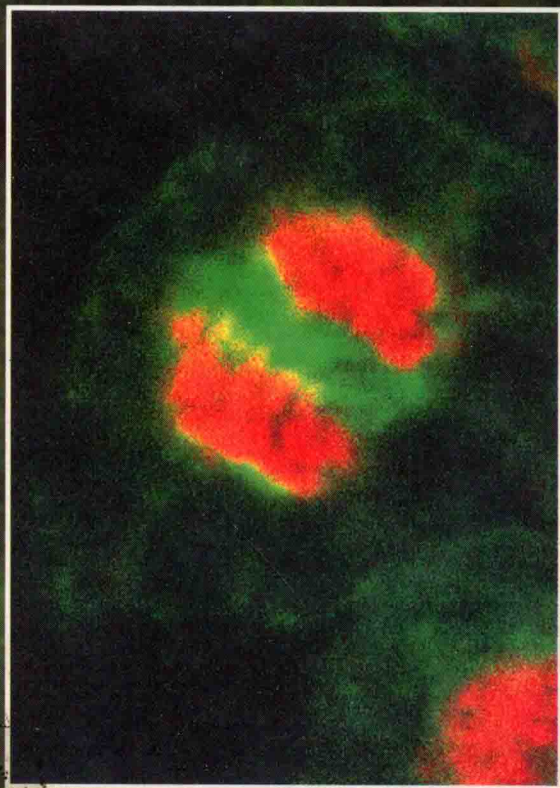


# *Membranes: Specialized Functions in Plants*



Edited by  
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# Membranes: Specialized Functions in Plants

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First published 1996

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A CIP catalogue record for this book is available from the British Library.

ISBN 1 85996 200 9

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**BIOS Scientific Publishers Ltd**

**9 Newtec Place, Magdalen Road, Oxford OX4 1RE, UK**

**Tel. +44 (0) 1865 726286. Fax +44 (0) 1865 246823**

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Toppan Company (S) PTE Ltd  
38 Liu Fang Road, Jurong  
Singapore 2262

*USA and Canada*

BIOS Scientific Publishers  
PO Box 605, Herndon  
VA 20172-0605

Typeset by Chandos Electronic Publishing, Stanton Harcourt, UK.

Printed by Biddles Ltd, Guildford, UK.

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**Cover illustration:** The inset on the front cover shows the cellular distribution of the endoplasmic reticulum (ER) in two daughter cells just after division of a tobacco cotyledon cell. The ER is visualized by the specific immunological detection of the ER resident protein calreticulin in combination with green fluorescent secondary antibodies. The DNA of the two daughter nuclei is visualized in orange by a subsequent propidium iodide staining. Note the accumulation of ER in the fragmoplast and the nuclear envelopes. The inset on the back cover shows a cell prior to cell division in the anaphase/metaphase, stained with the same procedure. The ER (green) is associated with the spindle figure on either side of the chromosomes (orange). The staining patterns suggest that, during cell division in plant cells, the ER moves along the microtubules in the opposite direction to the chromosomes and accumulates where the new cell plate is being formed. Original photographs courtesy of Dr Anna-Stina Höglund, Uppsala Genetic Center, Sweden.

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# Abbreviations

ABA	abscisic acid
ABP	actin-binding protein
ACC	aminocyclopropane-1-carboxylic acid
ACP	acyl carrier protein
ADF	actin depolymerizing protein
AGP	arabinogalactan-protein
ALP	alkaline phosphatase
AO	active oxygen
ARF	ADP-ribosylation factor
BFA	brefeldin A
BiP	binding protein
BL	barley lectin
BrHMA	bromohexamethylene amiloride
CaM	calmodulin
CAM	cell adhesion molecule
CaMV	cauliflower mosaic virus
CCV	clathrin-coated vesicle
CDPK	calmodulin-like domain kinase/calcium-dependent protein kinase
CHAPS	3-[(3-cholamidopropyl)dimethylammonio]-1-propanesulphonate
CHS	chalcone synthase
CLSM	confocal laser scanning microscopy
COP	coat protein
CPMV	cowpea mosaic virus
CPY	carboxypeptidase Y
CTPP	carboxyl-terminal propeptide
DAPI	4,6-diamidino-2-phenylindole
DCB	2, 6-dichlorobenzonitrile
DCCD	<i>N, N'</i> -dicyclohexylcarbodiimide
DCMU	3-(3,4-dichlorophenyl)-1,1-dimethylurea
DEAE	diethylaminoethyl
DEPC	diethylpyrocarbonate
DES	diethylstilbesterol
DG	diacylglycerol
DGDG	digalactosyldiacylglycerol
DHFR	dihydrofolate reductase
DMSO	dimethylsulphoxide
DP	degree of polymerization
DPAP	dipeptidyl aminopeptidase
DTT	dithiothreitol
ECM	extracellular matrix
EDTA	ethylenediamine tetra-acetic acid
EF	extracytoplasmic fracture
EGF	epidermal growth factor
EGTA	ethylene glycol-bis( $\beta$ -aminoethyl) ether <i>N, N, N', N'</i> -tetraacetic acid
EHM	extrahaustorial membrane
ELISA	enzyme-linked immunosorbent assay
EM	electron microscopy
ER	endoplasmic reticulum

ES	extracytoplasmic surface
EST	expressed sequence tag
F-actin	filamentous actin
FBPase	fructose-1, 6-bisphosphatase
FC	fusicoccin
FCR	ferricyanide reductase
FITC	fluorescein isothiocyanate
FN	fibronectin
FNR	ferredoxin:NADPH oxidoreductase
FPLC	fast protein liquid chromatography
$\beta$ GlcY	$\beta$ -glucosyl Yariv reagent
G-actin	globular actin
GAP	GTPase-activating protein
GC	generative cell
GC-MS	gas chromatography–mass spectroscopy
gMDH	glyoxysomal malate dehydrogenase
GNRP	guanine nucleotide release protein
GnT-I	<i>N</i> -acetylglucosaminyltransferase
GO	glycolate oxidase
GS I	$\beta$ -glucan synthase I
GS II	$\beta$ -glucan synthase II
GT	glucose transporter
GUS	$\beta$ -glucuronidase
HAO	haemagglutinin
HATS	high-affinity transport system
HC	haustorial complex
HPLC	high-pressure liquid chromatography
HPR	hydroxypyruvate reductase
HR	hypersensitive response
HRGP	hydroxyproline-rich glycoprotein
Hsc	heat shock cognate
Hsp	heat shock protein
HST	host-specific toxin
Hyp	hydroxyproline
IAA	indole-3-acetic acid
IC	intermediate compartment
ICL	isocitrate lyase
IF	intermediate filament
IMP	intramembrane particle
Ins(1,4,5)P <sub>3</sub>	inositol(1, 4, 5)triphosphate
IPA	inositol phosphate
JA	jasmonic acid
JIP	jasmonate-induced protein
LATS	low-affinity transport system
LHCP	light-harvesting chlorophyll-binding protein
LIMP	lysosomal integral membrane protein
LOX	lipoxygenase
LPS	lipopolysaccharide
LRR	leucine-rich repeat
LTP	lipid transfer protein
LYCH	Lucifer Yellow CH
M6P	mannose 6-phosphate
mAb	monoclonal antibody
MAP	microtubule-associated protein
Me-JA	methyl jasmonate

MF	microfilament
MFS	major facilitator superfamily
MGDG	male germ unit
MI	major intrinsic protein
MP	movement protein
MS	mechanosensitive
MT	microtubule
NAA	naphthyl-1-acetic acid
NBD-PC	nitrobenzoxadiazol-phosphatidylcholine
NEM	<i>N</i> -ethylmaleimide
NMR	nuclear magnetic resonance
NPTII	neomycin phosphotransferase II
NSF	<i>N</i> -ethylmaleimide-sensitive fusion protein
nsL-TP	non-specific lipid transfer protein
NTPP	amino-terminal propeptide
12-oxo-PDA	12-oxo-phytodienoic acid
$P_o$	channel open probability
PAL	phenylalanine ammonia-lyase
PAM	periarbuscular membrane
PAT	phosphoinothrian acetyl transferase
PBM	peribacteroid membrane
PC	phosphatidylcholine
PC-TP	proteins specifically transferring PC
PCMBs	<i>p</i> -chloromercuribenzyl sulphonic acid
PCR	partially coated reticulum
p.d.	potential difference
PDGF	platelet-derived growth factor
PE	phosphatidylethanolamine
PEP	phosphoenolpyruvate
PF	protoplasmic fracture
PG	phosphatidylglycerol
3-PGA	3-phosphoglycerate
PGA	polygalacturonic acid
PGA/RG-I	polygalacturonan/rhamnogalacturonan I
PHA	phytohaemagglutinin
PhyA	active phytochrome
PI	phosphatidylinositol
PI 3-kinase	phosphatidylinositol 3-kinase
PI-TP	proteins specifically transferring PI
PIC	phosphoinositidase C
PKC	protein kinase C
PLC	phospholipase C
PLD	phospholipase D
PM	plasma membrane
PPB	preprophase band
$PP_i$	pyrophosphate
$PP_i$ ase	pyrophosphatase
PPM	peripheral plasma membrane
PrA	proteinase A
PRK1	receptor-like kinase
PS	protoplasmic surface
PtdIns	phosphatidylinositol
PtdIns(4)P	phosphatidylinositol(4)phosphate
PtdIns(4,5)P <sub>2</sub>	phosphatidylinositol(4,5)bisphosphate
PTS	class-1 peroxisomal targeting signal

PUFA	polyunsaturated fatty acid
rER	rough endoplasmic reticulum
Rubisco	ribulose 1,5-bisphosphate carboxylase/oxygenase
SA	salicylic acid
SAM	substrate adhesion molecule
SAR	systemic acquired resistance
SBP	sucrose binding protein
SDS-PAGE	sodium dodecyl sulphate-polyacrylamide gel electrophoresis
SEL	size exclusion limit
SGAT	serine:glyoxylate amino transferase
SLG	S-locus glycoprotein
SNAP	soluble NSF attachment protein
SPP	stromal processing peptidase
SQDG	sulphoquinovosyldiacylglycerol
SRK	S-locus receptor kinase
SRP	signal recognition particle
SSU	small subunit
SUT	sucrose transporter
t-SNARE	target membrane SNAP receptor
TC	terminal complex
TEM	transmission electron microscope
Tes	<i>N</i> -[tris(hydroxymethyl)methyl]-2-aminomethanesulfonic acid
TGN	trans-Golgi network
TIP	tonoplast intrinsic protein
TLC	thin-layer chromatography
TMV	tobacco mosaic virus
TNF	tumour necrosis factor
TPP	thylakoidal processing peptidase
TPT	triose-phosphate translocator
triose-P	triose phosphate
UV	ultraviolet
v-SNARE	vesicle-specific SNAP receptor
VA	vesicular-arbuscular
VAMP	vesicle-associated membrane protein
VN	vitronectin
VSP	vegetative storage protein
XET	xyloglucan endotransglycosylase
XG	xyloglucan

# Preface

When we were invited to design a book on ‘membranes’ we decided to highlight features of membrane biology that are specific to plants. We chose this strategy because we wanted to develop a reference book and survey of membrane biology *in relation* to plant biology. First and foremost we are plant biologists and the contents of this book reflect our enthusiasm and excitement about plants fuelled by the ever-increasing understanding of plant form and function at the molecular level. In a sense, we used the opportunity as editors to invite chapters on all of the areas of plant membranes that we find fascinating. This may have produced a rather personal viewpoint of the range of topics included, but we hope that there is also some intellectual foundation to our choice!

The Contents List begins with a section entitled “Membranes and the Cell Surface”. The plasma membrane surrounds the protoplast and represent the junction and gateway linking it to the outer world of the symplast. It is increasingly recognized that the cell wall, plasma membrane and cytoskeleton interact to relay information across the hydrophobic barrier. The chapters in this section discuss the specialized functions of the plant plasma membrane within its cellular context: as a key site of synthesis of cell wall polysaccharides, as the major site of molecular recognition events, and as the location for the start of signalling cascades that link external stimuli to end-effect.

The second section, “Membrane Lipid Metabolism”, addresses specialized lipids of plant cell membranes. It covers the structural role(s) of the galactolipids and sterols, the putative role of inositol-containing lipids in cell signalling, and the lipid-transfer proteins that are now known to exist in both the symplast and the apoplast and play important roles trafficking lipids around and between the two hydrophilic compartments.

In Section 3, “Regulation of Membrane Permeability”, the authors address ion transport at the cell surface and vacuolar membranes. Movement of ions and the regulation of ion transport processes are fundamental to most, if not all, plant cell functions. We are now beginning to understand these events at the molecular level, with the aid of patch-clamp analyses, and this in turn is demonstrating the complexity of regulation both at the plasma membrane and, significantly for plants, at the tonoplast. Given the importance of turgor in the biology of plants, it is perhaps not surprising that the number of mechanosensitive channels identified is increasing. Ion fluxes have been linked causally as the stimulus–response coupling mechanism for some cellular responses. Interestingly, electrical activity is also now recognized as being of importance in long-distance systemic signalling although we are still some way from understanding the underlying molecular events leading to the variation potentials and action potentials that can be recorded.

The fourth section, “Membrane Compartments within the Cell”, addresses the endomembranes, and again highlights specialized functions in plants. Authors discuss the problem of protein targeting to the vacuole, how plant peroxisomes are formed and the action of the endoplasmic reticulum, Golgi apparatus and secretory vesicles in assembling, sorting and transporting newly synthesized proteins, glycoproteins and polysaccharides. The cortical endoplasmic reticulum is also a feature of all plant cells, yet is rarely highlighted in the literature on membranes. In

particular, the chloroplast is discussed with respect to events that control its division and thereby its biogenesis as well as events that lead to the import of nuclear-encoded gene products into the organelle.

Plasmodesmata, the topic of the fifth section, may seem an odd choice for a book on membranes, given that they are generally considered in texts discussing cell–cell junctions and cell signalling. Nevertheless, we chose to include plasmodesmata in this volume because of their significance to the understanding of the role of membranes in long-range communication throughout the plant. Given that membrane continuity through plasmodesmatal junctions is proven, fluidity of the lipid bilayer and mobility of protein and lipid components through plasmodesmata must be considered with the same emphasis as solute transport through the pore.

The book ends with a section on changes to membranes when plant cells are in intimate association with another organism; whether beneficial, in the context of symbiotic relationships, or detrimental, as when the cells of the plant are interacting with pathogens and pests. As yet, molecular information on these changes is limited. However, we wished to highlight this topic both for the light shed on fundamental processes in membrane biology and for the insights to be gained that may lead to novel crop protection applications.

We hope you as the reader will enjoy the selection of topics, and the very excellent reviews provided by the authors who have kindly contributed their time and enthusiasm to this book.

Margaret Smallwood  
Paul Knox  
Dianna Bowles

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