15

Role of Brassinosteroids (BRs) in Modulating Antioxidative Defense Mechanism in Plants Growing Under Abiotic and Biotic Stress Conditions

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Abstract

Brassinosteroids (BRs) are a group of steroidal phytohormone that plays an essential role in regulating various chemical and physiological processes involved in plant growth and development. Furthermore, physiological and molecular studies of BRs have revealed their potential of enhancing yield and productivity of crops by regulating variety of genes. But as per current scenario, variety of abiotic and biotic environmental stresses acts as major constraints in yield and productivity of crops. Furthermore, BRs act as nontoxic, environmentally safe steroidal compounds that has the potential in modulating plant responses against abiotic and biotic stresses. When applied exogenously at specific dose and at particular developmental stage of plant, they are known to enhance both quality and quantity of the crop plants. Moreover, BRs are also known to have antifungal, antiviral, and anti-ecdysteroidal properties, which make them potential alternate of chemical fungicide, pesticide, and herbicides. Therefore, keeping in view all these properties of BRs, the current book chapter focuses on the role of BRs in modulating enzymatic and nonenzymatic antioxidant defense mechanism of plants under abiotic and biotic stress conditions.

Keywords

Brassinosteroids · Antioxidants · Defense system · Abiotic stress · Biotic stress

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15.1 Introduction

Various abiotic and biotic stresses elicit threatening impact on productivity and yield of crops. Various abiotic stresses include thermal (high and low temperature), water (drought and flooding), heavy metal toxicity, salinity, and UV radiation stresses, and the biotic stress includes pathogenic stress. All these stresses have contributed in converting arable lands to unproductive barren lands, thus ultimately resulting in economic loss in agricultural field (Ahanger et al. 2018). All these stresses affect germination, growth, and various physiological processes in plants, and moreover, it has been predicted that if the similar situation continues, there will be scarcity of staple crops for human population (which is growing at an alarming rate) by 2050 (Ahanger et al. 2014). Keeping in mind, all these changes, biologists are trying to meet all these challenges by using various environmentally stable strategies like the use of biological components, drainage, water management, etc. One such strategy is the application of phytohormones, since various phytohormones play an essential role in regulating the normal and developmental processes and are also involved in combatting the effects caused due to various biotic and abiotic stresses by modulating several signaling pathways to evoke plants responses.

Among all plant hormones, brassinosteroids (BRs), a group of steroidal hormones found in lower as well as higher plants, are involved in regulating various mechanisms involved in growth and developmental processes in plants (Liu et al. 2017). BRs act as an essential regulator involved in photosynthesis, antioxidant defense system, and plant-water relation under normal as well as stress conditions, thus ultimately regulating the growth and developmental processes under normal as well as stress conditions. Furthermore, in the case of plants having mutations in BR biosynthesis, abnormal developmental phenotypes are generated, thus confirming the potencies of BRs (Sahni et al. 2016). Moreover, BR-induced ameliorating stress responses have been reported in various plants that were exposed to thermal, water, heavy metal, and pathogen stress (Hayat et al. 2010; Singh et al. 2012; Talaat et al. 2015; Zhao et al. 2016; Jasrotia and Ohri 2017a). BRs are applied exogenously to plants and are reported to have ability of mitigating different stresses in concentration-dependent manner and also on the developmental stage of plants as well as on the treated plant organs (Bao et al. 2004). So, in the current book chapter, efforts have been made to examine the potential of BRs in modulating antioxidant defense in plants growing under stress conditions. Moreover, cross talks of BRs with other phytohormones have also been summarized here.

15.2 Plant Responses to Environmental Stresses

Plants respond to various environmental stresses which include abiotic factors like heavy metals, drought, wounding, salinity, changes in temperature and light, pesticides, and nutrient stress and biotic factors such as pest and pathogen attack (Gull et al. 2019). Abiotic and biotic stresses induce morphological, biochemical, molecular, and physiological changes in plants. Extreme temperature, salinity

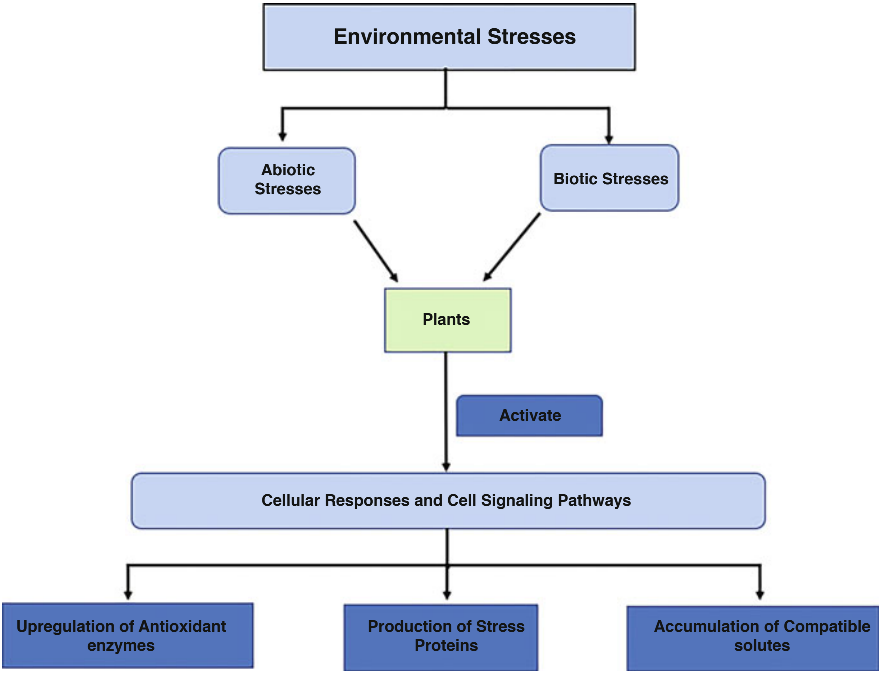

Fig. 15.1 Response of plants to different environmental stresses

drought, and oxidative stress are often interconnected and may lead to similar cellular damage. For example, salinity and drought condition are primarily evidenced as osmotic stress, leading to disruption of ion homeostasis in the cells (Samynathan et al. 2021). Denaturation of structural and functional proteins is caused by oxidative stress, which often accompanies high temperature, drought, or salinity stress (Chaki et al. 2020). As a result, various environmental stresses often activate similar cellular responses and cell signaling pathways (Sewelam et al. 2016), such as accumulation of compatible solutes, upregulation of antioxidants, and production of stress proteins (Kosová et al. 2018; Dumont and Rivoal 2019; Hasanuzzaman et al. 2020). Plants also undergo certain biochemical adaptations which involve various changes in cell biochemistry. These changes include detoxification mechanism, synthesis of special proteins, evolution of new metabolic pathways, accumulation of the metabolites, and changes in phytohormone level (Fujita et al. 2006) (Fig. 15.1).

15.3 Biosynthesis of BRs

The pathway leading to the biosynthesis of BRs and different genes involved in BR biosynthesis has been identified in *Arabidopsis* as well as in rice and tomato (Divi and Krishna 2009). Initially, BR-biosynthetic pathway was established by feeding

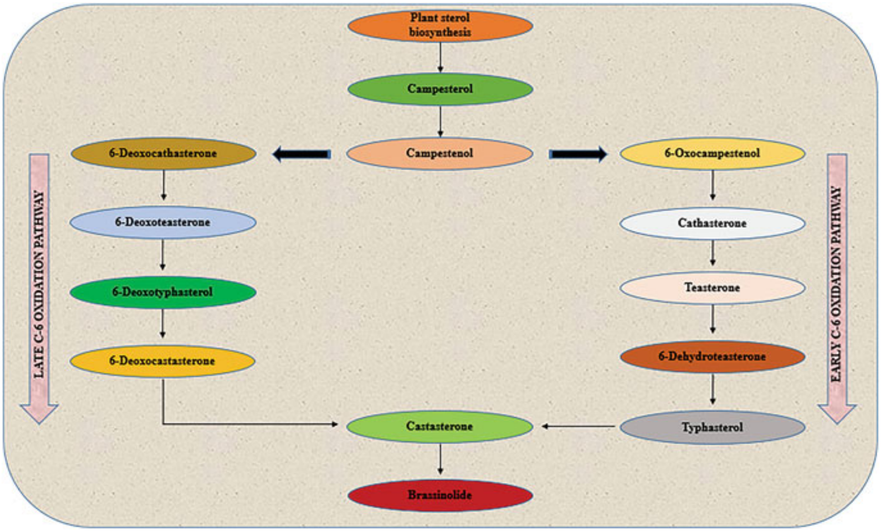

Fig. 15.2 Biosynthesis of brassinosteroids

cultured cells of *Catharanthus roseus* and *Arabidopsis* seedlings with deuterium-labeled substrates followed by identification of various metabolites and reaction sequences involved in biosynthetic pathway by utilizing gas chromatography-mass spectrometry (GC-MS) (Choi et al. 1996; Fujioka et al. 2000; Noguchi et al. 2000). The precursor for the biosynthesis of brassinolide (BL), the most active BR, is campesterol (CR). Earlier, BRs were thought to be biosynthesized from two parallel pathways, namely, early C-6 and late C-6 oxidation pathways (Fujioka et al. 1998). According to these pathways, CR is first converted to campesterol (CN), then to castasterone (CS), and finally to BL (Fig. 15.2). In early C-6 oxidation pathway, CN is first converted to 6-oxocampestanol, then to cathasterone, teasterone, 3-dehydroteasterone, typhasterol, and then CS. In late C-6 oxidation pathway, CN is first hydroxylated at C-22 to form 6-deoxocathasterone and is then converted to corresponding intermediates as in early C-6 oxidation pathway but in C-6 deoxy forms. These two pathways ultimately converge at CS, which is eventually converted to BL (Zhao and Li 2012). Another branching pathway termed as CN-independent pathway, which is an early C-22 oxidation branch, has been reported (Fujioka et al. 2002). Recently, a shortcut route involving C-23 hydroxylation leading to the conversion of CR to 6-deoxytyphasterol has been described (Ohnishi et al. 2006). Experimental data on different plant species have revealed that the CN-independent and late C-6 oxidation pathways are the predominant BR-biosynthetic pathways (Zhao and Li 2012). Different genes involved in BR-biosynthesis are *constitutive photomorphogenesis and dwarfism (CPD), de-etiolated-2 (DET2)*, and *DWARF4 (DWF4)* (Bartwal and Arora 2020). Constitutive expression of these genes can be modulated to regulate the endogenous levels of BR in plants (Fig. 15.2).

15.4 Role of BRs in Plant Growth and Development

BRs are steroidal phytohormones that are analogous to animal steroidal hormones. Mass spectrophotometric analysis such as UHPLC-ESI-MS/MS determined a total of around 22 natural BRs in a minute sample of plant tissue which exhibited a highly significant growth-promoting influence in plants (Tarkowska et al. 2016). They play imperative roles in divergent aspects of plant biology ranging from elongation and division of cell, root growth, photomorphogenesis, stomatal and vascular differentiation, seed germination, plant immunity, and its reproduction (Gudesblat and Russinova 2011; Vardhini and Anjum 2015; Wei and Li 2016) (Table 15.1). Besides, BRs regulate the production and oxidation of radicals and root gravitropic response and mediate plant responses to environmental cues (Krishna 2003; Bajguz and Hayat 2009; Vardhini 2019). Table 15.1 describes the physiological role of BRs in growth and development of different plant species.

15.5 Cross Talk of BRs with Other Plant Hormones

Several stress-responsive phytohormones act as a molecular regulatory element that assist sessile plants to maintain their growth plasticity and provide ability to adapt in tough environmental conditions. A cascade of interactions (occur mainly through phosphorylation/a common second messenger) that helps in regulating signaling network and persists among varied plant hormones which alter cellular dynamics is known as cross talk. This cross talk between phytohormones helps in revealing and targeting host resistance mechanisms under stress (Kohli et al. 2013; Wani et al. 2016; El-Esawi 2017; Li et al. 2021). On the basis of their action, phytohormones are grouped into two main categories: First group includes auxins (AUX), gibberellins (GA), brassinosteroids (BRs), strigolactones (SL), and cytokinins (CK) that coordinate during plant growth and development, while others play a vital role under environmental cues, namely, abscisic acid (ABA), brassinosteroids, ethylene (ET), jasmonic acid (JA), and salicylic acid (SA) (Pieterse et al. 2009; Santner et al. 2009; Denance et al. 2013; Fahad et al. 2015). Thus, BRs play a dual role in plants both under stress as well as during normal growth.

15.5.1 Interplay Between Brassinosteroids and Auxins

BRs and auxins are master hormones with coordinated effects on innumerable phases of plant growth and developmental pathways including the biosynthesis of BRs mediated by auxins (Yoshimitsu et al. 2011; Hao et al. 2013; Chaiwanon and Wang 2015). Physiological and genetic assays demonstrate opposite role of BR and AUX for controlling root growth by directing the expression of DWF4 (DWARF4) and BZR1 (BRASSINAZOLE-RESISTANT 1). On one hand, in roots where auxins enhance DWF4 expression, BRs suppress it through feedback mechanism (Yoshimitsu et al. 2011; Chaiwanon and Wang 2015). Also, during lateral root

Table 15.1 Effect of BRs on the various physiological aspects of plant growth and development in different plant species

Physiological parameters	Plant species	BR analogues/inhibitors used	Reference
Seed germination/ seedling growth	*Brassica juncea L.*	24-Epibrassinolide (EBL); 28-Homobrassinolide (HBL)	Sirhindi et al. (2009, 2011), Kumar et al. (2012), Soares et al. (2020)
	Raphanus sativus L.	EBL; HBL	Mahesh et al. (2013)
	Leymus chinensis	EBL	Guo et al. (2014)
	Acer pseudoplatanus L.; *Fraxinus excelsior* L.	EBL	Procházka et al. (2015)
	Tobacco	EBL	Bukhari et al. (2016)
	Picea abies, *Pinus sylvestris*, *Pseudotsuga menziesii*, and *Quercus robur*	2α,3α,17β-trihydroxy-5α-androstan-6-one (a Synthetic BR)	Kuneš et al. (2016)
	Solanum lycopersicum L.	EBL	Ahammed et al. (2012a), Shu et al. (2016)
	Solanum melongena	EBL	Xue-Xia et al. (2011), Wu et al. (2015), He et al. (2016), Wu et al. (2016)
	Cucumis sativus	EBL	Yuan et al. (2012a)
	Arabidopsis thaliana	Brassinazole	Yamagami et al. (2017)
	Vigna radiata L.	BL	Lalotra et al. (2017)
	Oryza sativa L.	7,8-Dihydro-8α-20-hydroxyecdysone (αDHECD; a BR mimic)	Sonjaroon et al. (2018)
	Pisum sativum	BL; EBL	Jiroutová et al. (2019)
	Triticum aestivum L.	BL	Toman et al. (2019)
	Gossypium hirsutum	EBL	Chakma et al. (2021)
Shoot and root growth	*Arachis hypogaea* L.	BR	Verma et al. (2012)
	Capsicum annuum L.	EBL	Abbas et al. (2013)
	Phaseolus vulgaris	EBL	Cheng et al. (2014)
	Oryza sativa	BR	Fahad et al. (2016)

(continued)

Table 15.1 (continued)

Physiological parameters	Plant species	BR analogues/inhibitors used	Reference
	Potatoes	BL	Hu et al. (2016)
	Arabidopsis thaliana	BL; Brassinazole	Vragovic et al. (2015), Yamagami et al. (2017)
	Vigna radiata L.	BL	Lalotra et al. (2017)
	Carica papaya L.	BR	de Assis-Gomes et al. (2018)
	Gossypium hirsutum	EBL	Chakma et al. (2021)
	Zea mays	EBL	Trevisan et al. (2020)
	Chenopodium quinoa Willd	BR	Sadak et al. (2020)
	Solidago canadensis	BR	El-Sayed et al. (2020)
	Pyrus ussuriensis	BL	Zheng et al. (2020)
	Solanum lycopersicum L.	EBL	Shu et al. (2016); Nazir et al. (2021)
	Berberis thunbergii L.	BL; EBL	Pacholczak et al. (2021)
Photomorphogenesis	*Arabidopsis thaliana*	BL	Kim et al. (2012); Zhiponova et al. (2013); Youn et al. (2016)
	Solanum melongena	EBL	Xue-Xia et al. (2011)
	Capsicum annuum L.	EBL	Abbas et al. (2013)
	Camellia oleifera	BL	Zhou et al. (2013)
	Solanum lycopersicum L.	EBL	Xia et al. (2014), Li et al. (2015), Nazir et al. (2021)
	Dwarf pear	BL	Chen et al. (2014)
	Leymus chinensis (Trin.) Tzvel.	BL	Niu et al. (2016); Wang et al. (2016)
	Oryza sativa	EBL; BR; 7,8-Dihydro-8α-20-hydroxyecdysone (αDHECD; a BR mimic)	Sun et al. (2015), Tong and Chu (2016), Fahad et al. (2016), Sonjaroon et al. (2018)
	Brachypodium distachyon L.	24-Epicastasterone	Xu et al. (2015)
	Chenopodium quinoa Willd	BRs	Sadak et al. (2020)
	Tobacco	EBL	Zhang et al. (2021)

(continued)

Table 15.1 (continued)

Physiological parameters	Plant species	BR analogues/inhibitors used	Reference
Photoperiodism and flower development	*Arabidopsis thaliana*	BR	Domagalska et al. (2010)
	Cucurbita pepo	Brassinozole	Manzano et al. (2011)
	Brassica napus	BL	Belmonte et al. (2011)
	Arachis hypogaea L.	BR	Verma et al. (2012)
	Solidago canadensis	BR	El-Sayed et al. (2020)
Photosynthesis	*Carica papaya* L.	BR	de Assis-Gomes et al. (2013)
	Secale cereale L.	EBL	Pociecha et al. (2016)
	Pisum sativum	EBL	Dobrikova et al. (2013)
	Helianthus annuus L.	EBL	Filova et al. (2013), Kaplan-Dalyan and Sağlam-Çağ (2013)
	Vigna radiata	HBL	Yusuf et al. (2014), Alyemeni and Al-Quwaiz (2016)
	Oryza sativa L.	BL; BR; 7,8-Dihydro-8α-20-hydroxyecdysone (αDHECD; a BR mimic)	Cao and Zhao (2008); Fahad et al. (2016); Sonjaroon et al. (2018)
	Glycine max L.	EBL	Bariş and Sağlam-Çağ (2016)
	Triticum aestivum L.	EBL; BL	Sağlam-Çağ (2007); Toman et al. (2019)
	Capsicum annuum L.	EBL	Yang et al. (2019)
	Solidago canadensis	BR	El-Sayed et al. (2020)
	Chenopodium quinoa Willd	BRs	Sadak et al. (2020)
	Solanum lycopersicum L.	EBL	Carvalho et al. (2013), Shu et al. (2016), Nazir et al. (2021)
Nitrogen metabolism	*Cajanus cajan* (L.) Millsp.	EBL	Dalio et al. (2013)
	Vigna radiata L.	HBL	Yusuf et al. (2014)
	Solanum lycopersicum L.	EBL	Shu et al. (2016)
	Arabidopsis thaliana	BL	Zhao et al. (2016)

(continued)

Table 15.1 (continued)

Physiological parameters	Plant species	BR analogues/inhibitors used	Reference
	Capsicum annuum L.	EBL	Yang et al. (2019)
	Vigna unguiculata L.	EBL	Cardoso et al. (2019)
Senescence	*Triticum aestivum* L.	EBL	Sağlam-Çağ (2007)
	Helianthus annuus L.	EBL	Kaplan-Dalyan and Sağlam-Çağ (2013)
	Citrus unshiu	EBL	Zhu et al. (2015)
	Solanum lycopersicum L.	EBL	Carvalho et al. (2013); Nazir et al. (2021)
	Glycine max L.	EBL	Bariş and Sağlam-Çağ (2016)
	Pisum sativum L.	EBL	Fedina et al. (2017)
	Carica papaya L.	BR	de Assis-Gomes et al. (2018)
	Capsicum annuum L.	EBL	Yang et al. (2019)
	Lilium orientalis	BR	Nergi and Ali (2020)

formation, BIN2 (BRASSINOSTEROID-INSENSITIVE2; a key component that mediate BR and auxin signaling during root development) plays an important role in auxin signaling, but BR signaling retards BIN2 activity which in turn couldn't activate transcription factors BES1 (BRI1-EMS-SUPPRESSOR 1) and BZR1 leading to downstream control of plant growth and development. But BIN2 causes the phosphorylation of ARF7 and ARF19 (AUXIN RESPONSE FACTOR), thereby enhancing their DNA-binding capacity at lower levels of BR (He et al. 2002; Yin et al. 2002; Cho et al. 2014). In shoot elongation, brassinosteroid treatment downregulates transcription factor ARF genes ARF4 and ARF8 in *Arabidopsis* wild-type (WT) seedlings in contrast to increased level of expression in BR-deficient mutants (Jung et al. 2010); however, the overexpression of ARF8 could suppress growth of hypocotyl resulting into a weaker apical dominance (Tian et al. 2004; Peres et al. 2019) (Fig. 15.3). These outcomes clearly indicated an elaborated and a dynamic interaction of ARFs through BZR1 and BIN2 both transcriptionally and post-transcriptionally to regulate plant growth and its development via BR-auxin cross talk (Peres et al. 2019).

15.5.2 Interplay Between Brassinosteroids and Gibberellins

A cooperative and an interdependent relationship exists between BRs and GAs, with multiple layers that interact in a species, tissue, and in a dose-dependent manner. The

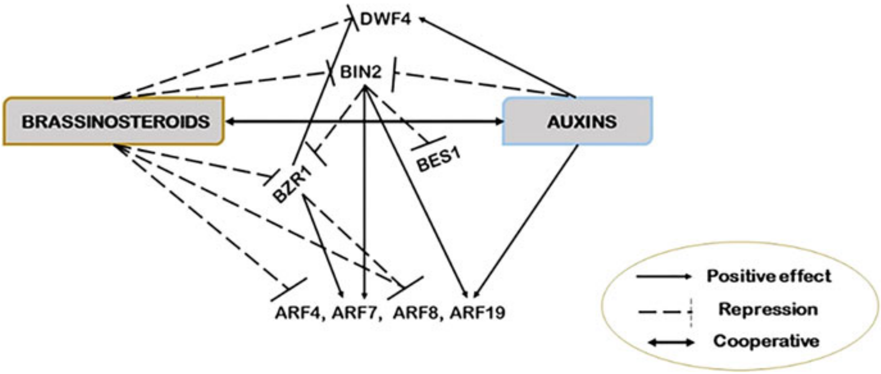

Fig. 15.3 A schematic model showing different signaling and biosynthesis genes during brassinosteroid-auxin interaction

studies revealed that the DELLA proteins (a key negative regulator of gibberellin signaling) have a suppressing effect on BZR1 transcriptional activity while interacting with BZR1/BES1 (Bai et al. 2012; Gallego-Bartolome et al. 2012; Li et al. 2012a; Peres et al. 2019). In *Arabidopsis* seedlings with lower levels of BR biosynthesis, hypocotyl elongation was promoted by GA or brassinazole treatment revealing the cooperative role of both hormones though it depends on the stage of growth, physiological conditions, and on the branched BR-regulated GA pathway (Gallego-Bartolome et al. 2012; Stewart Lilley et al. 2013; Unterholzner et al. 2015). BR influences GA biosynthesis not only in dicots but also in monocot plants as evident through the bioinformatics, chromatin immunoprecipitation (ChIP), and in vitro DNA binding studies, suggesting a direct binding of BZR1/BES1 to the target expression levels of two genes GA20ox, GA3ox, and GA2ox (encode enzymes in the rate-limiting step of GA production) from *Arabidopsis* and rice plants, respectively (Tong et al. 2014; Unterholzner et al. 2015; Peres et al. 2019). Thus, as per the postulates of the proposed model of BR-GA signaling involving the interaction between BZR1/BES1 and DELLA, BZR1/BES1 are activated post-translationally by BR to promote GA biosynthesis; further the escalated GA enhances DELLA degradation and releases the BZR1/BES1 activity. The stability of this proposed interaction is dependent upon the phosphorylation state of BZR1/BES1 proteins and the cellular localization of these processes (Ross and Quittenden 2016; Tong and Chu 2016; Unterholzner et al. 2016; Allen and Ptashnyk 2017) (Fig. 15.4). Additionally, the homeostasis between BR-GA is also affected during biotic stress where the biotic agents cause an interruption in the interplay between the hormones by producing hormonal mimicking signals for their own survival thereby disarming the immunity of their host (De Vleesschauwer et al. 2012; Peres et al. 2019).

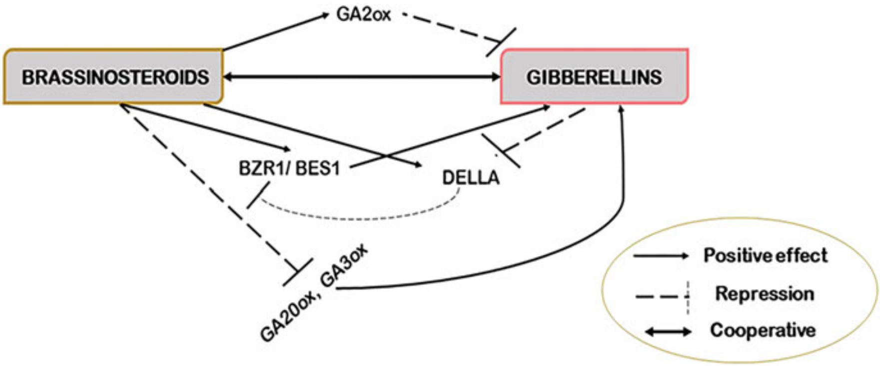

Fig. 15.4 A schematic diagram showing interaction between different signaling and biosynthesis genes during brassinosteroid-gibberellin cross talk

15.5.3 Interplay Between Brassinosteroids and Cytokinins

An indirect cross talk exists between brassinosteroids and cytokinins to regulate growth and development of plants. During lateral root formation, auxin transport is employed, and at molecular level, BR induces the expression of PIN genes (auxin efflux carriers) required for the development of root primordium, while CK suppresses its establishment by downregulating the expression of PIN genes, thus disturbing the auxin accumulation (Bao et al. 2004; Benjamins and Scheres 2008; Vercruyssen et al. 2011). Enzymatic targets of BR-mediated responses such as isopentenyl transferases (IPTs) and CKXs (CK oxidases/dehydrogenases) are responsible for the biosynthesis of bioactive cytokinins as well as its inactivation respectively. For example, in *Arabidopsis*, CKX3 gene directs the breakdown of CKs, and its overexpression under PYK10 (a root-specific promoter) reduces the levels of CKs in roots, causing minimal leaf and root growth. Reversibly, ectopic expression of CKX3 and BRI1 showed synergistic elevation in the leaf and root growth of plants (Werner and Schmülling 2009; Werner et al. 2010; Vercruyssen et al. 2011). In the regulation of several stress responses, negative role of CKs has been observed stating the gain and loss of function of CKX and IPT. On one hand, the overexpression of CKX implicated a deficiency of CK along with an elevated tolerance for drought and salinity; the suppression of IPT resulted in reduced levels of bioactive CK with enhanced stress tolerance. This negative relation may further be attributed to much repression of CK signaling pathway and inducing ABA signaling marker genes (such as AIL1, COR47, RAB18, RD29B, and SAG29) during cross talk between ABA and CK where ABA demonstrated similar results of increased stress tolerance via exogenous application (Nishiyama et al. 2011, 2012; Peres et al. 2019). Alternately, the role of BR can also be seen in drought stress such as in transgenic rice where it depends upon the physiological state of plant. The transgenic lines with IPT driven by PSARK (a stress- and maturation-induced promoter) showed increased CK levels before the start of senescence and BR

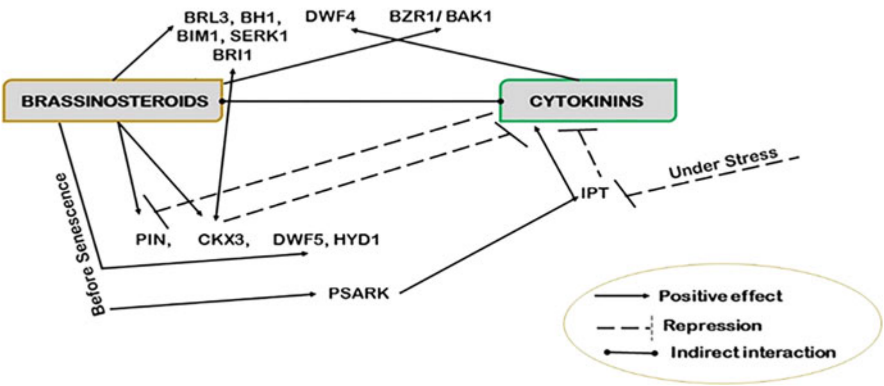

Fig. 15.5 Diagrammatic representation showing different signaling and biosynthesis genes during brassinosteroid-cytokinin interplay

signaling genes (BRL3, BRI1, BH1, BIM1, and SERK1) and its biosynthesis genes [DWF5 and HYD1 (HYDRA1)] were also upregulated under/no stress (Peleg et al. 2011) (Fig. 15.5).

15.5.4 Interplay Between Brassinosteroids and Ethylene

Cross talk between brassinosteroid and ethylene suggested indirect controls of different facets of plant growth and development. On one side, BR negatively regulates shoot gravitropism, and ethylene promotes shoot gravitropic reorientation through the involvement of auxin signaling genes (Guo et al. 2008; Vandenbussche et al. 2013). This is mainly achieved by activating and inhibiting negative and positive auxin signaling genes such as AUX/IAA and ARF7 and AR F19, respectively. However, ethylene works antagonistically by enhancing ARF7 and ARF19 and suppresses AUX/IAA to control shoot gravitropic responses (Vandenbussche et al. 2013). In case of root gravitropic responses also, the two hormones interact in opposite ways where BR increases root gravitropism while ET retards it by revamping auxin transport in the BR and ET mutants (Buer et al. 2006; Kim et al. 2007; Vandenbussche et al. 2013). Besides it, exogenously applied BR increases ET production in *Arabidopsis* seedlings by upregulating the expression of its key gene ACS (1-aminocyclopropane-1-carboxylate synthase) and stability of its proteins (mainly ACS5, ACS6, and ASC9) during external and internal stimuli thereby adjusting the ethylene synthesis in the plant tissues (Hansen et al. 2009; Muday et al. 2012). During root cell elongation, BRs and ET interaction has been observed in the root hair as well as the non-hair cells. In the case of root hair cells, the targeted expression of BRI1 activates the cell elongation in all tissues; however, it is retarded in non-hair cells due to elevation in the expression of two ACS genes: ACS5 and ACS9. Consequently, ACS genes catalyze the rate-limiting step of ET synthesis by forming ACC (1-aminocyclopropane-1-carboxylate) that accumulates and enhances

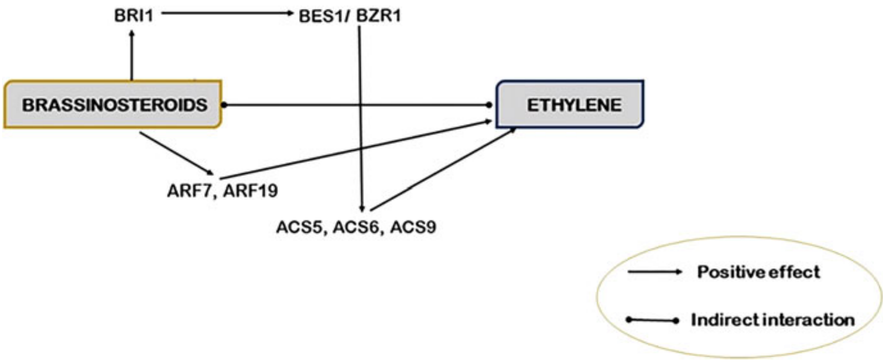

Fig. 15.6 A schematic representation of different signaling and biosynthesis genes in brassinosteroid-ethylene relationship

ethylene signaling, thereby inhibiting unidirectional cell expansion (Fridman et al. 2014; Zhu et al. 2016). On the contrary, synergistic relationship also exists between BR and ET in controlling hyponastic growth being employed by plants to cope the environmental strains. Here, ET is the main regulator and in turn is regulated by BR. C-23 hydroxylation of BR synthesis is mediated by ROT3 (ROTUNDIFOLIA3/CYP90C1), and any change in it impairs local cell expansion and inhibits BR synthesis which further lowers ethylene-induced upward leaf movement (Polko et al. 2013) (Fig. 15.6).

15.5.5 Interplay Between Brassinosteroids and Abscisic Acid

In plants, seed germination, root elongation, and even during stomatal closing, plants with defective BR signaling show enhanced sensitivity for ABA, thus showing antagonistic relationship between BRs and ABA (Steber and McCourt 2001; Zhang et al. 2009; Li et al. 2012b; Wang et al. 2020). During signaling process also, BR signaling opposes the ABA biosynthesis. This is evident through the removal of BSK5 (a positive regulator of BR signaling) which causes the induction of ABA3 and NCED3 (ABA biosynthesis-related genes) (Ha et al. 2016; Ha et al. 2018). Additionally, during BR-ABA cross talk, upstream of BIN2 kinase causes the downstream of BR receptor complex. In this, two negatively regulating ABA genes, ABI1 and ABI2, interact as well as dephosphorylate BIN2 (a negative regulator of BR signaling) to further regulate the phosphorylation of BES1. However, an in vitro ABA signal transduction mimicking showed that ABA through its receptors inhibit ABI2 which further promotes BIN2 phosphorylation (Zhang et al. 2009; Wang et al. 2018; Bulgakov and Avramenko 2020). Even under drought stress, BES1 impedes ABA induction of a drought-related transcription factor RD26 (RESPONSIVE TO DESICCATION 26) and it reciprocatively exhibits antagonism by modulating BES1-regulated transcription which hinders brassinosteroid-regulated growth (Chung et al. 2014; Ye et al. 2017). Moreover, early signaling of ABA is modified

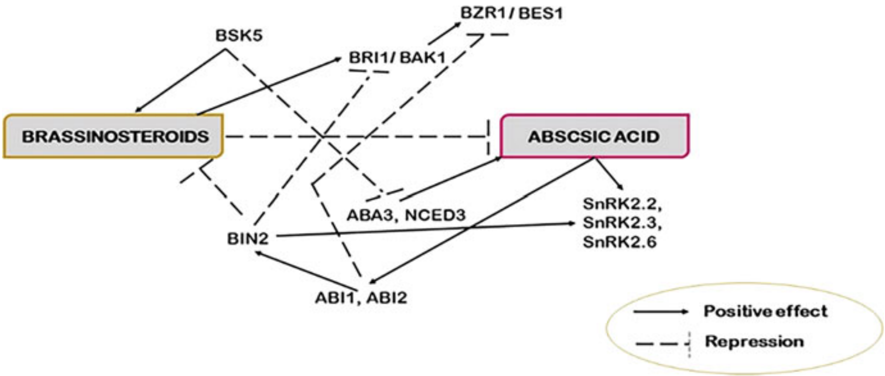

Fig. 15.7 Diagrammatic model showing interaction of signaling and biosynthesis genes during brassinosteroids-abscisic acid interlinkage

by BR as in the case of *Arabidopsis*, by directly affecting phosphorylation of the active ABA signaling participants such as SnRK2.2, SnRK2.3, and SnRK2.6. Here too, BIN2 kinase signaling acts as an interacting protein of SnRK2.2 causing its phosphorylation along with SnRK2.3 (Belin et al. 2006; Yoshida et al. 2010; Fujita et al. 2013; Cai et al. 2014) (Fig. 15.7).

15.5.6 Interplay Between Brassinosteroids and Salicylic Acid

The existence of the cross talk between BR and SA plays a key role in plants under a variety of environmental constraints. During biotic stress, though BR acts as an enhancer in vast range of disease resistance, this BR-mediated boosted resistance does not depend upon SA. However, the joint effect of BR and SAR (systemic acquired resistance) provides an additive protection against pathogens (Nakashita et al. 2003; Saini et al. 2015). Under biotic stress, APETALA2/ETHYLENE-RESPONSIVE FACTOR gene GhTINY2 is strongly enhanced. Its overexpression boost the plant's tolerance, and its underexpression makes the plant susceptible to infection. This is mainly because of more SA accumulation and its signal transduction through WRKY51 (WRKY transcription factor 51). However, the overexpression of GhTINY2 retards growth, knockdown of genes induced by BRs, and upregulation of BR-repressed genes. This occurs because of its interaction with BZR1 along with restraining of the transcriptional activation of IAA19 (INDOLE-3-ACETIC ACID INDUCIBLE 19) (Xiao et al. 2021). NPR1 (NON-EXPRESSOR OF PATHOGENESIS-RELATED GENES1) regulate BR signaling genes; BIN2 and BZRI induces stress tolerance in plants, and the interplay between BR and SA may be due to the NPR1 gene which stimulates expression of the SA-related genes involved in plant defense (Divi et al. 2010; Ohri et al. 2015). Additionally, negative cross talk also exists between SA and BR signaling pathways that resulted in the immune-suppressive effect of BR. Moreover, the external

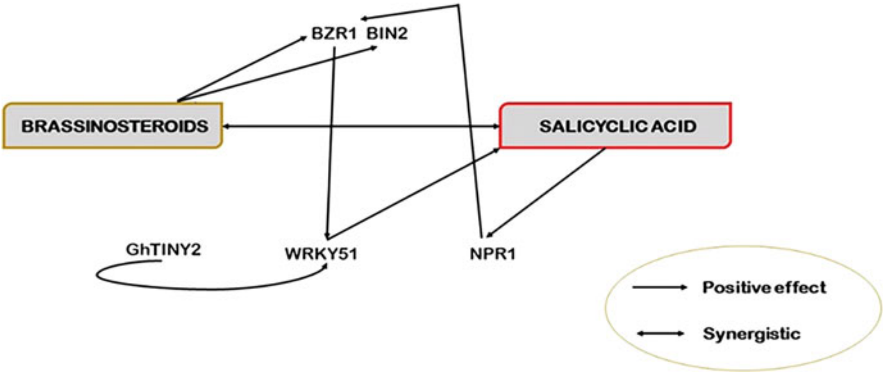

Fig. 15.8 A simplified model showing different signaling and biosynthesis genes during brassinosteroids-salicylic acid interaction

application of BRs activated the master defense regulators of SA pathway such as NPR1 and OsWRKY45 (WRKY transcription factor) (De Vleesschauwer et al. 2012) (Fig. 15.8).

15.5.7 Interplay Between Brassinosteroids and Jasmonic Acid

BR modulates JA signaling and inhibits JA-dependent growth and plays a vital role in both abiotic/biotic stresses in plants. Induced *OPR3* (encodes 12-oxophytodienoic acid reductase) jointly by BRs and JA signifies a potential integration node between BR action and JA synthesis (Zhang et al. 2009; Saini et al. 2015). In *Arabidopsis*, restoration of the sensitivity and hypersensitive reaction of JA was seen during a leaky mutation of DWF4 in coi1 mutant and a hypersensitive reaction in the wild type toward JA. But when BRs were applied exogenously, it mitigated root growth inhibition of JA because of downregulation of DWF4 in a COI1-dependent (CORONATINE INSENSITIVE1) manner by jasmonate (Ren et al. 2009; Jang et al. 2020). Jasmonate-induced anthocyanin accumulation is a hallmark of jasmonic acid-induced responses which reduces in BR-biosynthetic mutants, but the BR application helps plants accumulate anthocyanin. This occurs because of the minimal expression of MYB (transcription factor) genes PAP1 and PAP2 (PRODUCTION OF ANTHOCYANIN PIGMENT1) (Peng et al. 2011; Song et al. 2011; Wasternack and Hause 2013). In rice, thionin genes known for encoding antimicrobial peptides were greatly induced by JA but were enhanced by BR during stress (Kitanaga et al. 2006). Against insect herbivory also, BR-JA cross talk showed the defensive role of JA for anti-herbivory, while BR impedes it (Campos et al. 2009). In *Oryza sativa*, exogenous application of JA decreased expression of BR signaling gene, OSBRI1 and BR biosynthesis gene, and OsDWF4, during nematode infection revealing antagonistic interplay between JA and BR (Nahar et al. 2013) (Fig. 15.9).

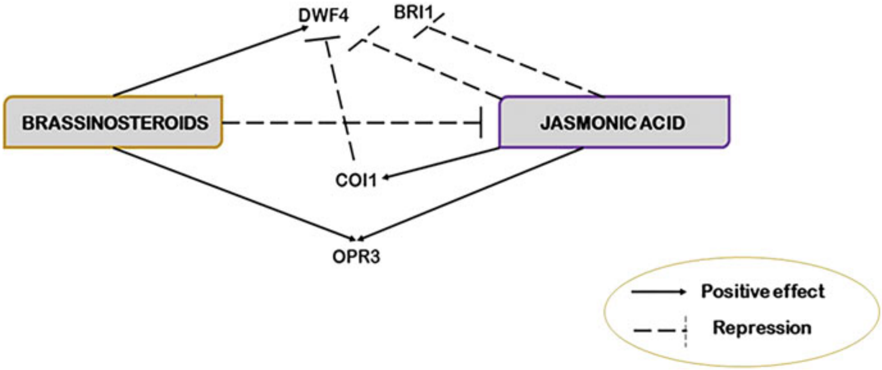

Fig. 15.9 A schematic representation showing different signaling and biosynthesis genes of brassinosteroids-jasmonic acid cross talk

15.5.8 Interplay Between Brassinosteroids and Strigolactones

Cross talk between BR and SL is still in its budding stage, and the inter-hormonal interaction pathways have been demonstrated recently (Faizan et al. 2020). Both BRs and SL help in regulating shoot branching in plants. This is achieved through the SL's key signaling component E3 ubiquitin ligase MAX2 (a shoot branching inhibitor) that continuously interacts with BR's transcription factors BZR1 and BRI1 EMS SUPPRESOR1 (BES1) by binding directly with them and causing their degradation. However, MAX2-mediated degradation of BR transcription factors is promoted by SL signaling resulting in suppressed shoot branching (Yin et al. 2002; He et al. 2005; Kim and Wang 2010; Wang et al. 2013). However, this has been contradicted in *bes1-D* mutant, where the role of BES1 was re-examined. The chosen phenotype with enhanced shoot branching does not show any association with the characteristic *bes1-D* leaf phenotype, thereby advocating that the branching defect described earlier might be wrongly referred to as a mutation in BES1 only (Bennett et al. 2016). Further, it is expected that advances in the studies of this new class of phytohormone will help in explaining the key underline players of the hormonal cross talk between BRs and SLs (Fig. 15.10).

15.6 BR-Mediated Modulation of Plant Antioxidant Defense System Under Abiotic Stress

Reactive oxygen species (ROS) are key regulatory and signaling molecules that play important role in plant growth and development. ROS, such as superoxide radical ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($^{\cdot}OH$) production, elevates when plant is exposed to certain stressed conditions. Brassinosteroids improve the scavenging mechanism of these ROS by modulating the antioxidative as well as

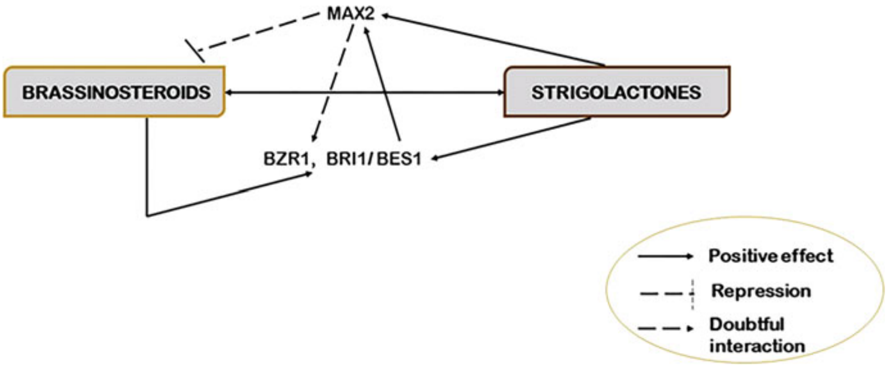

Fig. 15.10 Diagrammatic representation showing signaling and biosynthesis genes during brassinosteroid-strigolactone interaction

non-antioxidative system, thus playing an essential role in plant stress tolerance (Table 15.2).

15.6.1 Thermal Stress

In present scenario, with the increase in global greenhouse effect, changes in climatic conditions lead to rise in temperature, which has become one of the major detrimental stresses amid of constantly fluctuating environmental factors (Luo and Lau 2019; Karwa et al. 2020). Transcriptomic studies reveal that thermal/heat stress causes downregulation of critical gene(s) involved in the synthesis of cell wall, carbon assimilation, transport and accumulation of starch, and many metabolic pathways (Kothari and Lachowiec 2021). Plants in the environment are inevitable to such conditions but undergo some series of mechanisms to cope up with increased temperature, namely, osmoprotectants, ion transporters, antioxidant system, late embryogenesis abundant (LEA) proteins, heat shock proteins, signaling messenger, and factors of transcriptional machinery (Rodríguez et al. 2005). Various reports are available which depict BR-induced heat tolerance in plants. Though the underlined mechanism activated by BR for providing thermal stress tolerance is still not so clear, but different studies suggest that a signaling cascade is initiated by BR application which activates and brings together the small polypeptides and proteins, such as heat shock proteins (HSPs) or stress-induced proteins, to alleviate stress conditions (Bhandari and Nailwal 2020). BRs are believable to act as immunomodulators, protecting plants from injuries of HT stress. Several reports showed that BRs increase the production of heat shock proteins (HSPs) under thermal stress, thereby protecting proteins against irreversible heat-induced damage by preventing denaturation and facilitating the refolding of damaged proteins (Chauhan et al. 2011). BRs elevate the activities of various enzymes involved in the ascorbate–glutathione (AsA-GSH) cycle and maintain the homeostatic redox

Table 15.2 Role of BRs in modulating antioxidative defense system of plants under abiotic stress conditions

Type of abiotic stress	BR source	Mode of treatment	Plant species	Effect	References
Drought stress	BR	Seedling treatment	*Zea mays*	Enhanced water stress tolerance by increasing ABA biosynthesis	Zhang et al. (2011)
	BL	Soaking of roots	*Xanthoceras sorbifolia*	Increased leaf water content, relative water content, soluble sugar and protein content, SOD, POD, CAT, APOX activities	Li and Feng (2011)
	EBL	Foliar spray	*Capsicum annuum*	Enhanced antioxidant activity and prevented drought-induced inhibition photoinhibition	Hu et al. (2013)
	EBL HBL	Seed priming	*Raphanus sativus*	Increased levels of nucleic acids and soluble proteins, decreased activities of RNase and lowered lipid peroxidation and MDA content	Mahesh et al. (2013)
	BR	Seed priming	*Arachis hypogaea*	Improved oxidative enzyme levels and enhanced polyphenol and relative water content	Savaliya et al. (2013)
	HBL	Foliar spray	*Helianthus annuus*	Increased protein synthesis and acid inverters activity	Filova (2014)
	EBL	Foliar spray	*Capsicum annuum*	Elevation of stress-related transcription factors and antioxidant enzymes (*cAPX* and *MDAR*)	Hu et al. (2015)
	EBL	Foliar spray	*Lycopersicum esculentum*	Decreased ion leakage, lipoxygenase activity and ethylene production and increased SOD activity in leaves	Behnamnia (2015)
	EBL HBL	Seed priming	*Cajanus cajan*	Increased ABA, glycine betaine, proline accumulation, and decreased H_2O_2 and MDA content	Shahana et al. (2015)
	EBL + spermine	Foliar spray	*Zea mays*	Enhanced activities of dehydroascorbate reductase and monodehydroascorbate reductase	Talaat et al. (2015)
	EBL	Foliar spray	*Vigna unguiculata*	Improved photosystem II efficiency, gas exchange, and increased SOD, CAT, APX, and POX activities	Lima and Lobato 2017
	EBL	Seedling treatment	*Vitis vinifera*	Reduced the H_2O_2 content and superoxide radical (O_2^{*-} $^{-}$) production rate and enhanced content and activities of antioxidants	Wang et al. (2019)

Salinity stress	EBL + putrescine	Foliar spray	*Cucumis sativus*	Improved growth, chlorophyll content, and photosynthetic efficiency and promoted the activities of CAT, SOD, and POD	Fariduddin et al. (2013)
	EBL + putrescine	Foliar spray	*Lycopersicon esculentum*	Decreased MDA content and lipid peroxidation	Slathia et al. (2013)
	EBL + SA (salicylic acid)	Seed priming	*Phaseolus vulgaris*	Enhanced concentration of osmoprotectants and improved leaf water status and integrity of plasma membrane	Semida and Rady (2014)
	EBL + methyl jasmonate	Foliar spray	*Vitis vinifera*	Improved transpiration rate, pigments, photosynthesis, and proline content	Seif et al. (2014)
	EBL	Foliar spray	*Pisum sativum*	Improved osmolytes concentration and plant biomass.	Shahid et al. (2015)
	EBL + spermidine	Foliar spray	*Vigna radiata*	Increased activities of POX, SOD, and CAT and enhanced proline content, glycine betaine content, and gas exchange characteristics	Mir et al. (2015)
	EBL + ABA	Foliar spray	*Solanum tuberosum*	Enhanced various antioxidative defense enzyme activities	Upadhyaya et al. (2015)
	EBL	Seed priming	*Gossypium hirsutum*	Enhanced activities of GPX and SOD and improved proline content and pigments	Surgun et al. (2015)
Heat stress	EBL	Foliar spray	*Zea mays*	Alleviated protein degradation and enhanced cell membrane stability due to increased CAT, SOD, and POX activities	Yadav et al. (2016)
	BL	Foliar spray	*Leymus chinensis*	Enhanced biosynthesis of proline, sugars, and protein content and activation of antioxidant defense machinery	Niu et al. (2016)
	EBR	Spraying	*Solanum melongena* L.	Enhanced photosynthesis, seed germination, yield, and quality of crop	Wu et al. (2014)
	BRs	Seed priming	*Pinus sylvestris* L.	Enhanced seed germination	Cukor et al. (2018)
Zinc stress	EBL	Dipping	*Solanum nigrum*	Redox homeostasis	Sousa et al. (2020)
Cadmium stress	EBR	Spraying	*Vigna unguiculata* L.	Enhancement in leaf, root, and total dry matter. Elevated chlorophyll and gas exchange parameters	Santos et al. (2018)

(continued)

Table 15.2 (continued)

Type of abiotic stress	BR source	Mode of treatment	Plant species	Effect	References
Iron stress	EBR	Dipping	*Oryza sativa* L.	Enhanced electron transportation, photosynthetic activity	Tadaiesky et al. (2021)
Chromium stress	EBL	Seed priming	*Oryza sativa* L.	Improved ROS scavenging and maintain homeostasis	Basit et al. (2021)

potential during thermal stress in plants. BRs enhanced the expression of various genes encoding these enzymes (Zhang et al. 2014; Yadava et al. 2016; Kaur et al. 2018; Li et al. 2018; Surgun-Acar and Zemheri-Navruz 2019). Brassinosteroids alleviate the heat stress by regulating the glyoxylate and antioxidative system in the case of *Ficus* seedlings (Jin et al. 2015; Anwar et al. 2018). A study conducted by Sonjaron et al. (2018) revealed that 7,8-dihydro-8a-20-hydroxyecdysone (aDHECD), a mimic of brassinosteroid, improve the photosynthetic activity and carbohydrate content in rice seedlings under high temperature conditions. The mechanism of BR that contributes to plant heat stress (HS) tolerance is mediated by various essential complicated processes, namely, enhancing photosynthetic efficiency by maximizing the rate of carboxylation by Rubisco and improving the efficiency of PSII photochemistry; elevating photosynthetic pigments, stomatal conductivity, and membrane stability; activating antioxidant mechanisms; and maintaining redox homeostasis. Contrary to this, reduction in lipid peroxidation and production of ROS is observed (Hayat et al. 2010; Kaur et al. 2018; Kaya et al. 2019). Although a large number of studies demonstrated the heat stress-protective role of BR using exogenous applications, only a small number of studies are focused on molecular mechanism involved in heat stress tolerance (Ahammed et al. 2014; Zhou et al. 2014). It has been reported that a transient H_2O_2 production in the apoplast functions as a critical signal to mediate BR-induced heat stress tolerance in tomato (Zhou et al. 2014).

15.6.2 Heavy Metal Stress

Presently, heavy metals (HM) are regarded as major pollutants in the environment due to their toxic effect at very low concentration. “HM” is collective term, which applies to the group of metals and metalloids with greater atomic density than 4 g/cm^3, or five times, greater than water (Hawkes 1997; Gjorgieva Ackova, 2018). A number of HMs include cobalt (Co), nickel (Ni), lead (Pb), silver (Ag), iron (Fe), cadmium (Cd), chromium (Cr), zinc (Zn), arsenic (As), and the platinum group elements that are present in the environment affecting all its living components (Nagajyoti et al., 2010). Plants being sessile are exposed to various stress conditions in the environment, and HM constitutes one of the major obstacles in growth and development of plants. Anthropogenic activities and improper use of fertilizers and pesticides, urbanization, industrialization, and fossil fuel combustion have led to tremendous increase in concentrations of various hazardous chemicals in agricultural soils (Chen et al. 2015; Zhao et al. 2018). Toxic effect of HMs varies according to plant species, their concentrations, and chemical nature. HM reduces the rate of photosynthesis and the required precursors for the process. Also, there is significant reduction in quality and quantity of yield cultivated in polluted area with high risk of chemical consumption by human population (Wu et al. 2017; Hasan et al. 2019).

Recently, BRs, as an alternate eco-friendly tool for improving heavy metal (HM) stress tolerance in plants, have gained momentum (Bücker-Neto et al. 2017). BRs are reported for assimilation and metabolizing capacity for these chemicals (Santos et al. 2018). Plant exposed to HMs showed varied responses at the morphological, cellular, and molecular levels, and to study the complex mechanism underlining the improved tolerance by application of BRs**,** various studies have been conducted by worldwide scientists showing ameliorating effect of BRs during HM stress (Nawaz et al. 2017; Santos et al. 2018; Sharma et al. 2018; Wu et al. 2019; Ahammed et al. 2020; Soares et al. 2020; Betti et al. 2021). Study conducted by Jakubowska and Janicka (2017) decipher the potent role of BRs to provide stress tolerance during cadmium stress in cucumber plants. It has been observed that the BR stress tolerance is induced by the induction of plasma membrane NADPH oxidase and H^+ ATPase pump enzyme in cucumber during Cd stress. Similarly, BRs improve the tolerance against Cd in cowpea plants (Santos et al. 2018).

Exogenous application of EBL enhances the lead tolerance in both seeds and seedlings of *Brassica juncea* L. EBL alters the antioxidative enzyme activity and enhances the rate of ROS scavenging by their increased activity (Soares et al. 2020). Similar results have also been obtained by Wu and his coworkers (2019) in which EBL showed ameliorative effect against metalloid stress. Exogenously applied EBL (foliar spray) altered various enzymes and decreased the ROS level in wild *Arabidopsis thaliana* seedlings which improves stress tolerance against antimony. Similarly, EBL plays an important role in providing strength to rice plants against iron stress. Exogenous application of EBL can alter the light-capturing capacity and stomata conductance, increase thickness of epidermis of leaves, and maintain membrane integrity of leaves under Fe toxicity (Tadaiesky et al. 2021). Similarly, application of 28-Homobrassinolide improves the stress tolerance against Pb, Cd, and Zn and attenuates their toxic effect on growth and development of seedlings (Xu et al. 2019). Tolerance to high level of Zn has been reported in *Solanum nigrum* L by the foliar application of EBL, contributing in better physiological status and redox homeostasis in Zn-stressed seedlings (Sousa et al. 2020). BRs in combination with calcium play important role in amelioration of aluminum stress in plants (Ashraf et al. 2019). Improved root/shoot length and enhanced carotenoid, glutathione, ascorbic acid, and tocopherol content were reported with elevation in the expression catalase, peroxidase, glutathione reductase, and glutathione-S-transferase genes by EBL application during lead stress (Kohli et al. 2018). In conclusion, exogenous application of BR induce enhancement of tolerance to heavy metals is their involvement in substantial improvement in carbon metabolism, photosynthetic pigment content, antioxidative defense system, ROS scavenging capacity, glutathione content etc. (Choudhary et al. 2012; Rajewska et al. 2016). Though there are many reports available for stress tolerance properties of steroidal hormone (brassinosteroids), but there is still uncertainty about endogenous BR levels being modulated by exogenous BR under heavy metal stress.

15.6.3 Drought Stress

Water scarcity, which is one of the most deleterious of all environmental stresses, checks the growth of many crop varieties and declines the quality and quantity of crop production (Todorova et al. 2016). Severe drought stress conditions lead osmotic stress due to overproduction of reactive oxygen species (ROS) thereby reducing photosynthetic rate; revamping nitrogen and antioxidant metabolism, secondary metabolite accumulation, and mineral nutrition; and ultimately causing growth reduction in plants (Jatav et al. 2014; Ahanger et al. 2015; Ahanger et al. 2018). Various studies have reported that the exogenous application of plant growth regulators like BRs can mitigate the drought-induced adverse effects on the growth and metabolism of plants (Behnamnia 2015; Nawaz et al. 2015; Talaat et al. 2015; Ahanger et al. 2018). They enhance the antioxidative defense of plants to combat water deficiency. Exogenous application of BRs to plants suffering from drought stress causes reduction in H_2O_2 (hydrogen peroxide) and MDA (malondialdehyde) contents as a result of scavenging activities of antioxidative enzymes such as peroxidase (POD), catalase (CAT), superoxide dismutase (SOD), and ascorbate peroxidase (APX) (Li and Feng 2011; Vayner et al. 2014; Nawaz et al. 2017). Foliar application of EBL (0.01 mg/L) can also improve the antioxidant activity and drought-induced inhibition of photosynthetic functioning in *Capsicum annuum* (Hu et al. 2013).

It has been observed that exogenously applied BRs increase the concentration of abscisic acid and negate the toxic effects of water stress on plants (Wang et al. 2019). Supplementation of BRs (24-EBL and 28-HBL) alleviates the toxic effects of polyethylene glycol-6000 (PEG)-induced drought stress by enhancing seed germination, seedling length, and biomass (fresh and dry weight) in *Cajanus cajan* by increasing abscisic acid, glycine betaine, and proline accumulation (Shahana et al. 2015). It has been observed that the application of EBL and HBL to drought-stressed pigeon pea significantly decreases H_2O_2 and MDA accumulation by increasing antioxidative activities of SOD, CAT, POD, APX, and GR (glutathione reductase) (Shahana et al. 2015). Earlier, both EBL and HBL treatments have been found to reverse the inhibitory effects of PEG-6000-induced water stress on radish seedlings by increasing seed germination and seedling growth associated with enhanced levels of nucleic acids and soluble proteins and decreased activities of RNase. They also maintained the membrane integrity by lowering lipid peroxidation and MDA content (Mahesh et al. 2013). Recently, Tanveer et al. (2019) discussed the potential role of EBL in improving drought stress tolerance in plants. EBL ameliorates the negative effects of water stress by increasing carbon assimilation rate, perpetuating balance between ROS and antioxidants, and accumulating solutes especially proline (Tanveer et al. 2019). It enhances photosynthesis and other leaf gas exchange traits by protecting the ultrastructure of photosynthetic pigment apparatus from degradation (Tanveer et al. 2019).

BRs mediated plant defense mechanism against oxidative stress by maintaining the expression of genes involved in encoding xyloglucan endotransglucosylase/hydrolases (XTHs) or by escalating the activity of H^+-ATPase, sucrose synthase, and cellulose synthase (Clouse 2011; Nawaz et al. 2017). Application of BRs transmutes the expression of genes responsible for encoding both structural and regulatory proteins (Ahammed et al. 2020). It was studied that the overexpression of *Arabidopsis* BR biosynthetic gene *DWF4* in *Brassica napus* increased seed yield, root biomass, and length and enhanced stress tolerance caused by dehydration (Sahni et al. 2016). Duan et al. (2017) cloned a BR biosynthetic gene, *SoCYP85A1*, from *Spinacia oleracea* and studied its effect on abiotic stress tolerance in tobacco. They found that overexpression of the cloned gene improved drought tolerance and resulted in longer primary root and more lateral roots in transgenic tobacco as compared to wild types by eliminating ROS and MDA accumulation and improving proline content along with antioxidant enzyme activities (Duan et al. 2017).

15.6.4 Salinity Stress

Salinity is a major abiotic stress that renders most of the agricultural lands as barren wastelands resulting in food scarcity. It affects the water absorption capacity of plants that leads to overall decrease in plant growth (Bartwal and Arora 2020). Salinity stress, often termed as physiological drought, negatively affects plant development and productivity by inducing osmotic and ionic imbalances (Ahanger and Agarwal 2017; Kaur et al. 2018; Ahammed et al. 2020). Salt stress-induced toxic effects on plants include osmotic stress, ionic toxicity, truncated nitrogen metabolism, increased production of ROS that leads to oxidative damage, retarded photosynthetic functioning, and hindrance in uptake and translocation of mineral nutrients (Ahmad et al. 2010; Iqbal et al. 2015; Ahanger and Agarwal 2017). It is well established that exogenous application of BRs can reverse the negative effects induced by saline conditions on growth and development of plants. Time and again various studies have reported the role of BRs in mitigating the toxic effects of salt stress in wide range of plants including *A. thaliana,* rapeseed (*Brassica juncea*), mustard (*B. napus*), eggplant (*Solanum melongena*), pepper (*Capsicum annuum*), cucumber (*Cucumis sativus*), maize (*Zea mays*), and common bean (*Phaseolus vulgaris*) (Yuan et al. 2012a; Yue et al. 2018; Ahammed et al. 2020).

BRs help plants to cope up with salt stress by regulating antioxidative defense system. They activate the antioxidative defense machinery by influencing or controlling the transcription and/or translation of specific genes to improve the oxidative stress tolerance potential of plants (Cheng et al. 2015; Fariduddin et al. 2014). In a study, it was found that 24-EBL application enhanced growth, soluble proteins, and antioxidant activities of *Solanum tuberosum* suffering from salinity stress (Khalid and Aftab 2016). In another study, it was observed that exogenous application of BR conferred tolerance and mitigated the negative effects of NaCl-induced salt stress in cucumber by improving growth, chlorophyll content, and photosynthetic efficiency; promoting the activities of antioxidative enzymes, namely, CAT, SOD, POD; and increasing proline content (Fariduddin et al. 2013). In the same plant NaCl-induced production of ROS like O_2^- and H_2O_2 was mitigated by the enhancement of antioxidative defense system by EBL application (Lu and Yang 2013). Supplementation of watermelon with 24-EBL increased its salt tolerance by enhancing CO_2 accumulation and water use efficiency; BRs were suggested to promote photosynthesis through activation of photosynthetic enzymes like Rubisco under salt stress conditions (Cheng et al. 2015).

It is well documented that salinity stress reduces the percentage of seed germination and overall biomass of crops, but after treating stressed plants with brassinolide, an increase in germination rate as well as root and shoot length was seen, and nitrate reductase activity was also increased as compared to stressed plants (Lalotra et al. 2017). Apart from exogenous application of BRs, harmful effects of high salt content have been ameliorated, and stress tolerance has been improved by employing seed priming techniques (Ahanger et al. 2018). In an experiment Zhang and his co-workers pre-treated the seeds of *Medicago sativa* with EBL and then exposed them to saline conditions. They noticed that under the influence of EBL, seed germination increased and oxidative damage reduced by enhanced activities of antioxidant enzymes, namely, SOD, POD, and CAT (Zhang et al. 2007). It has been seen that BRs regulate DNA methylation that plays a pivotal role in salinity tolerance. In a study, cytosine DNA methylation was found to be decreased in *Linum usitatissimum* (flax) upon NaCl (150 mM) exposure; however, seed priming with 24-EBL induced total methylation and enhanced salt tolerance, suggesting its role in epigenetic modification under salinity stress (Amraee et al. 2019).

15.6.5 Other Major Abiotic Stress

Aside from the above discussed major abiotic stressors, BRs and related compounds can also play notable roles in plants to cope up with other abiotic stressors like pesticides, photoinhibition/light stress, nutrient stress, and water-logging/water-flooding stress (Ahammed et al. 2012b; Sharma et al. 2013, 2017; Xia et al. 2006; Ogweno et al. 2010; Ahanger et al. 2018; Janeczko et al. 2010; Kang et al. 2006, 2009; Liang and Liang 2009; Lu et al. 2006; Lu and Guo 2013). 24-Epibrassinolide can enhance the tolerance of *Oryza sativa* and *Brassica juncea* to stress generated by pesticide imidacloprid (IMI) by decreasing lipid peroxidation via enhanced activity of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APOX), guaiacol peroxidase (GPOX), glutathione reductase (GR), and monodehydroascorbate reductase (MDHAR), upregulating the expression of some genes like Fe-SOD, Mn-SOD, Cu/Zn-SOD, CAT, APOX, and GR (Sharma et al. 2013; Sharma et al. 2017). In $Ca(NO_3)_2$-exposed *Cucumis sativus,* EBL upregulated the ROS-scavenging metabolism of antioxidant enzymes and protected the photosynthetic membrane system (Yuan et al. 2012b). Mitigation of impacts caused by pyrene and phenanthrene toxicity in tomato has been observed as result of EBL-mediated decreased content of MDA and increased activity of CAT, APOX, GPOX, and GR (Ahammed et al. 2012a). Application of EBL decreased the lipid peroxidation and increased H_2O_2 metabolism via enhanced activity of GST and GSH content which were asserted to help *Solanum tuberosum* to counteract phenanthrene-accrued consequences (Ahammed et al. 2012b, c). In tomato exposed to phenanthrene and Cd co-contamination, decrease in lipid peroxidation and enhanced antioxidant defense system by EBL were reported by Ahammed et al. (2013a). Recently, Ahammed et al. (2013b) evidenced that EBL benefited the tomato to maintain photochemical quenching coefficient (Pq), quantum efficiency of PSII phytochemistry {(PS II)}, and photochemical efficiency of PSII (Fv/Fm) under polychlorinated biphenyls induced oxidative stress by enhancing the activities of antioxidant enzymes. Phytotoxicities of nine pesticides (abamectin, chlorpyrifos, Cuproxat, cyazofamid, Fluazifop-p-butyl, flusilazole, haloxyfop, imidacloprid, and paraquat) had been alleviated by pre-treating *Cucumis sativus* with EBL. EBL increased the CO_2 assimilation capacity and antioxidant enzyme activity in *C. sativus* (Xia et al. 2006). Application of EBL under light stress in tomato (*Lycopersicon esculentum*) enhanced the activity SOD, CAT, APOX, and GPOX enzymes and benefited the plants to maintain photochemical quenching (qP), quantum efficiency of PSII (PS II), and net photosynthetic rate (Pn) by decreasing lipid peroxidation (Ogweno et al. 2010). Significant role of EBL in enhancing the activity of antioxidant enzymes was evidenced in plants exposed to chlorpyrifos (Xia et al. 2009). Similarly, application of 24-epiBL to *Arachis hypogea* mitigated the oxidative stress induced by Fe-deficiency and reduced ROS production by enhancing activity of nitrate reductase, antioxidant system, and osmolyte accumulation (Song et al. 2016). Exogenous application of EBL (soaking and foliar) reduced uptake of iron and sodium and increased uptake of magnesium, calcium, and potassium in wheat (Janeczko et al. 2010). Foliar spray of EBL in *C. sativus* mitigated toxic effects of excess calcium on the uptake of necessary mineral elements such as potassium, magnesium, phosphorus, and manganese (Yuan et al. 2015). BRs and related compound were evidenced to furnish tolerance to water-logging/water-flooding stress to different crops such as oilseed rape (Liang and Liang 2009), soybean (Lu et al. 2006), and cucumber (Kang et al. 2006, 2009; Lu and Guo 2013) mainly by decreasing oxidative damage via increased activities of SOD and POD (peroxidase).

15.7 BR-Mediated Modulation of Plant Antioxidant Defense System Under Biotic Stress

Under natural conditions, plants are exposed to both abiotic stress (discussed above) and biotic stress (viruses, bacteria, fungi, insects, nematodes, parasites, and weeds). Plants use inducible defense mechanism to effectively tolerate different types of stress. Induced defense mechanism of plants against biotic stress is similar to defense induced against abiotic stress (Anwar et al. 2018). BRs and related compound not only help the plants to cope up with abiotic stresses but also play an important role to enhance the tolerance against biotic stresses (Krishna 2003; Ali et al. 2007; Jager et al. 2008; Bajguz and Hayat 2009; Nawaz et al. 2017) (Table 15.3). They involve complex signaling cascade to positively regulate antioxidant defense metabolism (Belkhadir et al. 2012) and induce innate immune response to protect the cells from different biotic stresses (Wang et al. 2012). Application of brassinolide (BL) in *A. thaliana* infected with cucumber mosaic virus (CMV) increased the activity of antioxidant enzymes like CAT, SOD, POD, and APOX; decreased photosystem damage; and modulated expression of genes related to defense (Zhang et al. 2015). Growth and activity of antioxidant enzymes in tomato also enhanced by

Table 15.3 Role of BRs in modulation of plant antioxidant defense system under various biotic stress

Type of biotic stress	BR source	Mode of BR treatment	Plant species	Effects	References
Bacteria	EBL	Injected in leaves	*Arabidopsis thaliana*	Inhibition of FLS2-mediated immune signaling	Albrecht et al. (2012)
Fusarium culmorum	EBL	Soil and foliar application	*Hordeum vulgare*	Inhibition of *Fusarium* head blight	Ali et al. (2013)
Oidium sp. and *Pseudomonas syringae and* TMV	EBL	Hydroponic system	*Hordeum vulgare*	Increased resistance against powdery mildew fungus *Oidium* sp. bacterium *Pseudomonas syringae* and TMV	Ali et al. (2014)
TMV	BL	Leaf treatment	*Nicotiana benthamiana*	Increased systemic TMV resistance	Deng et al. (2016)
Fusarium	EBL	Root and foliar application	*Cucumber sativus*	Reduced infection of *Fusarium* wilt	Ding et al. (2009)
Verticillium dahlia	BL	Soil application	*Gossypium barbadense* and *Gossypium hirsutum*	Enhanced resistance against wilt causing fungus	Gao et al. (2013)
Meloidogyne incognita	EBL	Seed dipping	*Solanum lycopersicum*	Increased tolerance against *M. incognita* by enhancing activity of antioxidant enzymes	Jasrotia and Ohri (2014, 2017a, b)
Meloidogyne graminicola	BL	Foliar application	*Oryza sativa*	Enhanced innate immunity against *M. graminicola*	Nahar et al. (2013)
Meloidogyne incognita	HBL EBL	Seed treatment	*Brassica juncea*	Increased tolerance against *M. incognita*	Ohri and Kaur (2011); Ohri et al. (2011)

(continued)

Table 15.3 (continued)

Type of biotic stress	BR source	Mode of BR treatment	Plant species	Effects	References
Pythium graminicola	BL	Media augmentation	*Oryza sativa*	Inhibited infection caused by root oomycete *Pythium graminicola*	De Vleesschauwer et al. (2012)
Cucumber mosaic virus (CMV)	BL	Foliar spray	*Arabidopsis thaliana*	Enhanced tolerance against CMV	Zhang et al. (2015)
Citrus disease	EBL	Fruit dipping	*Citrus unshiu*	Improved disease resistance and postharvest quality	Zhu et al. (2015)

28-homobrassinolide (HBL) application and resulted in reduced oxidative stress caused by nematodes (Kaur et al. 2013, 2014). In rice, induced systemic defense against nematode stress was stimulated by exogenous application of epibrassinolide (Nahar et al. 2013). At low temperature, management of *Botrytis cinerea* in postharvest grapes was reported by Liu et al. (2016) when EBL was applied exogenously. Similarly, Zhu et al. (2010) reported that exogenously applied brassinosteroid solution enhanced the activity of antioxidant enzymes like CAT, SOD, and POX and inhibited the development of blue mold decay caused by *Penicillium expansum* in harvested jujube fruit. Additionally, improved fruit quality and delayed senescence due to reduced ethylene production were observed suggesting that BR-mediated detain in fruit decay might be related with induction of disease resistance. *Citrus unshiu* fruit dipped in EBL manifested enhanced resistance against citrus disease due to increased activity of stress-related metabolites (Zhu et al. 2015). Reduced susceptibility against leaf blight and rice blast diseases in barley seedlings grown under hydroponic system containing EBL was also observed (Ali et al. 2014). Moreover, resistance in uzu barley lines against powdery mildew fungus *Oidium* sp., bacterium *Pseudomonas syringae* pv. Tabaci and tobacco mosaic virus (TMV) was also induced by EBL. Application of BL in tobacco and rice showed similar effects (Nakashita et al. 2003). Application of BR-containing extract of *Lychnis viscaria* seeds caused an enhanced resistance of tomato, cucumber, and tobacco to fungal and viral pathogens (*Botrytis, Sphaerotheca fuliginea,* and TMV, respectively) (Roth et al. 2000).

15.8 Conclusion

It is a well-established fact that different environmental stressors (biotic and abiotic) are responsible for negatively affecting the agricultural economy by directly reducing the productivity of different crop plants. Moreover, this decline in productivity is becoming more severe with passing times. Since, these stressors generate ROS in affected plants, this further leads to destructive effects on physiological and metabolic processes of plants. In order to overcome this ROS generation, various strategies have been developed, and one such strategy is the application of plant growth regulators, which can act as a feasible environmentally safe alternative. In this continuation phytohormones like BRs and its associated components have been reported to induce antioxidant defense system of plants under different stressful conditions. Furthermore, BRs have also the efficiency of interacting with other phytohormones under normal and stressed conditions thus making them more potent for the resistance in plants against different environmental stresses.

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