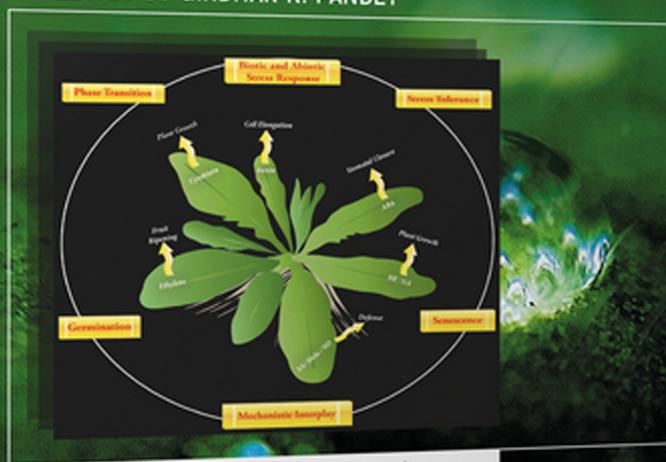


Mechanism of Plant Hormone Signaling Under

Mechanism of Plant Hormone Signaling Under Stress

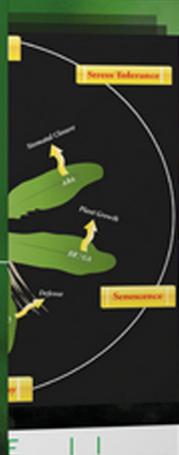
EDITED BY GIRDHAR K. PANDEY



VOLUME I

WILEY Blackwell

EDITED BY
PANDEY



WILEY Blackwell

VOLUME I

EDITED BY
PANDEY

Mechanism of Plant Hormone Signaling Under Stress

WILEY Blackwell

**Mechanism of Plant Hormone
Signaling under Stress**

Cover Image Description

The image presents a holistic view of the functional role of phytohormones. Different classes of plant hormones perform a myriad of functions starting from germination, vegetative, to reproductive phase transition; abiotic and biotic stress responses, defense against pathogens, and senescence. Plant hormones are known to regulate and interact with other hormones and more than one hormone is frequently involved in different signaling pathways, suggesting a mechanistic interplay among them in regulating plant growth, development, and physiological responses.

Mechanism of Plant Hormone Signaling under Stress

Edited by Girdhar K. Pandey

Department of Plant Molecular Biology,
University of Delhi South Campus,
New Delhi, India

Volume I

WILEY Blackwell

Copyright © 2017 by John Wiley & Sons, Inc. All rights reserved

Published by John Wiley & Sons, Inc., Hoboken, New Jersey

Published simultaneously in Canada

No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, recording, scanning, or otherwise, except as permitted under Section 107 or 108 of the 1976 United States Copyright Act, without either the prior written permission of the Publisher, or authorization through payment of the appropriate per-copy fee to the Copyright Clearance Center, Inc., 222 Rosewood Drive, Danvers, MA 01923, (978) 750-8400, fax (978) 750-4470, or on the web at www.copyright.com. Requests to the Publisher for permission should be addressed to the Permissions Department, John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, (201) 748-6011, fax (201) 748-6008, or online at <http://www.wiley.com/go/permission>.

Limit of Liability/Disclaimer of Warranty: While the publisher and author have used their best efforts in preparing this book, they make no representations or warranties with respect to the accuracy or completeness of the contents of this book and specifically disclaim any implied warranties of merchantability or fitness for a particular purpose. No warranty may be created or extended by sales representatives or written sales materials. The advice and strategies contained herein may not be suitable for your situation. You should consult with a professional where appropriate. Neither the publisher nor author shall be liable for any loss of profit or any other commercial damages, including but not limited to special, incidental, consequential, or other damages.

For general information on our other products and services or for technical support, please contact our Customer Care Department within the United States at (800) 762-2974, outside the United States at (317) 572-3993 or fax (317) 572-4002.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic formats. For more information about Wiley products, visit our web site at www.wiley.com.

Library of Congress Cataloging-in-Publication Data:

Names: Pandey, Girdhar K., editor.

Title: Mechanism of plant hormone signaling under stress / edited by Girdhar K. Pandey.

Description: Hoboken, New Jersey : John Wiley & Sons, Inc., 2017. | Includes bibliographical references and index.

Identifiers: LCCN 2016047893 (print) | LCCN 2016059906 (ebook) | ISBN 9781118888926 (cloth : alk. paper) | ISBN 9781118888964 (Adobe PDF) | ISBN 9781118888766 (ePub)

Subjects: LCSH: Plants--Effect of stress on. | Botanical chemistry. | Plant hormones. | Auxin. | Gibberellins.

Classification: LCC QK754 .M36 2017 (print) | LCC QK754 (ebook) | DDC 581.7--dc23

LC record available at <https://lccn.loc.gov/2016047893>

Set in 10/12pt WarnockPro by SPi Global, Chennai, India

Cover image: Mie Igarashi / EyeEm/Gettyimages

Cover designer: Wiley

10 9 8 7 6 5 4 3 2 1

Contents

About the Editor *xv*

List of Contributors *xvii*

Preface *xxiii*

Part I Action of Phytohormones in Stress *1*

- 1 Auxin as a Mediator of Abiotic Stress Responses** *3*
Branka Salopek-Sondi, Iva Pavlović, Ana Smolko, and Dunja Šamec
- 1.1 Introduction *3*
- 1.2 Auxin: A Short Overview of Appearance, Metabolism, Transport, and Analytics *4*
- 1.2.1 *De Novo* Synthesis *4*
- 1.2.2 Reversible and Irreversible Conjugation Pathways *5*
- 1.2.3 IBA to IAA Conversion *6*
- 1.2.4 Degradation Pathways *6*
- 1.2.5 Polar Auxin Transport *7*
- 1.2.6 Analytical Methods in Auxin Identification and Quantification *7*
- 1.3 How Auxin Homeostasis Shifts with Diverse Abiotic Stresses *9*
- 1.3.1 How the Auxin Pool is Affected by Abiotic Stress? *9*
- 1.3.2 Transcription of Auxin Metabolic Genes under Abiotic Stress *10*
- 1.3.3 What Can We Learn from Functional Analysis Research? *11*
- 1.4 How Does Auxin Signaling Respond to Abiotic Stress? *13*
- 1.4.1 Brief Overview of Auxin Perception and Signaling *13*
- 1.4.2 Auxin Signaling Attenuation under Stress Conditions: The Importance of miRNA Driven Post-Transcriptional Regulation *14*
- 1.5 Auxin and Redox State During Abiotic Stress *15*
- 1.6 Auxin-Stress Hormones Crosstalk in Stress Conditions *18*
- 1.6.1 Auxin-ABA Crosstalk *18*
- 1.6.2 Auxin-JA Crosstalk *19*
- 1.6.3 Auxin-Ethylene Crosstalk *20*
- 1.6.4 Auxin-SA Crosstalk *20*
- 1.7 Promiscuous Protein Players of Plant Adaptation: Biochemical and Structural Views *21*

1.7.1	IAR3 Auxin Amidohydrolase	21
1.7.2	GH3 Auxin Conjugate Synthetases	23
1.8	Conclusion	24
	Acknowledgment	24
	References	25
2	Mechanism of Auxin Mediated Stress Signaling in Plants	37
	<i>Lekshmy S, Krishna G.K., Jha S.K., and Sairam R.K.</i>	
2.1	Introduction	37
2.2	Auxin Biosynthesis, Homeostasis, and Signaling	37
2.3	Auxin Mediated Stress Responses in Model and Crop Plants	40
2.4	Regulation of Root System Architecture under Drought and Nutrient Stresses	41
2.5	Conclusions and Future Perspectives	45
	References	46
3	Integrating the Knowledge of Auxin Homeostasis with Stress Tolerance in Plants	53
	<i>Shivani Saini, Isha Sharma, and Pratap Kumar Pati</i>	
3.1	Introduction	53
3.2	Auxin Biosynthesis and its Role in Plant Stress	53
3.3	Auxin Transport and its Role in Plant Stress	57
3.4	Auxin Signaling and its Role in Plant Stress	60
3.5	Auxin Conjugation and Degradation and its Role in Plant Stress	61
3.6	Conclusions	63
	References	63
4	Cytokinin Signaling in Plant Response to Abiotic Stresses	71
	<i>Nguyen Binh Anh Thu, Xuan Lan Thi Hoang, Mai Thuy Truc, Saad Sulieman, Nguyen Phuong Thao, and Lam-Son Phan Tran</i>	
4.1	Introduction	71
4.2	CK Metabolism	72
4.2.1	CK Components and Regulatory Functions	72
4.2.2	CK Metabolism, Perception, and Signal Transduction	75
4.2.2.1	CK Metabolism	75
4.2.2.2	CK Perception and Signal Transduction	77
4.3	The Components of the CK Signaling Pathway	77
4.3.1	The CK Receptor Histidine Kinases	77
4.3.2	Histidine Phosphotransfer Proteins	79
4.3.3	Response Regulators	80
4.4	CK Signaling in Plant Responses to the Abiotic Stresses	81
4.5	Genetic Engineering of CK Content for Improvement of Plant Tolerance to Abiotic Stresses	82
4.6	Conclusions	88
	Acknowledgments	88
	References	88

5	Crosstalk Between Gibberellins and Abiotic Stress Tolerance Machinery in Plants	101
	<i>Ashutosh Sharan, Jeremy Dkhar, Sneha Lata Singla-Pareek, and Ashwani Pareek</i>	
5.1	Introduction	101
5.2	Gibberellins: Biosynthesis, Transport, and Signaling	102
5.3	GA Metabolism and Signaling During Abiotic Stress	106
5.3.1	Salinity Stress Induces GA2ox and GA20ox Gene Expression	106
5.3.2	Reduced GA Confers Tolerance to Drought Stress	111
5.3.3	Role of GA in Cold and Heat Stresses	112
5.4	Crosstalk between GA and Other Plant Hormones in Response to Abiotic Stresses	114
5.4.1	Crosstalk between GAs and Ethylene During Abiotic Stress	114
5.4.2	Crosstalk Between GAs and Abscisic Acid During Abiotic Stress	115
5.4.3	Crosstalk Between GAs and SA During Abiotic Stress	116
5.4.4	Crosstalk Between GAs and Jasmonic Acid During Abiotic Stress	116
5.5	Applications in Crop Improvement	117
5.5.1	Flower Development	117
5.5.2	Fruit Development	118
5.5.3	Brewing Industry	118
5.6	Conclusion	118
	Acknowledgment	119
	References	119
6	The Crosstalk of GA and JA: A Fine-Tuning of the Balance of Plant Growth, Development, and Defense	127
	<i>Yuge Li and Xingliang Hou</i>	
6.1	Introduction	127
6.2	GA Pathway in Plants	128
6.3	JA Pathway in Plants	129
6.4	GA Antagonizes JA-Mediated Defense	131
6.5	JA Inhibits GA-Mediated Growth	133
6.6	GA and JA Synergistically Mediate Plant Development	134
6.7	Conclusions	136
	Acknowledgments	136
	References	136
7	Jasmonate Signaling and Stress Management in Plants	143
	<i>Sirhindi Geetika, Mushtaq Ruqia, Sharma Poonam, Kaur Harpreet, and Ahmad Mir Mudaser</i>	
7.1	Introduction	143
7.2	JA Biosynthesis and Metabolic Fate	144
7.3	JA Signaling Network	146
7.4	Physiological Role of JAs	151
7.4.1	JA in Seed Germination	151
7.4.2	JA in Root Growth	151
7.4.3	JA in Tuber Formation	152
7.4.4	JA in Trichome Development	152

- 7.4.5 JA in Flower and Seed Development 153
- 7.4.6 JA in Abscission and Senescence 153
- 7.4.7 JA in Photosynthesis Regulation 154
- 7.4.8 JA in Secondary Metabolism 155
- 7.5 JA Regulated Stress Responses 156
- 7.5.1 JA in Antioxidant Management and Reactive Oxygen Species Homeostasis 156
- 7.5.2 JA in Biotic Stress 157
- 7.5.3 JA in Abiotic Stresses 157
- 7.6 Conclusion 159
- References 159

8 Mechanism of ABA Signaling in Response to Abiotic Stress in Plants 173

Ankush Ashok Saddhe, Kundan Kumar, and Padmanabh Dwivedi

- 8.1 Introduction 173
- 8.2 Signal Perception and ABA Receptors 175
- 8.3 Negative Regulators of ABA Signaling: Protein Phosphatase 2C (PP2C) 178
- 8.4 Positive Regulators of ABA Signaling: SnRK2 179
- 8.5 ABA Signaling Regulating Transcription Factor 181
- 8.5.1 Basic-Domain Leucine Zipper (bZIP) TF 181
- 8.5.2 AP2/ERF TF 182
- 8.5.3 NAC TF 183
- 8.5.4 WRKY TF 183
- 8.5.5 C₂H₂ ZF TF 184
- 8.5.6 MYB TF 185
- 8.5.7 bHLH TF 185
- 8.6 Crosstalk Between Various ABA Responsive Pathways in Abiotic Stress 186
- 8.7 Summary and Future Prospects 187
- Acknowledgments 188
- Abbreviations 188
- References 188

9 Abscisic Acid Signaling and Involvement of Mitogen Activated Protein Kinases and Calcium-Dependent Protein Kinases During Plant Abiotic Stress 197

Aryadeep Roychoudhury and Aditya Banerjee

- 9.1 Introduction 197
- 9.2 ABA Signaling in Plants 198
- 9.2.1 ABA as a Phytohormone 198
- 9.2.2 ABA Metabolism 199
- 9.2.3 ABA Transport 199
- 9.2.4 ABA Perception and Signal Transduction 201
- 9.2.4.1 ABA Receptors in Signal Transduction 202
- 9.2.4.2 PP2Cs as Negative Regulators of ABA Signaling 203
- 9.2.4.3 SnRK2 Acting as a Global Positive Regulator of ABA Signaling 205

9.3	The Signalosome and Signaling Responses Mediated by ABA: Structural Alterations in ABA by PYR/PYL/RCAR	207
9.4	Structural Alterations During PP2C Inhibition by ABA	208
9.5	The <i>abi1-1</i> Mutation Mystery Solved	208
9.6	Basic Leucine Zipper (bZIP) TFs in ABA Signaling	209
9.7	Mitogen-Activated Protein Kinase (MAPK) Cascades and Regulation of Downstream Signaling	210
9.7.1	Relevance and Crosstalk of MAPKs in Plant Abiotic Stresses	212
9.7.2	The MAPK Families of <i>Arabidopsis</i> and Rice	212
9.7.2.1	<i>Arabidopsis</i>	212
9.7.2.2	Rice	213
9.7.3	MAPK Cascades Regulating Abiotic Stress Signaling	215
9.7.3.1	Salt Stress	215
9.7.3.2	Drought Stress	215
9.7.3.3	Oxidative Stress	215
9.7.3.4	Ozone Stress	216
9.7.3.5	Heavy Metal Stress	216
9.7.3.6	Temperature Stress	216
9.7.3.7	ABA-Induced Activation of MAPKs	216
9.8	Calcium Dependent Protein Kinases (CDPKs)	219
9.8.1	CDPK Activities	221
9.8.1.1	Regulation of CDPK Activity	221
9.8.1.2	CDPK in ABA Signaling	221
9.8.2	Relevance and Crosstalk of CDPKs in Plant Abiotic Stresses	223
9.8.3	CDPKs as Potent Signaling Hubs	224
9.9	MAPK-CDPK Crosstalk	225
9.10	Conclusion and Future Perspectives	226
	Acknowledgments	227
	References	227
10	Abscisic Acid Activates Pathogenesis-Related Defense Gene Signaling in Lentils	243
	<i>Rebecca Ford, David Tan, Niloofar Vaghefi, and Barkat Mustafa</i>	
10.1	Plant Host Defense Mechanisms	243
10.1.1	Host versus Non-Host Resistance	243
10.1.2	Preformed and Induced Defense Responses	244
10.1.3	Reactive Oxygen Species (ROS) During an Oxidative Burst	245
10.1.4	Hypersensitive Response (HR)	245
10.1.5	Systemic Acquired Resistance (SAR)	246
10.2	Phytoalexins and Pathogenesis-Related (PR) Proteins	247
10.3	The Role of Plant Hormones in Pathogen Defense	247
10.3.1	Salicylic Acid	247
10.3.2	Jasmonic Acid	248
10.3.3	Ethylene	249
10.3.4	Abscisic Acid	249
10.3.5	Conservation and Crosstalk Within Signaling Pathways	250
10.4	The Lentil <i>Ascochyta lentis</i> Pathosystem	251

10.5	Key Defense-Related Genes Involved in <i>Ascochyta lentis</i> Defense	252
10.6	The Effect of Exogenous Hormone Treatment on PR4 and PR10 Transcription in Lentils	253
10.6.1	Bioassays and cDNA Production	255
10.6.2	PR Gene Amplification and Expression Profiling	255
10.6.3	Effects of ABA, ACC, MeJA, and SA on Lentil PR4 Gene Expression	256
10.6.4	Effects of ABA, ACC, MeJA, and SA on Lentil PR10 Gene Expression	256
10.7	Conclusions	259
	References	261

11 Signaling and Modulation of Non-Coding RNAs in plants by Abscisic Acid (ABA) 271

Raj Kumar Joshi, Swati Megha, Urmila Basu, and Nat N.V. Kav

11.1	Introduction	271
11.2	Biogenesis of Non-Coding RNAs in Plants	273
11.3	Mode of Action of ncRNAs in Plants	274
11.3.1	Mechanism of Action in Small RNAs	274
11.3.2	Mechanism of Action of lncRNAs	275
11.4	ABA Signaling in Plants	276
11.4.1	ABA Biosynthesis, Transport, and Catabolism	276
11.4.2	ABA Signal Transduction	278
11.4.3	Cis-Acting Elements and Transcription Factors in ABA-Mediated Gene Expression	278
11.4.4	ABA-Mediated Stomatal Closure During Pathogen Attack	280
11.5	Non-Coding RNAs and ABA Response	280
11.5.1	MiRNAs in ABA Signaling	280
11.5.2	Other ncRNAs in ABA Signaling	283
11.6	Conclusion and Future Prospects	285
	References	286

12 Ethylene and Stress Mediated Signaling in Plants: A Molecular Perspective 295

Priyanka Agarwal, Gitanjali Jiwani, Ashima Khurana, Pankaj Gupta, and Rahul Kumar

12.1	Introduction	295
12.2	Types of Stress	295
12.2.1	Temperature Stress	296
12.2.1.1	Cold Stress	296
12.2.1.2	Heat Stress	296
12.2.2	Water Stress	297
12.2.2.1	Drought Stress	297
12.2.2.2	Salinity stress	298
12.3	Overview of Stress Signaling	298
12.3.1	Perception of Stress	298
12.3.1.1	Perception at Plasma Membrane	298
12.3.1.2	Perception by Changed Ca ²⁺ Concentration	299
12.3.2	Action of Different Secondary Messengers	299
12.3.2.1	Reactive Oxygen Species (ROS)	299

12.3.2.2	Lipid Messengers	300
12.3.3	Ca ²⁺ as an Intermediate Signal Molecule	301
12.3.4	Role of MAPK in Stress Signaling	302
12.3.5	Role of Ethylene During Stress	302
12.3.5.1	Ethylene	302
12.3.5.2	Ethylene Biosynthesis	302
12.3.5.3	Ethylene Perception	303
12.3.5.4	Role of Ethylene in Fruit Ripening	303
12.3.6	Role of Ethylene in Abiotic Stress	304
12.3.6.1	Cold Stress	304
12.3.6.2	Heat Stress	306
12.3.6.3	Salinity Stress	307
12.3.6.4	Ethylene and Drought Stress	310
12.3.6.5	Ethylene and Flooding Tolerance	310
12.3.7	Role of Ethylene in Biotic Stress	310
12.3.7.1	Ethylene Signal Perception in Response to Biotic Stress in Plants	310
12.3.7.2	Mechanism of Action of Ethylene in Plant Pathogen Interaction	311
12.3.7.3	Crosstalk of Hormones in Plant Defense	312
12.3.7.4	Crosstalk of Ethylene with Other Hormones in Response to Biotic Stress	313
12.3.8	Role of ABA in Stress	315
12.3.9	Role of Other Phytohormones in Stress	316
12.4	Conclusion	316
	Acknowledgment	316
	References	317
13	Regulatory Function of Ethylene in Plant Responses to Drought, Cold, and Salt Stresses	327
	<i>Haixia Pei, Honglin Wang, Lijuan Wang, Fangfang Zheng, and Chun-Hai Dong</i>	
13.1	Functional Roles of Ethylene in Plant Drought Tolerance	328
13.2	Ethylene Signaling in Plant Cold Tolerance	330
13.3	Ethylene Signaling and Response to Salt Stress	333
13.4	Conclusion	336
	References	337
14	Plant Nitric Oxide Signaling Under Environmental Stresses	345
	<i>Ione Salgado, Halley Caixeta Oliveira, and Marília Gaspar</i>	
14.1	Introduction	345
14.2	Mechanisms of NO Action in Plants	346
14.3	The Control of NO Homeostasis in Plants	348
14.3.1	NO Synthesis in Plants	349
14.3.2	NO Degradation in Plants	350
14.3.3	Regulation of NO Homeostasis by S-Nitrosothiols Through the Nitrogen Assimilation Pathway	350
14.4	NO and the Response to Abiotic Stresses	351
14.4.1	Drought	351
14.4.2	Hypoxia Stress	352

- 14.4.3 Salt Stress 354
- 14.4.4 Heavy Metals 355
- 14.4.5 Low Temperature Stress 356
- 14.5 Conclusions and Future Prospects 358
- References 360

- 15 Cell Mechanisms of Nitric Oxide Signaling in Plants Under Abiotic Stress Conditions 371**
Yuliya A. Krasnylenko, Alla I. Yemets, and Yaroslav B. Blume
- 15.1 Introduction 371
- 15.2 Duality of RNS: Key Secondary Messengers in Plant Cells versus Nitrosative Stress Agents 373
- 15.3 Tyrosine Nitration as a Hallmark of Nitrosative Stress and Regulatory Post-Translational Modification 376
- 15.4 NO and Environmental Abiotic Challenges 380
- 15.4.1 Mechanical Wounding and Programmed Cell Death Progression 380
- 15.4.2 Chilling, Cold/Heat Stress, and Acclimation 380
- 15.4.3 Light Overexposure and UV Irradiation 382
- 15.4.4 Air (Ozone) and Soil Pollution (Heavy Metals, Herbicides) 384
- 15.4.5 Osmotic Stresses: High Salinity, Drought, and Flooding 386
- 15.5 Conclusions and Future Perspectives 388
- Acknowledgments 389
- References 389

- 16 S-Nitrosylation in Abiotic Stress in Plants and Nitric Oxide Interaction with Plant Hormones 399**
Ankita Sehwat and Renu Deswal
- 16.1 Introduction 399
- 16.2 S-Nitrosylation in Abiotic Stress 400
- 16.2.1 Salinity Stress 401
- 16.2.2 Cold Stress 406
- 16.2.3 Desiccation Stress 406
- 16.2.4 High Light Stress 406
- 16.2.5 Cadmium and 2,4-Dichlorophenoxy Acetic Acid (2,4-D) Stress 406
- 16.3 Nitric Oxide and Plant Hormone Interaction 407
- 16.4 Conclusions and Future Areas of Research 409
- References 409

- 17 Salicylic Acid Signaling and its Role in Responses to Stresses in Plants 413**
Pingzhi Zhao, Gui-Hua Lu, and Yong-Hua Yang
- 17.1 Introduction 413
- 17.2 Salicylic Acid Biosynthesis and Metabolism in Plants 414
- 17.2.1 SA Biosynthesis 414
- 17.2.2 SA Metabolism 416
- 17.3 Salicylic Acid: A Central Molecule in Plant Responses to Stress 417
- 17.3.1 SA-Mediated Plant Resistance to Disease 417

17.3.2	SA-Mediated Abiotic Stress Tolerance	419
17.3.2.1	Drought Stress	419
17.3.2.2	Cold and Heat Stress	421
17.3.2.3	Salinity Stress	423
17.3.2.4	Heavy Metal Stress	424
17.3.2.5	Ozone Stress and UV Radiation	425
17.3.3	Relationship Between Biotic and Abiotic Stress Factors	426
17.4	Salicylic Acid in Relation to Other Phytohormones in Response to Plant Stress Status	427
17.5	Conclusion	429
	References	429
18	Glucose and Brassinosteroid Signaling Network in Controlling Plant Growth and Development Under Different Environmental Conditions	443
	<i>Manjul Singh, Aditi Gupta, and Ashverya Laxmi</i>	
18.1	Introduction	443
18.2	Glucose Homeostasis and Signaling in Plants	444
18.3	Brassinosteroid Biosynthesis and Signaling	447
18.4	Role of Glc in Plant Adaptation to Changing Environmental Conditions	452
18.5	Role of BR in Plant Adaptation to Changing Environmental Conditions	454
18.6	Glc-BR Crosstalk and its Adaptive Significance in Plant Development	458
18.7	Conclusion and Future Perspective	459
	References	459
	Index	471

About the Editor



Girdhar K. Pandey received his B.Sc. (Hon.) in Biochemistry from Delhi University in 1992 and M.Sc. in Biotechnology in year 1994 from Banaras Hindu University (BHU). Subsequently, he joined the School of Life Sciences for his Ph.D., Jawaharlal Nehru University (JNU), and worked in the field of calcium signal transduction under abiotic stresses in plants. He was awarded the Ph.D. degree in 1999 and then pursued a post-doctoral career at the Department of Plant and Microbial Biology, University of California, Berkeley in 2000. There, he extended his work in the field of calcium-mediated signaling in *Arabidopsis* by studying

CBL-CIPKs, phosphatases, channels/transporters, and transcription factors involved in abiotic stresses. Currently, he is working as Professor in the Department of Plant Molecular Biology, Delhi University South Campus.

Pandey's research interests involve detail mechanistic interplay of signal transduction networks in plant under mineral nutrient deficiency (mostly potassium, calcium, and nitrate) and abiotic stresses such as drought, salinity, and oxidative stresses induced by heavy metals. His laboratory is working on the coding and decoding of mineral nutrient deficiency and abiotic stress signals by studying several signaling components such as phospholipases (PLA, PLC, and PLD), calcium sensors such as calcineurin B-like (CBL) and CBL-interacting protein kinases (CIPK), phosphatases (mainly PP2C and DSP), transcription factors (AP2-domain containing or ERF, WRKY), transporters and channels proteins (potassium and calcium channels/transporters), small GTPases, and Armadillo domain containing proteins in both *Arabidopsis* and rice. The long-term goal of his research group is to establish the mechanistic interplay and crosstalk of mineral nutrient deficient conditions and different abiotic stress signaling cascades in *Arabidopsis* and rice model systems by using the advance tools of bio-informatics, genetics, cell biology, biochemistry, and physiology with greater emphasis on functional genomics approaches.

See Pandey's web page for further information about his lab and research work: <https://sites.google.com/site/gkplab/home>; www.dpmb.ac.in/index.php?page=girdhar-pandey

List of Contributors

Priyanka Agarwal

Department of Plant Molecular Biology,
University of Delhi
New Delhi, India

Aditya Banerjee

Post Graduate Department of
Biotechnology,
St. Xavier's College
Kolkata, West Bengal, India

Urmila Basu

Department of Agricultural Food and
Nutritional Science,
University of Alberta,
Edmonton, Alberta, Canada

Yaroslav B. Blume

Department of Genomics and Molecular
Biotechnology,
Institute of Food Biotechnology and
Genomics,
National Academy of Sciences of Ukraine
Kyiv, Ukraine

Renu Deswal

Molecular Plant Physiology and
Proteomics Laboratory,
Department of Botany,
University of Delhi
Delhi, India

Jeremy Dkhar

Stress Physiology and Molecular Biology
Laboratory,
School of Life Sciences,
Jawaharlal Nehru University
New Delhi, India

Chun-Hai Dong

Qingdao Agricultural University
Qingdao, Shandong, China

Padmanabh Dwivedi

Department of Plant Physiology,
Institute of Agricultural Sciences,
Banaras Hindu University
Varanasi, India

Rebecca Ford

School of Natural Sciences,
Griffith University
Queensland, Australia

Krishna GK

Division of Plant Physiology,
Indian Agricultural Research Institute
New Delhi, India

Marília Gaspar

Núcleo de Pesquisa em Fisiologia e
Bioquímica,
Instituto de Botânica de São Paulo
São Paulo, Brazil

Sirhindi Geetika

Department of Botany,
Punjabi University
Patiala, India

Aditi Gupta

National Institute of Plant Genome
Research
Aruna Asaf Ali Marg,
New Delhi, India

Interdisciplinary Centre for Plant
Genomics,
University of Delhi South Campus
New Delhi, India

Pankaj Gupta

Central Research Institute for
Homeopathy
Noida, UP India

Kaur Harpreet

Department of Botany,
Punjabi University
Patiala, India

Xuan LanThi Hoang

School of Biotechnology,
International University,
Vietnam National University HCMC
Ho Chi Minh City, Vietnam

Xingliang Hou

Key Laboratory of South China
Agricultural Plant Molecular Analysis
and Genetic Improvement,
South China Botanical Garden,
Chinese Academy of Sciences,
Guangzhou, China

Gitanjali Jiwani

Department of Plant Molecular Biology,
University of Delhi
New Delhi, India

Raj Kumar Joshi

Department of Agricultural Food and
Nutritional Science,
University of Alberta,
Edmonton, Alberta, Canada and
Centre of Biotechnology,
Siksha O Anusandhan University
Bhubaneswar, India

Nat N.V. Kav

Department of Agricultural Food and
Nutritional Science,
University of Alberta,
Edmonton, Alberta, Canada

Ashima Khurana

Zakir Husain College,
University of Delhi
New Delhi, India

Yuliya A. Krasylenko

Department of Genomics and Molecular
Biotechnology,
Institute of Food Biotechnology and
Genomics,
National Academy of Sciences of Ukraine
Kyiv, Ukraine

Rahul Kumar

RTGR, Department of Plant Sciences,
University of Hyderabad
Hyderabad, India

Kundan Kumar

Department of Biological Sciences,
Birla Institute of Technology & Science
Pilani
Goa, India

Ashverya Laxmi

National Institute of Plant Genome
Research
Aruna Asaf Ali Marg,
New Delhi, India

Yuge Li

Key Laboratory of South China
Agricultural Plant Molecular Analysis
and Genetic Improvement,
South China Botanical Garden,
Chinese Academy of Sciences,
Guangzhou, China

Gui-Hua Lu

NJU–NJFU Joint Institute for Plant
Molecular Biology,
State Key Laboratory of Pharmaceutical
Biotechnology,
School of Life Sciences,
Nanjing University,
Nanjing, China

Swati Megha

Department of Agricultural Food and
Nutritional Science,
University of Alberta,
Edmonton, Alberta, Canada

Ahmad Mir Mudaser

Department of Botany,
Punjabi University
Patiala, India

Barkat Mustafa

Department of Environment and Primary
Industries,
Victorian AgriBiosciences Centre, La
Trobe University
Victoria, Australia

Halley Caixeta Oliveira

Departamento de Biologia Animal e
Vegetal,
Centro de Ciências Biológicas,
Universidade Estadual de Londrina (UEL),
Londrina, Brazil

Ashwani Pareek

Stress Physiology and Molecular Biology
Laboratory,
School of Life Sciences,
Jawaharlal Nehru University
New Delhi, India

Pratap Kumar Pati

Department of Biotechnology,
Guru Nanak Dev University
Amritsar, Punjab, India

Iva Pavlović

Department for Molecular Biology,
Ruđer Bošković Institute
Zagreb, Croatia

Lekshmy S

Division of Plant Physiology,
Indian Agricultural Research Institute
New Delhi, India

Haixia Pei

Qingdao Agricultural University
Qingdao, Shandong, China

Sharma Poonam

Department of Botany,
Punjabi University
Patiala, India

Sairam RK

Division of Plant Physiology,
Indian Agricultural Research Institute
New Delhi, India

Aryadeep Roychoudhury

Post Graduate Department of
Biotechnology,
St. Xavier's College
Kolkata, West Bengal, India

Mushtaq Ruqia

Department of Botany,
Punjabi University
Patiala, India

Jha SK

Division of Genetics,
Indian Agricultural Research Institute
New Delhi, India

Ankush Ashok Saddhe

Department of Biological Sciences,
Birla Institute of Technology & Science
Pilani
Goa, India

Shivani Saini

Department of Biotechnology,
Guru Nanak Dev University
Amritsar, Punjab, India

Ione Salgado

Departamento de Biologia Vegetal,
Instituto de Biologia,
Universidade Estadual de Campinas
(UNICAMP), Campinas, Brazil

Branka Salopek-Sondi

Department for Molecular Biology,
RuđerBošković Institute
Zagreb, Croatia

Dunja Šamec

Department for Molecular Biology,
RuđerBošković Institute
Zagreb, Croatia

Ankita Sehrawat

Molecular Plant Physiology and
Proteomics Laboratory,
Department of Botany,
University of Delhi
Delhi, India

Ashutosh Sharan

Stress Physiology and Molecular Biology
Laboratory,
School of Life Sciences,
Jawaharlal Nehru University
New Delhi, India

Isha Sharma

Department of Biotechnology,
Guru Nanak Dev University
Amritsar, Punjab, India

Manjul Singh

National Institute of Plant Genome
Research
Aruna Asaf Ali Marg,
New Delhi, India

Interdisciplinary Centre for Plant
Genomics,
University of Delhi South Campus
New Delhi, India

Sneh Lata Singla-Pareek

Plant Molecular Biology,
International Centre for Genetic
Engineering and Biotechnology,
New Delhi, India

Ana Smolko

Department for Molecular Biology,
RuđerBošković Institute
Zagreb, Croatia

Saad Sulieman

Signaling Pathway Research Unit,
RIKEN Center for Sustainable Resource
Science,
Yokohama, Japan and
Department of Agronomy, Faculty of
Agriculture,
University of Khartoum
Khartoum North, Sudan

David Tan

Faculty of Veterinary and Agricultural
Sciences,
The University of Melbourne
Victoria, Australia

Nguyen Phuong Thao

School of Biotechnology,
International University,
Vietnam National University HCMC
Ho Chi Minh City, Vietnam

Nguyen Binh Anh Thu

School of Biotechnology,
International University,
Vietnam National University HCMC
Ho Chi Minh City, Vietnam

Lam-Son Phan Tran

Signaling Pathway Research Unit,
RIKEN Center for Sustainable Resource
Science
Yokohama, Japan

Mai Thuy Truc

School of Biotechnology,
International University,
Vietnam National University HCMC,
Ho Chi Minh City, Vietnam and
John Carroll University,
University Heights, OH, USA

Nilofar Vaghefi

Cornell University,
Plant Pathology & Plant-Microbe Biology
Section
Geneva, NY, USA

Honglin Wang

Qingdao Agricultural University
Qingdao, Shandong, China

Lijuan Wang

Qingdao Agricultural University
Qingdao, Shandong, China

Yong-Hua Yang

NJU–NJFU Joint Institute for Plant
Molecular Biology,
State Key Laboratory of Pharmaceutical
Biotechnology,
School of Life Sciences,
Nanjing University,
Nanjing, China

Alla I. Yemets

Department of Genomics and Molecular
Biotechnology,
Institute of Food Biotechnology and
Genomics,
National Academy of Sciences of Ukraine
Kyiv, Ukraine

Pingzhi Zhao

NJU–NJFU Joint Institute for Plant
Molecular Biology,
State Key Laboratory of Pharmaceutical
Biotechnology,
School of Life Sciences,
Nanjing University,
Nanjing, China

Fangfang Zheng

Qingdao Agricultural University
Qingdao, Shandong, China

Preface

One of the basic biological differences between plants and animals is in their habit of growth and development. During the processes of evolution, unlike animals, plants adopted sessile and relatively immobile growth habits to complete their lifecycle. However, common key chemical communicators called “hormones” regulate growth and development in a similar fashion in plants and animals. Plant hormones are known as “phytohormones,” which act locally and systemically to regulate their growth and development. The importance of phytohormones in a plant’s biological activities can be perceived well typically in a tissue culture system, where a slight alteration in the level of various hormones lead to development of undifferentiated mass of cells called the *callus*.

The Phytohormones act at a very low concentration, usually in nano- to micro molar amounts within a plant cell. Owing to this, initial attempts to understand the biochemical and functional role of phytohormones remained inconclusive. However, with the help of chemical synthesis, large-scale purification, and through mutant based genetic approaches, valuable information to understand the underlying mechanism has been unearthed for the role of phytohormones over the past few decades. The detailed biosynthetic and signal transduction pathways have been identified for most of the classical phytohormones like auxin, abscisic acid, gibberlin, cytokinin, and ethylene along with the newly discovered brassinosteroids, salicylic acid, jasmonic acid, nitric oxide, and others. Using the tools of genetics, biochemistry, and molecular biology, plant biologists are now able to develop a concrete roadmap starting from the biosynthesis to perception and action of many of these phytohormones in regulating physiological and developmental responses.

Mounting evidence suggest that, besides regulating the growth of plants, phytohormones are the critical factors that also play a role in fine-tuning the metabolism and physiology of the plants under varying environmental cues. In the natural growth environment, plants perceive a large number of favorable (nutrient, water, light) and unfavorable stimuli (abiotic and biotic stresses), which influence their growth and development. To counteract these adverse conditions, plants have developed an intricate web of complex machineries to translate perceived stress signal into effective response by modulating the gene expression or directly affecting the physiology of the cell. Phytohormones or plant growth regulators are the key chemical molecules that are involved in broad spectrum of signaling pathways in response to a particular abiotic or biotic stress mounting an effective defense response.

Similar to other signaling molecules, phytohormones act coordinately to generate synergistic, antagonistic, and additive or subtractive responses. The direct indication of this cross talk is considered to be based on molecular interactions between factors regulating phytohormone signal action pathways. Thus, to elucidate the molecular mechanism of possible integration of phytohormone signaling pathways with the intermediates of other signaling cascades under a given condition requires the major attention of plant biologists.

More than ever, in the current state where aggressive climate change, rapidly growing population, and diminishing fertile land due to increased exploitation of natural resources imposes serious threat to crop production worldwide. And so, the major focus of plant biologists across the world is to improve crop productivity and yield. With the development of gene cloning, genetic engineering, and genome editing, modification of a food crop's genetic makeup to accustom it toward changing conditions paves way for the possibility of development and enhancement of tolerance against these stresses. In the field conditions, crops are constantly exposed to multitude of stresses and efforts are being focused towards generating new crop varieties that can tolerate these multiple stresses without yield loss. Detail molecular understanding of the cross talk and interaction of different phytohormones would certainly open new directions to design strategies to generate stress tolerant high yielding crop varieties.

In the post-genomic era, one of the major challenges is the functional analysis and understanding of plant hormone associated multiple genes and gene families regulating a particular physiological and developmental aspect of plant lifecycles. One of the important physiological processes is stress response regulation, which leads to adaptation in response to adverse stimuli. With the holistic understanding of the molecular mechanism of plant hormones associated signaling involving more than one gene family, plant biologist can lay the foundation for designing and generating future crops, which can withstand adverse environmental conditions without compromising on yield and productivity.

This book on *Mechanism of Plant Hormone Signaling under Stress* comprises of two volumes (Volume I and Volume II with 18 chapters in each). Several plant biologists throughout the world have contributed in the field of 'mechanisms of plant hormone action' in plants with a special emphasis on 'stress signaling in plants'. This book describes the timely and state-of-art contribution to knowledge in the field of 'phytohormone mediated signaling under stress' to develop a better and holistic understanding of hormone stress perception, transduction followed by the generation of response.

Despite of availability of large number of publications in the field of action of phytohormones during stress conditions, the in-depth analysis of this aspect has not been covered in previous books and volumes. Above all, the topics include a greater emphasis on genomics and functional genomics aspects in order to understand the global and whole genome level changes under particular stress conditions through a functional genomics perspective.

With functional genomics tools, the mechanisms of phytohormone signaling and their target genes can be defined in a more systematic manner. The integrated analysis of phytohormone signaling under single or multiple stress conditions may prove exceptional to design stress tolerant crop plants in field conditions. Toward achieving

this goal, the book is divided into four sections. Volume I comprises the first part where 18 chapters on *Action of Phytohormones in Stress* discusses the mechanistic action of the most common phytohormones, and their roles in stress signaling in plants. These chapters will aware the readers primarily on the detailed signaling pathways and their roles in various stress conditions in plants. The first three chapters (Chapter 1–3) are dealing with the various aspects of biosynthesis, signaling, and action of classical phytohormone, auxin in multiple stress conditions. The Chapter 4 describes the metabolism, homeostasis, and signaling pathways of another classical phytohormone, cytokinin, known to regulate growth and differentiation in plants, also involved in various stress conditions. GA also belongs to the category of classical phytohormone regulating plant growth by cell division and elongation. Chapter 5 and 6 discuss the various roles of GA, its metabolism, signal transduction pathways, and also its interaction with JA in stress conditions in plants. In continuation with Chapter 6, where interaction of GA with JA is discussed, their elaborate role, metabolism, and signaling pathway is discussed in detail in Chapter 7 with a special emphasis of JA in stress management. The another typical phytohormone, ABA, long known to regulate stress related responses in plants is extensively discussed in Chapters 8–11, where different contributors have discussed its in-depth signal transduction and mechanism of action in regulating both abiotic and biotic stresses. Ethylene is also a conventional gaseous hormone known to regulate fruit ripening and senescence in plants. Chapters 12 and 13 discusses the elaborate aspects of ethylene signal transduction and responses under both abiotic and biotic stresses and cross talk with other phytohormones. Chapters 14 to 16 emphasizes the signal transduction and detail role of another gaseous hormone, nitric oxide or NO and the process of S-nitrosylation in several abiotic stress conditions in plants. Salicylic acid (SA) is mostly appreciated as an important phytohormone regulating biotic stress. SA is also well elaborated upon in multiple abiotic stresses in Chapter 17. The last chapter of the Part I (Chapter 18) describes the complex interplay of brassinosteroid (BR) and glucose in growth and development, and also during environmental stress conditions.

Volume II of this book contains three parts (Parts II–IV) consisting of 18 chapters in total. Part II of this book describes the role of several different factors that are intangibly linked with phytohormone signaling under biotic and abiotic stresses. Chapters 1 and 2 elaborate the role of reactive oxygen species (ROS) in regulating both abiotic and biotic stress responses. ROS are key signaling molecules, which are also interacting and participating in multiple phytohormone-mediated signaling and response pathways during various stress conditions in plants. Calcium (Ca^{2+}) is a metal ion involved in regulating a plethora of biological processes including stress signal transduction pathways in plants. Ca^{2+} acts as second messenger and is involved in signaling pathways of several phytohormones. The most studied phytohormone where Ca^{2+} is a pivotal signaling molecule is abscisic acid (ABA) regulating several abiotic stress responses. Chapter 3 focuses on the role of Ca^{2+} signaling components and their complex interplay with multiple phytohormones in plants. Chapter 4 reports the role of phospholipids in regulating various signaling pathways during biotic and abiotic stresses and their interaction with phytohormones. Emerging evidences showing effects of biotic and abiotic stresses on cytoskeletal protein network mediated through different phytohormone is highlighted in Chapter 5. In the Chapter 6, the role of several proteins involved in metabolism, transport, and signal transduction of different phytohormones is discussed. Further, increased use of man-made chemicals such as organic compounds mainly used as

pesticides, herbicides, and fungicides has resulted in the accumulation of these xenobiotic compounds in the environment that leads to interference with plant hormone signaling and metabolism. Chapter 7 articulates important aspects of interaction of xenobiotic compounds with phytohormone signaling and metabolism, and opens up new possibilities to investigate these aspects at molecular levels. In Chapter 8, the role of phytohormone mediated signaling in several metal stresses and how plants changes their growth and development in response to toxic metal ions is well documented.

Part III (in Volume II) of this book comprised of three chapters, which mainly discusses the role of transcription factors, transcription activators, and microRNA in the regulation of phytohormones related gene expression under stress and developmental conditions. In Chapter 9, the development of stomata by several transcription factors and their regulation by multiple phytohormones is described. Since stomata is the gate-keeper that controls the passage of gases like CO₂, O₂, and are responsible for the transpirational pull of water and nutrients from the soil, their opening and closure is thoroughly fine-tuned by several phytohormones, majorly by ABA. This chapter details the interplay of phytohormones in the development of stomata and their regulation under abiotic stresses mediated by multiple phytohormones. Chapter 10 describes the role of the phytohormone regulated mediator complex. This is a large multimeric transcriptional activator complex, involved in regulating the transcription of multiple stress inducible genes. In Chapter 11, the complex regulatory roles of micro-RNA in modulating the gene expression in phytohormones and abiotic stress conditions are extensively elucidated.

The last part of this book (in Volume II), Part IV is comprised of seven chapters, mainly discussing the roles of multiple phytohormones in diverse stress adaptive responses. The first chapter in this section, i.e., Chapter 12 confers on the role of multiple phytohormones and microbial elicitors in regulating the signaling pathway in guard cell during stomatal closure. Chapter 13 elaborates on how phytohormones are involved in regulating pathogen infection and plant defense and immune response during biotic stress. In Chapter 14, the role of multiple phytohormones is described in regulating both seed development and stress responses. The important role and interaction of multiple phytohormones is once more discussed in abiotic and biotic stress responses in Chapter 15 with special emphasis on SA and its interaction with other phytohormones. With the identification of multiple phytohormones signaling pathways, it is well appreciated that many of these phytohormone shows the complex interaction because of convergence and overlap of signal transduction components such as kinases, phosphatases, transcription factors, and other signaling molecules. Chapters 16 and 17 highlight the complex interplay of several phytohormones in abiotic and biotic stress regulation and crosstalk. The last chapter of this section, Chapter 18, emphasizes on the transgenic approaches to manipulate crop productivity by altering the levels of several phytohormones. With an in-depth understanding of several signal transduction components mediated by phytohormones, the ultimate goal is to translate this mechanistic knowledge into useful tools to generate crop varieties with either genetic alteration of these signaling components, or to utilize this knowledge for molecular-marker assisted breeding, which ultimately augment stress tolerance in crop plants without compromising their productivity.

Despite my rigorous attempts, not all aspects of phytohormone signaling and components could be discussed here because of space constraints. Nevertheless, I strongly

believe that this book, covering different characteristics of phytohormone signal transduction machinery with a special emphasis on the mechanistic action under stress conditions will prove extremely useful to students, teachers, and research scientists.

I am grateful to all the contributors of this work, which could not be possibly compiled without their significant contributions. At last, I would like to express my sincere thanks to Dr. M.C. Tyagi, Dr. Amita Pandey, and Ms. Manisha Sharma for critical reading and constructive suggestions related to this book. Ms. Manisha Sharma is also acknowledged for designing the cover page of this book. I am also thankful to Delhi University, University Grant Commission, Department of Biotechnology, Department of Science and Technology, and Council of Scientific and Industrial Research, India for supporting research in my laboratory.

Girdhar K. Pandey
(Editor)

