

Mohd Tanveer Alam Khan
Mohammad Yusuf
Fariduddin Qazi
Aqeel Ahmad *Editors*

Brassinosteroids Signalling

Intervention with Phytohormones and
Their Relationship in Plant Adaptation
to Abiotic Stresses

Brassinosteroids Signalling

Mohd Tanveer Alam Khan • Mohammad Yusuf •
Fariduddin Qazi • Aqeel Ahmad
Editors

Brassinosteroids Signalling

Intervention with Phytohormones and Their
Relationship in Plant Adaptation to Abiotic
Stresses

Editors

Mohd Tanveer Alam Khan
College of Life Science and Technology
Huazhong Agricultural University
Wuhan, China

Mohammad Yusuf 
Department of Biology
United Arab Emirates University
Al Ain, United Arab Emirates

Fariduddin Qazi
Department of Botany
Aligarh Muslim University
Aligarh, Uttar Pradesh, India

Aqeel Ahmad
Vegetable Research Institute,
Guangdong Academy of Agricultural
Sciences/Guangdong Key Laboratory
for New Technology Research
of Vegetables,
Guangzhou, China

ISBN 978-981-16-5742-9

ISBN 978-981-16-5743-6 (eBook)

<https://doi.org/10.1007/978-981-16-5743-6>

© Springer Nature Singapore Pte Ltd. 2022

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Singapore Pte Ltd.

The registered company address is: 152 Beach Road, #21-01/04 Gateway East, Singapore 189721, Singapore

Dedicated to my Parents
(MOHD AYYUB KHAN AND ANJUM
AFROJ)

Preface

The book attempts to update on the state of the art of the knowledge on brassinosteroids signaling and crosstalk with phytohormones and their relationship in plant adaptation to abiotic stresses involving physiological, biochemical, and molecular processes. Due to progressively adverse environmental conditions and scarce natural resources, high-efficient crops become more important than ever. More importantly, sustainable agriculture and food security are a major concern, especially for the areas prone to abiotic stress conditions. Abiotic stress such as cold, drought, salt, and heavy metals largely influences plant development and crop productivity. It is becoming a major threat to food security due to the constant change of climate and the deterioration of the environment caused by human activity. To cope with abiotic stress, plants can initiate a number of molecular, cellular, and physiological changes to respond and adapt to such stresses. Better understanding of plant responsiveness to abiotic stress will aid in both traditional and modern breeding applications towards improving stress tolerance. For successful development of stress-tolerant plants, it is important to understand precise signaling mechanisms that plants use to tolerate stresses and how much these mechanisms are induced by phytohormones. Moreover, it is debatable at which point plants could have acquired brassinosteroids (BRs) signaling from an evolutionary perspective. BRs are involved in modulating a large array of important functions throughout a plant's life cycle. BRs are considered as one of the most important plant steroidal hormones that show varied role in observing a wide range of developmental practices in plants. At cellular levels, BRs regulate cell elongation, division, and differentiation. At whole plant levels, BRs regulate male fertility, flowering time, root meristem size, and development of stomata and are involved in diverse abiotic and biotic stress responses. Exogenously applied BRs have the ability to substantially enhance plants yield and improve stress tolerance by inducing cellular changes like stimulation of nucleic acid and protein synthesis, activation of ATPase pump, antioxidant enzymes and accumulation of osmoprotectants, induce other hormone responses, regulate expression of stress-responsive genes, and improve

photosynthetic efficiency. Our grip of brassinosteroids signaling has rapidly expanded over the past two decades, due in part to the isolation of the components involved in the signal transduction pathway. The book offers a helpful guide for plant scientists and graduate students in related areas.

Chapter 1 of this book (which represents a total of 16 chapters) talks about molecular links between BR and several other signaling pathways under abiotic stress. In this chapter, we provide a summary of the highly incorporated BR signaling network and elucidate how this steroid hormone functions as a master regulator of plant growth, development, and metabolism. Chapter 2 discusses the specific role of BRs at different stages of seed germination, focuses on the signaling factors, and categorizes the signaling mechanisms. However, all the details have been provided with a special focus on proteins associated with BR. The chapter has also enlisted the BR-sensitive proteins along with their specific roles in cell physiology and metabolism. It describes the details of BR-sensitive proteins at three stages of seed germination and differentiates BR signaling into two distinct pathways. A total number of 88 protein species have been found to be BR-sensitive, for which the international identifiers and cellular activities have been described. Nitric oxide and brassinosteroids positively influence plant responses to abiotic stresses, such as temperature stress, heavy metal stress, water stress, oxidative stress, salt stress, and UV radiation, which is discussed in Chap. 3. The intent of the chapter is to explain how BRs and NO interact with each other and regulate various metabolic processes in plants and improve growth, photosynthesis, antioxidative defense system, and ROS homeostasis under normal and abiotic stress conditions. Chapter 4 provides an overview of current understanding on the signaling of BRs and H_2O_2 and their interplay in modulating plant growth and development, in particular seed germination, root growth, stomatal movement, leaf senescence, and fruit ripening, in addition to providing an overview of their interaction under diverse abiotic stress factors. More importantly, gene expression by mitogen-activated protein kinases, BZR1, BES1, SINAC2, and other transcription factors which modulate abiotic stresses in plants have also been sectioned. In Chap. 5, we provide some insights on brassinosteroids and strigolactones signaling pathways and emphasize on recent findings on the mechanisms and networks for BR and SL-regulated gene expression and various transcriptional networks involved in the signaling pathways. Chapter 6 describes brassinosteroids (BRs) and gibberellins (GAs), which play their role to promote plant growth-related developmental processes. Recent advancements in molecular tools have now provided a better understanding of phytohormones biosynthesis, signaling, and degradation pathways. For the elaboration of signaling crosstalk between BRs and GAs, different studies have been performed with the conclusion that, to control cell elongation in *Arabidopsis*, signaling crosstalk between BRs and GAs is mediated by the interaction between BZR1/BES1 and DELLA proteins which are the transcriptional regulators from BR and GA signaling pathways. Chapter 7 examines the interrelation of ethylene and BRs during different developmental stages. It also highlights the two hormones' role

during fruit ripening, stomatal closure, reproduction, abiotic stresses, and biotic stresses. The BRs and ethylene possess an antagonistic influence on the expansin gene *AtEXPA5* expression. That antagonistic interrelation is responsible for the hook formation during the gravitropic growth of hypocotyls. The ethylene and BRs crosstalk comprises a complex network of signaling pathways, e.g., the ACC synthase pathway. Chapter 8 is devoted to different groups of plant hormones (Auxin and BRs), which regulate many processes from seed germination to fruit development independently. But in recent years, several studies have revealed a common link between these two hormones in regulation of plant developmental processes. A recent advancement in molecular tools has made it possible to better understand the mechanism of signal transduction of the interaction of BRs and auxin. So, in this book chapter we discuss the physiological responses of plants induced through the interplay of BRs and auxin and its detailed mechanism of signal transduction pathway. In Chap. 9 we provide an overview of the role of BR in plant growth and development and then discuss how BRs react under different environmental stress conditions. We will also highlight how BRs function with ABA to regulate plant growth and development. At the end, we review our understanding of BRs crosstalk with ABA and elaborate its genetic basis to overcome the gap in our knowledge related to BR crosstalk with ABA. Chapter 10 inspects the interrelation of cytokinins and BRs throughout diverse developmental points. It also highlights the physiological response of plants convinced through interaction of BRs and cytokinins and its detailed mechanism of signal transduction pathway. Chapter 11 gives us an opportunity to improve the growth efficiency of plants and their adaptation under heavy metal stress through modulation in BR signaling pathway, hormone interactions, and crosstalk at organ, tissue, and cell levels to better understand how plants respond to heavy metal stress. In Chap. 12 an attempt has been made to give a comprehensive idea over the uptake, transportation, effect, and detoxification mechanism of pesticides in plants. However, BRs strengthen the plant's defense potential by stimulating the enzymatic and nonenzymatic antioxidative mechanisms which scavenge the generated ROS and activate the pesticidal detoxifying transcripts. Therefore, understanding the BRs-mediated pesticide degradation process in plants is vital for global food security. Chapter 13 specially debates the role of glyphosate and brassinosteroids applications in plants. So, this chapter offers to reveal the function of BRs in the management of glyphosate, and current research illuminates the detoxification of BR-regulated glyphosate in plants. Chapter 14 focuses on the basic information regarding distribution of important SM and in vitro strategies involved for optimal metabolite production with special reference to the use of BR as abiotic elicitor in improving metabolite yields in hairy root cultures. Chapter 15 discusses how heat stress could function in protein folding during BR action is poorly understood. This chapter focuses on the current status of our understanding about the role of BRs in protein folding under high temperature stress. In Chap. 16, we focus on representing the molecular mechanism, genes, and cascades in plants (both *Arabidopsis* and crop plants) for controlling growth-related factors. These techniques upon allocation in crops can set out

perceptible biological and cellular BR mechanism and its future application in controlling traits that can serve as a potential tool for enhancing yield and quality.

Wuhan, China
Al Ain, United Arab Emirates
Aligarh, Uttar Pradesh, India
Guangzhou, China

Mohd Tanveer Alam Khan
Mohammad Yusuf
Fariduddin Qazi
Aqeel Ahmad

Acknowledgements

First and foremost I thank Almighty God, the most merciful, who showered His gracious blessings upon us all and directed all the networks to work in consistency and coordination from the conception of the idea to the progress of the final version of this book *Brassinosteroids Signalling: Intervention with Phytohormones and Their Relationship in Plant Adaptation to Abiotic Stresses* till the successful completion of the work.

With great preference, we extend our heartfelt appreciation to all the contributors for their well-timed response, their outstanding and current contributions, and consistent support and collaboration. We are also thankful to Prof. Shamsul Hayt, Department of Botany, Aligarh Muslim University, Aligarh, for his inspiration. We are greatly thankful to Springer Singapore for speedy acceptance of our proposal and completion of the review process. Succeeding cooperation and understanding of their staff is also thankfully acknowledged. Finally, we express our sincere cheers to the members of our family for all the support they provided and the neglect and loss they hurt during the preparation of this book.

Mohd Tanveer Alam Khan
Mohammad Yusuf
Fariduddin Qazi
Aqeel Ahmad

Contents

1	Signal Transduction of Brassinosteroids Under Abiotic Stresses . . .	1
	Mohd Tanveer Alam Khan, Mohammad Yusuf, Waheed Akram, and Fariduddin Qazi	
2	Plant Proteomics and Metabolomics Investigations in Regulation of Brassinosteroid	17
	Aqeel Ahmad, Iqra Shahzadi, Waheed Akram, Nasim Ahmad Yasin, Waheed Ullah Khan, and Tingquan Wu	
3	Crosstalk Between Brassinosteroids and Nitric Oxide Regulates Plant Improvement During Abiotic Stress	47
	Fareen Sami, Shamsul Hayat, and Fariduddin Qazi	
4	Interaction Between Brassinosteroids and Hydrogen Peroxide Networking Signal Molecules in Plants	59
	Faroza Nazir, Fariduddin Qazi, and Mohd Tanveer Alam Khan	
5	Brassinosteroids and Strigolactone Signaling in Plants	81
	Anjuman Hussain, Faroza Nazir, and Fariduddin Qazi	
6	Mechanism Associated with Brassinosteroids Crosstalk with Gibberellic Acid in Plants	101
	Hafiz Muhammad Khalid Abbas, Syed Muhammad Hassan Askri, Sajid Ali, Ammara Fatima, Muhammad Tahir ul Qamar, Shu-Dan Xue, Zafarullah Muhammad, Waheed Akram, and Yu-Juan Zhong	
7	Brassinosteroid and Ethylene-Mediated Cross Talk in Plant Growth and Development	117
	Iqra Shahzadi, Aqeel Ahmad, Zarish Noreen, Waheed Akram, Nasim Ahmad Yasin, and Waheed Ullah Khan	

8	Interplay of Brassinosteroids and Auxin for Understanding of Signaling Pathway	137
	Gausiya Bashri, Abreeq Fatima, Shikha Singh, and Sheo Mohan Prasad	
9	Brassinosteroids Cross Talk with ABA Under Stress Condition . . .	155
	Samavia Mubeen, Wajid Saeed, Aqeel Ahmad, and Iqra Shahzadi	
10	Cross Talk Between Brassinosteroids and Cytokinins in Relation to Plant Growth and Developments	171
	Nasim Ahmad Yasin, Anis Ali Shah, Aqeel Ahmad, and Iqra Shahzadi	
11	Role of Brassinosteroids and Its Cross Talk with Other Phytohormone in Plant Responses to Heavy Metal Stress	179
	Mohammad Yusuf, Mohd Tanveer Alam Khan, Mohammad Faizan, Radwan Khalil, and Fariduddin Qazi	
12	Mechanism Associated with Brassinosteroids-Mediated Detoxification of Pesticides in Plants	203
	Palak Bakshi, Shagun Bali, Pooja Sharma, Mohd Ibrahim, Kamini Devi, Neerja Sharma, Ashutosh Sharma, Amrit Pal Singh, Bilal Ahmad Mir, and Renu Bhardwaj	
13	Glyphosate: Is Brassinosteroids Application a Remedy?	223
	Taiba Saeed, Aqeel Ahmad, Mohd Tanveer Alam Khan, and Iqra Shahzadi	
14	The Production of High-Value Secondary Metabolites Through Hairy Root Transformation in the Presence of Brassinosteroids . . .	239
	Taiba Saeed, Anwar Shahzad, and Vikas Yadav	
15	Role of Brassinosteroids in Protein Folding Under High-Temperature Stress	259
	Mohammad Faizan, Fangyuan Yu, Vishnu D. Rajput, Tatiana Minkina, and Shamsul Hayat	
16	Molecular Mechanism of Brassinosteroids in Boosting Crop Yield	269
	Reena Dubey and Deepti Tiwari	
	Index	293

Editors and Contributors

About the Editors

Mohd Tanveer Alam Khan is a Leibniz-DAAD postdoctoral fellow at Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany. His main focus of research is in understanding the integrative analysis of low temperature stress defense responses in *Arabidopsis thaliana* with respect to brassinosteroids signaling and metabolite patterns. He completed his BSc, MSc, and PhD from the Department of Botany at Aligarh Muslim University, Aligarh, India. Before joining the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany, he has worked as a postdoctoral fellow at National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan, P.R. China. His area of research is to dissect the abiotic stress tolerance mechanism in plants through engineered signaling, proteomics, metabolomics, and biochemical traits in the presence and absence of phytohormones. During the span of eight and half years as researcher, he has published more than 21 research articles in the journal of international repute, with a total impact factor of more than 50 and 500 citations along with an h-index of 16 and also contributed two book chapter to book edition published by Springer. During his PhD and post-PhD tenure, he was awarded several research fellowships, including CST-UP-RA, SERBNPDF, and international PDF at Huazhong Agricultural University in Wuhan, China, and at the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany.

Mohammad Yusuf is Lecturer in the Department of Biology at United Arab Emirates University, Al Ain, UAE. Mohammad received his PhD in Plant Physiology and MSc in Botany (Plant Physiology) from Aligarh Muslim University, India. He has worked as the SERB-Young Scientist and also an awardee of the prestigious Dr. D.S. Kothari Postdoctoral Fellowship from the Government of India. He has also been invited to present his work at Huazhong Agricultural University (HAU), Wuhan, China. Mohammad's research contribution includes more than 50 research

articles in the international journal of repute and also more than 2500 google scholar citations with 26 h-index. He is exploring phytohormones-mediated abiotic stress tolerance mechanism in crop plants through proline metabolism.

Fariduddin Qazi is Professor of Botany at Aligarh Muslim University, Aligarh, India, where he has been serving as faculty since 2006. He has been extensively working in the field of agricultural biotechnology to explore the abiotic stress tolerance mechanism in plants through physiological and molecular approaches. The findings of his work have revealed that brassinosteroids (BRs) and salicylic acid improved the yield and quality of plants under low temperatures, salt, water, and heavy metal stress and could be exploited as a farmer-friendly tool to overcome the menace of crop losses due to various abiotic stresses. Moreover, his findings have also revealed the potential role of hydrogen peroxide and polyamines in conferring tolerance to abiotic stresses in crop plants. His lab is extensively using proteomic approaches to reveal the novel pathway protein expressed under various abiotic stresses in plants. He had visited Göttingen University, Göttingen, Germany, for six months under BOYSCAST Fellowship and conducted experiments related to the topic “Molecular studies of salt tolerance in *Arabidopsis thaliana*.” He has visited Michigan State University, Michigan, USA, on an International Research Project with a specific objective to generate information on “Host target modification as a strategy to counter pathogen hijacking of the jasmonate hormone receptor” (Published in PNAS, 2015). He has published more than 80 research papers in the international journal of high impact factor such as *Proceedings of the National Academy of Sciences, USA, Food Chemistry, Plant Physiology and Biochemistry, Chemosphere, Journal of Integrative Plant Biology, Environmental and Experimental Botany, Ecotoxicology and Environmental Safety*, and many more with a total citation of 4925 and an h-index of 32. He had presented his findings in various conferences held in the USA, Germany, China, Malaysia, etc. He has successfully completed various funded research projects from reputed funding agencies. He has also supervised six doctoral students and three MPhil students and a number of master’s students, and presently five students are enrolled under his supervision for PhD degrees.

Aqeel Ahmad is a young and energetic researcher, working in the field of stress physiology. He earned his doctoral degree (PhD) from the University of the Punjab, Lahore, Pakistan, and performed his research work at the University of Florida, USA. Then, he joined Huazhong Agricultural University as a Postdoctoral Fellow, and now he is serving Guangdong Academy of Agricultural Sciences as Postdoctoral Fellow. He extensively studied plant defense responses (i.e., defense genes, hormones, PR proteins, and biochemicals) against the plant pathogens. His core skills are proteomics (profiling, characterization, and supramolecular kinetics) and metabolomics, by using which he elucidated cell signaling to understand plant defenses, based on oxidative enzymes of the phenylpropanoid pathway. Transcriptomics further strengthened his scientific findings concerning cell responses towards pathogenic invasions and abiotic stresses. He has devised

bioactive metabolites (e.g., benzimidazole and benzenedicarboxylic acid) to control plant pathogens and to augment the nutritional quality of our plant-based foods. He has developed techniques to make edible plants tolerant against environmental stressors by reharmonizing their osmoregulatory systems, oxidative machinery, and physiological responses. He has published 59 research manuscripts in world-renowned journals and won three research grants and one research honor award at such a young age of 32 years. A wide spectrum of publication platforms is evident from his scientific articles including the leading journals of *Food Chemistry*, *Chemosphere*, etc. His editorial activities in multiple Impact Factor journals have made him a distinctive and progressive figure in the researchers' pool.

Contributors

Hafiz Muhammad Khalid Abbas Vegetable Research Institute, Guangdong Academy of Agricultural Sciences/Guangdong Key Laboratory for New Technology Research of Vegetables, Guangzhou, China

Aqeel Ahmad Vegetable Research Institute, Guangdong Academy of Agricultural Sciences/Guangdong Key Laboratory for New Technology Research of Vegetables, Guangzhou, China

Waheed Akram Vegetable Research Institute, Guangdong Academy of Agricultural Sciences/Guangdong Key Laboratory for New Technology Research of Vegetables, Guangzhou, China

Sajid Ali Department of Agronomy, Institute of Agricultural Sciences, University of the Punjab, Lahore, Pakistan

Syed Muhammad Hassan Askri College of Agriculture and Biotechnology, Provincial Key Laboratory of Crop Gene Resources, Zhejiang University, Hangzhou, People's Republic of China

Palak Bakshi Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Shagun Bali Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Gausiya Bashri Department of Botany, Aligarh Muslim University, Aligarh, Uttar Pradesh, India

Renu Bhardwaj Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Kamini Devi Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Reena Dubey Department of Plant Production, Mediterranean Agronomic Institute of Zaragoza (IAMZ-CIHEAM), Zaragoza, Spain

Hongbing Dung School of Resource and Environmental Science, Wuhan University, Wuhan, Hubei, China

Mohammad Faizan Collaborative Innovation Centre of Sustainable Forestry in Southern China, Tree Seed Center, College of Forest Science, Nanjing Forestry University, Nanjing, Jiangsu, China

Abreeq Fatima Ranjan Plant Physiology and Biochemistry Laboratory, Department of Botany, University of Allahabad, Prayagraj, Uttar Pradesh, India

Ammara Fatima Department of Environmental Science, Lahore College for Women University, Lahore, Pakistan

Shamsul Hayat Plant Physiology and Biochemistry Section, Department of Botany, Faculty of Life Sciences, Aligarh Muslim University, Aligarh, India

Anjuman Hussain Plant Physiology and Biochemistry Section, Department of Botany, Faculty of Life Sciences, Aligarh Muslim University, Aligarh, India

Mohd Ibrahim Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Radwan Khalil Botany Department, Faculty of Science, Benha University, Benha, Egypt

Mohd Tanveer Alam Khan Vegetable Research Institute, Guangdong Academy of Agricultural Sciences/Guangdong Key Laboratory for New Technology Research of Vegetables, Guangzhou, China

Waheed Ullah Khan Department of Environmental Science, University College of Agriculture and Environmental Sciences, Baghdad-UI-Jadeed Campus, The Islamia University of Bahawalpur, Bahawalpur, Pakistan

Tatiana Minkina Academy of Biology and Biotechnology, Southern Federal University, Rostov-on-Don, Russia

Bilal Ahmad Mir Department of Botany, School of Life Science, Satellite Campus, Kargil, University of Kashmir, Jammu and Kashmir, India

Samavia Mubeen State Key Laboratory for Biocontrol, School of Life Sciences, Sun Yat-Sen University, Guangzhou, China

Zafarullah Muhammad Institute of Sericulture and Agricultural Products Processing, Guangdong Academy of Agricultural Sciences, Guangzhou, People's Republic of China

Faroza Nazir Plant Physiology and Biochemistry Section, Department of Botany, Faculty of Life Sciences, Aligarh Muslim University, Aligarh, India

Zarish Noreen HealthCare Biotechnology, Atta-Ur-Rahman School of Applied Biosciences, National University of Sciences and Technology (NUST), Islamabad, Pakistan

Sheo Mohan Prasad Ranjan Plant Physiology and Biochemistry Laboratory, Department of Botany, University of Allahabad, Prayagraj, Uttar Pradesh, India

Muhammad Tahir ul Qamar College of Life Science and Technology, Guangxi University, Nanning, People's Republic of China

Fariduddin Qazi Plant Physiology and Biochemistry Section, Department of Botany, Faculty of Life Sciences, Aligarh Muslim University, Aligarh, India

Vishnu D. Rajput Academy of Biology and Biotechnology, Southern Federal University, Rostov-on-Don, Russia

Taiba Saeed Plant Biotechnology Laboratory, Department of Botany, Aligarh Muslim University, Aligarh, India

Wajid Saeed College of Agriculture, Guangxi University, Guangxi, Nanning, People's Republic of China

Fareen Sami Plant Physiology and Biochemistry Section, Department of Botany, Faculty of Life Sciences, Aligarh Muslim University, Aligarh, India

Anis Ali Shah Department of Botany, University of Narowal, Narowal, Punjab, Pakistan
Senior Superintendent Gardens, RO II Wing, University of the Punjab, Lahore, Punjab, Pakistan

Anwar Shahzad Plant Biotechnology Laboratory, Department of Botany, Aligarh Muslim University, Aligarh, India

Iqra Shahzadi School of Resource and Environmental Science, Wuhan University, Wuhan, Hubei, China
Vegetable Research Institute, Guangdong Academy of Agricultural Sciences/
Guangdong Key Laboratory for New Technology Research of Vegetables, Guangzhou, China

Ashutosh Sharma Faculty of Agricultural Sciences, DAV University, Jalandhar, Punjab, India

Neerja Sharma Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Pooja Sharma Department of Microbiology, DAV University, Jalandhar, Punjab, India

Amrit Pal Singh Department of Pharmaceutical Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Shikha Singh Ranjan Plant Physiology and Biochemistry Laboratory, Department of Botany, University of Allahabad, Prayagraj, Uttar Pradesh, India

Deepti Tiwari Division of Plant Physiology, ICAR – Indian Agricultural Research Institute, New Delhi, India

Tingquan Wu Vegetable Research Institute, Guangdong Academy of Agricultural Sciences/Guangdong Key Laboratory for New Technology Research of Vegetables, Guangzhou, China

Shu-Dan Xue Vegetable Research Institute, Guangdong Academy of Agricultural Sciences/Guangdong Key Laboratory for New Technology Research of Vegetables, Guangzhou, China

Vikas Yadav Plant Biotechnology Laboratory, Department of Botany, Aligarh Muslim University, Aligarh, India

Nasim Ahmad Yasin Senior Superintendent Gardens, RO II Wing, University of the Punjab, Lahore, Punjab, Pakistan

Fangyuan Yu Collaborative Innovation Centre of Sustainable Forestry in Southern China, Tree Seed Center, College of Forest Science, Nanjing Forestry University, Nanjing, Jiangsu, China

Mohammad Yusuf Department of Biology, College of Science, United Arab Emirates University, Al Ain, UAE

Yu-Juan Zhong Vegetable Research Institute, Guangdong Academy of Agricultural Sciences/Guangdong Key Laboratory for New Technology Research of Vegetables, Guangzhou, China

List of Figures

Fig. 1.1	Effect of brassinosteroids and abiotic stress tolerance in plants. (Yan et al., 2009; Luo et al., 2010; Ryu et al., 2010; Jaillais et al., 2011; Choudhary et al., 2012)	10
Fig. 2.1	Schematic representation of genomic and non-genomic signaling of brassinosteroids	20
Fig. 2.2	Number of protein species involved in seed germination. The results revealed by the proteomic analysis of brassinazole (BRZ1) treated plants and a mutant d61-125 rice plant during the germination period	23
Fig. 2.3	Chain event of protein species starting from brassinosteroid receptors associated with the plasma membrane and leading to physiological responses of plant cells	24
Fig. 4.1	Signaling pathway of brassinosteroid	61
Fig. 4.2	A model of H ₂ O ₂ signaling cascade for heavy metal stress	64
Fig. 4.3	Interactions between BRs and H ₂ O ₂ during various abiotic stress responses	71
Fig. 5.1	SL Signaling pathway, SL receptor D14 recognize the SL molecules Receptor hydrolyses SL molecules causing conformation changes of the D14 protein. In the presence of SLs, the receptor is able to bind the F-box protein (MAX2/D3) from the SCF complex and the SL repressor (D53/ SMXL6-8). The receptor is degraded in the proteasome, and receptor is destabilized because of its changed conformation. Degradation of repressor allows the expression of TFs which stimulates SL responsive genes	84
Fig. 5.2	Signaling pathway of brassinosteroid	88

Fig. 6.1	A model to represent the brassinosteroid (BR) signaling in <i>Arabidopsis</i> (Li & He, 2013). BRs are recognized by the BR receptor, BRI1. This binding causes the activation of BRI1 via the homo-dimerization and hetero-dimerization of BAK1 and releases it from BKI1 which is an inhibitory protein. After that, BRI1 activates (through phosphorylation) BSK1 and CDG1 and BSUI (Ser/Thr phosphatase to inactivate the BIN2 kinase (negative regulator for BR signaling)). Furthermore, BR signaling stimulates the PP2A to activate BES1 and BZR1 transcription factors. BES1 and BZR1 (dephosphorylated) bind with BRRE or target gene's E-box motif to regulate their expression. During the absence of BR signal, BKI1 inhibits the interaction of BRI1 with BAK1. Cytoplasmic 14-3-3 proteins retain the phosphorylated BES1 and BZR1 and then degrade them with the help of 26S proteasome. Arrows correspond to the positive effect, while bars correspond to the negative effect	103
Fig. 6.2	GA biosynthesis and signaling in plants (Ross & Quittenden, 2016). BZR1 works as principle positive regulator for BR growth response. DELLA proteins, negative regulators of GA signaling, coordinate with BZR1 to lessen the BR growth response. Arrows correspond to the positive effect, while bars correspond to the negative effect. Red and blue arrows correspond to the GA signaling	105
Fig. 6.3	A graphical representation of crosstalk of gibberellins (GAs) with brassinosteroids (BRs). Various key genes and transcription factors engaged in the transcriptional regulation of plant growth and development have briefly been represented here. Arrows represent the positive effect, while bars represent the negative effect	106
Fig. 6.4	Transcriptional network in plants regulated by the DELLA and BZR1/BES1 (Li & He, 2013). An interaction of DELLAs with different transcription factors (MYC2, JAZs, ALC, SCL3, EIN3/EIL1, PIFs, BZR1, and BES1) to control different growth and developmental processes has been represented here. BZR1 and BES1 also directly bind with their different target genes or other transcriptional regulators (14-3-3 s, BIM1, MYB30, ELF6, REF6, etc.) to regulate the plant developmental processes. Arrows represent the positive effect, while bars represent the negative effect	111
Fig. 7.1	Ethylene interaction with brassinosteroids (BRs) under light and dark conditions Furthermore, the interactions have been demonstrated on the growth and development of the plants. The arrows show positive interaction, while blunt head arrows show a negative interaction	122

Fig. 7.2	Ethylene interaction with brassinosteroids (BRs) and abiotic stressors (i.e., salinity, drought, chilling, and oxidative stress) Arrows show positive interaction, while blunt head arrows show negative interaction	127
Fig. 7.3	Ethylene interaction with brassinosteroids (BRs), pathogens, and phytotoxins The interaction leads to some physical outcome in the plant's stature. Black arrows show positive interaction, while blunt head arrows show negative interaction. Red arrows show an abrupt elevation in the contents due to some external stimuli/applications. Reception signals of pathogen or phytotoxins have been shown with dotted arrows	131
Fig. 8.1	Diagrammatic illustration of brassinosteroid (BRs) and auxin (AUX)-mediated interplay responsible for the growth and development of the plants BRs is involved in the biosynthesis and signaling of auxin. BRI1 (BRs) and TIR1 (AUX) receptors are responsible for signal perception. When the signal is perceived, BRs binds to the extracellular domain of BRI1 and interacts with co-receptor BAK1 and forms active BRs complex. It causes inactivation of BIN2 and leads to the dephosphorylation of BZR1 and BZR2 (TF). This in turn activates transcription of genes containing BRRE in nucleus. BIN2 suppresses AUX/IAAs by phosphorylating ARF and increases transcriptional activity of the target genes. On the other hand, TIR1 interacts with AUX/IAA proteins. Then AUX/IAA is degraded, and auxin response factors (ARFs) are released. It activates the transcription of genes with auxin-responsive elements (AUXRE). ARFs bind to BRI1 and regulate its expression which activates the BRs signaling. At last the cross talk occurs by the activation of genes containing both BRRE and AUXRE and promotes integrated signaling pathways (BRs and AUX) to regulate the transcription of various target genes	145
Fig. 8.2	A pictorial representation of PILS-dependent brassinosteroid and auxin cross-talk When brassinosteroid (BR) binds with its receptor BRI1, signals are transmitted to BIN2 for the stimulation of BZR1 which enter in the nucleus, where BZR1 suppresses the expression of PILS genes. In this way, auxin sequestration into the endoplasmic reticulum is decreased and nuclear auxin concentration is increased. This ultimately leads to enhanced expression of auxin-responsive genes by the release of auxin response factors (ARF) from inhibition by AUX/IAA proteins, which are degraded by auxin-regulated interaction with TRANSPORT TIR1 family of auxin receptors. (Modified from Rana & Hardtke, 2020; Sun et al., 2020)	148

Fig. 12.1	Mechanism of pesticide detoxification in plants. (Modified from Jan et al., 2020)	215
Fig. 14.1	Strategies employed for improved in vitro production of bioactive compounds	244
Fig. 15.1	Brassinosteroids recover plant tolerance to abiotic stresses	263
Fig. 15.2	Transcription factor model for regulating abiotic stress signaling pathways	265
Fig. 16.1	Brassinosteroid structure, class of polyhydroxy steroids categorized as C27, C28, or C29 (C = dissimilar alkyl-substitution outlines of the side chains)	270
Fig. 16.2	BRs are recognized at apoplast of cell membrane with co-receptor intricate made of BRI1 and BAK1, in exhibition of BR, BKI1 form BRI1 and BRI1:BAK1 complex is generated. (This intricate is involved in inactivation of BIN2 (BR binds to the BRI1:BAK1 composite, BKI1 is released, and a phosphorylation cascade is activated resulting in the deactivation of additional kinase, brassinosteroid insensitive 2 (BIN2). BIN2 and its adjacent homologues prevent numerous transcription factors) and transcription factors can then exert their effects. BRI1 activity get blocked in lack of BR, and BKI1 and BIN2 constrain the transcription factors. The box represents the synthesis of BR in the endoplasmic reticulum from which it gets activated upon getting the perception and binding with BR biosynthesis enzymes)	272
Fig. 16.3	Regulation of stress retorts via BR-ABA crosstalk ABA is documented by PYR/PYL/RCAR receptors and improves the phosphorylation and activation of SnRKs, therefore alleviating them from PP2C-mediated constraint. SnRKs, thusly, phosphorylate downstream transcription factors, for example, ABI5 that modulates the transcription of several stress-responsive genes. BIN2, which is a negative modulator of BR signaling, can openly phosphorylate and trigger SnRKs and ABI5, while PP2C can deactivate BIN2. ABI5 is additionally an immediate target of BZR1, which inhibits its transcription to regulate the stress-responsive genes negatively (Planas-Riverola et al., 2019)	275

- Fig. 16.4 BR regulated developing model in Arabidopsis
 Temperature and light regulate PHYB activity, harmonize concentration of PIF4, and determine the levels of PIF4–BES1 heterodimerization. These interactions dictate the gene targets and lead to variable cellular responses. TRACHEARY ELEMENT DIFFERENTIATION INHIBITORY FACTOR signaling pathway determines the xylem differentiation. In addition, GSK3s act as negative controllers of xylem differentiation and allow the crosstalk with signaling pathway, thereby acting as crucial component. BIN2 is responsible for the controlling the stomatal development. In nucleus, BIN2 negatively regulates the SPCH activity while in complex with BASL and POLAR, it rearranges the PM polarized region of MMC and acts as a negative regulator of YDA and MKKs, which leads to SPCH activation. BRs prevent flowering by expressing FLC, a flowering inhibitor. In addition, the articulation BR biosynthetic genes show diurnal changes. During the root epidermal cell determination step, BIN2 phosphorylates EGL3, prompting its dealing from the nucleus to cytosol in trichoblast cells, which facilitates its transfer from trichoblast to atrichoblast cells. BIN2 can similarly phosphorylate TTG1 to repress the action of the WER–GL3/EGL3–TTG1 transcriptional complex. In the root apical meristem, BRs control the size of the stem cell by adjusting the outflow of BRAVO, which contrarily directs cell divisions in the quiescent center. BR signaling levels increase along the longitudinal axis, with more elevated levels present in cells nearer to the differentiation/elongation zone. BRAVO, BRASSINOSTEROIDS AT VASCULAR AND ORGANIZING CENTER; BSU1, BRI1 SUPPRESSOR1; EGL3, ENHANCER OF GLABRA3; EPF1/2, EPIDERMAL PATTERNING FACTOR 1/2; FLC, FLOWERING LOCUS C; GL2, GLABRA2; MKK4/5/7/9, MITOGEN-ACTIVATED PROTEIN KINASE KINASE4/5/7/9; MMC, Meristemoid mother cell; P, phosphorylation; PHYB, PHYTOCHROME B; QC, Quiescent center; TDIF, TRACHEARY ELEMENT DIFFERENTIATION INHIBITORY FACTOR; TDR, TDIF RECEPTOR; TTG1, TRANSPARENT TESTA GLABRA1; WER, WEREWOLF; WOX4, WUSCHEL RELATED HOMEODOMAIN4; YDA, YODA (Nolan et al., 2020) 280

Chapter 1

Signal Transduction of Brassinosteroids Under Abiotic Stresses



Mohd Tanveer Alam Khan, Mohammad Yusuf, Waheed Akram,
and Fariduddin Qazi

Abstract Plants live in regularly fluctuating surroundings that are critical for progression and enlargement. Divergent environmental circumstances comprise biotic and abiotic stress. The opposing things of abiotic indications are impaired by environmental variation, which has been forecast to outcome in an improved rate of dangerous climate. However, brassinosteroids (BRs), a unique polyhydroxy steroidal hormones in plants and capable for endogenous signals for the directive of plant growth and enlargement. It plays an imperative function in plant like seed sprouting, flowering and elongation of hypocotyl, etc. Moreover, BRs have capability to ameliorate the numerous abiotic difficulties like metal stress, temperature stress, water stress, oxidative damage, and salt injury. Furthermore, BR signaling is transduced by a receptor kinase-mediated signal transduction pathway, which is distinct from animal steroid signaling systems. Newest studies entirely associated with the signal pathway of BR have recognized numerous BR marker genes, associating with BR signaling to several cellular practices. This chapter summarizes the BR signaling system in wide detail and discusses how steroid hormone plays a key role in controlling plant growth, size, and metabolism.

Keywords Abiotic stress · Brassinosteroid · Signaling · Target genes

M. T. A. Khan (✉) · W. Akram

Vegetable Research Institute, Guangdong Academy of Agricultural Sciences/Guangdong Key Laboratory for New Technology Research of Vegetables, Guangzhou, China

M. Yusuf

Department of Biology, College of Science, United Arab Emirates University, Al Ain, UAE

F. Qazi

Plant Physiology and Biochemistry Section, Department of Botany, Faculty of Life Sciences, Aligarh Muslim University, Aligarh, India

Introduction

Plants live in regularly fluctuating surroundings that are critical for progression and enlargement. These opposing environmental circumstances comprise biotic and abiotic stress. The opposing things of abiotic practices are impaired by environmental alteration, which has been forecast to outcome in an improved rate of risky climate (Fedoroff et al., 2010). Plants acclimate to opposing environments through stress signals acting as biological queries. Plant stress encounter is dangerous for farming and environmental sustainability due to the excessive consumption of water and manure resources to load the environment. However, plant growth regulators recover over all plant development and productivity (He & Zhu, 2008; Khan et al., 2019). Wang et al. (2005) revealed that environmental stresses influence the endogenous concentration of many phytohormones, as a result alter numerous signaling pathways. These modifications cause severe metabolic complaints most important to embarrassment of overall plant growth performance in stress environments (Lerner & Amzallag, 1994). A decent strategy to overcome abiotic stresses is the exogenous use (either through the seed or soil management) of PGRs (Ashraf et al., 2008). Brassinosteroids (BRs) show dynamic roles in improving growth and enlargement of plants and can upgrade the opposing things of numerous abiotic stresses in a varied range of plant species (Fariduddin et al., 2011; Jiang et al., 2013; Khan et al., 2015, 2019; Nazir et al., 2021). In this chapter, we deliver the summary of latest improvements in revealing the signaling trails for BRs under abiotic stresses. Furthermore, this chapter emphasizes on the possible mechanisms to decipher the molecular and biochemical levels of BR signaling linked to upstream sensing and to downstream alterations in gene expression, metabolic rate, physiology, growth, and expansion.

Physiological Roles of Brassinosteroids

Brassinosteroids are the steroidal growth controllers related to plant easiness. These entities show essential roles in many biological practices like cell division, cell elongation, xylem disparity, initiation of stem elongation, proton pump activation, leaf epinasty, tissue disparity, morphogenesis, pollen tube progression, and photosynthesis (Clouse & Sasse, 1998; Xia et al., 2009; Clouse, 2011). BRs have been used to upgrade the adversarial response of plants contrary to various stresses such as metal stress (Yusuf et al., 2011), cold stress (Fariduddin et al., 2011), salinity stress (Deng et al., 2012), and oxidative impairment (Cao et al., 2005). The foliar practice of BRs can upregulate the manifestation of stress connected genes, resultant stimulation of antioxidant enzymes, proline, repairs of photosynthesis activity, and some other favorable retorts (Divi & Krishna, 2009; Fariduddin et al., 2015; Khan et al., 2015, 2019; Nazir et al., 2020).

Effect of Brassinosteroids on Seed Germination

Numerous studies have provided that BRs promote seed sprouting. It has been renowned that BRs encourage seed propagation in tobacco (Leubner-Metzger, 2001), wheat (Hayat & Ahmad, 2003), tomato (Ahammed et al., 2012), *Brassica juncea* (Sirhindi et al., 2009), and *Arachis hypogaea* (Vardhini & Rao, 1997). BRs stimulated the sprouting of pre-chilled seeds of BRs-lacking biosynthesis *det2-1* mutant and the BRs-unresponsive reply mutant *bri1-1* exposed to light in *Arabidopsis thaliana* (Zhang et al., 2009). Seed germination of *det2-1* mutant and *bri1-1* is further powerfully repressed by ABA associated with their wild type. Further, pre-treatment with BL encouraged growth and sprout appearance of old rice grains. Hayat and Ahmad (2003) reported that seeds soaked in BRs had increased activity of α -amylase in *Lens culinaris*. In *Arabidopsis*, BR-signal reversed the ABA-convinced dormancy, therefore encouraging the sprouting (Steber & McCourt, 2001). BRs promoted the break of endosperm in tobacco in dose dependent method (Leubner-Metzger, 2001).

Effect of Brassinosteroids on Growth

BRs have imperative character in plant developmental courses comprising cell division, cell elongation, pollen tube progression, xylem disparity, proton pump activation, initiation of stem elongation, leaf epinasty, tissue disparity, morphogenesis, and photosynthesis (Xia et al., 2009; Clouse, 2011; Gudesblat & Russinova, 2011). Mussig et al. (2003) have reported that BRs deficient mutants of *Arabidopsis* showed increased root elongation after exogenous applications of BRs and auxins. Sun et al. (2010) revealed that improved plant growth could be recognized to the BRs skill to control cell growth and central events over the upregulation of xyloglucan endo-transglycosylase. It has also been stated that BRs improved the growth of *Raphanus sativus* seedlings (Choudhary et al., 2012).

Brassinosteroids and Plant Abiotic Stress Tolerance

Various researches over the years have indicated the active involvement of BRs in plants when showing to different abiotic practices such as low temperature (Khan et al., 2015, 2019), high temperature, and chilling stresses (Janeczko et al., 2009, 2011). Some previous studies highlight the status of BRs and associated composites in diverse plants under drought (Mahesh et al., 2013), light (Li et al., 2012a), salinity (Abbas et al., 2013), heavy metal (Yusuf et al., 2011), submerging (Liang & liang, 2009), herbicide (Sharma et al., 2013a). Therefore, recent reports regarding the role of BRs in the modulation of abiotic stresses in plants are appraised in Table 1.1.

Table 1.1 Effect of brassinosteroids and abiotic stress tolerance in plants

BR analogues	Abiotic stress	Plant species	Responses	References
BRs (EBL or HBL)	Cd	<i>Raphanus sativus</i>	Activated antioxidant enzymes like catalase, superoxide dismutase, peroxidase, and glutathione in the plantlets treated by cd and BRs	Anuradha and Rao (2007)
BRs (EBL/HBL)	Low temperature	<i>Lycopersicon esculentum</i>	BRs facilitated enhancement in photosynthetic machinery and proline content	Khan et al. (2015)
BRs (EBL/HBL)	Cd	<i>Lycopersicon esculentum</i>	BRs mediated upgradation in stomatal conductance, transpiration rate, proline accumulation, and antioxidant system	Hasan et al. (2011)
BR	Drought	<i>Glycine max</i>	Raised the activities of POX and SOD, augmented the concentration of soluble sugars and proline that eventually caused reduced MDA concentration and electrical conductivity	Zhang et al. (2008)
EBL/HBL	Water stress	<i>Raphanus sativus</i>	Mediated a decline in the deleterious outcome of water stress on seed development and sprout progression by enhancing the antioxidant and free proline	Mahesh et al. (2013)
EBL	Mn	<i>Brassica juncea</i>	Enriched growth, water relations, and photosynthesis and improved several antioxidant enzymes like CAT, POX, and SOD and proline	Fariduddin et al. (2015)
EBL	Salinity	<i>Cucumis sativus</i>	Better seedlings growth as outcome upgraded activities of several antioxidant enzymes	Lu and Yang (2013)
EBL	Drought	<i>Chorispora bungeana</i>	Deliberated tolerance to drought-stress by reducing the lipid peroxidation, membrane permeability as consequence of augmented antioxidant enzymes and non-enzymatic antioxidants like ascorbate and GSH	Li et al. (2012b)
EBL	Cd	<i>Brassica napus</i>	EBL reduced the lethal result of cadmium on photochemical practices by falling injury of photochemical reaction centers also O ₂ developing centers as well as retaining effective photosynthetic electron transport	Janeczko et al. (2005)
EBL	Cd	<i>Raphanus sativus</i>	EBL minimized the harmful role of cd on plant growth,	Anuradha and Rao (2007)

(continued)

Table 1.1 (continued)

BR analogues	Abiotic stress	Plant species	Responses	References
			photosynthesis related attributes, and enzymes activity	
HBL	Cu	<i>Vigna radiata</i>	Improved photosynthetic associated traits and carbonic anhydrase activity	Fariduddin et al. (2014)
EBL	Ni	<i>Raphanus sativus</i>	Elevated activities of antioxidant that ultimately caused in dropping lipid peroxidation. Greater proline and protein contents, and upgraded the overall plant growth	Sharma et al. (2011)
EBL	Co	<i>Brassica juncea</i>	EBL improved the stress created by co and suggestively improved the activities of antioxidant enzymes	Arora et al. (2012)
EBL	Zn	<i>Brassica juncea</i>	Augmented activities of superoxide dismutase, catalase, ascorbate peroxidase, MDHAR, DHAR, and the GSH contents	Arora et al. (2010)
EBL	Pb	<i>Raphanus sativus</i>	Decreased Pb harmfulness and improved overall plant growth and activities of antioxidant enzymes and reducing peroxidase	Anuradha and Rao (2007)
HBL	B	<i>Vigna radiata</i>	Upgraded the growth, water relationships, net photosynthesis, stomatal conductance, and transpiration rate by improving antioxidant enzymes and level of proline	Yusuf et al. (2011)
HBL	Zn	<i>Raphanus sativus</i>	Conferred tolerance to Zn harmfulness by improving antioxidant enzymes, establishment of GSH metabolic rate and redox grade, and enlightening the contents of non-enzymatic antioxidants	Ramakrishna and Rao (2013)
BR	High temperature	<i>Oryza sativa</i>	Displayed significant improvement in the expression of POX and SOD; decreased level of MDA and electrolytes leakage	Cao and Zhao (2007)
EBL	High temperature	<i>Lycopersicon esculentum</i>	Significantly improved high temperature convinced reduction of photosynthesis via improving the antioxidant enzymes and decreasing H ₂ O ₂ and MDA contents	Ogwen et al. (2008)
HBL	Chilling	<i>Cucumis sativus</i>	Improved growth and photosynthesis by improving proline content	Fariduddin et al. (2011)

(continued)

Table 1.1 (continued)

BR analogues	Abiotic stress	Plant species	Responses	References
BR	Cold	<i>Cucumis sativus</i>	Protected photosynthetic related cold convinced harm by triggering the enzymes of Calvin cycle and improving the antioxidant capacity, alleviated the influence of photo-oxidative stress and impairment	Jiang et al. (2013)
EBL	Low temperature	<i>Brassica juncea</i>	Improved the lethal consequence of H ₂ O ₂ through improving the activities of several enzymes involved in antioxidant defense systems such as CAT, APX, and SOD	Kumar et al. (2010)
EBL	Low temperature	<i>Vitis vinifera</i>	Improved antioxidant defense and osmoregulation	Xi et al. (2013)
EBL	Cd	<i>Phaseolus vulgaris</i>	Mediated improved activity of antioxidant enzymes, proline content, and later enhancement in the membrane stability index and relative water content	Rady (2011)
EBL	Ni	<i>Brassica juncea</i>	Ameliorated Ni-stress by improving the movement of antioxidant enzymes	Kanwar et al. (2013)
EBL	Cu and NaCl	<i>Cucumis sativus</i>	Greater the actions of several antioxidant enzymes such as CAT, POX, SOD that ultimately enhanced growth, nitrate reductase activity, and photosynthetic efficacy	Fariduddin et al. (2013)
EBL	Salinity	<i>Oryza sativa</i>	Displayed enhancement in growth, levels of protein, proline contents, and activities of antioxidant enzymes over the expression of several BRs and salt responsive genes	Sharma et al. (2013b)

Brassinosteroids and Low Temperature Stress

BRs have been successfully used to make plants resistant contrary to cold stress. BRs could be exogenously functional either by seed soaked, root dipping, and foliar application. However, foliar spray and seed soaking methods have been generally adopted. Janeczko et al. (2009) stated that application of EBL earlier to cold stress minimized the ion leakage in freezing showing rape plants, while it improved the antioxidant system and proline in freezing worried young grapevines (Xi et al., 2013). The characters of BRs in cold stress are concise in Table 1.2.

Table 1.2 Effect of brassinosteroids and abiotic stress tolerance in plants

BR analogues	Abiotic stress	Plant species	Responses	References
HBL	Chilling	<i>Cucumis sativus</i>	Improved the growth photo-synthesis and water relation by improving antioxidant enzymes such as CAT, POX, and SOD	Fariduddin et al. (2011)
BR	Cold	<i>Cucumis sativus</i>	Protected the photosynthetic tool from cold convinced impairment by triggering the enzymes of Calvin cycle and improving the antioxidant ability	Jiang et al. (2013)
BL	Chilling	Maize	Improved the growth and rescue of seedlings after freezing treatment	He et al. (1991)
EBL	Low temperature	<i>Brassica juncea</i>	Improved the lethal outcome of H ₂ O ₂ over improving the accomplishments of several enzymes intricate in antioxidant defense arrangement such as CAT, APX, and SOD	Kumar et al. (2010)
EBL	Low temperature	<i>Vitis vinifera</i>	Augmented antioxidant system and osmoregulation	Xi et al. (2013)
BL	Chilling	<i>Solanum lycopersicum</i>	Inhibited the events of phospholipase D and lipoxygenase in fruits, subjected to chilling stress	Aghdam and Mohammadkhani (2014)
BL	Chilling	<i>Capsicum annum</i>	Effectively reduced freezing damage of <i>Capsicum annum</i> fruit put in storing on 3 °C for longer duration via decreasing the ion leakage, MDA content; aggregate the activities of antioxidant enzymes like CAT, POX, APX, and GR	Wang et al. (2012b)
EBL	Chilling	<i>Cucumis sativus</i>	Improved the chilling-convinced embarrassment of photosynthesis in <i>Cucumis sativus</i> by minimizing ROS generation and accumulation over increased activities of antioxidants	Hu et al. (2010)
EBL	Chilling	<i>Chorispora bungeana</i>	Alleviated chilling-prompted oxidative injury over the antioxidant defense mechanism and decreased the intensities of ROS as well as lipid peroxidation, thereby improved the freezing tolerance	Liu et al. (2009)

(continued)