# PHOTOSYNTHESIS

## VOLUME I

# ENERGY CONVERSION BY PLANTS AND BACTERIA

EDITED BY
GOVINDJEE

Cell Biology : A Series of Monographs

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# Photosynthesis

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**Edited by**

GOVINDJEE

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## PHOTOSYNTHESIS
## Volume I: Energy Conversion by Plants and Bacteria

This two-volume work is a comprehensive examination of the molecular mechanisms of the conversion of light energy into chemical energy. Serving as both a review of fundamental theory and a summary of recent research, these two volumes will be a valuable reference for researchers and a fine introductory text for students of the biological, biochemical, and plant sciences.

The uniqueness of these volumes lies in their treatment of the energy conversion phenomenon in both plants and bacteria. A principal theme is the need for a thorough understanding of the molecular mechanisms involved in order to manipulate the biological systems to improve the overall rates of photosynthesis and, consequently, to increase food and biomass productivity. A second theme is that knowledge of the molecular aspects of the energy conversion process will facilitate the design of artificial systems to utilize solar energy for the production of chemical and electrical energy. The emphasis is on the biochemical and biophysical aspects of the topics covered.

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# Photosynthesis

VOLUME I

**Energy Conversion by Plants and Bacteria**

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*I am especially indebted to my daughter*
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*for her technical and editorial assistance during the preparation of this volume.*

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# Preface

Sunlight is a plentiful, continuously available source of energy. Photosynthesis converts this radiant energy into chemical energy in a highly efficient manner. Plants and cyanobacteria use water as a hydrogen donor and produce oxygen as a by-product; energy is stored in complex organic molecules. Photosynthetic bacteria use chemicals such as $H_2S$ as their hydrogen donors. Hence, they do not produce oxygen as a by-product. In plants, there is a noncyclic electron flow from water to nicotinamide adenine dinucleotide phosphate ($NADP^+$) producing NADPH and adenosine triphosphate (ATP). In photosynthetic bacteria, except, perhaps, in green bacteria, there is a cyclic electron flow producing ATP; the pyridine nucleotide, nicotinamide adenine dinucleotide ($NAD^+$), is reduced through reversed (uphill) electron flow by utilizing ATP and the externally added hydrogen donors. The complete sequence of the conversion of light energy into the production of ATP and NADPH (or NADH) in both plants and bacteria is the subject of this volume. The uniqueness of this volume lies in its integrated approach to both plant and bacterial photosynthesis. A separate volume (*Photosynthesis: Development, Carbon Metabolism, and Plant Productivity,* Vol. II) includes discussion on how ATP and NADPH are used to fix carbon dioxide into organic compounds and on the relationship between photosynthesis and plant productivity.

The contributors discuss the various aspects of the energy conversion process in both plants and bacteria in an integrated fashion, except, of course, when they deal with a process unique to one system. Most chapters have two authors—one an expert in plant photosynthesis and the other in bacterial photosynthesis. This volume emphasizes the biochemical and biophysical aspects of photosynthesis. It also contains a review of the historical development of major concepts, analysis of experimental data, and an exposition of recent findings. Since both background and up-to-date information is included, the book will serve not only as a reference source for researchers but also as an introductory work for



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graduate and advanced undergraduate students in cell biology, plant physiology, biochemistry, and biophysics.

It is our belief that a basic understanding of photosynthesis is needed before we can use it to improve the overall rate of photosynthesis of a single plant or learn how to build photosynthesis-based artificial devices to convert light energy efficiently into electrical and chemical energy.

The reader is encouraged to read both Chapters 1 and 2 before going on to the later ones, since Chapter 1, in addition to introducing the various chapters briefly, presents some of the past concepts, and Chapter 2 discusses the current attitudes in research and presents a comparative biophysical chemistry of both plants and bacteria.

GOVINDJEE

# Acknowledgments

I am grateful to my wife, Rajni, and my children, Anita and Sanjay, for their patience during the preparation of this book. I am thankful to my past graduate students for having provided me with an intellectual atmosphere for photosynthesis research, long before this book was ever planned: Maarib Bazzaz, Glenn Bedell, Fred Cho, Paul Jursinic, Rita Khanna, Ted Mar, Prasanna Mohanty, John Munday, George Papageorgiou, Alan Stemler, David vanderMeulen, Daniel Wong, Tom Wydrzynski, and Barbara Zilinskas. My present graduate students (Danny Blubaugh, William Coleman, Julian Eaton-Rye, and James Fenton) deserve my gratitude for not complaining when I was busy preparing this volume. I am also thankful to Shubha Govind, Wim F. J. Vermaas, Christa Critchley, and Ion Baianu for their cooperation. The courtesy extended by the personnel in the Department of Physiology and Biophysics, particularly by Nan Miller and Margaret McWhorter, is gratefully acknowledged.

Thanks are due to all the contributors for writing excellent chapters for this volume. I wish to thank Tony Crofts, Don DeVault, Tom Ebrey, Herb Gutowsky, Don Ort, Gregorio Weber, and John Whitmarsh for discussions on photosynthesis and related topics.

# Bessel Kok (1918–1979): A Tribute

Bessel Kok was born and educated in Holland, receiving the degrees of Candidate in Natural Philosophy in 1938, Doctor of Natural Philosophy in 1941 from the University of Leiden, and the Ph.D. in biophysics at the University of Utrecht in 1948. While pursuing his Ph.D. he worked in Utrecht for a distilling company where he became acting manager.

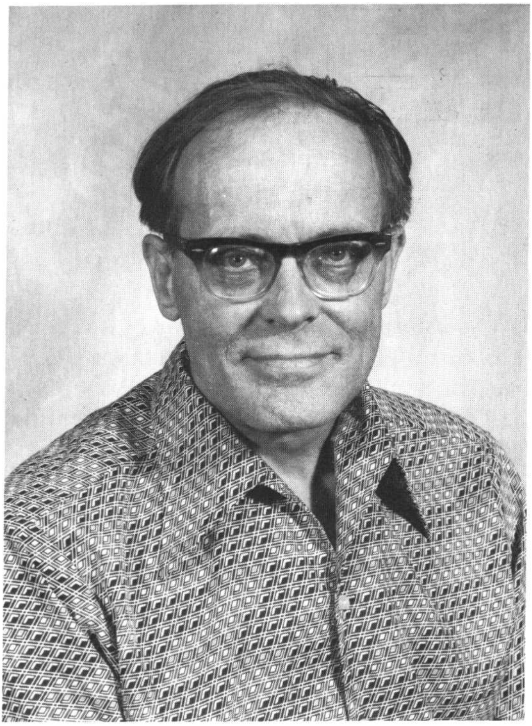
From 1949 to 1958, he worked for the Dutch Central Organization for Applied Research (T.N.O.) at the University of Wageningen (except during 1951–1952, when he was a Fellow at the Carnegie Institute of Washington at Stanford, California).

In 1958, Bessel became director of the Bioscience Group of the Research Institute for Advanced Studies (RIAS) in Baltimore, Maryland. He was subsequently promoted to the rank of associate director of research of this Martin-Marietta-sponsored laboratory and served in this capacity until his untimely death on April 27, 1979.

Bessel's scientific accomplishments were celebrated by a number of awards, including the C. F. Kettering Award (1972), the Stephen Hales Prize (1978) of the American Society of Plant Physiologists, and election to membership (1974) in the United States National Academy of Sciences.

Of the many aspects of research on the process of photosynthesis there are few which do not bear some imprint left by Bessel Kok. His work yielded more than 100 publications over 31 years. However, the number of publications is less distinctive than the critical character of the questions addressed and the results obtained.

Bessel's dissertation was a critical study of the quantum yield of photosynthesis and its measurement. In the course of that work he discovered the partial suppression of dark respiration by light, which came to be called the *Kok Effect.* In the early 1950s he made in-depth studies of solar energy conversion by algae in the context of mass culture as a potential source of food. For the maximum conversion efficiency of light to algal cell material his measured value of 20% stands as a benchmark.



**Bessel Kok**

Interest in intermittancy light effects on yields in mass culture led to the study of flashing light at a time when there were divergent data and interpretations for the $O_2$ flash yield. Elegant experimentation revealed the effect of flash duration on flash yield and eliminated the then current doubts on the conceptual validity of the photosynthetic unit.

The concept of the photosynthetic unit led to the prediction of an *ultimate photoreceptor.* Bessel's search for it by increasingly more sophisticated experimentation led to his discovery and characterization of P700, a milestone in work on the primary reactions of photosynthesis. Study of the reversible bleaching of P700 by different actinic wavelengths provided evidence for the proposal of Kok and George Hoch, made almost simultaneously with that of Robert Hill and Fay Bendall, for two photoreactions interacting in what has come to be called the *Z-scheme.* There followed widely ranging work on pool sizes, component interaction, and transfer times of electron carriers linking the two photoreactions. Collaboration with Pierre and Anne Joliot added $O_2$ evolution as a kinetic measure of events between photosystems I and II and led subsequently to extension of the Joliots' observations on $O_2$ yields from single flashes. From this emerged the clearly proposed and generally accepted cyclic four-step model for $O_2$ evolution, in Bessel's language the *oxygen clock.* A development of techniques followed which allowed critical measurements of $H^+/e^-$ accompanying $O_2$ evolution and the $e^-$-transfer steps between the photoacts. Almost obscured by the rapid pace of these exciting achievements was the development of mass spectrometric measurements applied to the interactions between photosynthesis and respiration and to an extraterrestrial life-detection system.

Undoubtedly our abridged account is incomplete, especially in its recognition of Bessel's many collaborators. Our intent was to sketch his scientific history in order that we might turn to more personal thoughts.

As a practitioner of science, Bessel was distinguished by his creativity. His keen and imaginative mind was guided into complex problems by a remarkable intuition. Identifying and finding the *nuggets* (his word) allowed simplification of a complex picture to its bare essentials. Such was his art. He often claimed that his successes came from *gadgeteering.* In perspective, however, one might say that his science was the product of artistry, craftmanship, and intensity of effort.

Bessel's scientific accomplishments reveal too little of a unique character that had many facets. Some may have seen only the outer veneer as a brusque and, at times, even boorish personality. Some have felt his patience and his sensitivity to all people, whatever their walk in life. Some have seen his intolerance of the trappings or of the pomp and ceremony of science. Some have enjoyed him as a witty and boisterous drinking companion.

Bessel was an uncommonly dedicated man, dedicated to his family, to his science, and to the joys of life. He pursued each endeavor with unrelenting fervor and passion and with enormous mental and physical stamina. He wore only a thin cloak of inhibitions, happily shared warmth and encouragement, but also gave sharp and sometimes brutal criticisms. His standards for his own work were uncompromisingly high, and he expected as much from others. Many of us earned his criticisms, some experienced his praise and encouragement, but all of us learned from Bessel.

On behalf of all of the authors, the editor of this volume, and many others, we salute and toast you, Bessel, for your scientific accomplishment, for your free spirit, and for all the fond personal remembrances you gave us.

GEORGE CHENIAE
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