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

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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

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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, SlNAC2, 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.

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Mohd Tanveer Alam Khan
Mohammad Yusuf
Fariduddin Qazi
Aqeel Ahmad

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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-Ul-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

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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

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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	*Raphanus sativus*	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	*Lycopersicon esculentum*	BRs facilitated enhancement in photosynthetic machinery and proline content	Khan et al. (2015)
BRs (EBL/HBL)	Cd	*Lycopersicon esculentum*	BRs mediated upgradation in stomatal conductance, transpiration rate, proline accumulation, and antioxidant system	Hasan et al. (2011)
BR	Drought	*Glycine max*	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	*Raphanus sativus*	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	*Brassica juncea*	Enriched growth, water relations, and photosynthesis and improved several antioxidant enzymes like CAT, POX, and SOD and proline	Fariduddin et al. (2015)
EBL	Salinity	*Cucumis sativus*	Better seedlings growth as outcome upgraded activities of several antioxidant enzymes	Lu and Yang (2013)
EBL	Drought	*Chorispora bungeana*	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	*Brassica napus*	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	*Raphanus sativus*	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	*Vigna radiata*	Improved photosynthetic associated traits and carbonic anhydrase activity	Fariduddin et al. (2014)
EBL	Ni	*Raphanus sativus*	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	*Brassica juncea*	EBL improved the stress created by co and suggestively improved the activities of antioxidant enzymes	Arora et al. (2012)
EBL	Zn	*Brassica juncea*	Augmented activities of superoxide dismutase, catalase, ascorbate peroxidase, MDHAR, DHAR, and the GSH contents	Arora et al. (2010)
EBL	Pb	*Raphanus sativus*	Decreased Pb harmfulness and improved overall plant growth and activities of antioxidant enzymes and reducing peroxidase	Anuradha and Rao (2007)
HBL	B	*Vigna radiata*	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	*Raphanus sativus*	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	*Oryza sativa*	Displayed significant improvement in the expression of POX and SOD; decreased level of MDA and electrolytes leakage	Cao and Zhao (2007)
EBL	High temperature	*Lycopersicon esculentum*	Significantly improved high temperature convinced reduction of photosynthesis via improving the antioxidant enzymes and decreasing H_2O_2 and MDA contents	Ogweno et al. (2008)
HBL	Chilling	*Cucumis sativus*	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	*Cucumis sativus*	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	*Brassica juncea*	Improved the lethal consequence of H_2O_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	*Vitis vinifera*	Improved antioxidant defense and osmoregulation	Xi et al. (2013)
EBL	Cd	*Phaseolus vulgaris*	Mediated improved activity of antioxidant enzymes, proline content, and later enhancement in the membrane stability index and relative water content	Rady (2011)
EBL	Ni	*Brassica juncea*	Ameliorated Ni-stress by improving the movement of antioxidant enzymes	Kanwar et al. (2013)
EBL	Cu and NaCl	*Cucumis sativus*	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	*Oryza sativa*	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	*Cucumis sativus*	Improved the growth photosynthesis and water relation by improving antioxidant enzymes such as CAT, POX, and SOD	Fariduddin et al. (2011)
BR	Cold	*Cucumis sativus*	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	*Brassica juncea*	Improved the lethal outcome of H_2O_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	*Vitis vinifera*	Augmented antioxidant system and osmoregulation	Xi et al. (2013)
BL	Chilling	*Solanum lycopersicum*	Inhibited the events of phospholipase D and lipoxygenase in fruits, subjected to chilling stress	Aghdam and Mohammadkhani (2014)
BL	Chilling	*Campsicum annum*	Effectively reduced freezing damage of *Campsicum annum* 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	*Cucumis sativus*	Improved the chilling-convinced embarrassment of photosynthesis in *Cucumis sativus* by minimizing ROS generation and accumulation over increased activities of antioxidants	Hu et al. (2010)
EBL	Chilling	*Chorispora bungeana*	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)