Plant Biochemistry

Fourth edition

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Hans-Walter Heldt

Birgit Piechulla

in cooperation with Fiona Heldt

Translation of the 4th German edition

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Dedicated to my teacher, Martin Klingenberg
Hans–Walter Heldt

Preface

The present textbook is written for students and is the product of more than three decades of teaching experience. It intends to give a broad but concise overview of the various aspects of plant biochemistry including molecular biology. We attached importance to an easily understood description of the principles of metabolism but also 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 it was appropriate. Thus special attention was given to the generation and utilization of transgenic plants.

Since there are many excellent textbooks on general biochemistry, we 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. We 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 and a specialized textbook.

To ensure the continuity of the textbook in the future, Birgit Piechulla is the second author of this edition. We have both gone over all the chapters in the fourth edition, HWH concentrating especially on Chapters 1–15 and BP on the Chapters 16–22. All the chapters of the book have been thoroughly revised and incorporate the latest scientific knowledge. Here are just a few examples: the descriptions of the metabolite transport and the ATP synthase were revised and starch metabolism and glycolysis were dealt with intensively. The descriptions of the sulfate assimilation and various aspects of secondary assimilation, especially the isoprenoid synthesis, have been expanded. Because of the rapid advance in the field of phytohormones and light sensors it was necessary to expand and bring this chapter up to date. The chapter on gene technology takes into account the great advance in this field. The literature references for the various chapters have been brought up to date. They relate mostly to reviews accessible via data banks, for example PubMed, and should enable the reader to attain more detailed information about the often rather compact explanations in the

textbook. In future years these references should facilitate opening links to the latest literature in data banks.

I (HWH) would like to express my thanks to Prof. Ivo Feussner, director of the biochemistry division – as emeritus, I had the infrastructure of the division at my disposal, an important precondition for producing this edition.

Our special thanks go to the Spektrum team, particularly to Mrs. Merlet Behncke-Braunbeck who encouraged us to work on this new edition and gave us many valuable suggestions. We also thank Fiona Heldt for her assistance.

We are very grateful to the Elsevier team for their friendly and very fruitful cooperation. Our thanks go in particular to Kristi Gomez for the vast effort she invested in advancing the publication of our translation. We also thank Pat Gonzalez and Caroline Johnson for their thoughtful support for our ideas about the layout of this book and their excellent work on its production.

Once again many colleagues have given us valuable suggestions for the latest edition. Our special thanks go to the colleagues listed below for critical reading of parts of the text and for information, material and figures.

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We have tried to eradicate as many mistakes as possible but probably not with complete success. We are therefore grateful for any suggestions and comments.

Hans-Walter Heldt
Birgit Piechulla
Göttingen and Rostock, May 2008 (German edition)
July 2010 (Translation)

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 to day the leaves have to 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 due to 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 is also instrumental in breeding productive varieties of crop plants.

Plants are the source of important industrial raw material such as fat and starch but they are also the basis for the production of pharmaceutics. It is to be expected that in 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 is also an applied science which, 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, co-operate closely with one another. Only the integration of the results and methods of working with 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 will try to describe how this could be achieved.

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

1

A leaf cell consists of several metabolic compartments

In higher plants photosynthesis occurs mainly in the **mesophyll,** the chloroplast-rich tissue of leaves. Figure 1.1 shows an electron micrograph of a mesophyll cell and Figure 1.2 shows a schematic presentation of the cell structure. The cellular contents are surrounded by a **plasma membrane**

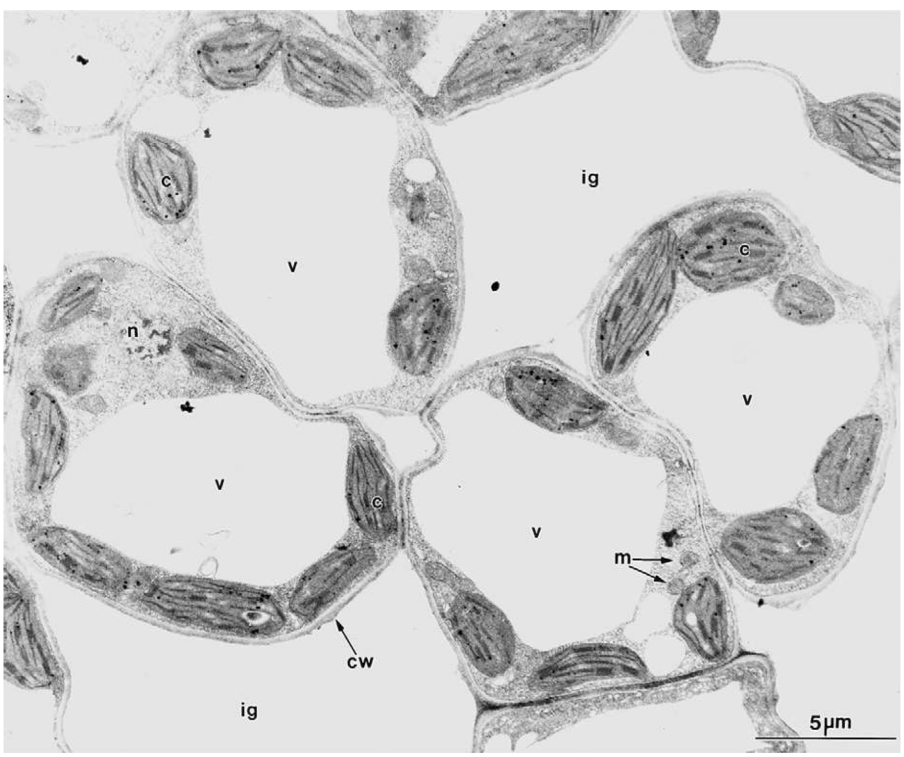

Figure 1.1 Electron micrograph of mesophyll tissue from tobacco. In most cells the large central vacuole is to be seen (v). Between the cells are the intercellular gas spaces (ig), which are somewhat enlarged by the fixation process. c: chloroplast; cw: cell wall; n: nucleus; m: mitochondrion. (By D. G. Robinson, Heidelberg.)

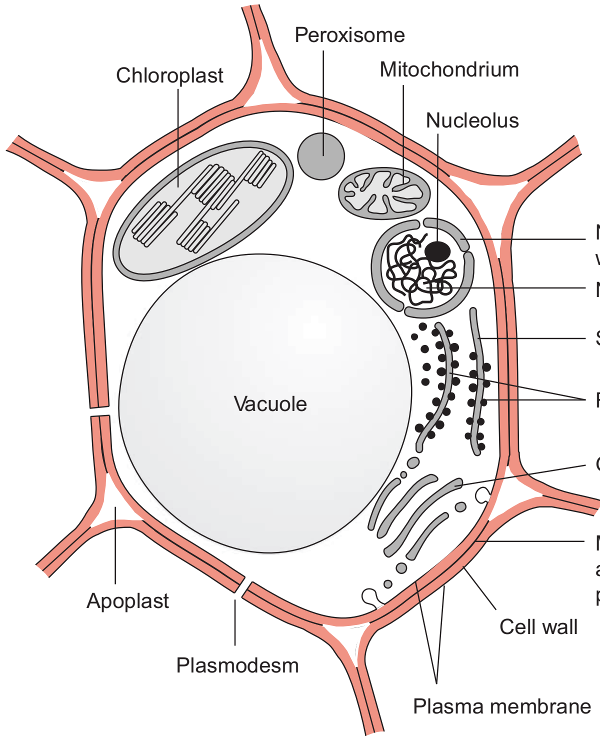

Figure 1.2 Schematic presentation of a mesophyll cell. The black lines between the red cell walls represent the regions where adjacent cell walls are glued together by pectins.

called the plasmalemma and are enclosed by a **cell wall**. The cell contains organelles, each with its own characteristic shape, which divide the cell into various compartments (subcellular compartments). Each compartment has specialized metabolic functions, which will be discussed in detail in the following chapters (Table 1.1). The largest organelle, the vacuole, usually fills about 80% of the total cell volume. Chloroplasts represent the next largest compartment, and the rest of the cell volume is filled with mitochondria, peroxisomes, the nucleus, the endoplasmic reticulum, the Golgi bodies, and, outside these organelles, the cell plasma, called **cytosol**. In addition, there are oil bodies derived from the endoplasmic reticulum. These oil bodies, which occur in seeds and some other tissues (e.g., root nodules), are storage organelles for triglycerides (see Chapter 15).

The **nucleus** is surrounded by the **nuclear envelope**, which consists of the two membranes of the endoplasmic reticulum. The space between the two membranes is known as the **perinuclear space**. The nuclear envelope is interrupted by **nuclear pores** with a diameter of about 50 nm. The nucleus contains **chromatin**, consisting of DNA double strands that are stabilized