



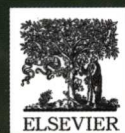
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Plant Biochemistry 植物生物化学

(第三版)

Hans-Walter Heldt, Fiona Heldt



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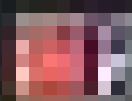
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Plant Biochemistry 植物生物化学

(第三版)

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Hans-Walter Heldt
in cooperation with Fiona Heldt

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导 读

我有幸阅读了负有盛名的最新德文第三版《植物生物化学》英译本教科书 (Hans-Walter Heldt 著, 2005 年版), 收益良多, 因而愿意介绍给在校研读生命科学的大学生、研究生和从事植物生物化学及相关领域的其他学科的研究人员, 作为教学和研究工作的参考。

本书具有知识的系统性: 全书共有 22 章, 内容涵盖了植物生物化学基础而前沿的知识: 细胞结构和功能、光合作用、脂肪和多糖代谢、固氮作用、植物韧皮部运输、类异戊二烯的合成与功能、苯基丙酸类物质和其他次生代谢物、植物生长调节与发育等内容, 读者从中可以获得从光合作用到各种基因工程及其商业应用的整个领域的基本而系统的知识。

本书的写作与以往的《植物生物化学》教科书有所不同, 它没有从氨基酸、碳水化合物及核酸的结构与功能, 蛋白质的结构与功能及酶催化作用等生物化学的基本概念入手, 而只是在有助于理解问题时才给予一定的介绍, 因此本书是一本介于普通和专业教科书之间的折衷教材。本书对于具备一定生物化学基础知识的学生和研究人员拓展知识和深入思考问题很有益处。

本书贯穿一条写作路线。大家知道生命科学中包括人类和所有生命的生存及其延续相关的两大元素是碳、氮代谢及其循环。2006 年美国《Science》(5 月 5 日出版, 312 卷, 708~709 页) 杂志的相关评论认为, “从我们的地球中心观点看, 没有碳和氮难于想象生命” (From our Earth-centric point of view, it is equally difficult to imagine life without carbon and nitrogen)。本书恰恰以这方面内容作为写作主线, 突出了生物化学中的物质来源及其代谢作用。植物的光合作用将空气中的 CO_2 和水合成了碳水化合物(糖类), 构成了包括人类在内的所有生命能量来源的基础。生物固氮作用将空气中无法利用的 N_2 变成可利用的 NH_3 (或 NH_4^+), 合成了生命的物质基础——核酸和蛋白质。在这两大基础物质上, 衍生出了千变万花的构成生命的组成物质, 产生了生命体的合成代谢和分解代谢的路线和调控网络, 并行使各种生命功能, 从而形成了地球上多姿多彩的生命世界。

本书具有新颖性: 每一章的标题都具有吸引力, 告诉读者本章所阐述的科学问题的重要性。例如“光合作用利用太阳能是地球上生命的基础”; “固氮作用使空气中的氮气为植物生长所用”; “类异戊二烯多样性在植物代谢中具有多种功能”; “多重信号调控植物器官的生长和发育并使植物能适应环境条件”等等。每一章节先用几句话扼要地点出基本概念, 随后切入正题, 把每一科学问题的基本概念和物质的合成与分解代谢路线及其之间的联系分析得清清楚楚, 并告诉读者物质代谢在细胞结构的哪个区域进行。例如“叶细胞由多个代谢区域组成”; “线粒体是细胞的‘动力站’”等。这种写法很有新意, 在以往的教科书中很少见到。

本书具有科学前沿性: 几乎在每一章节均点出了研究的重点和热点。从大到光合作

用和固氮作用的信号传导、基因表达和网络调控,小到具体的蛋白,如“14-3-3 蛋白”的功能(参与植物质膜上 H^+ -ATP 酶活性调节,转录因子活性和蛋白传递到叶绿体的调节,参与信号转导的调节,并对生物和非生物因子所引起的逆境的防御反应等)、植物多肽激素(systemin)、 CO_2 固定产物形成后 Acetyl-CoA 的形成机制等,点出了研究的最新进展、存在的不足和今后需要探索的方向。

本书点出了重大基础研究和应用研究的关系:作者指出了与植物生物化学研究领域中的多次重大突破相关的诺贝尔奖。例如 20 世纪初揭示了光的电磁波和光量子的双重特性,并由此引入光合作用中的研究;1910 年表明异戊二烯(isoprene)是萜烯(terpene)类物的基本组成成分研究;1931 年糖代谢的三羧酸循环(Krebs cycle)研究;1932 年生物氧化作用研究;1961 年卡尔文(Calvin)循环($CO_2 + NADPH$ 同化作用)研究;1939 年异戊二烯是合成许多天然化合物的基本元件的研究;1964 年磷酸异戊二烯(isopentenyl pyrophosphate)是活性异戊二烯(active isoprene)来源的研究;1978 年 ATP 合成的化学渗透假说及其在光合磷酸化中的研究;1983 年玉米转座子研究;1988 年紫色光细菌(*Rhodospseudomonas viridis*)膜蛋白光反应中心的结构分析研究等等。正是在这些重大发现和突破的基础上,发展起来了很多的基础理论和应用研究。其中,作者着重介绍了植物根癌农杆菌(*Agrobacterium tumefaciens*)的研究意义:由于对它的深入研究,1984 年三家实验室同时发表了文章,首次获得了转基因研究的成功,从而奠定了基因工程的基础,随后逐步发展并完善了植物生物技术,产生了农业新的绿色革命。截至 2003 年,美国有 80% 的大豆,70% 的棉花、38% 的玉米都是基因工程产品,带来了巨大收益。因此,植物生物化学不仅是阐明植物分子功能理论的重要基础,也是应用科学的重要领域。生物技术在现代农业中的广泛运用,正在为人类创造一个无限广阔的前景。

本书是一本综合性和比较性很强的教科书,不仅讲述了植物生物化学的多个领域,而且还与动物、微生物(包括病毒)生物化学进行了比较,使读者了解三者的生物化学知识,特别是三者物质代谢方面的异同,拓展了生物化学的知识面,并加深了理解。在本书阅读过程中可以看出,植物生物化学领域的研究需要有分子生物学、植物生理学、细胞生物学等学科的互相配合和各种方法的紧密整合,才有助于我们更好地理解植物发挥的功能及如何用于经济发展。最后在每一章后面附上了深入阅读的关键文献,感兴趣的读者可以进一步获取相关知识。

荆玉祥研究员、博士生导师

北京中国科学院植物研究所

2006 年 10 月 25 日

序

这是一本专为学生而写的教材，也是我三十多年教学经验的结晶。它旨在对植物生物化学包括分子生物学的各个方面进行广泛而又精练的介绍。我着重以一种易于理解的方式描述代谢的规律，同时又对内容有所限制，这样就不至于使学生被那些不必要的细节分散了精力。考虑到植物生物技术的重要性，书中在适当的地方介绍了植物生物化学的工业应用。因此，本书对转基因植物的产生及其应用给予了特别的关注。

考虑到已经有了很多非常优秀的普通生物化学教材，在本书中我把诸如氨基酸、碳水化合物及核酸的结构和功能，蛋白质的结构和功能及酶催化作用等生物化学的基本要素都有意略去，仅仅在对于理解当前问题十分必要时才给予一定的介绍。因此本书最终成为一本介于普通教材与专业教材之间的折衷教材。

本书是德文本第三版的英译本。与此前的英文本教材相比，本教材已作了全面的修订，纳入了该领域的最新进展，尤其是对关于植物激素的章节作了极大的调整。由于德文第三版本在一年前就已经完成，而 2003 年该学科迅猛发展，本书对相关内容作了彻底的更新。

我非常感激我的诸多同事。他们通过讨论和及时向我发送他们特定领域的最新进展，使我掌握了大量的信息，让我能够撰写本书的多个版本。随后名单中所列出的同事们都对本书的某个或多个章节进行了认真而严格的审阅，不时提醒我注意修订各种错误，这对我十分有益，同时他们还提出了改进的建议，对此我尤为感激。我要特别感谢我的妻子兼合作者，Fiona Heldt。没有她的全力支持，我不可能完成本书，更不可能有此英文版问世。

我试图根除所有错误，看来不是很成功。因此，对任何的建议和批评，我都十分感激。

Hans-Walter Heldt

2004 年 1 月

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(金治平 译, 荆五祥 校)

Dedicated to my teacher Martin Klingenberg

Preface

This textbook is written for students and is the product of more than three decades of my teaching experience. It intends to give a broad but concise overview of the various aspects of plant biochemistry, including molecular biology. I have attached importance to an easily understood description of the principles of metabolism but also have restricted the content in such a way that a student is not distracted by unnecessary details. In view of the importance of plant biotechnology, industrial applications of plant biochemistry have been pointed out wherever appropriate. Thus, special attention has been given to the generation and utilization of transgenic plants.

Since there are many excellent textbooks on general biochemistry, I have deliberately omitted dealing with elements such as the structure and function of amino acids, carbohydrates, and nucleotides; the function of nucleic acids as carriers of genetic information; and the structure and function of proteins and the basis of enzyme catalysis. I have dealt with topics of general biochemistry only when it seemed necessary for enhancing understanding of the problem in hand. Thus, this book is, in the end, a compromise between a general textbook and a specialized textbook.

This book is a translation of the third German edition. Compared to the previous English edition, it has been fully revised to take into account the progress in the field. In particular, the chapter about phytohormones has undergone extensive changes. As a year has passed since the third German edition was completed, the text has been thoroughly updated, taking into account the rapid development of the discipline in 2003.

I am very grateful to the many colleagues who, through discussions and the reprints they have sent me on their special fields, have given me the information that made it possible for me to write the various editions of this book. It was especially helpful for me that the colleagues in the following list went to great trouble to read critically one or more chapters, to draw my attention to mistakes, and to suggest improvements for which I am particularly grateful. My special thanks go to my coworker and wife, Fiona Heldt. Without her intensive support, it would not have been possible for me to write this book or to prepare the English version.

I have tried to eradicate as many mistakes as possible, probably not with complete success. I am therefore grateful for any suggestions and comments.

Hans-Walter Heldt
Göttingen, January 2004

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导 言

植物生物化学是研究植物生命的分子机理，其中主题之一是光合作用。高等植物的光合作用主要在叶中进行，利用太阳光能将水、二氧化碳、硝酸盐和硫酸盐合成碳水化合物和氨基酸。大部分的光合产物通过微管系统从叶片由茎转运到植物的其他部位，例如，建成根系和供给能量。因而，也给植物叶名为“源”，根名为“库”。种子储藏物也是重要的库组织部分，取决于品种不同，储存了像碳水化合物、蛋白质和脂肪等许多农业产品。

与动物相比，植物有非常巨大的叶表面。通常叶片很薄，以便尽可能保持 CO_2 极短的扩散途径，获得尽可能多的日光。植物根毛中有从土壤吸收水分和无机营养的有效系统。然而，巨大的叶表面使植物处于多变的环境，因而植物必须能够忍耐诸如干旱、热、冷或冻霜以及强光辐射的极端条件。叶片必须日复一日地与白天的光合代谢及夜间的氧化代谢之间的变化进行抗争。在外部条件的极端变化中，植物拥有了极具灵活的各种调节过程参与的代谢作用。植物不能够逃离它的敌人，因而它们形成了一整套的防御物质作为武器，以保护自己免被吞食。

植物农业产品是人类营养的基础。植物基因技术是植物生物化学的一部分，将对世界人口巨大增长带来的日益紧迫的全球食品短缺作出贡献。借助基因技术，利用环境友好的除草剂和保护植物免受病毒或真菌感染的研究具有重大的经济意义。植物生物化学对于培育作物高产也非常有用。

植物是油脂和淀粉工业原材料的重要来源，也是药物生产的基础。可以预计，将来基因技术将更广泛地利用植物生产具有工业目的的可持续原材料。

列出本书简短目录的目的是显示植物生物化学不仅是阐明植物分子功能基础科学的重要领域，也是应用科学的重要领域。现在是植物生物化学发展的革命性阶段，处于为解决重要经济问题作贡献的位置。

为达此目的，植物生物化学领域的生物能源、中间代谢的生物化学和植物次生化化合物，分子生物学以及植物科学其他领域的植物生理学和植物细胞生物学，相互间需要紧密合作。只有将植物科学不同领域的工作结果和方法整合在一起，才能帮助我们理解植物怎样发挥功能，并将这些知识用于经济发展。这本书描述了怎样为此而达目的。

以前已经有许多好的关于生物化学的通用教科书，因此普通生物化学的基本要素就不在此考虑，读者可从其他教科书获得普通生物化学的知识。

(金治平 译，荆玉祥 校)

Introduction

Plant biochemistry examines the molecular mechanisms of plant life. One of the main topics is photosynthesis, which in higher plants takes place mainly in the leaves. Photosynthesis utilizes the energy of the sun to synthesize carbohydrates and amino acids from water, carbon dioxide, nitrate, and sulfate. Via the vascular system, a major part of these products is transported from the leaves through the stem into other regions of the plant, where they are required, for example, to build up the roots and supply them with energy. Hence, the leaves have been given the name *source*, and the roots the name *sink*. The reservoirs in seeds are also an important group of the sink tissues, and, depending on the species, act as a store for many agricultural products such as carbohydrates, proteins, and fat.

In contrast to animals, plants have a very large surface, often with very thin leaves in order to keep the diffusion pathway for CO_2 as short as possible and to catch as much light as possible. In the finely branched root hairs, the plant has an efficient system for extracting water and inorganic nutrients from the soil. This large surface, however, exposes plants to all the changes in their environment. They must be able to withstand extreme conditions such as drought, heat, cold, or even frost, as well as an excess of radiated light energy. Day after day the leaves must contend with the change between photosynthetic metabolism during the day and oxidative metabolism during the night. Plants encounter these extreme changes in external conditions with an astonishingly flexible metabolism in which a variety of regulatory processes take part. Since plants cannot run away from their enemies, they have developed a whole arsenal of defense substances to protect themselves from being eaten.

Plant agricultural production is the basis for human nutrition. Plant gene technology, which can be regarded as a section of plant biochemistry, makes a contribution to combat the impending global food shortage resulting from the enormous growth of the world population. The use of environmentally compatible herbicides and protection against viral or fungal infestation by means of gene technology is of great economic importance. Plant biochemistry also is instrumental in breeding productive varieties of crop plants.

Plants are the source of important industrial raw material such as fat and starch, but they also are the basis for the production of pharmaceuticals. It is to be expected that in the future gene technology will lead to the extensive use of plants as a means of producing sustainable raw material for industrial purposes.

The aim of this short list is to show that plant biochemistry is not only an important field of basic science explaining the molecular function of a plant, but also an applied science that, now at a revolutionary phase of its development, is in a position to contribute to the solution of important economic problems.

To reach this goal, it is necessary that sectors of plant biochemistry such as bioenergetics, the biochemistry of intermediary metabolism and the secondary plant compounds, as well as molecular biology and other sections of plant sciences, such as plant physiology and the cell biology of plants, cooperate closely with one another. Only the integration of the results and methods of working of the different sectors of plant sciences can help us to understand how a plant functions and to put this knowledge to economic use. This book describes how this may be achieved.

Since there are already many good general textbooks on biochemistry, the elements of general biochemistry are not considered here, and it is presumed that the reader will obtain the knowledge of general biochemistry from other textbooks.