Subcellular Biochemistry

Volume 10

Edited by

Donald B. Roodyn

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Contributors

Paul S. Agutter Department of Biological Sciences, Napier College, Edinburgh EH10 5DT, United Kingdom

B. B. Biswas Department of Biochemistry, Bose Institute, Calcutta 700009, India

Maryse A. Block Physiologie Cellulaire Végétale, Département de Recherche Fondamentale, Laboratoire de Biologie Végétale, Centre d'Etudes Nucléaires et Université Scientifique et Médicale de Grenoble, 85 X, F-38041 Grenoble cedex, France

Albert-Jean Dorne Physiologie Cellulaire Végétale, Département de Recherche Fondamentale, Laboratoire de Biologie Végétale, Centre d'Etudes Nucléaires et Université Scientifique et Médicale de Grenoble, 85 X, F-38041 Grenoble cedex, France

Roland Douce Physiologie Cellulaire Végétale, Département de Recherche Fondamentale, Laboratoire de Biologie Végétale, Centre d'Etudes Nucléaires et Université Scientifique et Médicale de Grenoble, 85 X, F-38041 Grenoble cedex, France

B. Ghosh Department of Biochemistry, Bose Institute, Calcutta 700009, India

Enrique Herrero Departamento de Microbiología, Facultad de Farmacia, Universidad de Valencia, Valencia 10, Spain

Jacques Joyard Physiologie Cellulaire Végétale, Departement de Recherche Fondamentale, Laboratoire de Biologie Végétale, Centre d'Etudes Nucléaires et Université Scientifique et Médicale de Grenoble, 85 X, F-38041 Grenoble cedex, France

Germán Larriba Departamento de Microbiología, Facultad de Ciencias, Universidad de Extremadura, Badajoz, Spain

Arun Lahiri Majumder Biochemistry Laboratory, Department of Botany, School of Life Sciences, Visva Bharati University, Santiniketan 731235, India

José P. Martínez-García Departamento de Microbiología, Facultad de Farmacia, Universidad de Valencia, Valencia 10, Spain

Günter A. Peschek Biophysical Chemistry Group, Institute for Physical Chemistry, University of Vienna, A-1090 Vienna, Austria

Gerald Schatten Department of Biological Science, Florida State University, Tallahassee, Florida 32306, U.S.A.

Rafael Sentandreu Departamento de Microbiología, Facultad de Farmacia, Universidad de Valencia, Valencia 10, Spain

Héctor N. Seuánez Laboratório de Citogenética, Departamento de Genética, Instituto de Biologia, Universidade Federal do Rio de Janeiro, 21.941 Rio de Janeiro, R.J., Brazil

Preface

The broad aim of this series is to work toward "an integrated view of the cell." It is perhaps fitting that this tenth volume, corresponding to roughly a decade of endeavor in this direction, should cover a wide range of topics from apparently disparate subject areas and yet reveal a strong underlying unity of approach in each topic. The unifying element is the remarkable extent to which diverse biological processes can now be described (even if not fully explained) in terms of fundamental molecular biology.

Chapter 1, by R. Douce, M. A. Block, A.-J. Dorne, and J. Joyard, surveys the great advances that have been made in our understanding of the properties, functions, and biogenesis of plastid envelope membranes. In Chapter 2, G. A. Peschek deals in a most comprehensive way with respiratory membranes of cyanobacteria (blue-green algae); his article fills a gap in the literature in a subject that is now attracting increasing attention. R. Sentandreu, E. Herrero, J. P. Martinez-García, and G. Larriba then describe in Chapter 3 the important advances that have been made in our understanding of the structure and biogenesis of the yeast cell wall. B. B. Biswas, B. Ghosh, and A. L. Majumder deal in Chapter 4 with a generally neglected area, namely, the role of *myo*-inositol polyphosphates in metabolism. They propose an interesting metabolic cycle involving glucose-6-phosphate and *myo*-inositol phosphates; this cycle may well be of general importance in many cell types. In Chapter 5, P. S. Agutter provides an extensive and erudite analysis of current research into the important subject of nucleocytoplasmic RNA transport; various theories are critically assessed, and the importance of correct methodology is stressed.

In Chapter 6, G. Schatten describes in a most comprehensive way the striking morphological and molecular changes that occur in the cytoskeleton during fertilization. Completing this volume is Chapter 7, an extensive and erudite account by H. N. Seuánez of modern approaches to the study of the evolution of the human chromosome.

Readers of Volume 10 of *SUBCELLULAR BIOCHEMISTRY* will no doubt be impressed by the extent and rapidity of the advances now being made on a broad front of cell biology. We are indeed living in exciting times, and it

is hoped that future volumes of this series will continue to reflect these great developments.

D. B. Roodyn

London

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Chapter 1

The Plastid Envelope Membranes: Their Structure, Composition, and Role in Chloroplast Biogenesis

Roland Douce, Maryse A. Block, Albert-Jean Dorne, and Jacques Joyard

Physiologie Cellulaire Végétale, ERA au CNRS No. 847
Département de Recherche Fondamentale
Laboratoire de Biologie Végétale
Centre d'Etudes Nucléaires et Université Scientifique et Médicale de Grenoble
85X, F-38041 Grenoble cedex, France

1. INTRODUCTION

The feature shared by all members of the plastid family (proplastids, elaioplasts, leukoplasts, amyloplasts, chromoplasts, etioplasts, and chloroplasts) is a pair of outer membranes, known as the envelope. These membranes together provide a flexible boundary between the plastid and the surrounding cytosol (Thomson, 1974). This applies even to highly senescent plastids (Priestley, 1977), and to plastids devoid of ribosomes (Börner *et al.*, 1976; Feierabend and Schrader-Reichhardt, 1976)—from which all other membraneous structures have disappeared—and to dividing plastids (Chaly *et al.*, 1980). Consequently, the plastid envelope is a permanent structure in the sense that every existing envelope membrane could theoretically be traced back through generations of cells and organisms maintaining uninterruptedly for millions of years some specific structural organization.

The chloroplast envelope maintains the so-called "soluble" Benson–Calvin cycle enzymes in close contact with the thylakoid network (Figure 1A). These enzymes, which are probably organized into large complexes close to the inner envelope membrane, are rapidly released into the medium when the plastid envelope membranes are damaged.

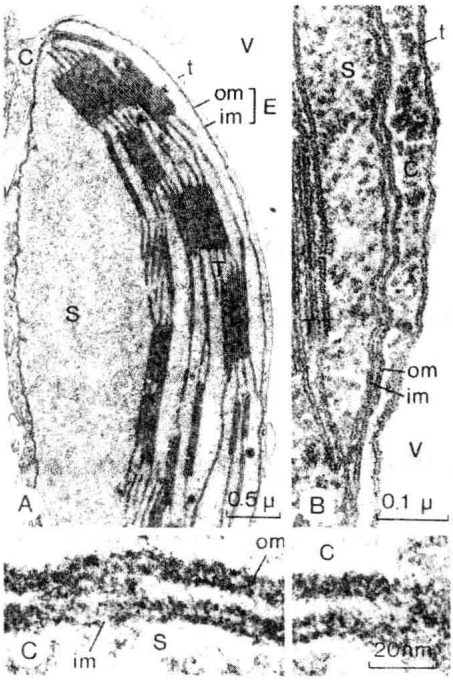

FIGURE 1. Thin sections of parts of spinach (*Spinach oleracea* L.) leaf cells at different magnifications. The chloroplast envelope of higher plants consists of two morphologically and topologically distinct membranes. In these thin sections, the two envelope membranes stain with approximately equal electron density. The trilaminar appearance of each envelope membrane is readily observed when tannic acid is used during sample processing (for technical details, see Carde *et al.*, 1982). (V) Vacuole; (C) cytoplasm; (S) stroma; (T) thylakoids; (E) envelope; (om) outer membrane; (im) inner membrane; (t) tonoplast. Micrographs adapted from Carde *et al.* (1982) with permission.

The investigations of the permeability properties of the outer membrane of the chloroplast envelope have led to the almost universally accepted view that this structure is freely permeable to small molecules such as sucrose and other molecules either charged or uncharged up to a molecular weight of about 10,000 (Heldt and Sauer, 1971). In contrast, the inner envelope membrane surrounding the stroma space is impermeable to sucrose and is a highly effective barrier against unidirectional movement of most anions and cations (Walker, 1976; Heldt, 1976). The selective permeability of the inner envelope membrane to a few species of anions is now known to be due to specific translocators. Over the past decade, several important reviews have appeared that have discussed, in considerable detail, the transport properties of intact chloroplasts isolated from plants having the Benson–Calvin pathway of photosynthesis (C3 plants) or the C4 dicarboxylic acid pathway of photosynthesis (C4 plants). The reader is referred to these reviews to obtain an interesting and global view of this important topic (Heber, 1974; Walker, 1974, 1976; Heldt, 1976; Heber and Walker, 1979; Heber and Heldt, 1981). Besides this important role, the envelope membranes regulate the transport of cytoplasmically synthesized chloroplast proteins (Chua and Schmidt, 1979) and can catalyze the synthesis of galactolipids (Douce and Joyard, 1980, 1983), carotenoids

(Douce and Joyard, 1983), and prenyllipids (Douce and Joyard, 1983). It is therefore our main purpose in this review to give an account of our knowledge of the structure and chemical composition of the envelope of higher plant plastids and to indicate the current areas of uncertainty and controversy. It is also our intention to point out the multiple functions of this membraneous system involved in the synthesis of lipids and in the regulation of the uptake of the many chloroplast proteins that are made on the cytoplasmic polysomes.

2. STRUCTURE OF THE PLASTID ENVELOPE

The thickness of each envelope membrane from higher plant chloroplasts is reported to be 5.5 nm (Gunning and Steer, 1975; Sprey and Laetsch, 1976a; Carde *et al.*, 1982) (Figure 1). This thickness is less than that of the tonoplast (6 nm) or plasma membrane (7 nm), but is comparable to that of mitochondrial membranes and the peroxisomal membrane as well as the smooth or rough endoplasmic reticulum. The two envelope membranes are separated by a gap 2–10 nm wide, the average being 6 nm, and generally stain with approximately equal density (Figure 1). Kagan-Zur *et al.* (1980) have shown that glutaraldehyde fixation reveals changes in the staining properties of the envelope of pea chloroplasts kept in the light or in the dark prior to fixation. They suggest that these changes are presumably conformational and rapidly reversible. When tannic acid is used in addition to glutaraldehyde and osmium tetroxide on thin-section material (Carde *et al.*, 1982), the trilaminar appearance of both envelope membranes is readily observed by electron microscopy (Figure 1). In fact, by its complementary fixative action on membrane proteins (Futaesaku *et al.*, 1972), on phosphatidylcholine (Kalina and Pease, 1977), and perhaps on other components of the envelope membranes, tannic acid seems to stabilize the chloroplast envelope against lipid extraction resulting from dehydration and subsequent processing. At irregular intervals, electron-dense areas (zones of fusion?) seem to punctuate both membranes (Carde *et al.*, 1982) (Figure 2). It is possible that the zones of fusion may serve to maintain the overall structure of the envelope. A further function may be that of protein transport (Chua and Schmidt, 1979).

Unfortunately, thin sectioning of isolated plastid envelope membranes alone has not resulted in sufficient ultrastructural evidence on the specificity of these membranes. Contrarily to examination by freeze–fracturing, the main disadvantage of thin sectioning is that surface views as well as cross sections of chemically unaltered membranes in their natural surroundings cannot be obtained. Freeze–fracture of each envelope membrane yields two faces designated the protoplasmic fracture (PF) and the endoplasmic fracture (EF) face in the terminology of Branton *et al.* (1975). Freeze–cleavage of the outer and