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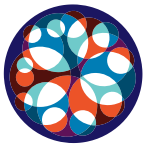
Plant Hormone Signalling

Edited by Thomas Guilfoyle and Gretchen Hagen



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CONTENTS

PREFACE

Plant hormones or phytohormones are small signalling molecules that function at low concentrations to regulate a wide variety of growth, developmental and environmental responses within both flowering and non-flowering plants. These signals have also been referred to as plant growth substances, although this latter terminology may be too narrow to encompass all aspects of plant hormone action. The five 'classical' plant hormones (i.e. auxins, cytokinins, gibberellins, ethylene and abscisic acid) were the first to be discovered and characterized, but today the categories of phytohormones have been expanded to include jasmonates, brassinosteroids, salicylic acid and strigolactones. Beyond these, florigen and signalling peptides have in some cases (and here) also been included in the list of plant hormones.

Historically, the bulk of investigations into plant hormone signalling have restricted the focus to a single hormone, but more recent studies have begun to consider cross-talk among the different classes of hormones and whether signalling among hormones is antagonistic or synergetic. These cross-talk studies have revealed that selected hormones rarely act in isolation, but rather co-ordinate with other hormones in signalling. In this volume of *Essays in Biochemistry*, authors discuss what is thought to be the primary functions of individual hormones, but also the host of interactions among the different classes of plant hormones.

Our understanding of the molecular mechanisms involved in plant hormone signalling has increased dramatically in the last two decades due largely to employment of facile genetic systems (e.g. generation and selection of hormone signalling mutants and availability of entire genomic sequences) and powerful molecular and cell biology tools. This has led to the assimilation of detailed hormone signal-transduction pathways, including the identification of unconventional hormone receptors, *cis*-elements in promoters that confer hormone responsiveness, transcription factors that target the *cis*-elements and confer activation or repression on the hormone response genes, and downstream gene products involved in hormone responses. Interestingly, these recent studies have uncovered similar signalling processes used by different classes of plant hormones. In some cases, these processes are unique to plants, and in other cases, they are related to bacterial signalling. Some of the information gained from these basic studies suggests future directions, including those aimed at crop improvement.

In this volume of *Essays in Biochemistry* on plant hormone signalling, Chapters 1-10 focus on individual hormones, including auxin, cytokinin, abscisic acid, gibberellins, ethylene, brassinosteroids, jasmonic acid, salicylic acid, peptides and florigen, but also discuss cross-talk with other hormones. Chapter 11 discusses seed germination as a well-studied example of hormone cross-talk. Chapter 12 addresses similarities and differences among different plant hormone pathways, and includes some preliminary information on signalling by strigolactone, the most recently discovered plant hormone. Overall, these chapters summarize current information on plant hormone signalling and address some of the questions that are under investigation.

We would like to thank all of the authors for their willingness in providing up-to-date, informative, critical and engaging chapters that target upper level undergraduates and graduate students in this field of biochemistry. We would also like to thank Professor Nigel Hooper,

Series Editor of *Essays in Biochemistry*, and the Advisory Panel for the invitation to serve as Guest Editors for the volume on Plant Hormone Signaling, and to give special thanks to Clare Curtis, Executive Editor of *Essays in Biochemistry*, for her many efforts and perseverance in recruiting authors and for keeping submissions, reviews, revisions and production of chapters on schedule.

Thomas J. Guilfoyle and Gretchen Hagen
June 2014

AUTHORS

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Aaron M. Rashotte is an Associate Professor in the Department of Biological Sciences at Auburn University, and has been studying hormones, including cytokinin and auxin, for more than 15 years. Current research in his laboratory is focused on understanding the functional role of the cytokinin response factors (CRFs) in growth, development, stress and cytokinin-regulated processes in both *Arabidopsis* and tomato.

Inhwan Hwang is currently working as a Professor in the Division of Integrative Biosciences and Biotechnology at Pohang University of Science and Technology, South Korea. He completed B.S. and M.S. degrees in the Chemistry Department of Seoul National University, South Korea, a Ph.D. in the Department of Biochemistry and Biophysics, University of North Carolina at Chapel Hill, U.S.A., and postdoctoral training at the Department of Molecular Biology, Massachusetts General Hospital and Genetics Department, Harvard Medical School, U.S.A. Currently he is studying the mechanisms underlying abscisic acid (ABA) homeostasis and signalling, protein trafficking and targeting, and the biogenesis and function of organelles in plants, and actively seeking to apply his findings to the development of plants as a biomaterial production platform.

Ting Dong completed a Ph.D. in Integrative Biological Engineering under the supervision of Professor Inhwan Hwang at Pohang University of Science and Technology, South Korea. Her study focused on the catabolism and homeostasis of ABA, and the role of ABA in the abiotic stress response. She had previously received an M.S. in Botany from the School of Life Science, Shandong University, China, and a B.S. majoring in Biotechnology from the School of Life Science, Shaanxi Normal University, China.

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Thomas Hartwig is a Postdoctoral Fellow at the Carnegie Institution for Science, Department of Plant Biology at Stanford University in California. He previously received his Ph.D. from Purdue University, U.S.A., and his Masters degree from the University of Rostock, Germany. Hormone networks that control plant development are the central focus of his research. He is particularly interested in the signal cross-talk that regulates branching patterns and sex determination in maize.

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Dr. Marta Boter graduated in Biology at the University of Barcelona. During her Ph.D. under the supervision of Dr. Salomé Prat at the Centro de Investigación y Desarrollo (CID-CSIC), Barcelona, she specialized in plant responses to abiotic and biotic stresses and hormone signalling, focusing on jasmonate (JA) signalling. She then joined Dr. Ken Shirasu's group at the Sainsbury Laboratory, Norwich, UK, where she was awarded a Marie Curie Intra-European Fellowship to work on effector-triggered immunity (ETI). She subsequently joined Roberto Solano's laboratory at the Centro National de Biotecnología (CNB-CSIC), Madrid, where she has continued her research on plant hormone signalling and disease resistance.

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Ayane Motomitsu began her scientific career in the Faculty of Science at Kumamoto University, Japan. In 2014, before completing her undergraduate programme, she skipped a grade and began an M.Sc. in the Graduate School of Science and Technology, Kumamoto University, Japan. She is studying the molecular basis of the apical meristem in *Arabidopsis thaliana*. Since 2014 she has also worked as a visiting student at Temasek Life Sciences Laboratory (TLL), Singapore.

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Takashi Ishida graduated from Meiji University, Japan, and received his Ph.D., for which he studied the molecular mechanisms underlying cortical microtubule dynamics in plant cells, from the Nara Institute of Science and Technology (NAIST), Japan. He then worked as a Postdoctoral Fellow at RIKEN, Japan, where he studied the developmental regulation of the phase transition from cell proliferation to cell differentiation. He subsequently moved to the Nara Institute of Science and Technology (NAIST), Japan, and then became an Assistant Professor at Kumamoto University, Japan, where he is studying the intracellular signal transduction mechanisms of peptide hormones in the regulation of stem cells.

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Antoine Larrieu completed his Ph.D. at the University of Nottingham and at the Plant Systems Biology Department in the University of Ghent under the supervision of Professor Malcolm Bennett and Professor Tom Beeckman. During his Ph.D. he used chemical genetics approaches to study auxin signalling and its role in regulating root architecture. He is currently a Postdoctoral Fellow working in the laboratory of Dr. Teva Vernoux. His main research interest is the development of novel fluorescent hormone biosensors to study plant development, with a particular focus on studying the regulation by auxin of organ initiation and positioning at the shoot apical meristem.

ABBREVIATIONS

AA	ascorbic acid
ABA	abscisic acid
ABA-GE	ABA-glucosyl ester
ABC	ATP-binding cassette
ABRE	ABA-responsive element
ACC	1-aminocyclopropane-1-carboxylic acid
ACO	ACC oxidase
ACS	ACC synthase
AHA2	H^+-ATPase 2
AHK	Arabidopsis histidine kinase
AHP	Arabidopsis histidine phosphotransferase
ARF	auxin response factor
ARR	Arabidopsis response regulator
AuxRE	auxin response element
AZ	abscission zone
AZA	azelaic acid
BABA	β-aminobutyric acid
bHLH	basic helix-loop-helix
BiFC	bimolecular fluorescence complementation
BiP2	binding protein 2
BL	brassinolide
bp	base pair
BR	brassinosteroid
bZIP	basic-leucine zipper
CBF	CRT-binding factor
CE	coupling element
CEP	C-terminally encoded peptide
CK	cytokinin
CLE	CLAVATA3/embryo surrounding region
CLV	CLAVATA
CO	CONSTANS
COR	coronatine
COR-MO	coronatine-O-methyloxime
CPPU	*N*-phenyl-N′-(2-chloro-4-pyridyl)urea
CPS	*ent*-copalyl diphosphate synthase
CRF	cytokinin response factor
CRSP	CO_2 response secreted protease
CRT	C-repeat
CRT3	calreticulin 3
CRY	cryptochrome

CTD	C-terminal domain
CTR	constitutive triple response
CYP	cytochrome P450
cZ	*cis*-zeatin
DA	dehydroabietinal
DBD	DNA-binding domain
DIR1	defective in induced resistance 1
DPA	dihydrophaseic acid
DRE	dehydration-responsive element
DREB	DRE-binding protein
DZ	dihydrozeatin
EPF	epidermal patterning factor
ER	endoplasmic reticulum
ERAD	endoplasmic-reticulum-associated degradation
ERF	ethylene-responsive factor
ERQC	endoplasmic reticulum quality control
ESF	embryo surrounding factor
ET	ethylene
FCA	flowering time control protein A
FD	flowering locus D
FMI	floral meristem identity
FPI	floral pathway integrator
FR	far red
FRET	fluorescence resonance energy transfer
FT	flowering locus T
FTIP1	FT-interacting protein 1
G3P	glycerol-3-phosphate
GA	gibberellin
GC	guard cell
GGDP	*trans*-geranylgeranyl diphosphate
GID1	gibberellin insensitive dwarf 1
GMC	guard mother cell
GS	glucosinolate
GSK3	glycogen synthase kinase 3
GT	glucosyltransferase
GTF	general transcription factor
GUS	β-glucuronidase
HDA	histone deacetylase
HK	histidine kinase
HPt	histidine phosphotransfer protein
HR	homologous recombination
HSL	hormone-sensitive lipase
IAA	indole-3-acetic acid
IC	isochorismate
ICS	isochorismate synthase

IDA	inflorescence deficient in abscission
IDD	indeterminate domain protein
iP	isopentenyladenine
IP5	inositol pentakisphosphate
IPA	indole-3-pyruvate
IPL	isochorismate pyruvate lyase
IPP	isopentenyl diphosphate
IRE1	inositol-requiring enzyme 1
JA	jasmonic acid; jasmonate
JA-Ile	(+)-7-*iso*-jasmonoyl-L-isoleucine
JAZ	jasmonate ZIM domain
LD	long day
LDP	long-day plant
LRR	leucine-rich repeat
MAMP	microbe-associated molecular pattern
MAP	mitogen-activated protein
MAPK	mitogen-activated protein kinase
MAPKKK	mitogen-activated protein kinase kinase kinase
MeSA	methyl ester of salicylic acid
miRNA	microRNA
MLPK	M-locus protein kinase
MMC	meristemoid mother cell
MoCo	molybdenum cofactor
NCED	9-*cis*-epoxycarotenoid dioxygenase
NO	nitric oxide
NPR1	nonexpressor of pathogenesis-related genes 1
NRAMP	natural resistance-associated macrophage protein
NT	N-terminal
2ODD	2-oxoglutarate-dependent dioxygenase
PA	phaseic acid
PAL	phenylalanine ammonia-lyase
PC	phospholipid phosphatidylcholine
PCD	programmed cell death
PEBP	phosphatidylethanolamine-binding protein
PIF	phytochrome-interacting factor
PM	plasma membrane
PP2C	protein phosphatase 2C
PR	pathogenesis-related
PRR	pseudo-response regulator
PSK	phytosulfokine
PSKR	phytosulfokine receptor
PSY	peptide-containing sulfated tyrosine
PTM	post-translational modification
PYR	pyrabactin resistance
QC	quiescent centre

RALF	rapid alkalinization factor
RCAR	regulatory component of ABA receptor
RdDM	RNA-directed DNA methylation
RIDD	regulated IRE1-dependent decay
RIDS	regulated IRE1-dependent splicing
RLCK	receptor-like cytoplasmic kinase
RLK	receptor-like kinase
RNAi	RNA interference
RR	response regulator
SA	salicylic acid
SAM	*S*-adenosylmethionine; shoot apical meristem
SAR	systemic acquired resistance
SCF	Skip–Cullin–F-box
SCR	S-locus cysteine-rich protein
SD	short day
SDP	short-day plant
SDR	short-chain dehydrogenases/reductases
siRNA	small interfering RNA
SL	strigolactone
SLG	S-locus glycoprotein
SLGC	stomatal lineage ground cell
SnRK	SNF1-related protein kinase
SRK	S-locus receptor kinase
SUMO	small ubiquitin-like modifier
TAA	tryptophan aminotransferase
TDIF	tracheary element differentiation inhibitory factor
TDZ	thidiazuron
TF	transcription factor
TMK	transmembrane kinase
TMV	tobacco mosaic virus
TPST	tyrosylprotein sulfotransferase
Tre6P	trehalose-6-phosphate
TSF	twin sister of FT
tZ	*trans*-zeatin
UDP	uridine diphosphate
UGT	uridine diphosphate glucosyltransferase
UPR	unfolded protein response
UPS	ubiquitin–proteasome system
UV-A	ultraviolet A
UV-B	ultraviolet B
WT	wild type
WUS	WUSCHEL
Y2H	yeast two-hybrid
ZEP	zeaxanthin epoxidase