Sulfur Metabolism in Phototrophic Organisms
The scope of our series, beginning with volume 11, reflects the concept that photosynthesis and respiration are intertwined with respect to both the protein complexes involved and to the entire bioenergetic machinery of all life. *Advances in Photosynthesis and Respiration* is a book series that provides a comprehensive and state-of-the-art account of research in photosynthesis and respiration. Photosynthesis is the process by which higher plants, algae, and certain species of bacteria transform and store solar energy in the form of energy-rich organic molecules. These compounds are in turn used as the energy source for all growth and reproduction in these and almost all other organisms. As such, virtually all life on the planet ultimately depends on photosynthetic energy conversion. Respiration, which occurs in mitochondrial and bacterial membranes, utilizes energy present in organic molecules to fuel a wide range of metabolic reactions critical for cell growth and development. In addition, many photosynthetic organisms engage in energetically wasteful photorespiration that begins in the chloroplast with an oxygenation reaction catalyzed by the same enzyme responsible for capturing carbon dioxide in photosynthesis. This series of books spans topics from physics to agronomy and medicine, from femtosecond processes to season long production, from the photophysics of reaction centers, through the electrochemistry of intermediate electron transfer, to the physiology of whole organisms, and from X-ray crystallography of proteins to the morphology or organelles and intact organisms. 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, respiration and related processes.

*The titles published in the Series are listed at the end of this volume.*
Cover Image: Glutathione is the most important low molecular weight thiol in nearly all living cells with numerous functions including stress tolerance and redox signal transduction. Shown is the in situ labelling of glutathione in the cytosol of plant cells (green colour) using a fluorescent dye.

Left panels: heterotrophic cells from suspension culture of Arabidopsis thaliana. Red indicates staining of cell walls and integral plasmamembranes with propidium iodide. Right panels: stoma cells of Nicotiana tabacum. Red colour indicates autofluorescence from chlorophyll. Dark areas within cells are caused by vacuoles. For detailed description see chapter 24 by A.J. Meyer and M. Fricker.

The photograph was generously provided by Dr. Andreas J. Meyer, University of Heidelberg, Germany, and Dr. Mark Fricker, University of Oxford, UK.

Printed on acid-free paper
From the Series Editor

Advances in Photosynthesis and Respiration

Volume 27: Sulfur Metabolism in Phototrophic Organisms

I am delighted to announce the publication, in Advances in Photosynthesis and Respiration (AIPH) Series, of a book Sulfur Metabolism in Phototrophic Organisms. Four distinguished authorities (Rüdiger Hell, Christiane Dahl, David Knaff, and Thomas Leustek) have edited this volume: Hell is an authority from the University of Heidelberg (Germany), Dahl from the University of Bonn (Germany), Leustek from Rutgers University (USA), and Knaff from Texas Tech University (USA). Taken together, these editors have a unique combination of expertise in Biochemistry, Microbiology, Plant Physiology, and Molecular Biology. Their joint efforts have provided a comprehensive overview of Sulfur Metabolism in Phototrophic Organisms. The editors have presented an authoritative decisive volume on sulfur metabolism in both phototrophic eukaryotes and prokaryotes. This book is unique in my Series since it is the first time, we have covered the metabolism of this important element in photosynthetic systems.

Published Volumes (2007–1994) in the Series are:


Further information on these books and ordering instructions can be found at <http://www.springeronline.com> under the Book Series ‘Advances in Photosynthesis and Respiration.’ Table of Contents of Volumes 1–25 can be found at <http://www.life.uiuc.edu/govindjee/photosynSeries/ttoc.html>. Special discounts are available to members of the International Society of Photosynthesis Research, ISPR (<http://www.photosynthesisresearch.org/>).

Other Volumes, at the typesetters are:

• Biophysical Techniques II (Editors: Thijs Aartsma and Jörg Matisyk) (expected to be Volume 26) ; and
• The Purple Phototrophic Bacteria (Editors: C. Neil Hunter, Fevzi Daldal, Marion Thurnauer and J. Thomas Beatty).

About Volume 27: Sulfur Metabolism in Phototrophic Organisms

Sulfur Metabolism in Phototrophic Organisms has 24 authoritative Chapters, and is authored by 55 international authorities from 10 countries (Australia, Canada, Denmark, Germany, Israel, Italy, Japan, Netherlands, United Kingdom, United States of America). It is a truly an international
book and the editors deserve our thanks and our congratulations this gift for our future.

**Sulfur** is one of the most versatile elements in life due to its reactivity in different oxidation and reduction states. In phototrophic organisms, the redox properties of sulfur in proteins, and of sulfur-containing metabolites, are particularly important in the interaction between the reductive assimilation processes of photosynthesis and reactive oxygen species that arise as by-products of electron transport chains. Thiol groups in proteins and metabolites are targets of reactive oxygen species, resulting in potential damage and at the same time giving rise to redox signal cascades that trigger repair reactions and adaptation to environmental stress. Further, reduced sulfur compounds play a prominent role as electron donors for photosynthetic carbon dioxide fixation in anoxygenic phototrophic sulfur bacteria. Interest in the investigation of the multiple functions of sulfur-related processes has exponentially increased in recent years, especially in molecular and cellular biology, biochemistry, agrobiotechnology and ecology. This book provides, for the first time, in-depth and integrated coverage of the functions of sulfur in phototrophic organisms including bacteria, plants and algae; it bridges gaps between biochemistry and cellular biology of sulfur in these organisms, and of biology and environments dominated by them. This book is designed to be a comprehensive resource on sulfur in phototrophic organisms for advanced undergraduate and graduate students, beginning researchers and teachers in the area of photosynthesis, bacterial energy metabolism, biotechnology, plant nutrition, plant production and plant molecular physiology.

The readers can easily find the titles and the authors of the individual chapters in the Table of Contents of this book. Instead of repeating this information here, I prefer to thank each and every author by name (listed in alphabetical order) that reads like a “Who’s Who in Sulfur Metabolism in Phototrophic Organisms”:

Christoph Benning; Don Bryant; Meike Burow; Leong-Keat Chan; Christiane Dahl; Luit De Kok; Mark D. Fricker; Niels-Ulrik Frigaard; R. Michael Garavito; Jonathan Gershenzon; Mario Giordano; Arthur Grossman; Robert Hänsch; Thomas E. Hanson; Günther Hauska; Malcolm J. Hawkesford; Rüdiger Hell; Cinta Hernández-Sebastiá; Holger Hesse; Rainer Hoefgen; Josef Horne; Timothy J. Hurse; Johannes Imhoff; Ulrike Kappler; Patrick Keeling; Jürg Keller; David Knaff; Stanislav Kopriva; Thomas Leustek; Frédéric Marsolais; Ralf R. Mendel; Andreas Meyer; Hartwig Modrow; Rachael Morgan-Kiss; Alessandra Norici; Jörg Overmann; Lolla Padmavathi; Nicola Patron; Marinus Pilón; Elizabeth A. H. Pilon-Smits; Alexander Prange; Simona Ratti; Thomas Rausch; John A. Raven; Kazuki Saito; Yosepha Shahak; Nakako Shibagaki; Mie Shimojia; Hideki Takahashi; Michael Taus; Luc Varin; Markus Wirtz; Ute Wittstock; Hong Ye; Fangjie Zhao.

**Timeline for Sulfur in Phototrophic Organisms**

A timeline of discoveries is one way to assess the progress and the status of a field. See for example:


Below, we provide a timeline for sulfur in phototrophic organisms (courtesy of Rüdiger Hell):

1836: Christian Gottfried Ehrenberg describes the discovery of the first purple sulfur bacteria “Monas okeni” and “Ophidomonas jenensis”

1861 and 1882: Sulfate is found to be an essential plant mineral nutrient by German plant physiologists J.A.L.W. Knoop and J. v. Sachs using hydroponic cultures

1872 and 1875: The German botanist founder of bacterial systematics, Ferdinand Cohn, unequivocally proved that the cellular inclusions of the above purple bacteria consisted of elemental sulfur

1883: Theodor W. Engelmann discovered and described action spectrum of photosynthesis in purple bacteria
1919: Johannes Buder confirmed Engelmann’s theories that the purple bacteria perform a photosynthetic metabolism. They assimilate carbon dioxide or organic compounds anaerobically in the light.

1931: The definite proof for the phototrophic nature of the purple and green sulfur bacteria, by the Dutch American microbiologist Cornelis B. van Niel, working in Pacific Grove, CA: For the phototrophic sulfur bacteria the reducing agent is hydrogen sulfide (or sulfur or thiosulfate) and for the photosynthesis of plants, algae and cyanobacteria, it is water, with the oxidation products being molecular sulfur (and/or sulfate) and molecular oxygen, respectively.


1973: Jerome Schiff begins to identify the eukaryotic sulfate assimilation pathway in Euglena.

1988 and 1995: First genetics in green (John Ormerod) and purple sulfur bacteria (Christiane Dahl).

1996: Tom Leustek and John Wray isolate genes for adenosine phosphosulfate reductase, the decisive enzyme in plant sulfate reduction.

2002: The first genome sequence of a green sulfur bacterium by Jonathan A. Eisen and coworkers.


Future AIPH 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):

● Abiotic Stress Adaptation in Plants: Physiological, Molecular and Genomic Foundation (Editors: Ashwani Pareek, Sudhir K. Sopory, Hans J. Bohnert and Govindjee);

● C-4 Photosynthesis and Related CO$_2$ Concentrating Mechanisms (Editors: Agepati S. Raghavendra and Rowan Sage);

● The Chloroplast Biochemistry, Molecular Biology and Bioengineering, Part I and Part 2 (Editors: Constantin Rebeiz, Hans Bohnert, Christoph Benning, Henry Daniell, Beverley R. Green, J. Kenneth Hooper, Hartmut Lichtenthaler, Archie R. Portis and Baishnab C. Tripathy);

● Photosynthesis: Biochemistry, Biophysics, Physiology and Molecular Biology (Editors: Julian Eaton-Rye and Baishnab Tripathy);

● Photosynthesis In Silico: Understanding Complexity from Molecules to Ecosystems (Editors: Agu Laisk, Ladislav Nedbal and Govindjee).

In addition to these contracted books, we are in touch with prospective Editors for the following topics, among others:

Books, that are relevant to Sulfur metabolism, arranged chronologically since 1970 (courtesy of Rüdiger Hell).

Researchers and lecturers who wish to examine all published material in the area of sulfur metabolism in plants, algae and bacteria would benefit by consulting all of the following books listed below.


Readers are encouraged to send their suggestions for these and future Volumes (topics, names of future editors, and of future authors) to me by E-mail (gov@uiuc.edu) or fax (1-217-244-7246).

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

I take this opportunity to thank and congratulate all the four editors (Rüdiger Hell, Christiane Dahl, David Knaff, and Thomas Leustek) for their outstanding and painstaking editorial work. I thank all the 55 authors (see the list above) of this book in our AIPH Series: without their authoritative chapters, there would be no such Volume.

I thank Rüdiger Hell for his contribution to the Timeline of Sulfur in plant, algal and bacterial metabolism and for providing the list of books on this topic, cited above. We owe Jacco Flipsen and Noeline Gibson (both of Springer) thanks for their friendly working relation with us that led to the production of this book. Thanks are also due to Jeff Haas (Director of Information Technology, Life Sciences, University of Illinois at Urbana-Champaign, UIUC), Evan DeLucia (Head, Department of Plant Biology, UIUC) and my dear wife Rajni Govindjee for constant support.

October 24, 2007
Govindjee
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Govindjee, born in 1932, obtained his B.Sc. (Chemistry, Biology) and M.Sc. (Botany, Plant Physiology) in 1952 and 1954, from the University of Allahabad, India. He learned his Plant Physiology from Prof. Shri Ranjan, who was a former student of Felix Frost Blackman. For his Ph.D. (in Biophysics, 1960), he studied under the pioneers of photosynthesis: Profs. Robert Emerson and Eugene Rabinowitch, both at the University of Illinois at Urbana-Champaign (UIUC), IL, U.S.A. He considers Eugene Rabinowitch as his main role model and his mentor.

Govindjee is best known for his research on the mechanisms of excitation energy transfer, light emission, the primary photochemistry and the electron transfer in Photosystem II (PS II). His research, with many collaborators, has 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 effects in Chl \(a\) fluorescence and in NADP (nicotinamide dinucleotide phosphate) reduction in chloroplasts (Emerson Enhancement). Further, he has worked on the existence of different spectral fluorescing forms of Chl \(a\) and the temperature dependence of excitation energy transfer down to 4 K; basic relationships between Chl \(a\) fluorescence and photosynthetic reactions; unique role of bicarbonate on the acceptor side of PS II, particularly in the protonation events involving the Q\(_b\) binding region; the theory of thermoluminescence in plants; picosecond measurement on the primary photochemistry of PS II; and the use of Fluorescence Lifetime Imaging Microscopy (FLIM) of Chl \(a\) fluorescence in understanding photoprotection against excess light.

Govindjee’s current focus is on the ‘History of Photosynthesis Research,’ in ‘Photosynthesis Education,’ and in the ‘Possible Existence of Extraterrestrial Life.’ He is the founding Historical Corner Editor of ‘Photosynthesis Research’, and the founding Series Editor of ‘Advances in Photosynthesis and Respiration’. He has served on the faculty of the UIUC for ~40 years. Since 1999, he has been Professor Emeritus of Biochemistry, Biophysics and Plant Biology at the same institution. His honors include: Fellow of the American Association of Advancement of Science (AAAS); Distinguished Lecturer of the School of Life Sciences, UIUC; Fellow and Life member of the National Academy of Sciences (India); President of the American Society for Photobiology (1980–1981); Fulbright Scholar and Fulbright Senior Lecturer; Honorary President of the 2004 International Photosynthesis Congress (Montréal, Canada); the 2006 recipient of the Lifetime Achievement Award from the Rebeiz Foundation for Basic Biology, and most recently, the 2007 recipient of the ‘Communications Award’ of the International Society of Photosynthesis Research (ISPR).

Further information on Govindjee and his research can be found at his web site: http://www.life.uiuc.edu/govindjee. He can always be reached by e-mail at gov@uiuc.edu.
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Sulfur is one of the most versatile elements in life due to its reactivity in different oxidation and reduction states. In phototrophic organisms, the redox properties of sulfur in proteins, and of sulfur-containing metabolites, are particularly important for the mediation between the reductive assimilation processes of photosynthesis and reactive oxygen species that arise as byproducts of electron transport chains in chloroplasts and mitochondria. Further, reduced sulfur compounds play a prominent role as electron donors for photosynthetic carbon dioxide fixation in anoxygenic phototrophic sulfur bacteria. Indeed, sulfur together with iron may be assumed to have contributed to early electron transport processes in protolife. Reductive atmospheric conditions before the invention of oxygenic photosynthesis probably promoted the functional evolvement of processes based on the redox properties of the different oxidation states of sulfur. When the atmospheric environment became oxidative as a consequence of the effective development of photosynthesis in bacteria and later in algae and plants, the cellular milieu remained reductive. Reduced sulfur moieties such as cysteine and methionine changed into targets of abundant reactive oxygen species that were derived from respiration or photosynthesis. It is still a matter of speculation whether defense reactions to prevent oxidation led to the development of redox signal transduction. Interest in the investigation of such dualistic functions of sulfur-related processes has exponentially increased in recent years, especially in molecular and cellular biology, biochemistry, agrobiotechnology and ecology.

Sulfur metabolism is thus of truly elemental importance for life, but complex in its biochemical, biophysical and metabolic functions. The editors of this book come from different backgrounds (biochemistry, microbiology, plant physiology, molecular biology) and joined their efforts to provide a comprehensive overview of Sulfur Metabolism in Phototrophic Organisms. The aim was to present a definitive volume on sulfur metabolism in phototrophic eukaryotes (plants, algae) and prokaryotes (anoxygenic and oxygenic phototrophic bacteria). The most recent informations available in these fields have been compiled. Contributors had the freedom to develop their topics in depth, and we feel that nothing significant in this field has been neglected.

The book is organized along four major themes: (1) sulfate activation and reduction, biosynthesis of sulfur containing amino acids, (2) sulfur in plants and algae, (3) sulfur in phototrophic prokaryotes, and (4) ecology and biotechnology. For each theme several chapters contributed by leading experts in the field are combined to yield a detailed picture of the current state of art.

A comprehensive volume combining the aspects of sulfur metabolism not only in eukaryotic phototrophs but also in phototrophic bacteria has never been published. Here, we try to emphasize the common characteristics of the processes of assimilatory sulfate reduction in eukaryotic and prokaryotic phototrophs. Ample parallels are also found in the uptake of sulfate into the cell, sulfation pathways, in the biosynthetic pathways of sulfur-containing amino acids, or sulfur donation reactions in the biosynthesis of other sulfur-containing cell constituents.

This book provides for the first time a comprehensive and integrated knowledge of the functions of sulfur in phototrophic organisms including bacteria, plants and algae; it bridges gaps between biochemistry and cellular biology of sulfur in these organisms, and of biology and environments dominated by them. Specialized functions of sulfur in animals in reductive environments such as sediments have purposely been omitted. As the contents of this book have been compiled for plant scientists, agronomists and microbiologists alike, we see an ideal opportunity to unite the common interest in sulfur metabolism. Many plant scientists might not be aware of the important role sulfur compounds play in anoxygenic sulfur bacteria where they serve as photosynthetic electron donors. In order to provide the reader specializing in plant issues with a comprehensive introduction into and overview about various groups of anoxygenic phototrophic bacteria, we included chapters about systematics and ecology of anoxygenic phototrophic bacteria. In other chapters the role of sulfur compounds for these organisms and the biochemistry of dissimilatory sulfur transformations in this group are described in depth.
We hope this book will be of use for advanced students as well as teachers and researchers in the fields of photosynthesis, bacterial energy metabolism, plant nutrition, plant production and plant molecular physiology and stimulates further research to close the gaps of our knowledge on sulfur in plants.

We have many people to thank. First of all, we would like to take this opportunity to acknowledge all authors for providing uniformly excellent chapters. Each author is a leading authority in his/her field and has generously offered the time and effort to make this book a success. All authors were willing to look beyond their research specialties to give the reader a more encompassing view. In addition, they put up with the inevitable delays in publication. We also acknowledge the help received from Noeline Gibson and Jacco Flipson (of Springer). And, of course, we wish to thank the series editor Govindjee. His patience, good humor and professional competence helped us immensely.

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Rüdiger Hell was born in a small village in the west of Germany and enjoyed rural life and excellent early education on nearly everything except biology. He developed a strong interest in the special life of plants and, after civil service, studied biology at the technical University of Darmstadt, Germany. He specialized in the combination of biochemistry and ecology in the hope this would help him to understand how plants function. He graduated with a diploma thesis on Crassulacean Acid Metabolism (CAM) in cell cultures in 1985. During his PhD research, he studied under the supervision of his excellent teacher Prof. Ludwig Bergmann at the University of Cologne, Germany. He worked out the biosynthesis of glutathione in plants and demonstrated the still valid concept of redox control and feedback sensitivity of the first enzyme of the glutathione pathway. After graduation in 1989, he moved into the regulatory interactions between chloroplasts and the cytosol. The German Science Foundation (DFG, Deutsche Forschungsgemeinschaft) provided him a fellowship from 1990 to 1993 to work with Prof. Wilhelm Gruissem at the University of California, Berkeley. There he was introduced into the powerful techniques of molecular biology and plant genetic transformation to study the control of chloroplast RNA stability by nucleus-encoded RNA-binding proteins. The inspiring atmosphere by wonderful colleagues in the laboratory and the scientific and cultural spirit at Berkeley enabled him to extend experiments to the regulation of metabolic reactions that are distributed between chloroplasts and the cytosol. This became his major research area and led him to choose primary sulfur metabolism for investigation which at that time was hardly understood.

In 1993 he returned to Germany to take a position as research group leader at the Department of Plant Physiology at the Ruhr-University Bochum, where he was allowed to independently follow his ideas on cloning genes of plant sulfur metabolism. The aim was to establish the regulatory mechanism that control this pathway and relate it to the network of primary assimilatory pathways of carbon and nitrogen. Again funded by DFG, he set up a research program and quickly provided evidence for the significance of protein–protein interaction in the cysteine synthase complex. Within five years of intense teaching and research, the license of university teaching (Habilitation) was achieved in 1998. In order to broaden his research interest Rüdiger Hell accepted a position as head of the Molecular Mineral Assimilation group at the Leibniz-Institute of Plant Genetics and Crop Plant Research (IPK) at Gatersleben in what used to be Eastern Germany. Until 2003 he taught plant physiology at the University of Halle and used the excellent research facilities and high quality plant research community at IPK to investigate sulfate assimilation, iron allocation and nitrogen use efficiency in Arabidopsis thaliana as well as in crop plants.

In 2002, he received invitations for professorships in Heidelberg and in Düsseldorf, Germany. In 2003, he accepted the chair of Molecular Biology of Plants at the University of Heidelberg, Germany’s oldest University and particularly strong in biosciences. In recent years, his laboratory has demonstrated that the cysteine synthase protein complex
is a sensor for sulphide in plant cells, that glutathione is a part of signal transduction of cellular redox state, and that sulfur metabolism has an important and special role in mounting the plant’s defence against pathogens. Rüdiger Hell has served as Dean of the Faculty of Biosciences at Heidelberg from 2005 to 2007, and continues to regularly review for national and international funding agencies and the most important journals in plant sciences.

Rüdiger Hell’s work is funded by DFG and the German Academic Exchange Service (DAAD, Deutscher Akademischer Austauschdienst). He is indebted to the lively and excellent fellows in his research group and the Heidelberg Institute of Plant Sciences. He owes incredibly much to his wife, Dr. Helke Hillebrand, who always supported him and advises him best when life becomes tough.

Further information can be found at the Heidelberg Institute of Plant Sciences web site: http://www.bot.uni-heidelberg.de. He can be reached by e-mail at rhell@hip.uni-heidelberg.de.
Christiane Dahl is a lecturer of Microbiology in the Institute of Microbiology & Biotechnology at the Rheinische Friedrich-Wilhelms Universität in Bonn, Germany. She studied Biology at University of Bonn from 1982 to 1987 and received her diploma for a thesis on “Comparative enzymology of sulfur metabolism in the purple sulfur bacterium Thiocapsa roseopersicina under chemo- and photolithoautotrophic conditions”. She received her PhD in 1992 for a thesis on a much “hotter” topic, the biochemistry of dissimilatory sulfate reduction in the hyperthermophilic archaeon Archaeoglobus fulgidus. Both theses were supervised by her much esteemed academic teacher Hans G. Trüper. During the work for the PhD, a research visit to the laboratory of Nicholas M. Kredich at the Department of Biochemistry, Duke University, Durham, North Carolina, proved most rewarding. In 1993 she accepted a position as a research group leader, at the Institute of Microbiology & Biotechnology in Bonn. She then switched back to anoxygenic phototrophic sulfur bacteria, to study their oxidative sulfur metabolism in more depth. Up to that point, biochemical techniques had been used for analysis of the various enzymatic steps involved. Now, she introduced targeted genetics to explore the mechanisms of reduced sulfur compound oxidation. Allochromatium vinosum was the first purple sulfur bacterium for which methods like conjugational transfer of plasmids, insertionnal mutagenesis and in frame deletion of genes, epitope tagging and complementation of genes were employed. In the meantime, this purple sulfur bacterium had been developed into a model for studying oxidative sulfur metabolism. In 1999, she completed her Habilitation in Microbiology at the University of Bonn. The expertise of her group includes methods in molecular genetics and biology, protein biochemistry and analysis of inorganic sulfur compounds. Current research focuses on the uptake of insoluble elemental sulfur by bacterial cells, the oxidation of thiosulfate, and the oxidation of intracellularly stored sulfur by the so-called Dsr system with sulfite reductase as a component of major importance. She also initiated the complete genome sequencing of Allochromatium vinosum within the Community Sequencing Program 2008 of the United States DOE (Department of Energy) Joint Genome Institute. Together with Cornelius G. Friedrich (Dortmund, Germany) she organized the first “International Symposium on Microbial Sulfur Metabolism” held in June 2006 in Münster, Germany. Since 1998, she is a member of the Editorial Board of FEMS Microbiology Letters and is also a member of the Scientific Committee for the International Symposium on Phototrophic Prokaryotes.

Dahl’s research is supported by the generous funding by the Deutsche Forschungsgemeinschaft and by the Deutscher Akademischer Austauschdienst. Her studies have been facilitated by the enthusiastic collaboration of students and technical assistants in her group and past and ongoing cooperation with many research groups, both in
Germany and overseas. The latter include productive studies on the Sox system for thiosulfate oxidation with Ulrike Kappler (Brisbane, Australia) and Cornelius G. Friedrich (Dortmund, Germany), speciation of stored sulfur via XANES (X-ray Absorption Near Edge Spectrum) spectroscopy with Alexander Prange (Mönchengladbach, Germany, and Baton Rouge, LA), detection of siroamide in *Allochromatium vinosum* with Russ Timkovich (Tuscaloosa, AL), the solution structure of DsrC via Nuclear Magnetic Resonance (NMR) with John Cort (Richland, WA), the crystal structure of DsrEFH (Dong-Hae Shin, Seoul, Korea) and on sulfur globule proteins with Dan C. Brune (Tempe, AZ). Christiane Dahl is deeply indebted to her mentor Hans G. Trüper. He incited her interest in sulfur metabolism and his never ceasing support and continuous encouragement is invaluable to her. She appreciates very much the support of her husband, Achim Heidrich, who always provides encouragement in all her endeavours.

Further information can be found at her web site: http://www.ifmb-a.uni-bonn.de/ag-dahl.htm. She can be reached by e-mail at ChDahl@uni-bonn.de.
David Knaff is a native New Yorker and received his early education in New York City. He was lucky enough to attend the Bronx High School of Science, where he not only received a superb education, but also had the good fortune to work with inspiring teachers who introduced him to the rewards of scientific inquiry. After receiving a B.S. in chemistry from the Massachusetts Institute of Technology (MIT) in 1962, he obtained M.S. (in 1963) and Ph.D. (in 1966) degrees, both in chemistry, from Yale University with the support of a National Science Foundation (NSF) pre-doctoral fellowship. His Ph.D. research, under the direction of Prof. Jui Wang, focused on developing model systems for photosynthetic energy conservation using illuminated solutions of metal-containing porphyrins in non-aqueous polar solvents. This work stimulated his interest in all aspects of photosynthesis and, despite the fact that he had never had any formal training in biochemistry, he was able to obtain, in 1966, a three-year National Institutes of Health (NIH) post-doctoral fellow in the Department of Cell Physiology at the University of California at Berkeley, where he received his first direct training in the biochemistry of photosynthetic systems under the mentorship of Prof. Daniel I. Arnon. He remained at Berkeley until 1976 as a Cell Physiology research scientist and was fortunate enough to share laboratory space with Richard (Dick) Malkin, Peter Schürmann and Bob Buchanan, who were wonderful colleagues and who introduced him to areas of biophysics and of plant and bacterial photosynthesis beyond those encountered in his work with Prof. Arnon.

In 1976, he moved to Lubbock, Texas to assume a faculty position in the Department of Chemistry and Biochemistry at Texas Tech University, where he is currently the Paul W. Horn Professor of Chemistry and serves as Co-Director of the Texas Tech Center for Biotechnology and Genomics. He served six years, from 1990 through 1996, as chair of his academic department. His early work in photosynthesis focused on biophysical and biochemical studies of membrane-bound electron transfer chains in plant chloroplasts, cyanobacteria and in purple and green anoxygenic photosynthetic bacteria. More recently, the emphasis in his research group has shifted to the study of soluble enzymes that catalyze electron transfer reactions involved in the early stages of sulfate and nitrate assimilation in oxygenic photosynthetic organisms, with a particular emphasis on enzymes that use reduced ferredoxin as an electron donor. His interest in ferredoxin-dependent enzymes led, with considerable assistance from Peter Schürmann and Bob Buchanan, to opening a new area of investigation in his lab at Texas Tech in redox-regulation of enzyme activity and gene expression in systems related to the chloroplast ferredoxin/thioredoxin system. The thioredoxin work produced extremely rewarding collaborations with the research groups of
Jean-Pierre Jacquot, Myroslawa Miginiac-Maslow and Jean-Marc Lancelin (supported in its early days by a joint NSF/CNRS (Centre National de la Recherche Scientifique) grant) in France, and with Carl Bauer’s group at Indiana University in the U.S.

David Knaff, who is currently half-way through his second five-year term as editor-in-chief of the journal *Photosynthesis Research*, has published more than 200 refereed scientific articles and is co-author, with William (Bill) Cramer, of “Energy Transduction in Biological Membranes”. His work continues to be supported generously by U.S federal agencies (the Department of Energy and the Department of Agriculture) and by the Robert A. Welch Foundation.

Further information can be found at the Department of Chemistry and Biochemistry, University of Texas, Lubbock, web site: http://www.depts.ttu.edu/chemistry. David Knaff can be reached by e-mail at david.knaff@ttu.edu.
Thomas Leustek

**Thomas Leustek** is a professor at the Biotechnology Center for Agriculture and the Environment of Rutgers University, New Brunswick, NJ. He had the privilege to spend and enjoy most of his academic career in the New Jersey/New York metropolitan area. In 1981, he received his B.A. from Newark College of Arts and Sciences, Newark, New Jersey. Early on he was interested in plant sciences. In 1987, he obtained his Ph.D. working on nutritional aspects of plants. During his period as a postdoctoral fellow (1986–1988) at the Roche Institute of Molecular Biology in Nutley, New Jersey, he worked on protein folding and heat stability in *E. coli* and *Rhodospirillum* under the supervision of Prof. Herbert Weissbach, who became an important teacher and mentor for him; Weissbach introduced him into the world of Biochemistry. He stayed on at the Roche Institute as a research fellow (1988–1991) and extended the work on heat-shock proteins to plant cells.

In 1991 he accepted an offer to join the Plant Science Department at Rutgers University, New Brunswick as an Assistant Professor. There, he developed a comprehensive research program on the plant assimilatory sulfate reduction pathway. He was among the first to clone genes and cDNAs and developed functional complementation of *E. coli* to perfection. The reward was the identification of adenosine-phosphosulfate reductase, the enigmatic central enzyme of the sulfate reduction pathway. His discoveries closed a long-standing biochemical controversial discussion on the nature of electron transfer to free or bound reaction intermediates and helped to establish the now accepted mechanisms in plants and different groups of bacteria. As an Associate Professor and since 2001 as a Professor at the newly founded Biotechnology Center for Agriculture, he also worked intensively on the improvement of crop plants with respect to their nutritional value. More recently, he has embarked on a new challenge to the biochemists: the biosynthesis of essential amino acids in plants. At Rutgers, he is Director of the Plant Biology Graduate Program; he has received several awards for his outstanding teaching and sustained research.

Tom Leustek has received numerous honors and serves on a number of panels, such as the editorial boards of *The Plant Journal* and *Photosynthesis Research*. He advises scientific panels including USDA (United States Department of Agriculture) and NRI (National Resources Institute) but also biotech companies and is a regular reviewer for the most important journals in plant biology.

Further information can be found at a web site: http://www.cook.rutgers.edu/~biotech/faculty/index.html. Thomas Leustek can be reached by e-mail at leustek@AESOP.Rutgers.edu.
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Fig. 2. Three-dimensional structures of prokaryotic SAT and OAS-TL. The figure depicts the overall homomeric quaternary structure of SAT (A) and OAS-TL (D). In both cases the monomers are shown in different colours in order to illustrate the sterical position of the monomers. Each SAT monomer (B) consists of an α-helical domain (green), a β-sheet domain (golden) that included a random coil loop (red) and the C-terminal tail (dark blue), which is responsible for CSC formation. Please note that the last 11 amino acid residues of the C-terminal tail are missing in the structural presentation, since they were not solved by X-ray crystallography. (C) Top view on an SAT trimer, where α-helical domains are deleted for better overview. The active site of SAT lies in between the β-sheet domain of two monomers, thus a SAT ‘dimer of trimers’ (A) contains six independent active sites. The most important residues for binding of substrates and the enzymatic activity are named and shown in sticks. Each OAS-TL monomer (E) of the native OAS-TL dimer (B) contains one PLP (red) that is bound via an internal Schiff base by Lys41. The asparagine loop, which is important for substrate binding and induction of the global conformational change of OAS-TL during catalysis is shown in dark blue. The green colour indicates the β8a–β9a loop that seems to be important for interaction with SAT. Both structural elements are in close proximity to the active site of OAS-TL (F). Important residues for binding of substrates and the enzymatic activity are highlighted in F. The software UCSF Chimera V1.2422 (University of California, San Francisco) was used to visualize SAT (pdb: 1T3d) and OAS-TL (pdb: 1OAS). See Chapter 4, p. 67.
Fig. 1. Typical composition of a pelagic community of phototrophic and chemotrophic bacteria. Samples from the chemocline of dimictic Lake Dagow (North Brandenburg, Eastern Germany; obtained in September 2006) were left overnight after sampling for sedimentation of microbial cells. A. Purple sulfur bacteria (psb) containing numerous yellowish sulfur droplets. Pr, brown-colored phototrophic consortium “Pelochromatium roseum” in a partially disaggregated state. B. Brown- and green colored forms of Chlorobium clathratiforme (Ccl) and platelet-like microcolony of the purple sulfur bacterium Thiopedia rosea (Tr). C. Intact “Pelochromatium roseum” (Pr), one disintegrated phototrophic consortium “Chlorochromatium aggregatum” (Ca). Green-colored epibions surround the central chemotrophic bacterium. Tr, Thiopedia rosea; Cn, filamentous green bacterium Chloronema sp. (Chloroflexaceae); Plr, filamentous cyanobacterium Planktothrix rubescens. Highly refractile and irregular intracellular regions in the latter three bacteria are gas vacuoles. Bar, 10 µm. See Chapter 19, p. 377.