Photosynthesis

Overviews on recent progress and future perspectives

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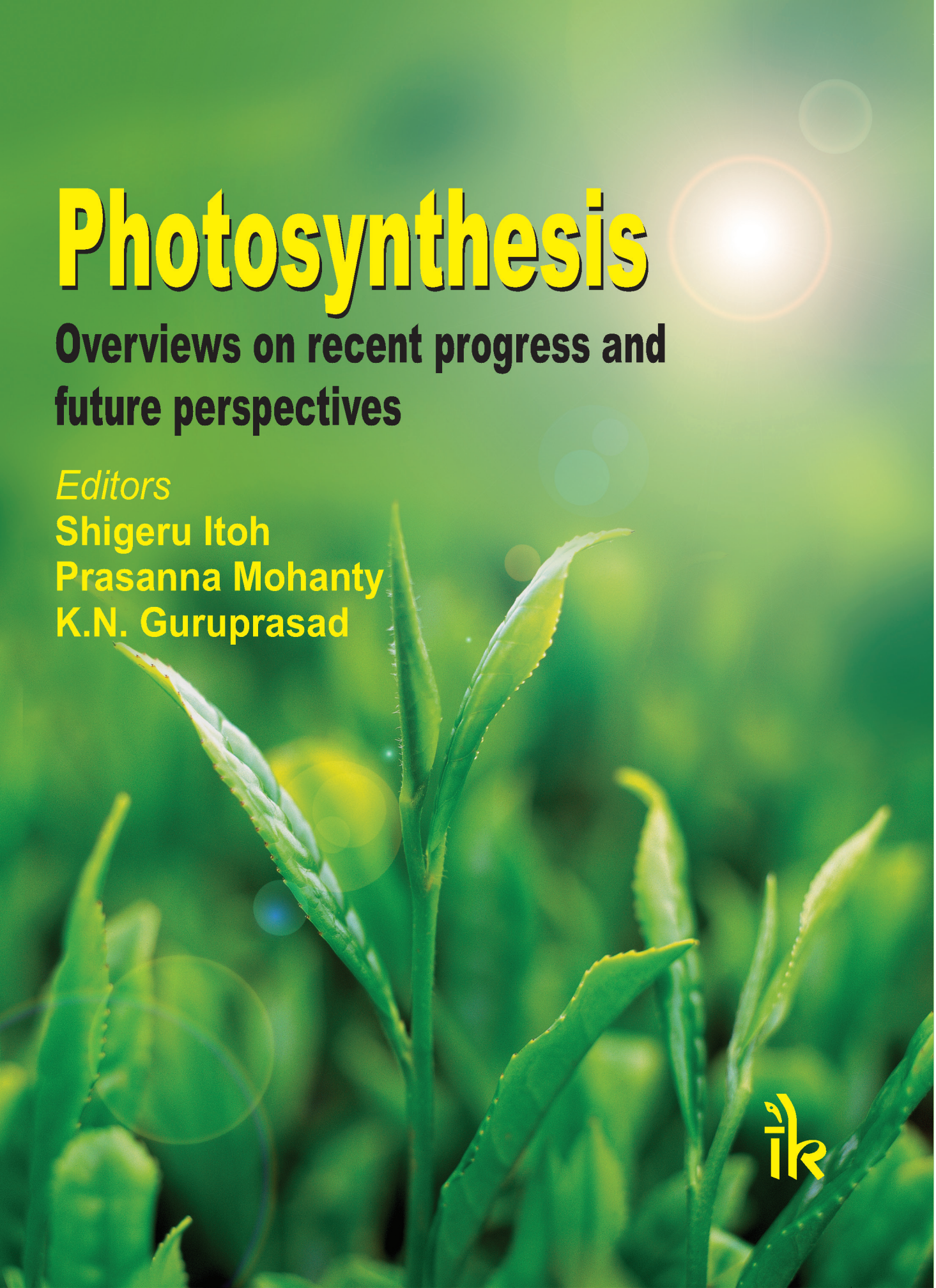

Photosynthesis: Overviews on Recent Progress and Future Perspectives

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Dedication

A 2010 portrait of Govindjee in his home at Urbana, Illinois, USA.
Photo by Rajni Govindjee.

We dedicate this book to **Govindjee**, born on October 24, 1932, in Allahabad, Uttar Pradesh, India, and to his many distinguished students and associates for their pioneering discoveries in oxygenic photosynthesis, particularly on Photosystem II (PS II), the waterplastoquinone oxido-reductase, and on the understanding and the relationship of the light emission by chlorophyll *a* (Chl *a*) (prompt fluorescence, delayed fluorescence and thermoluminescence) with various specific reactions of photosynthesis by plants, algae and cyanobacteria. Govindjee is best known for discovering that a 670 nm–absorbing form of Chl *a* belongs to PSII, for the discovery of the *two-light effect* in Chl *a* fluorescence, and in NADP reduction, and for the discovery of the specific role of the bicarbonate anion in photosynthetic electron flow to (and protonation of) a plastoquinone molecule on the electron acceptor side of PS II. In particular, we, honour him for his love and passion in communicating the concepts of *photosynthesis*, and in identifying the scientists behind their discoveries, to both young and old people around the world. He achieved these goals through truly inspiring lectures and through various publications that include books, reviews, Scientific American articles, and many edited volumes. For further information, see the *Foreword* in this book by George C. Papageorgiou, his first PhD student.

Govindjee's honours include: Fellow of the American Association of Advancement of Science (AAAS); Distinguished Lecturer of the School of Life Sciences, University of Illinois at Urbana-Champaign (UIUC); Fellow and Life Member of the National Academy of Sciences (Allahabad, India); President of the American Society for Photobiology (1980–1981); Honorary President of the 2004 International Photosynthesis Congress (Montréal, Canada); 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 the Alumni Lifetime Achievement Award of the College of the Liberal Arts and Sciences, UIUC, 2008.

Foreword

Photosynthesis: Overviews on Recent Progress and Future Perspectives, is dedicated to Professor Govindjee of the University of Illinois at Urbana-Champaign, Illinois, USA, by his students and colleagues in recognition of his great contributions to the advancement and the interpretation of the science of photosynthesis. Its inspiration was an International Conference on "Photosynthesis in the Global Perspective" held in honour of Govindjee at the University of Indore, India, in November 27-29, 2008 (see Jajoo et al. 2009). The book, however, is not a proceedings volume. It is a collection of research and review articles invited by its editors, Professors S. Itoh, Division of Materials Science, University of Nagoya, Japan, P. Mohanty, formerly of the Jawaharlal Nehru University of New Delhi and presently at the Department of Agricultural Biotechnology, Bhubaneswar, Orissa, India and K. N. Guruprasad at the School of Life Sciences, Devi Ahilya University, Indore, India from selected participants of the conference.

The chapters of the book pertain to various subjects, such as to the effects of environmental stresses on photosynthesis, to regulatory mechanisms triggered by ground state redox signals or by carotenoid absorption, to the application of optical probes to photosynthesis research, notably of chlorophyll fluorescence, and to the historical evolution of the concepts of modern photosynthesis, particularly with respect to photosynthetic oxygen evolution. Although the theme of the global perspective of photosynthesis – namely exploiting science for improved food production and energy storage – was behind this book, none of its chapters addresses such themes. Instead, they provide a glimpse of how far the science of photosynthesis has advanced to ensure the successful confrontation of these crucial and controversial global issues.

The honoured person here, Professor Govindjee, was born in Allahabad, Northern India, in 1932, the youngest child of (Mrs) Savitri Devi Asthana and (Mr) Vishveswar Prasad Asthana. He finished elementary school, high school, college, and university up to the level of MSc (subjects: chemistry, botany, zoology) in Allahabad, and in 1956 he went to the University of Illinois at Urbana-Champaign as a Fulbright Scholar, where he was accepted as graduate student in the laboratory of the famous Robert Emerson of the Botany Department.

From the early 1930s through late 1950s Robert Emerson was a dominant personality in photosynthesis research. A gifted experimentalist he made radical discoveries that seemingly violated fundamental and firmly established chemical laws and concepts (see reviews by Myers, 1974; Govindjee, 2000; Govindjee and Krogmann 2004; and Govindjee and Björn, this volume). Thus, his discovery with William Arnold of a stoichiometric ratio of ~2480 chlorophylls per 1 O_2 evolved (Emerson and Arnold, 1932a, b) not only was way out exopragmatic, but also against what one would expect from an organic-magnesium compound like chlorophyll, for which a Chl.CO_2 complex, analogous to those of the organic-magnesium Grignard reagents form ($RMgX + CO_2 \rightarrow RCOOMgX$ where X is a halogen atom) seemed more likely. Likewise, the discovery that the unicellular green alga *Chlorella* requires a minimum of 8 ~12 quanta in order to release 1 O_2 (Emerson and Lewis, 1941, 1943) appeared to be in direct conflict with the Stark-Einstein law of photochemical equivalence, which prescribes 1 chemical event per absorbed photon. And

lastly, Emerson's idea of two separate, but closely cooperating, photochemical systems (Emerson and Rabinowitch, 1960) had no precedent in photobiology (although and quite remarkably, it was predicted by Eugene Rabinowitch; see Govindjee and Björn, this volume).

These three discoveries of Emerson and coworkers, together with van Neil's (1941) discovery that both the anoxygenic (bacteria) and oxygenic (algae, plants) photosyntheses do not photo-deoxygenate CO_2 but they do photo-reduce it by photo-dissociating hydrogen donors are today the mainstays of the modern theory of photosynthesis. At the time of Govindjee's arrival in Urbana, however, they were still debated. Govindjee started working on his doctoral thesis under Emerson, seeking further evidence to consolidate the concept of the two light reactions in photosynthesis. Emerson, however, was killed in 1959, in an airplane accident, so Govindjee continued and completed his thesis requirements in 1960 under the supervision of Emerson's associate, Professor Eugene Rabinowitch, a physical chemist of many talents and countless interests including photosynthesis (see Brody 1995, 2002). Its appropriate title was *"Action Spectra of the Emerson Enhancement Effect in Algae"*.

Like an impatient race car at the starting line, Govindjee set off in his scientific race at top speed. In the years that followed he devoted his energy, mainly, to four areas of intellectual activity: education, scientific research, book and journal editing and in the chronicling of emerging concepts, trends and of the individuals behind them that occurred in the Gnostic area of photosynthesis. He is recognized as a truly inspirational educator, with a talent of adding drama to his teaching, as the numerous students he proselytized to photosynthesis research do prove. The first such proselyte (in 1963) was the author of this Foreword, and shortly after, Prasanna Mohanty, one of the editors of this volume, did join in. Since that magic time, both of us, Mohanty and Papageorgiou, are in continuous contact and collaboration with Govindjee. From the very beginning, through his retirement and beyond, his research output was always near or in the moving frontline of advancing photosynthesis. Govindjee is best known for his research on the various functional manifestations of the Photosystem II (PS II) supercomplex (light-driven water-plastoquinone oxidoreductase), including excitation energy transfer, light emission, primary photochemistry and electron transfer. His major achievements further include an understanding of the basic relationships between Chl a fluorescence and photosynthetic reactions; an unique role of the bicarbonate ion in protonations in the QB–binding region; a 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 to understand photoprotection by plants against excess light. He was and is an innovative editor, having edited several important volumes, but most remarkable for the editorial guidance he provided to the journal *Photosynthesis Research* and to the series of volumes for Kluwer/Springer under the title *Advances in Photosynthesis and Respiration*. As a chronicler, he initiated and steered the *Historical Corner in Photosynthesis Research* (Govindjee, 2006). Although, a section like this may be more appropriate for a periodical or for a magazine, and not for a technical scientific journal like Photosynthesis Research, the plethora of the contributed historical articles over the years and the fact that succeeding editors (Robert Blankenship and David Knaff) kept it on, shows beyond doubt that the Historical Corner was indeed quite well received by the photosynthesis community.

All these, and much more, including rich anecdotal material contributed by past students and colleagues of Govindjee, are presented in detail in two excellent guest editorials published in the journal Photosynthesis Research in 2007 and 2008 by his former student, Julian Eaton-Rye, of the University of Otago, New Zealand. His early times in the family home at Allahabad, with his parents, two brothers and one sister, come alive in an informal family volume published by Govindjee in 2007.

Govindjee retired from the University of Illinois to become an Emeritus Professor in 1999, after 38 years of service. With his retirement, the famous Photosynthesis Laboratory of Emerson–Rabinowitch–Govindjee in the Botany Department was dissolved and its historical equipment was donated at best, or somehow disposed of. However, even without a laboratory, Govindjee continued unabatedly his research activity, mostly by orchestrating international collaborations, as well as his editorial leadership of the Advances in Photosynthesis and Respiration series, as well as in several volumes and special issues of journals. After retirement, he received various distinctions and awards for outstanding contributions to the advancement of the science of photosynthesis and for the interpretation of its mechanism and its global significance for the benefit of the general scientific and non-scientific public (Eaton-Rye 2007a; also *http://www.life.illinois.edu/govindjee/*).

The 2008 International Conference held at the University of Indore, and the present volume are two such distinctions.

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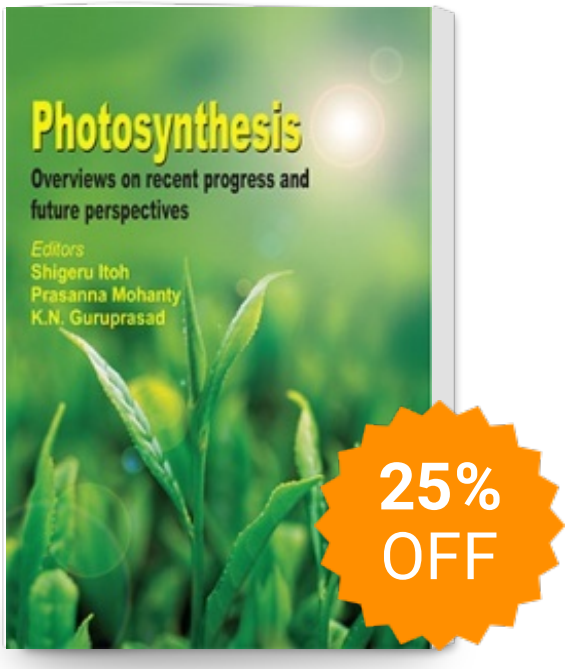

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