THE BIOCHEMISTRY OF PLANTS

A COMPREHENSIVE TREATISE

Volume 4

Lipids: Structure and Function

P. K. Stumpf, editor

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P. K. Stumpf, editor

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Davis, California

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General Preface

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 which have been developed by those working with other organisms . . .
>
> Certain important aspects of biochemistry have been entirely omitted from the present volume simply 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 thus 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 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 phytochemical organizations in Europe and in 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 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 were able to invite over 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 the neurobiochemist to become better informed about the interesting and often unique problems which the plant cell provides. It is hoped, too, the senior graduate student will be inspired by one or more comments in chapters of this Treatise and will orient his 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 nor 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.

Finally, we wish to thank all our colleagues for their enthusiastic cooperation in bringing these eight volumes so rapidly into fruition. We are grateful to Academic Press for their gentle persuasive pressures and we are indebted to Ms. Barbara Clover and Ms. Billie Gabriel for their talented assistance in this project.

P. K. Stumpf
E. E. Conn

Preface to Volume 4

The study of plant lipid biochemistry is expanding rapidly. In recent years a number of excellent books based on the successful proceedings held every two years in Europe under the auspices of the "International Symposium on Plant Lipids" have added much to the literature.

This volume has several goals in mind; it brings together the current knowledge on plant lipids; it gathers into one volume the views of authorities writing on their specialized areas and raising problems for further investigations; and equally important it will serve as a source of information for the lipid biochemist who worries about animal and bacterial lipid biochemistry and is blissfully unaware of the important area of plant lipid biochemistry.

The subjects covered in this volume are not unique, with the exception of Chapter 6 on ethylene biosynthesis. This subject was added to this volume because it describes the synthesis of the simplest two-carbon double bond system. Its mechanism of synthesis from methionine is unusual and may indeed serve as one of several models for the equally complex desaturation systems found in plants.

I wish to thank the contributors to this volume who accepted the challenge of writing their chapters, kept their schedules, and made the task of editing this volume hardly an onerous one. I particularly wish to thank Ms. Barbara Clover and Mrs. Billie Gabriel who handled all the secretarial work with efficiency and good nature.

P. K. Stumpf

Contents

List of Contributors xi

General Preface xiii

Preface to Volume 4 xv

1 **Plant Acyl Lipids: Structure, Distribution, and Analysis**
J. L. HARWOOD
I. Introduction 2
II. Plant Fatty Acids 2
III. Complex Acyl Lipids 12
IV. Distribution of Acyl Lipids 20
V. Age-Related Changes in the Lipid Composition of Plant Tissues 36
VI. Methods for Lipid Analysis 44
References 48

2 **Membrane Lipids: Structure and Function**
JOHN K. RAISON
I. Introduction 57
II. Membrane Structure 58
III. Lipid Dependency of Purified Membrane Proteins 63
IV. Temperature Effects on Lipid Structure and Membrane Function 64
V. Membrane Structure and Phytochrome Action 79
VI. Conclusions 80
References 81

3 Degradation of Acyl Lipids: Hydrolytic and Oxidative Enzymes
T. GALLIARD

I. Lipolytic Enzymes 85
II. Oxidative Enzymes 105
References 114

4 The Role of the Glyoxylate Cycle
HARRY BEEVERS

I. Introduction: The Problem Posed by the Conversion of Fat to Carbohydrate 117
II. Elucidation of the Glyoxylate Cycle 119
III. Enzymes of the Glyoxylate Cycle in Plants 120
IV. Experiments with Labeled Acetate: Confirmation of the Pathway 121
V. Compartmentation of the Glyoxylate Cycle: The Glyoxysome 126
References 129

5 Lipoxygenases
T. GALLIARD AND H. W.-S. CHAN

I. Introduction 132
II. Distribution of Lipoxygenases 134
III. Characterization of Lipoxygenases 135
IV. Assay Methods 138
V. Mechanism of Lipoxygenase Reactions 140
VI. Enzymatic Conversions of Lipoxygenase Products 150
VII. Nonenzymatic Reactions of Hydroperoxides 155
VIII. Physiological Aspects of Lipoxygenase 156
References 157

6 Biosynthesis of Ethylene
S. F. YANG AND D. O. ADAMS

I. Introduction 163
II. Olefin-Forming Biochemical Reactions 164
III. Conversion of Methionine to Ethylene in Model Systems 167
IV. Methionine as a Biochemical Precursor of Ethylene 169
V. Regulation of Ethylene Biosynthesis 172
References 174

7 Biosynthesis of Saturated and Unsaturated Fatty Acids
P. K. STUMPF
I. Biosynthesis of Saturated Fatty Acids 177
II. Biosynthesis of Unsaturated Fatty Acids 193
III. Termination Mechanisms 198
References 202

8 The Biosynthesis of Triacylglycerols
M. I. GURR
I. Introduction 205
II. Structure of Triacylglycerols 208
III. Accumulation of Triacylglycerols in Plant Cells 216
IV. The Storage of Oil in Plant Cells 223
V. Pathways for the Biosynthesis of Triacylglycerols in Plants 234
VI. Future Trends 244
References 246

9 Phospholipid Biosynthesis
J. B. MUDD
I. Introduction 250
II. Phospholipid Composition of Tissues and Organelles 250
III. Fatty Acid Composition of Phospholipids 254
IV. Enzymatic Steps of Phospholipid Biosynthesis 256
V. The Use of Intact Tissue and Labeled Precursors for the Study of Phospholipid Metabolism 270
VI. Factor Effecting Changes in Phospholipids 276
VII. Turnover of Phospholipids 278
VIII. Conclusions 279
References 280

10 Phospholipid-Exchange Systems
PAUL MAZLIAK AND J. C. KADER
I. Introduction 283
II. Organelles Involved in Membrane Lipid Biosynthesis 284
III. Phospholipid Exchange *in Vitro* 287
IV. Phospholipid-Exchange Proteins (PLEP) 294
V. Phospholipid Exchange *in Vivo* 297
VI. Conclusions 297
References 298

11 Sulfolipids
J. L. HARWOOD
I. Introduction 301
II. Identification and Characterization of Diacylsulfoquinovosylglycerol 302
III. Occurrence and Distribution of Diacylsulfoquinovosylglycerol 303
IV. Metabolism of Diacylsulfoquinovosylglycerol 304
V. Possible Functions of Diacylsulfoquinovosylglycerol 311
VI. Other Sulfur-Containing Lipids 315
References 318

12 Plant Galactolipids
ROLAND DOUCE AND JACQUES JOYARD
I. Introduction 321
II. Structure 322
III. Occurrence and Distribution 325
IV. Biological Function 340
V. Metabolism 342
References 357

13 Biochemistry of Terpenoids
W. DAVID LOOMIS AND RODNEY CROTEAU
I. Introduction 364
II. Hemiterpenes (Isoprene) (C_5) 368
III. Monoterpenes (C_{10}) 370
IV. Sesquiterpenes (C_{15}) 386
V. Diterpenes (C_{20}) 395
VI. Sesterterpenes (C_{25}) 399
VII. Triterpenes (C_{30}) 400
VIII. Polyterpenes $(C_5)_n$ 404
IX. Prenols and Prenyl Side Chains 407
X. Conclusions 409
References 410

14 Carotenoids
SANDRA L. SPURGEON AND JOHN W. PORTER
I. Introduction 420
II. Structure and Nomenclature 421
III. Chemistry 428
IV. Distribution 440
V. Biosynthesis 447

VI. Function 471
References 476

15 **Biosynthesis of Sterols**
T. W. GOODWIN
I. Introduction 485
II. Cyclization of Squalene 491
III. Alkylation Reactions 493
IV. Opening of the Cyclopropane Ring 498
V. Later Stages 501
VI. Transformations Involving 24-Methylene Lophenol and 24-Ethylidene Lophenol 503
VII. Conclusion 504
References 505

16 **Sterol Interconversions**
J. B. MUDD
I. Introduction 509
II. Analytical Data 510
III. Metabolism 517
IV. Physiological Observations 525
V. Physical Properties 528
VI. Function 530
VII. Sterol Derivatives in Fungi 530
VIII. Conclusions 531
References 532

17 **Biosynthesis of Acetate-Derived Phenols (Polyketides)**
N. M. PACKTER
I. Introduction 535
II. Early Considerations 536
III. Biosynthesis of Phenols in Fungi 538
IV. Biosynthesis of Phenols in Higher Plants 549
V. Modifications of Assembly 555
VI. Regulation of Phenol Synthesis in Fungi 561
VII. Assembly Patterns 565
References 567

18 **Cutin, Suberin, and Waxes**
P. E. KOLATTUKUDY
I. Introduction 571
II. Chemistry of Cutin, Suberin, Sporopollenin, and Waxes 573

III. Biosynthesis of Waxes, Cutin, and Suberin 600
IV. Degradation of Waxes, Cutin, and Suberin 623
V. Function of Cellular Lipids 631
VI. Conclusion 634
References 635

19 Biosynthesis of Cyclic Fatty Acids
H. K. MANGOLD AND F. SPENER
I. Introduction 647
II. Cyclopropanoid and Cyclopropenoid Fatty Acids 648
III. Cyclopentenyl Fatty Acids 652
IV. Other Cyclic Fatty Acids 659
V. Conclusions 661
References 661

Index 665

Contents of Other Volumes 688

Plant Acyl Lipids: Structure, Distribution, and Analysis

1

J. L. HARWOOD

I. Introduction 2
II. Plant Fatty Acids 2
A. Major Fatty Acids 2
B. Minor Fatty Acids 4
C. Unusual Fatty Acids 4
III. Complex Acyl Lipids 12
A. Glycerol-Based Compounds 12
B. Glycosphingolipids 15
C. Acylated Steryl Glycosides 16
D. Other Acyl Lipids 17
E. Composition of Cutin and Suberin 17
IV. Distribution of Acyl Lipids 20
A. Lipid Composition of Seed and Storage Tissues 20
B. Lipid Composition of Leaf Tissue 24
C. Other Tissues 26
D. Tissue Cultures 26
E. Lipid Distribution among Cell Organelles 26
F. Fatty Acid Content of Individual Complex Lipids 32
V. Age-Related Changes in Lipid Composition of Plant Tissues 36
A. Seed and Fruit Development 37
B. Seed Germination 39
C. Leaf Development 41
D. Senescence 44
VI. Methods for Lipid Analysis 44
A. Extraction 44
B. Separation Methods 45
C. Identification and Quantitation 47
References 48

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I. INTRODUCTION

Acyl lipids are major constituents of plant tissue. They comprise a wide variety of different structures of which the majority contain fatty acid esters, though in a few cases the fatty acids are present in ether linkages or as amide derivatives. The lipids are mainly present as triacylglycerols (triglycerides) in seeds or in the fleshy part of fruits where they act as food stores. These tissues provide very important commercial sources of fats and oils. In other plant tissues such as leaves, roots, or shoots, acyl lipids are mainly present as glycolipids and phospholipids. The reason that acyl lipids are fats (i.e., preferably soluble in organic solvents rather than water) is because of their fatty acid constituents whose long hydrocarbon chains are basically hydrophobic. It is, therefore, logical to consider the fatty acids of plants first.

II. PLANT FATTY ACIDS

A. Major Fatty Acids

Although the number of fatty acids detected in plant tissues approaches 300, most of them only occur in a few plant species (Hitchcock and Nichols, 1971). The major fatty acids are all saturated or unsaturated monocarboxylic acids with an unbranched even-numbered carbon chain. The saturated fatty acids, lauric (dodecanoic), myristic (tetradecanoic), palmitic (hexadecanoic), and stearic (octadecanoic), and the unsaturated fatty acids, oleic (*cis*-9-octadecenoic), linoleic (*cis*-9,*cis*-12-octadecadienoic), and linolenic (all-*cis*-9,12,15-octadecatrienoic (Table I), together account for almost all of the fatty acid content of higher plants. For example, about 94% of the total fatty acids of commercial oils and 89–97% of leaf fatty acids consist of these seven structures alone. It will be noted that the unsaturated acids all contain a cis-9 double bond and that the polyunsaturated acids contain a methylene-interrupted structure. The four saturated fatty acids differ from each other by two carbons. These structural relationships are due to the principal pathways of fatty acid biosynthesis in plants (see Stumpf, this volume, Chapter 7).

A shorthand nomenclature is in common usage for fatty acids. They are written as two numbers separated by a colon. The number before the colon indicates the carbon chain length, and the figure after corresponds to the number of double bonds. Additional figures in parentheses show the position of double bonds, and the letters *c*, *t*, *a*, and *e*, show whether the bond is *cis*-olefinic, *trans*-olefinic, acetylenic, or ethylenic. The position of the double bonds is numbered from the carboxyl group, but where it is more meaningful to number from the methyl end it is prefixed by ω. These abbreviations

TABLE I

Structures of the Major Fatty Acids[a,b]

World distribution (%)[c]	Common name	Symbol	Structure	Systematic name
4	Lauric	12:0	$CH_3(CH_2)_{10}COOH$	Dodecanoic acid
2	Myristic	14:0	$CH_3(CH_2)_{12}COOH$	Tetradecanoic acid
11	Palmitic	16:0	$CH_3(CH_2)_{14}COOH$	Hexadecanoic acid
4	Stearic	18:0	$CH_3(CH_2)_{16}COOH$	Octadecanoic acid
34	Oleic	18:1 (9c)	$CH_3(CH_2)_7CH\overset{c}{=}CH(CH_2)_7COOH$	Octadecenoic acid
34	Linoleic	18:2 (9c 12c)	$CH_3(CH_2)_4CH\overset{c}{=}CHCH_2CH\overset{c}{=}CH(CH_2)_7COOH$	Octadecadienoic acid
5	Linolenic[d]	18:3 (9c 12c 15c)	$CH_3(CH_2CH\overset{c}{=}CH)_3(CH_2)_7COOH$	Octadecatrienoic acid

[a] From Hitchcock and Nichols (1971).

[b] The major fatty acids are those responsible for a large proportion of fatty acids present in most plant lipids; other acids are ubiquitous but usually present in small quantities (minor acids) or are found in a few sources only (unusual acids).

[c] Estimation of the percentage distribution of each acid in all commercial vegetable fats grown throughout the world in 1969–1970. Other acids accounted for about 6%, including 3% erucic acid [22:1 (13*c*)], 1% ricinoleic acid (12-hydroxy-18:1, 9*c*), 0.7% arachidic acid (20:0), and 0.3% eleostearic acid [18:3 (9*c* 11*t* 13*t*)]. The total annual production of these fats was about 30 million tons.

[d] Also called α-linolenic acid to distinguish it from its minor isomer γ-linolenic acid [18:3 (6*c* 9*c* 12*c*)].