

PREFACE TO VOLUME 1

Volumes published during the 1980s that made up the series on *"The Biochemistry of Plants—A Comprehensive Treatise"*, edited by Eric Conn and Paul K. Stumpf, covered many of the then known aspects of plant biochemistry. During the last two decades, however, our knowledge on plant biochemistry, physiology, and molecular genetics has been augmented to an astonishing degree. This remarkable revolution has been brought about by new techniques, new concepts that are now summarized as "genomics", "proteomics" and "metabolomics," as well as to a large degree by new forms of instrumentation for each type of application. This volume has been designed to incorporate new concepts and insights in plant biochemistry and biology as part of a new series titled *"Advances in Plant Biochemistry and Molecular Biology"* edited by Professor Norman Lewis. To put this into suitable context, attached is a Foreword by Eric Conn and the late Paul K. Stumpf as regards the need for this new series.

The increased knowledge about the structure of genomes in a number of species, about the complexity of their transcriptomes, and the nearly exponentially growing information about mutant phenotypes have now set off the large scale use of transgenes to answer basic biological questions, and to generate new crops and novel products. This volume includes thirteen chapters, which to variable degrees describe the use of transgenic plants to explore possibilities and approaches for the modification of plant metabolism, adaptation or development. The interests of the authors of these chapters range from tool development, to basic biochemical know-how about the engineering of enzymes, to exploring avenues for the modification of complex multigenic pathways, and include several examples for the engineering of specific pathways in different organs and developmental stages.

Kruger and Ratcliffe focus on the tools for analyzing metabolic network structures and provide a conceptual framework about the challenges faced in engineering pathways. Sections on metabolic flux and control analysis as well as kinetic modeling that measure the impact of changes on network structure, with excellent discussion of the literature, are destined to set a standard. Enzyme engineering with theoretical and practical considerations is discussed by Shanklin with a focus on structure models as the guiding light. Examples of success from the author's laboratory provide lucid documentation.

The engineering potential for altering photosynthetic performance, discussed by Yokota and Shigeoka, addresses a fundamental set of pathways, whose improvements would be of great importance, although complexity and barriers to change have shown to be still considerable. The authors, nevertheless, provide an overview of the failures and discuss prospects provided by the emerging new

biology. In another example on the engineering of primary metabolism, Galili and colleagues describe approaches and progress with respect to altering amino acid metabolism. The conspicuous successes in this area are discussed with respect to individual amino acid families and with respect to metabolic fluxes.

Three chapters discuss progress and potential in the engineering of metabolic end-products that are of vast economical importance: the genetic engineering of cellulose by Saxena and Brown, of seed storage proteins by Holding and Larkins, and of content and composition of edible and industrial oils by Cahoon and Schmid. Owing to the different complexities that these three "pathways" present to engineers, these chapters present views of how to go about in dissecting complexity into manageable partitions. Nawrath and Poirier focus on pathways for the synthesis of polyesters in plants, with examples for the engineering of existing plant pathways, cutin and suberin, and the engineering of a foreign pathway, leading to polyhydroxyalkanoates. As in many of the chapters in this volume, the authors point to the necessity for more fundamental research into plant metabolic pathways. Addressing a problem of yet higher complexity, Bressan and coworkers tackle genetic engineering for salinity tolerance. They point to the multitude of pathways, developmental ages, and tissues that must be integrated to achieve a goal that can stand the test of performance in the real world.

Finally, four chapters are devoted to the engineering of secondary metabolism. Kutchan and coworkers, on the progress and prospects of plant alkaloid biosynthetic pathways, discuss the substantial progress in the identification of pathways and metabolites. Similarly, Sato and Yamada provide an overview on the engineering and use of cells in culture for the biosynthesis of secondary metabolites as a source for medicinal compounds. Zhou and colleagues describe strategies for bioengineering of sterol methyltransferases. The chapter covers enzyme and pathway structure and proceeds to the ecology of sterol functions. Lewis and colleagues discuss prospects of engineering allylphenols, lignins and lignans, based on tremendous progress made in recent years. This theme, in combination with the discussion on cellulose biosynthesis and engineering by Saxena and Brown, is of particular relevance in the light of efforts to develop energy from renewable lignocellulosic materials.

The challenges that lie ahead for genetic manipulation of plant pathways to become truly productive are several. Minimizing unexpected detrimental, pleiotropic effects on plant growth and development, owing to complex regulation of biochemical pathways is one of these challenges. To achieve the desired levels of metabolites and end-products will require that the information, presently in part available for a few model species, on genome structure, transcript abundance and regulation, on pathway and protein regulation, and on metabolic flux become understood on a more fundamental mechanistic level. This volume presents concepts and strategies that are required to overcome limitations that obstruct coordinated pathway regulation.

The older volumes on the biochemistry of plants contained the sum of our knowledge at the time. They have provided basic knowledge, much of it still useful, that many plant scientists used as a start point and springboard for creative new approaches. It is hoped that the present volume with its emphasis on plant engineering will have a similarly inspiring influence such that, in the future, we can proceed from the modification of individual genes or a few proteins and enzymes to metabolic pathway engineering on a fundamental scale.

Hans Bohnert
Henry Nguyen
January 2007

General Preface to The Biochemistry of Plants
In 1939, James Bohnert wrote the following preface to the first edition of his book, *Biochemistry of Plants*, published by Academic Press:

There is much work to be done in plant biochemistry. Our understanding of many vital metabolic pathways in the higher plant is fragmentary, while the emphasis in this book is on the higher plant, it will frequently be necessary to call attention to analogous pathways in bacteria and animals, or to other higher organisms. Fundamental problems in plant biochemistry could undoubtedly be illuminated by the direct application of the information and the techniques that have been developed by those working with other organisms.

Certain important aspects of biochemistry have been entirely omitted from the present volume because of lack of pertinent information from the domain of higher plants.

This volume had 31 chapters and a total of 570 pages. Many of the illustrations, examples cited in the text were derived from studies on the then known and model systems. Despite these shortcomings, the book had a profound effect on a number of young biochemists, which challenged them to enter the field of plant biochemistry and to correct the lack of pertinent information from the domain of higher plants.

Since 1939, an explosive acquisition of knowledge in biochemistry has occurred. Unfortunately, the study of plants has not a corresponding biochemical community. With the exception of photosynthesis, biochemists have avoided tackling, for one reason or another, the incredibly growing problems associated with plant tissues. Leading biochemical journals have frequently rejected second manuscripts for the trivial reason that the reaction had been well described by *E. coli* and that there was of little interest to again describe its presence in green plants. The recent Federal granting agencies, the National Science Foundation excepted, have also been reluctant to fund applications where

PROLOGUE

A good way to introduce the new series of volumes entitled *Advances in Plant Biochemistry and Molecular Biology* is to examine the state of plant biochemistry in 1980, when an earlier series was initiated. At that time, Paul Stumpf and Eric Conn undertook the task of organizing a collection of volumes edited and written by leaders in the field of plant biochemistry. The General Preface to that collection, which we wrote in 1980, explained why we thought it was time for a series entitled *The Biochemistry of Plants*.

General Preface to *The Biochemistry of Plants*¹

In 1950, James Bonner wrote the following prophetic comments in the Preface of the first edition of his *Plant Biochemistry*, published by Academic Press.

There is much work to be done in plant biochemistry. Our understanding of many basic metabolic pathways in the higher plant is lamentably fragmentary. While the emphasis in this book is on the higher plant, it will frequently be necessary to call attention to conclusions drawn from work with microorganisms or with higher animals. Numerous problems of plant biochemistry could undoubtedly be illuminated by the closer application of the information and the techniques that have been developed by those working with other organisms....

Certain important aspects of biochemistry have been entirely omitted from the present volume because of the lack of pertinent information from the domain of higher plants.

The volume had 30 chapters and a total of 490 pages. Many of the biochemical examples cited in the text were derived from studies on bacterial, fungal, and animal systems. Despite these shortcomings, the book had a profound effect on a number of young biochemists, since it challenged them to enter the field of plant biochemistry and to correct "the lack of pertinent information from the domain of higher plants."

Since 1950, an explosive expansion of knowledge in biochemistry has occurred. Unfortunately, the study of plants has had a mixed reception in the biochemical community. With the exception of photosynthesis, biochemists have avoided tackling, for one reason or another, the incredibly interesting problems associated with plant tissues. Leading biochemical journals have frequently rejected sound manuscripts for the trivial reason that the reaction had been well described in *E. coli* and liver tissue and was of little interest to again describe its presence in germinating pea seeds! Federal granting agencies, the National Science Foundation excepted, have also been reluctant to fund applications when

¹ Stumpf, P. K., and Conn, Eric E., eds. in chief. (1980). *The Biochemistry of Plants: A Comprehensive Treatise*, Vol. 1, pp. xiii-xiv. Academic Press, New York.

it was indicated that the principal experimental tissue would be of plant origin despite the fact that the most prevalent illness in the world is starvation.

The second edition of *Plant Biochemistry* had a new format in 1965 when J. Bonner and J. Varner edited a multiauthored volume of 979 pages; in 1976, the third edition containing 908 pages made its appearance. A few textbooks of limited size in plant biochemistry have been published. In addition, two continuing series resulting from the annual meetings and symposia of photochemical organizations in Europe and North America provided the biological community with highly specialized articles on many topics of plant biochemistry. Plant biochemistry was obviously growing.

Although these publications serve a useful purpose, no multivolume series in plant biochemistry has been available to the biochemist trained and working in different fields who seeks an authoritative overview of major topics of plant biochemistry. It therefore seemed to us that the time was ripe to develop such a series. With the encouragement and cooperation of Academic Press, we invited six colleagues to join us in organizing an eight-volume series to be known as *The Biochemistry of Plants: A Comprehensive Treatise*. Within a few months, we obtained commitments from more than 160 authors to write authoritative chapters for these eight volumes.

Our hope is that this Treatise not only will serve as a source of current information to researchers working in plant biochemistry, but equally important will provide a mechanism for the molecular biologist who works with *E. coli*, or for the neurobiochemist to become better informed about the interesting and often unique problems that the plant cell provides. It is hoped too that the senior graduate students will be inspired by one or more comments in chapters of this Treatise and will orient their future career to some aspect of this science.

Despite the fact that many subjects have been covered in this Treatise, we make no claim to have been complete in our coverage or to have treated all subjects in equal depth. Notable is the absence of volumes on phytohormones and on mineral nutrition. These areas, which are more closely associated with the discipline of plant physiology, are treated in multivolume series in the physiology literature and/or have been the subject of specialized treatises. Other topics (e.g., alkaloids, nitrogen fixation, flavonoids, plant pigments) have been assigned single chapters even though entire volumes, sometimes appearing on an annual basis, are available.

These sixteen volumes, covering many aspects of plant biochemistry as was known at that time, were published during 1980 and 1990. Since then, a remarkable revolution has occurred as the techniques of molecular biology burst on the scene and extended our knowledge on many aspects of plant growth and development. With this new approach, a large number of transgenic plants have been designed specifically to function well under harsh environments of drought and salinity as well as withstand attacks by microbial, fungal, viral, and insect populations. Highly sophisticated techniques can now probe the secrets of the plant life cycle and identify genes involved in germination, growth, flowering seed formation, and other processes. Thus, it is appropriate that a new series will again summarize the recent advances in plant biochemistry and molecular biology.

It will be most welcome as plants continue to affect the many aspects of life in this ever more complicated world.

The overall goals and aims of Volume 1 of the present series are summarized in the following overview by Hans Bohnert and Henry Nguyen.

Paul K. Stumpf

Eric E. Conn

Metabolic Organization in Plants: A Challenge for the Metabolic Engineer

Nicholas J. Kruger and R. George Ratcliffe

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Abstract Predictive models of plant metabolism with sufficient power to identify suitable targets for metabolic engineering are desirable but elusive. The problem is particularly acute in the presence of primary carbon metabolism and ultimately is due to the complexity of the plant metabolic network and the limitations of information components that determine the observed fluxes. This complexity is manifested most explicitly in the

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