

Hormones, Signals and Target Cells in Plant Development

The term target cell, first conceived in animal biology, is generally taken to mean a cell that has a pre-determined competence to respond in a defined way to a specific hormone signal. In this volume, the authors present the theory that every plant cell is a target cell for one or more of the plant hormones or other regulatory signals. The different types of cells seen in a mature plant arise as a result of selective responses of meristematic cells to chemical inputs. In this context, the authors provide an overview of plant signals as well as evidence for both short- and long-distance cell-to-cell communication. An interpretation of the target cell concept at the biochemical and molecular levels is then presented using a wide range of examples. This volume will serve as a valuable reference for those working in the field of plant developmental biology.

Daphne J. Osborne is a Visiting and Honorary Professor with the Oxford Research Unit of the Open University, Oxford, United Kingdom, where her research focuses on the hormonal control of physiological and biochemical processes in plant differentiation and development.

Michael T. McManus is Associate Professor in Plant Biology at the Institute of Molecular BioSciences, Massey University, Palmerston North, New Zealand. His research is concerned with the control of biochemical pathways in plants, including the biosynthesis of hormones.



Developmental and Cell Biology Series

SERIES EDITORS

Jonathan B. L. Bard, *Department of Anatomy, Edinburgh University* Peter W. Barlow, *School of Biological Sciences, University of Bristol* David L. Kirk, *Department of Biology, Washington University*

The aim of the series is to present relatively short critical accounts of areas of developmental and cell biology, where sufficient information has accumulated to allow a considered distillation of the subject. The fine structure of cells, embryology, morphology, physiology, genetics, biochemistry, and biophysics are subjects within the scope of the series. The books are intended to interest and instruct advanced undergraduates and graduate students, and to make an important contribution to teaching cell and developmental biology. At the same time, they should be of value to biologists who, while not working directly in the area of a particular volume's subject matter, wish to keep abreast of developments relevant to their particular interests.

RECENT BOOKS IN THE SERIES

20. V. Raghavan Developmental biology of fern gametophytes	0521 33022 X
21. R. Maksymowych Analysis of growth and development in Xanthium	0521 35327 0
22. B. John Meiosis	0521 35053 0
23. J. Bard Morphogenesis: the cellular and molecular processes of	
developmental anatomy	0521 36196 6
24. R. Wall This side up: spatial determination in the early development of	
animals	0521 36115 X
25. T. Sachs Pattern formation in plant tissues	0521 24865 5
26. J. M. W. Slack From egg to embryo: regional specification in early	
development (second edition)	0521 40108 9
27. A. I. Farbman Cell biology of olfaction	0521 36438 8
28. L. G. Harrison Kinetic theory of living pattern	0521 30691 4
29. N. Satoh Developmental biology of ascidians	0521 35221 5
30. R. Holliday Understanding ageing	0521 41788 0
31. P. Tsonis Limb regeneration	0521 44149 8
32. R. Rappaport Cytokinesis in animal cells	0521 40173 9
33. D. L. Kirk Volvox: molecular genetic origins of multicellularity and cellular	
differentiation	0521 45207 4
34. R. L. Lyndon The shoot apical meristem: its growth and development	0521 40457 6
35. D. Moore Fungal morphogenenesis	0521 55295 8
36. N. Le Douarin & C. Kalcheim The neural crest (second edition)	0521 62010 4
37. P. R. Gordon-Weeks Neuronal growth cones	0521 44491 8
38. R. H. Kessin Dictyostelium	0521 58364 0
39. L. I. Held, Jr. Imaginal discs: the genetic and cellular logic of pattern	
formation	0521 58445 0
40. D. Häder, R. Hemmersbach, & M. Lebert Gravity and the behavior of	
unicellular organisms	0521 82052 9
41. D. J. Osborne & M. T. McManus Hormones, Signals and Target Cells in	
Plant Development	0521 33076 9



Hormones, Signals and Target Cells in Plant Development

DAPHNE J. OSBORNE

Open University, Oxford, United Kingdom

MICHAEL T. McMANUS

Massey University, Palmerston North, New Zealand





CAMBRIDGE UNIVERSITY PRESS

Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press 40 West 20th Street, New York, NY 10011-4211, USA

www.cambridge.org

Information on this title: www.cambridge.org/9780521330763

© Cambridge University Press 2005

This book is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 2005

Printed in the United States of America

A catalog record for this publication is available from the British Library.

Library of Congress Cataloging in Publication Data

Osborne, Daphne J.

Hormones, signals and target cells in plant development / Daphne J. Osborne, Michael T. McManus.

p. cm. – (Developmental and cell biology series; 41)

Includes bibliographical references and index.

ISBN 0-521-33076-9 (hardback)

1. Plant hormones. 2. Plant cellular signal transduction. 3. Plants – Development.

I. McManus, Michael T. II. Title. III. Series.

QK898.H67O83 2004

571.7'42 – dc22 2004019647

ISBN-13 978-0-521-33076-3 hardback ISBN-10 0-521-33076-9 hardback

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party Internet Web sites referred to in this book and does not guarantee that any content on such Web sites is, or will remain, accurate or appropriate.



Contents

Pr	Preface po	
1	Introduction	1
	What is a target cell?	3
	Cells, simple and complex tissues	3
	How are signals defined?	4
	Intracellular signal transduction	5
	Cellular competence	5
	Cell and tissue sensitivity to signal inputs	5
2	Hormones and Signals: Identification and Description	
	of Signalling Molecules	6
	Auxin	6
	Auxin biosynthesis	6
	Auxin conjugation	8
	Sites of auxin biosynthesis and transport	9
	Gibberellins	10
	Gibberellin biosynthesis	10
	Cytokinins	11
	Abscisic acid (ABA)	14
	Ethylene	17
	1-Aminocyclopropane-1-carboxylic acid (ACC)	19
	Brassinosteroids	19
	Jasmonates	22
	Salicylic acid	25
	Methylsalicylate and methyljasmonate as signalling volatiles	27
	Nitric Oxide	27
		vii



viii CONTENTS

	Oligosaccharins	28
	Oligogalacturonides (OGAs)	29
	Xyloglucan derivatives	30
	Arabinogalactan proteins	31
	Unconjugated N-glycans	32
	Lignans as signalling molecules	33
	Peptides as signals in plants	34
	Systemin	34
	Systemin-like peptides	35
	RALF peptides	36
	CLAVATA peptides	37
	Phytosulfokines	38
	S-locus cysteine-rich proteins (SCRs)	40
	Major and satellite signals	41
3	Cell-to-Cell Signalling: Short and Long Distance	42
	Origins of cell-to-cell signalling	43
	Short-distance signalling	44
	Meristems	44
	Controlling meristem size	49
	Other short-distance signals	51
	Inter-wall signals	54
	Saccharide-derived signals	54
	Lignin-derived signals	60
	Long-distance signals	62
	Hormones and root-to-shoot signalling	63
	Systemin as a long-distance signalling molecule	70
	Plant nutrients and shoot-to-root signalling	74
	Volatiles and signalling	74
	Methylsalicylate	74
4	Population Diversity of Cell Types and Target Identification	
	in Higher Plants	76
	Evolution of cell types	78
	Meristems as stem cells	80
	Flexibility and plant cell differentiation options	82
	Meristem centres	82
	Options for cell enlargement	84
	The search for molecular markers	85
	Cell performance and ageing in the target state	89
	Senescence and cell death	91
	Is regeneration possible?	95
5	Flexibility of Cell Types and the Target Cell Status	98
	Epidermis as a target state	100
	Flexibility in epidermal cells	100



	CONTE	NTS ix
	Dorsiventrality in the epidermis	102
	The epidermis as a target tissue – Evidence from	
	experiments in vitro	102
	Epidermal cross-talk	103
	Epidermal outgrowths – Trichomes	104
	Epidermis and shoot elongation	105
	Cortical parenchyma cells	107
	Aerenchyma	112
	Loss of flexibility with age	113
	Pith parenchyma	113
	Lignified cells	115
6	Terminally Committed Cell Types and the Target Status	117
	Statocytes	118
	Abscission cells	125
	The aleurone	131
	Stomata and trichomes	138
	Stomata	138
	Trichomes	142
	Vascular tissue	143
7	The Mechanisms of Target Cell Perception and Response to	
	Specific Signals	146
	The emergence of the receptor concept in higher plants	147
	Auxins and the receptor concept	148
	Identification and characterisation of auxin binding proteins	148
	Aux/IAA proteins and auxin action at the gene level	157
	How does auxin exert its cellular effects on target tissues -	
	A working model	161
	Ethylene perception	163
	Evidence that receptor proteins perceive ethylene	163
	Characterisation of ETR function	165
	Evidence that the expression of receptors is developmentally	170
	regulated in plant tissues	172
	Does receptor abundance confer a target status to the cell?	175
8	Hormone Action and the Relief of Repression	179
	Cytokinin perception in the context of receptors and target cells	179
	Identification and characterisation of cytokinin receptors and	
	their downstream elements	181
	Response elements and modulating the cytokinin input	184
	A model for cytokinin signalling in plants	185
	Gibberellin perception and the search for receptors	187
	Summary of the candidates for gibberellin binding proteins and	
	receptors	187



x CONTENTS

	GA perception and signalling	188
	The role of the DELLA protein in regulating the GA response	189
	Perception of the brassinosteroids	192
	A molecular model of plant hormone action and the target cell	
	concept	196
9	The Phenomenon of Hormonal Cross-Talk	198
	Concluding remarks	201
Re	ferences	205
Inc	dex	249



Preface

This volume presents a conceptual approach to plant cell differentiation that differs in a number of respects from those already present in the literature. We seek to show how every cell has an individual competence to respond to the signal inputs that may impinge upon it and how every cell then has an individual qualitative and quantitative response. Central to this target cell concept is the premise that each cell is selective and can therefore discriminate amongst the many incoming signals to which it is exposed by an ability to perceive them and to respond to them.

Because each cell occupies its individual position within the plant body, the intensity or diversity of the signal inputs that it receives are not themselves identical. Hence, each cell is a unique individual and displays a unique target status even though it may also possess considerable commonality with its neighbours. We define this target status of a cell as the selectivity of its response to a signal and the intensity of that response.

The target cell concept arose originally from notions that were current amongst insect and mammalian scientists stating that a regulatory chemical produced in one organ would be perceived and activated upon by the cells in a distant organ – a specificity that operated between two distinct cell types. As the evidence for specificity of response to hormonal inputs increased during the twentieth century, developmental biologists saw this ability of cells to discriminate amongst the multitude of chemical signals to which they were exposed as a marker of the cell's ability to discriminate between them. For a passing hormone, the cell that responded was a target cell.

For the purposes of this volume, we will consider those signals that are endogenously produced or transmuted to chemical signals within the plant. We define such signals as the agents of cell-to-cell communication. This does not imply, however, that we consider electrical signals, gravity signals or differential light inputs

хi



xii PREFACE

to be unimportant, but the scope of this book focuses on the molecular communicators that can be isolated from plants as chemical entities with growth regulatory properties. It is these signal molecules that provide the messages that coordinate the processes of differentiation. We shall not, therefore, consider in any detail the formative influence of all the many external cues that a plant encounters directly from the environment.

Our aim is to present the reader with our interpretation of how the unique target status of each cell is expressed at the biochemical and molecular levels and how this forms the basis for specificity in signal-directed responses. Some of the examples that we discuss here are selected from research studies fitting most easily into the target cell concept. Other examples are those that we have re-interpreted in this light. The target cell concept, as we present it here, has arisen from the many years of our own research. However, it is also our purpose to stimulate debate on the validity of this concept when interpreting other studies of plant cell differentiation and development.

In terms of the structure of the volume, we begin by defining the concept of target cells (Chapter 1), then introduce the repertoire of signals that operate in plants (Chapter 2), and present evidence for both short- and long-distance cell-to-cell signalling (Chapter 3). The concept of the higher plant body in which the majority of cells retain a flexible differentiation status, while some functionally specialised cell types attain a state of terminal commitment, is introduced in Chapter 4. We submit though, that every cell, irrespective of its differentiation status, is a target cell and so we examine the target status of both flexible cell types and terminally committed cell types in Chapters 5 and 6 respectively. Finally, our understanding of the molecular mechanism of hormone action has the potential to be advanced by the identification of receptors and proteinaceous regulators of these signals. In Chapters 7 and 8, we review this literature and speculate on its current and future impact on the target cell concept. In Chapter 9 we consider implications of signal cross-talk.

We hope that this volume will become a useful reference to those working in the field of plant developmental biology.

We wish to acknowledge the assistance of Mrs. Vivian Reynolds, Mrs. Cynthia Cresswell, Ms. Rae Gendall, and Glenda Shaw during the preparation of this volume.