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Biochemistry of Plant Secondary Metabolism

Second Edition

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CONTENTS

Contributors x
Preface xiii

1 Introduction: biochemistry, physiology and ecological functions of secondary metabolites 1
Michael Wink

1.1 Introduction 1
1.2 Biosynthesis 2
1.3 Transport, storage and turnover 9
1.4 Costs of secondary metabolism 13
1.5 Ecological role of secondary metabolites 14
References 17

2 Biosynthesis of alkaloids and betalains 20
Margaret F. Roberts, Dieter Strack and Michael Wink

2.1 Introduction 20
2.2 Nicotine and tropane alkaloids 23
2.3 Pyrrolizidine alkaloids (PAs) 33
2.4 Benzylisoquinoline alkaloids 35
2.5 Monoterpene indole alkaloids (MIA) 46
2.6 Ergot alkaloids 56
2.7 Acridone alkaloid biosynthesis 60
2.8 Purine alkaloids 61
2.9 Taxol 62
2.10 Betalains 66
2.11 Conclusions 75
References 75

3 Biosynthesis of cyanogenic glycosides, glucosinolates and non-protein amino acids 92
Dirk Selmar

3.1 Introduction 93
3.2 Cyanogenic glycosides 94
3.3 Glucosinolates 128
3.4 Non-protein amino acids 146
Acknowledgements 157
References 157

4 Biosynthesis of phenylpropanoids and related compounds 182
Maike Petersen, Joachim Hans and Ulrich Matern

4.1 Introduction 182
4.2 General phenylpropanoid pathway and formation of hydroxycinnamate conjugates 183
4.3 Coumarins 197
4.4 Lignans 209
4.5 Gallotannins and ellagitannins 223
4.6 Conclusion 229
References 230

5 Biochemistry of terpenoids: monoterpenes, sesquiterpenes and diterpenes 258
Mohamed Ashour, Michael Wink and Jonathan Gershenzon

5.1 Introduction 259
5.2 Function 260
5.3 Biosynthesis 263
5.4 Conclusions 285
References 286

6 Biochemistry of sterols, cardiac glycosides, brassinosteroids, phytoecdysteroids and steroid saponins 304
Wolfgang Kreis and Frieder Müller-Uri

6.1 Introduction 305
6.2 Sterols 308
6.3 Cardiac glycosides 319
6.4 Brassinosteroids 336
6.5 Phytoecdysteroids 341
6.6 Steroid saponins and steroid alkaloids 343
6.7 Conclusions 347
References 348

7 Chemotaxonomy seen from a phylogenetic perspective and evolution of secondary metabolism 364
Michael Wink, Flavia Botschen, Christina Gosmann, Holger Schäfer and Peter G. Waterman

7.1 Introduction 365
7.2 Establishment of chemotaxonomy as a research discipline 365
7.3 Developments in small molecule chemotaxonomy over the past 35 years 380
7.4 Molecular biology and plant taxonomy 382
7.5 Comparison between patterns of secondary metabolites and molecular phylogeny 383

7.6 Evolution of plant secondary metabolism 406
Acknowledgements 426
References 426

Index 434
Color plate can be found between pages 368 and 369.

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PREFACE

A characteristic feature of plants is their capacity to synthesize and store a wide variety of low molecular weight compounds, the so-called *secondary metabolites* (SMs) or natural products. The number of described structures exceeds 100 000; the real number in nature is certainly much higher because only 20–30% of plants have been investigated in phytochemistry so far. In contrast to primary metabolites, which are essential for the life of every plant, the individual types of SMs usually occur in a limited number of plants, indicating that they are not essential for primary metabolism, i.e. anabolism or catabolism.

Whereas SMs had been considered to be waste products or otherwise useless compounds for many years, it has become evident over the past three decades that SMs have important roles for the plants producing them: they may function as signal compounds within the plant, or between the plant producing them and other plants, microbes, herbivores, predators of herbivores, pollinating or seed-dispersing animals. More often SMs serve as defence chemicals against herbivorous animals (insects, molluscs, mammals), microbes (bacteria, fungi), viruses or plants competing for light, water and nutrients. Therefore, SMs are ultimately important for the fitness of the plant producing them. Plants usually produce complex mixtures of SMs, often representing different classes, such as alkaloids, phenolics or terpenoids. It is likely that the individual components of a mixture can exert not only additive but certainly also synergistic effects by attacking more than a single molecular target. Because the structures of SMs have been shaped and optimized during more than 500 million years of evolution, many of them exert interesting biological and pharmacological properties which make them useful for medicine or as biorational pesticides.

In this volume of *Annual Plant Reviews*, we have tried to provide an up-to-date survey of the biochemistry and physiology of plant secondary metabolism. A companion volume – M. Wink (ed.) *Functions of Plant Secondary Metabolites and Biotechnology* – published simultaneously provides overviews of the modes of action of bioactive SMs and their use in pharmacology as molecular probes, in medicine as therapeutic agents and in agriculture as biorational pesticides.

In order to understand the importance of SMs for plants, we need detailed information on the biochemistry of secondary metabolism and its integration into the physiology and ecology of plants. Important issues include

characterization of enzymes and genes of corresponding biosynthetic pathways, and of transport and storage mechanisms, regulation in space/time and compartmentation of both biosynthesis and storage. The study of secondary metabolism has profited largely from the recent progress in molecular biology and cell biology and the diverse genome projects. Although *Arabidopsis thaliana* is not an excellent candidate to study secondary metabolism on the first view, the genomic analyses, EST-libraries, mutants and other tools of *A. thaliana* have been extremely helpful to elucidate secondary metabolism in other plants.

The present volume is the second edition of a successful first edition which was published in 1999 and which has received many positive responses from its readers. To achieve a comprehensive and up-to-date summary, we have invited scientists who are specialists in their particular areas to update their previous chapters. This volume draws together results from a broad area of plant biochemistry and it cannot be exhaustive on such a large and diverse group of substances. Emphasis was placed on new results and concepts which have emerged over the last decades.

The volume starts with a bird's eye view of the biochemistry, physiology and function of SMs (M. Wink), followed by detailed surveys of the major groups of SMs: alkaloids and betalains (M.F. Roberts *et al.*); cyanogenic glucosides, glucosinolates and non-protein amino acids (D. Selmar); phenyl propanoids and related phenolics (M. Petersen *et al.*); terpenoids, such as mono-, sesqui-, di- and triterpenes, cardiac glycosides and saponins (M. Ashour *et al.*, W. Kreis and F. Müller-Uri). The final chapter discusses the evolution of secondary metabolism (M. Wink *et al.*). The structural types of SMs are often specific and restricted in taxonomically related plant groups. This observation was the base for the development of 'chemotaxonomy'. A closer look indicates that a number of SMs have a taxonomically restricted distribution. Very often, we find the same SMs also in other plant groups which are not related in a phylogenetic context. There is evidence that some of the genes, which encode key enzymes of SM formation, have a much wider distribution in the plant kingdom than assumed previously. It is speculated that these genes were introduced into the plant genome by horizontal gene transfer, i.e. via bacteria that developed into mitochondria and chloroplasts (endosymbiont hypothesis). Evidence is presented that a patchy distribution can also be due to the presence of endophytic fungi, which are able to produce SMs.

The book is designed for use by advanced students, researchers and professionals in plant biochemistry, physiology, molecular biology, genetics, agriculture and pharmacy working in the academic and industrial sectors, including the pesticide and pharmaceutical industries.

The book brought together contributions from friends and colleagues in many parts of the world. As editor, I would like to thank all those who have

taken part in writing and preparation of this book. I would like to thank Theodor C. H. Cole for help, especially in preparation of the index. Special thanks go to the project editor Catriona Dixon from Wiley-Blackwell and her team for their interest, support and encouragement.

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