an oxygen electrode, confirmed the work of Emerson and showed equivalence of the action spectra of the enhancement effect with the chromatic transients discovered by Larry Blinks (Myers and French 1960). This was at the time I was finishing my PhD and had shown that in addition to chlorophyll b (that Emerson and Myers had shown), a short-wavelength form of chlorophyll a was present in the chlorophyll b-containing system (Govindjee and Rabinowitch 1960). Jack then focused more on cyanobacteria, the topic of this book. Fujita and Myers (1965) studied hydrogenase and NADP reduction in the cyanobacterium *Anabaena cylindrica*. Holten and Myers (1967a, b) provided the most thorough research on the many cytochromes in the cyanobacterium *Anacystis nidulans*. I will end describing Jack's research by mentioning his remarkable work with C. Bonaventura, where he thoroughly investigated oxygen evolution and chlorophyll a fluorescence (remember his 1940 work with Macalister, cited above) and discovered the phenomena of opposite effects in the photochemical efficiencies of the two light reactions as caused by changes due to light absorbed by *pigment systems I* or *II*; they had called it *light state 1* or *light state 2* (Bonaventura and Myers 1969); most now call this regulation phenomenon *"state transitions"*, but some call it *"state shifts"* (see Papageorgiou and Govindjee 2011, for a full history).

Jack was a humble man. I was particularly humbled when once he wrote: "other more patient and perceptive (as Govindjee, see Govindjee 1995) would later find gold in the mine". Jack, you have always been much more patient and perceptive that I could ever hope to be, and you certainly have discovered more gold than I could ever hope to see.

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A tribute to Mamoru Mimuro (1949–2011)

Professor Mamoru Mimuro, the principal author of Chapter 9 **"Bioenergetics in a Primordial Cyanobacterium *Gloeobacter violaceus* PCC 7421"**, passed away on February 8, 2011, only few days after he sent back the corrected author's proof.

Three years ago Mamo Mimuro was diagnosed with colon cancer. In spite of the after effects of surgery and chemotherapy, he continued his active research and teaching at Kyoto University. After three months of intravenous feeding at home, he even attended the Master's thesis presentations of his students at the university on February 2, 2011. His untimely death at the age of 61 has left us with a feeling of deep sadness about the loss of a remarkable scientist and a wonderful friend.

Mamo Mimuro started his research on excitation energy transfer in cyanobacteria in 1973, while he was a Master's student in the laboratory of Dr. Yoshihiko Fujita at the Ocean Research Institute of the University of Tokyo. After he moved to the National Institute of Basic Biology at Okazaki in 1980 as an assistant professor, he started a series of studies on time-resolved fluorescence spectral analysis of excitation energy transfer in photosynthesis. In collaboration with the physical chemist, Dr. Iwao Yamazaki, and his coworkers, Mamo made beautiful and fantastic discoveries on the excited singlet state energy transfer between different spectral components of the antenna complexes, using a single photon counting method with very fast time (less than 10 ps) and high spectral resolution (better than 1.5 nm). Kinetic analysis of spectral components among phycobilin pigments in red algae and cyanobacteria revealed that the rise and decay kinetics of spectral components were proportional to the square root of time. This method was applied by Mamo and collaborators to analyze antenna systems of plants and bacteria, especially chlorosomes of the green bacteria, and the presence and relevance of various minor spectral components were reported. His pioneering work on excitation energy transfer in red algae has been recognized by Govindjee in his 2004 review on the basics and history of chlorophyll fluorescence.

After Mamo moved to Yamaguchi University as a professor in 1997, he started the study of a primordial cyanobacterium, *Gloeobacter violaceus,* with interests in early evolution of oxygenic photosynthesis. Details of the *Gloeobacter* studies from his group are reviewed in Chapter 9 of this book. His earlier research on **"Photon Capture, Exciton Migration and Trapping and Fluorescence Emission in Cyanobacteria and Red Algae"** has been beautifully reviewed by Mamo himself in Chapter 7 of the 2004 book "Chlorophyll a Fluorescence: A Signature of Photosynthesis", volume 19 of Advances in Photosynthesis and Respiration, edited by G.C. Papageorgiou and Govindjee, and published by Springer.

Mamo was enthusiastic in stimulating international exchange of information and ideas in the field of photosynthesis. He organized many meetings and symposia. Among these, he organized the "International Symposium on Molecular Structure and Regulation of Photosynthetic Pigment Systems" in 1992 at Sanda, Japan, as a satellite meeting of the IXth International Congress on Photosynthesis. He also took an initiative to invite 11th International Symposium on Photosynthetic Prokaryote in 2003 in Tokyo. In 2007, he organized "7th International conference on the tetrapyrrole photoreceptors in photosynthetic organisms" in Kyoto. In those symposia, Mamo was the key person for the relaxed atmosphere and fruitful discussions.

In the words of Govindjee (University of Illinois at Urbana-Champaign, USA), who speaks on behalf of a very large community of friends and well-wishers of Mamo: "The entire photosynthesis community has lost a great scientist, a great friend, a great human being, and the major pioneer of this decade in the field of excitation energy transfer in photosynthesis. He will be sorely missed by all of us; no one can come close to his breadth of knowledge and dedication."

Tokyo Metropolitan University Katsumi Matsuura
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One of the editors of this book (Günter Peschek) has highly enjoyed the privilege to stay in Mamoru Mimuro's laboratory at the University of Kyoto as a visiting coworker of "Mamo" several times during almost a decade from 2000 and 2009, when being on sabbatical leaves from the Institute of Physical Chemistry at the University of Vienna, Austria. Günter not only performed experiments on cyanobacteria in Mamo's group but also joined him in teaching and instructing his graduate students. During these visits Günter had the great chance to enjoy Mamo's extremely hospitable, helpful and friendly personality and, in particular, he will never forget the great welcome and farewell parties that Mamo had arranged each time, together with his whole research group. Everybody who ever got the opportunity to know him personally will keep an everlasting brilliant memory of Professor Mamoru Mimuro. Another editor of this book (Gernot Renger) gratefully remembers enjoyable talks and discussions at international meetings and in particular he was deeply impressed by the extraordinary constructive and exceptionally friendly cooperation when he invited Mamo as the author of a chapter for the book on the *"Primary Processes of Photosynthesis"*.

We all – the colleagues and friends in Japan and around the world – will very much miss the big smile and friendly words of this outstanding person.

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Preface

The evolutionary "invention" of a system that enabled water-splitting into molecular dioxygen and metabolically bound hydrogen was the "Big-Bang" in the development of the biosphere. This event occurred about three billion years ago at the level of cyanobacteria and enriched the hitherto essentially anoxic terrestrial atmosphere with O_2 which had dramatic global consequences: (1) the efficiency of free energy exploitation from food increased by more than a factor of ten through the possibility of aerobic respiration thus opening the "thermodynamic door" for the development and sustenance of all higher forms of life, (2) the ozone layer was formed and provided the essential protective umbrella to UV radiation as prerequisite for populating the land with plants and animals, and (3) the oxidation of minerals gave rise to large-scale changes of the earth crust including geological phenomena. At the same time most of the existing organisms were killed due to oxidative degradation (in geological terms called "the O_2 cataclysm or O_2 catastrophe") unless they were able to develop suitable protective mechanisms or to find anaerobic ecological niches for survival.

Cyanobacteria have effectively colonized our whole planet. They are rather flexible in adaptation to a great variety of different environments and even capable of occupying arctic water bodies, or hot (alkaline) springs by forming the significant family of thermophilic organisms. A unique and common characteristics of all species is their "dual nature" of a prokaryotic (bacterial) cell structure and an O_2-evolving photosynthesis which is typical for (green) plants. Accordingly, the cyanobacteria can be classified in two ways, i.e. either as blue-green or *cyano*-bacteria or as (prokaryotic) blue-green algae (plants). In the past, both terms have been used but nowadays the term cyanobacteria—introduced about 50 years ago by the leading French-Canadian microbiologist Roger Y. Stanier—is universally accepted in the biological literature of nomenclature and systematics.

Due to the paramount importance for our entire biosphere it is not surprising and highly justified that several books and monographs on cyanobacteria have been published in recent years, and specialized scientific meetings and congresses exclusively or predominantly devoted to cyanobacteria are being regularly organized. Therefore the question arises: Why another book on this subject? Mainly two reasons should be mentioned: (a) A book is missing which focuses on *bioenergetics* of cyanobacteria primarily addressing questions of energy conversion by the fundamental bioenergetic processes: (Oxygenic) photosynthesis, (aerobic) respiration, and (anaerobic) fermentation which uniquely occur together in these prokaryotic cells, and (b) thermophilic cyanobacteria offer the most suitable material for high resolution structure analyses of Photosystem I and II and other electron transport complexes by X-ray crystallography (for example, at present the structure of Photosystem II at atomic resolution is only known for these organisms). These achievements during the last decade represent a milestone in our understanding of the complexes which are crucial for solar energy exploitation through photosynthetic water splitting.

Based on these considerations we feel confident that it is worth publishing this book and sincerely hope that it will find a positive resonance. It represents an ambitious attempt to achieve the goal of a synoptic state-of-the-art picture on the bioenergetics of cyanobacteria by casting together the mosaics of detailed knowledge described by leading experts in the field. It contains 24 chapters written by 51 authors from Austria, Finland, France, Germany, India, Israel, Japan, Netherlands, Portugal, Spain, UK and USA. The book is aimed at reaching a broad audience ranging from students to experienced scientists in chemistry, physics, biology and physiology. It is devided into seven parts: **Part I** offers in seven chapters a general description of cyanobacteria and their environment, with occasional historic and philosophic excursions into the phenomenon of life as such, the living cell and our universe. **Part II** contains three chapters on the history and function of electron transport and ATP-synthesis including brand-new results on *Gloeobacter*. Details on the oxygenic photosynthesis and aerobic respiration are outlined in **Part III** by presenting five chapters. **Part IV** focuses in two chapters on electron entry systems. **Part V** addresses in five chapters the connection between the various electron transfer complexes, and **Part VI** in three chapters reactions of terminal oxidation. The book finishes in **Part VII** by a single chapter which describes most recent progress with tools for genetic manipulation of cyanobacteria.

We have many people to thank. First of all, the authors for their efforts to offer the readers excellent chapters and for their positive response to our suggestions. Without their invaluable cooperation there would be no book. The book has grown out from a pertinent discussion of Govindjee with one of us (G.A.P.) in March 2007 and the editors want to express their particular thanks to Govindjee for his untiring encouragement during the years. We also gratefully acknowledge the editorial staff of Springer, especially Dr. Jacco Flipsen and Mrs. Ineke Ravesloot, for their generous help in all respects. Last, but not the least, we also thank Martin Pairer, BOKU—University of Natural Resources and Life Sciences, Vienna, who has taken the utmost care in achieving a uniform style of all manuscripts and to satisfy all editorial requirements set by Springer, Dordrecht. We made all efforts to reach the goal of presenting a book which may significantly contribute to the deepening and broadening of scientific knowledge and interest in cyanobacteria.

We wish all the readers a pleasant and stimulating journey through the fascinating "world" of the bioenergetics of cyanobacteria. It is our sincere hope that this book will entice young people into this exciting research area with the aim to address successfully the challenging problems of high relevance that are still waiting for satisfactory answers.

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