



Brassinosteroids Regulate Growth in Plants Under Stressful Environments and Crosstalk with Other Potential Phytohormones

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Abstract

Brassinosteroids (BRs) are an important group of plant steroidal hormones that are actively involved in a myriad of key growth and developmental processes from germination to senescence. Moreover, BRs are known for their effective role in alleviation of stress-induced changes in normal metabolism via the activation of different tolerance mechanisms. Efforts to improve plant growth through exogenous application of BRs (through different modes such as foliar spray, presowing seed treatment, or through root growing medium) have gained considerable ground world over. It has been widely demonstrated that the exogenous application of BRs to stressed plants imparts the stress tolerance mechanisms. In BR-induced regulation of physio-biochemical processes in plants, interaction (crosstalk) of BRs with other phytohormones has been reported. This crosstalk may fine-tune the effective roles of other hormones in regulating stress tolerance. The multifaceted role of BRs consolidated so far has reflected their immense potential to help plants in counteracting the stress-induced changes. The effects of introgression and up- and down-regulation of BR-related genes reported so far to improve crop productivity have been presented here. Strong evidence exists that BRs are involved in signal transduction particularly in the regulation of the mitogen-activated protein kinase (MAPK) cascade, which in turn is involved in controlled development, cell death, and the perception of pathogen-associated molecular pattern (PAMP) signaling. How far BRs are involved in signal transduction pathways operative under stressful environments has also been comprehensively discussed in this review.

Keywords Brassinosteroids · Abiotic stress tolerance · Signaling · Crosstalk

Introduction

Stresses (both abiotic and biotic) have been recognized as the prime potential threats to the normal growth maintenance of plants and agricultural productivity. Stresses

including water, salinity, alkalinity, lodging, metal(loid)s, UV radiation, ozone, and temperature (high and low) alter plant growth by affecting physiological, biochemical, and molecular aspects of metabolism. Climate change and the anthropogenic interferences have aggravated the situation leading to conversion of arable lands to unproductive wastelands and also reduce the yield of most crops below their potential (Ahanger et al. 2014, 2015, 2017; Ahmad et al. 2010, 2011, 2015, 2016a, b, 2017a, b, 2018a, b). Stresses affect germination, growth pattern, and the yield productivity significantly and it has been proposed that by 2050 there will be a severe scarcity of staple food for the progressively growing human population (Ahanger et al. 2014). In view of this changing scenario, agriculturalists and plant biologists have made enough strides to meet the challenges. Several growth-promoting alternatives and agricultural practices like proper mineral supplementation, water management, drainage, use of pesticides and fungicides have been tested and employed to meet the cumbersome challenges of increasing crop productivity for feeding the ever-increasing

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human population. However, understanding of the genetic, molecular, and hormonal regulation of growth in response to stresses has remained under intensive research trials for the last few decades, and some satisfactory and fruitful achievements have been attained (Divi et al. 2010, 2016; Deng et al. 2016; Sahni et al. 2016; Ahanger et al. 2017a, b).

Phytohormones play an important role in plant growth regulation and are actively involved in counteracting the abiotic and biotic stresses by mediating signaling cascades for better response elicitation (Fig. 1). BRs are involved in growth regulation through their active involvement in processes like photosynthesis, antioxidant metabolism, osmolyte accumulation, nitrogen metabolism, and plant–water relations under normal and stressful conditions (Ali et al. 2007, 2008a, b; Hayat et al. 2012; Krumova et al. 2013; Fariduddin et al. 2014; Ahmad et al. 2018a, b). It has been demonstrated that plants defective in BR biosynthesis exhibit abnormalities in developmental phenotypes and the underlying signaling pathways regulating such processes (Sahni et al. 2016). Genetic and molecular studies have witnessed their active role in development of root, anther and pollen, stem elongation, vasculature differentiation, and cellulose biosynthesis suggesting involvement of BR is

far beyond promoting the cell elongation (Yang et al. 2011; Clouse 2015).

BRs are known to exist in a wide range of organisms including lower and higher plants. These steroidal plant hormones mediate growth elevation via activation of different mechanisms (Bajguz and Hayat 2009; Liu et al. 2017). BRs have been shown to be beneficial for growth regulation by imparting the induction of genes related to a stress and other defense mechanism for better growth adaptability (Yang et al. 2004; Zhao et al. 2016) (Fig. 1). Effective stress amelioration due to application of BRs has been reported in crops exposed to water/drought (Talaat et al. 2015), salinity, high temperature (Hayat et al. 2010), cold (Singh et al. 2012), and metal stress (Zhao et al. 2016). Commercial use of BRs for improving growth through exogenous application is attracting the interests of researcher's world over. It has been reported that BRs impart growth stimulation and stress mitigation in a concentration-dependent manner. Application of BRs to stressed plants exogenously either through spraying, priming, or feeding along with nutrient solution has been reported to impart and strengthen the stress tolerance mechanisms (Anuradha and Rao 2007; Hayat et al. 2007, 2010; Ali et al. 2008a, b; Fariduddin et al. 2009; Talaat et al.

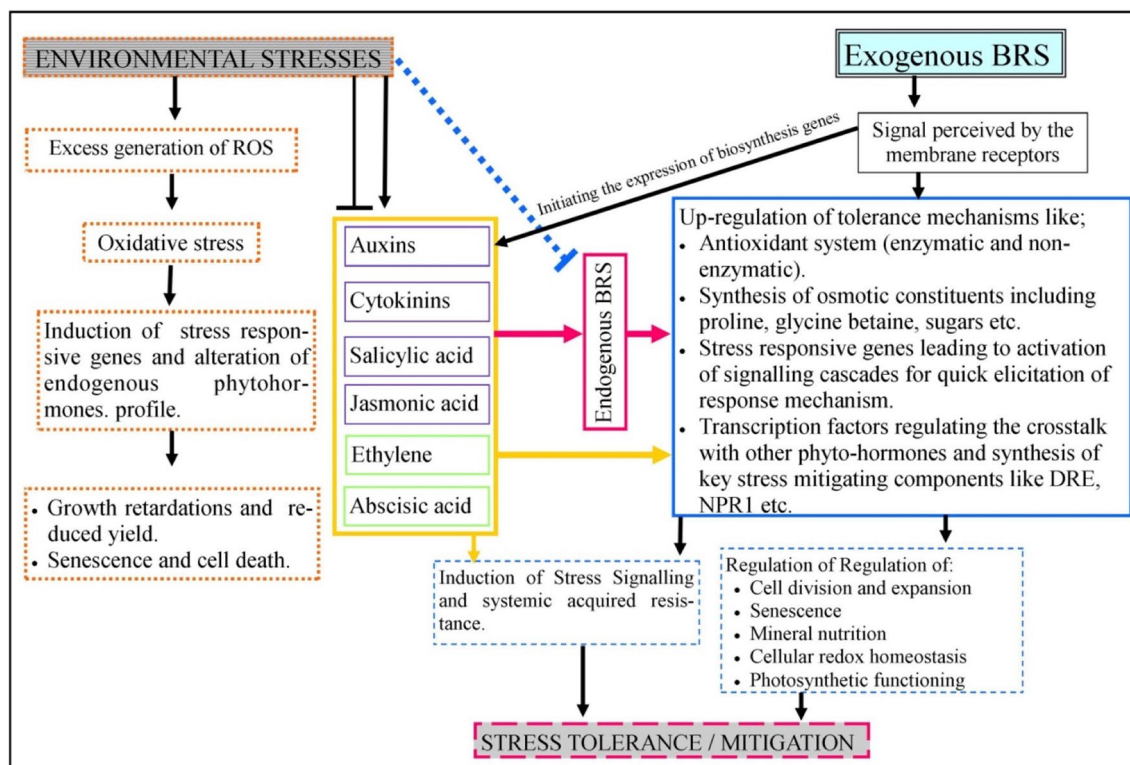


Fig. 1 Stress tolerance mechanisms and the underlying pathways triggered by brassinosteroids (Brs) in plants. Moderate stress can initiate the synthesis of phytohormones for controlling growth which is, however, negatively affected after stress crosses certain levels. BRs (generated either after moderate stress exposure or supplemented exogenously)

can either show antagonistic or synergistic interactions with other endogenous phytohormones for elicitation of stress response. (Arrows and lines ending in bars indicate positive and negative regulation, respectively)

2015; Sharma et al. 2016; Ahmad et al. 2018a, b). However, induction or inhibition of growth is determined by the concentration applied and such variation in plant responses are reported to be dependent on the type of plant species and the intensity of stress. For example, Ali et al. (2008a, b) have reported that application of 24-epibrassinolide (EBL) and 28-homobrassinolide (HBL) to aluminum (1 and 10 mM)-stressed bean seedlings mitigated the stress more significantly in 1 mM Al-treated plants as compared to 10 mM Al-treated counterparts. Application of EBL improved cold tolerance of *Zea mays* up to 1 μM , while declined growth was observed with higher EBL (10 μM) concentration (Singh et al. 2012). However, in addition to a concentration applied, the effect of exogenous BR application, inhibitory or stimulatory, can vary with the developmental stage, plants species, and the plant organ treated (Bao et al. 2004). Some studies have also revealed the involvement of BRs in expression of genes having an important role in regulation of various processes of stress tolerance. For example, BRs induce expression of late anthocyanin biosynthetic genes including those of dihydroflavonol reductase, leucoanthocyanidin dioxygenase, and UDP-glucose: flavonoid-3-O-glucosyl transferase and the transcription factors like production of anthocyanin pigment 1 (PAP1), glabra 3 (GL3), and enhancer of glabra 3 (EGL3) involved in their regulation (Yuan et al. 2015). It is imperative to note here that excessive application of BRs can interfere with the endogenous BRs biosynthesis by inhibiting gene expression concomitant with the up-regulation of BR-inactivation genes, thereby causing growth reduction (Tanaka et al. 2005; Zhu et al. 2013). Recent studies have evidenced the involvement of BRs in the regulation of the mitogen-activated protein kinase (MAPK) cascade (Kim et al. 2011; Khan et al. 2013) and possible interaction of the BR receptor (BRI1), for example, BRI1-associated protein receptor kinase (BAK1), by its role as co-receptor for several receptor-like kinases (RLKs) to bring controlled development, cell death, and the perception of pathogen-associated molecular pattern (PAMP) signaling (Li 2003, 2005; Kemmerling and Nurnberger 2008; Greeff et al. 2012).

Research on exploring the role of BRs is currently gaining ground due to their role in plant growth modulation and more importantly their integration with other signaling molecules including auxins, abscisic acid (ABA), ethylene, salicylic acid (SA), and gibberellic acid. With respect to this, developing ideotypes for acquiring the agricultural sustainability by improving plant performance under changing climatic conditions, it would be imperative to exploit the existing knowledge about the involvement of BRs in plant stress tolerance. So in the present review, efforts have been made to examine that how far BRs play an effective role in regulating growth and physio-biochemical processes in plants exposed to abiotic stresses. In addition, the BR-mediated

signaling and crosstalk with other hormones are also briefly summarized here.

BRs and Plant Stress Tolerance

It is now evident that BRs can induce considerable resistance in plants against a variety of abiotic stress factors including salinity, water logging, drought, metals, high and low temperature (Anuradha and Rao 2007; Hayat et al. 2007, 2010; Ali et al. 2008a, b; Fariduddin et al. 2009; Talaat et al. 2015; Sharma et al. 2016; Ahmad et al. 2018a, b). However, the effects of BRs in counteracting the adverse effects of different stresses may vary and it depends on the type of a stress, plant species, BR dose, and plant ontogenic phase at which BRs are applied. Thus, manipulation of intrinsic BR levels either through genetic engineering or exogenous application results in enhanced yield in crops exposed to stressful environments.

Drought Stress

One of the main challenges to sustainable agricultural production is the frequently occurring chronic or sporadic drought stress particularly in arid and semi-arid regions of the globe. Often characterized by reduced relative water content (RWC), drought stress causes considerable reduction in crop growth and ultimate yield (Jatav et al. 2014; Ahanger et al. 2014, 2015; Ahanger and Agarwal 2017a, b). Drought stress-induced growth reduction generally occurs due to reduced photosynthetic rate, and alteration in nitrogen and antioxidant metabolism, secondary metabolite accumulation, and mineral nutrition (Jatav et al. 2014; Ahanger et al. 2015, 2017). However, drought-induced adverse effects on plant growth and metabolism can be mitigated by exogenous application of a variety of growth regulating substances including BRs. For example, in *Phaseolus vulgaris*, application of EBL or HBL to water-stressed plants resulted in improved growth and yield by enhancing root nodulation and nitrogenase activity, thereby providing strength to the plants to withstand drought (Upreti and Murti 2004). Similarly, in another study with *Brassica juncea*, application of 0.01 μM HBL to drought-stressed plants at two different developmental stages enhanced the photosynthetic rate by improving RWC, stomatal conductance, and water use efficiency by increasing the accumulation of proline (Fariduddin et al. 2009). Kocova et al. (2010) have also demonstrated improved growth performance in field grown maize due to application of EBL (10^{-12} M) through improved chlorophyll synthesis, Hill reaction, and PSI activity, and specific leaf mass production. Exogenous application of HBL has been reported to counteract the detrimental effects of

drought in *Zea mays* by causing improvement in the activity of antioxidant enzymes, soluble protein content, and water uptake (Anjum et al. 2011). Drought-induced improvement in antioxidant activity and photosynthetic functioning was observed in *Capsicum annum* due to exogenously applied EBL (0.01 mg L⁻¹) (Hu et al. 2013). Similarly, *Raphanus sativus* plants subjected to simulated drought stress using PEG-6000 exhibited considerable growth retardation, but presoaking with EBL and HBL caused a significant stress amelioration by enhancing the activity of antioxidant enzymes concomitant with reduction in RNase activity depicting the protective role of BRs for RNA (Mahesh et al. 2013).

It has been widely reported that exogenous BR application up-regulates the activity of antioxidant enzymes and the levels of non-enzymatic antioxidants for mediating efficient removal of reactive oxygen species (ROS) and thereby providing protection to membrane lipids for maintaining membrane integrity and functioning (Li et al. 2012a, b; Shahana et al. 2015; Ahmad et al. 2017a). For example, application of EBL reduced drought-induced oxidative damage in tomato plants by down-regulating lipoxygenase activity and up-regulating the antioxidant defense system by enhancing the expression of antioxidant isozymes (Behnamnia 2015). A study carried out by Talaat et al. (2015) has shown a significant modulation of the antioxidant system and enhanced osmolyte accumulation due to exogenous EBL application in drought-stressed *Zea mays* cultivars. EBL when applied in combination with spermine up-regulated the oxidative defensive mechanisms by reducing the production of superoxide and hydrogen peroxide radicals reflecting lower lipid peroxidation and higher membrane stability (Talaat et al. 2015). Similarly, in maize, application of EBL to drought-stressed plants showed enhanced production of polyamines by up-regulating the activity of biosynthetic enzymes, while it down-regulated the catabolizing enzymes resulting in enhanced drought stress tolerance by protecting Rubisco enzymes through enhanced production of osmolytes (Talaat and Shawky 2016).

BRs are believed to play a vital role in expressing genes involved in the mechanism of drought tolerance. For example, Sahni et al. (2016) observed enhancement in drought stress tolerance in transgenic *Brassica napus* over-expressing the BR biosynthetic gene, DWF4. It has also been observed that application of EBL augments drought tolerance by up-regulating the transcription factors regulating the expression of the drought-responsive element, DRE, as observed in *Arabidopsis thaliana* and *Brassica napus* (Kagale et al. 2007). Gruszka et al. (2016) reported that barley genotypes defective in BR synthesis display less drought stress tolerance, and drought induced accumulation of castasterone and EBL imparted regulation of the hormonal profile at the whole plant level. Crosstalk between drought

and BR signaling is regulated by the transcription factor RD26 which when over-expressed can inhibit BR-regulated growth. Such negative regulation is under direct control of BRASSINOSTEROID INSENSITIVE1-EMS-SUPPRESSOR 1/ BRASSINAZOLE-RESISTANT 1 (BES1/BZR1) repressing the expression of RD26 at transcriptional levels; however, RD26 protein interacts with BES1 and inhibits its transcriptional activity. RD26 antagonistically regulates BR as revealed by the over-expression and knockout studies of RD26 leading to repressed and increased BR response (Ye et al. 2017). It is believed that BR signaling controls the activities of BES1/BZR1 transcription factors. Additionally, other transcription factors like WRKY (46, 54, and 70) have been shown to regulate both BR-regulated plant growth as well as drought response. As reported, *wrky46 wrky54 wrky70* triple mutants having defects in BR-regulated growth are more tolerant to drought stress; however, their global role in promoting BR-mediated gene expression and inhibition of drought responsive genes often regulated by the direct interaction between WRKY54 and BES1 has been recently established (Chen et al. 2017). Phosphorylation and destabilization of WRKY54 by GSK3-like kinase BR-INSENSITIVE2 lead to negative regulation of the BR pathway. Therefore, it can be concluded that elucidating the factors involved in controlling the antagonistic regulation of BR and drought-responsive genes can be interesting. Sahni et al. (2016) concluded that enhanced drought tolerance in transgenic plants over-expressing BR biosynthesis is likely mediated by BES1/BZR1, and therefore further studies using genomics integrated with proteomics can be helpful in dissecting the exact pathway.

Salt Stress

Increasing salt concentrations in soils have rendered most of the agricultural lands as unproductive wastelands resulting in an increased food crisis. In view of some projections, about 45 million hectares of irrigated land are salt affected (Munns and Tester 2008; Machado and Serralheiro 2017). Salinity reduces plant productivity by adversely affecting growth through induction of osmotic and ionic imbalances (Ahanger and Agarwal 2017; Ahmad et al. 2017b, 2018b; Kaur et al. 2018). Salinity-induced deleterious effects include ionic toxicity, osmotic stress, reduced nitrogen metabolism, elevated production of ROS leading to oxidative damage, hampered photosynthetic functioning and photosynthate translocation, impeded uptake and translocation of mineral nutrients (Turkan and Demiral 2009; Ahmad et al. 2010, 2016a, b; Iqbal et al. 2015; Ahanger and Agarwal 2017) (Fig. 1). Although plants employ various mechanisms to counteract salinity stress, often they fail to fully counteract the negative effects. Therefore, devising strategies and management

techniques for achieving improved salt tolerance is imperative. Significant contributions of exogenously supplied BRs to assuaging the salinity-induced growth retardation have been reported from time to time. The role of BRs in regulating salinity tolerance mechanisms has been reported in several crops like *Oryza sativa* (Anuradha and Rao 2003), *Cicer arietinum* (Ali et al. 2007), *Brassica juncea* (Ali et al. 2008), *Vigna sinensis* (El-Mashad and Mohamed 2012), and *Mentha piperita* (Coban and Baydar 2016). The most studied metabolic mechanism with respect to the effect of BRs is the oxidative defense. A number of reports can be deciphered from the literature wherein researchers have shown a marked regulatory effect of BRs on the antioxidative defense system. For example, in a study with wheat, foliar application of EBL counteracted the adverse effects of salinity by enhancing the activity of peroxidase and catalase in wheat cultivars with contrasting degrees of salt tolerance (Shahbaz and Ashraf 2007). Similarly, in salt-stressed *Cucumis sativus*, supplementation of EBL caused a marked enhancement in growth by up-regulating the activity of superoxide dismutase (SOD), peroxidase, and catalase (CAT) concomitant with reduced electrolyte leakage and malondialdehyde (MDA) content (Song et al. 2006). In the same vegetable crop, Lu and Yang (2013) have demonstrated NaCl-accrued production of ROS like O_2^- , H_2O_2 imparting considerable loss in membrane functioning, but application of EBL significantly mitigated the oxidative damage by strengthening the antioxidative system. Application of 0.01 μM EBL to *Vigna radiata* (Hayat et al. 2010) and *Cucumis sativus* (Fariduddin et al. 2013) proved significant in inducing enhancement in the photosynthetic attributes by modulating the antioxidant defense system and carbonic anhydrase activity, and such growth-promoting effect of exogenous EBL was maintained under NaCl treatments.

Despite using foliar application of BRs, some researchers have employed seed priming techniques to achieve enhanced stress tolerance. For example, the seeds of *Medicago sativa* pretreated with 5.0 μM EBL and then exposed to salinity of 13.5 dS m^{-1} showed enhanced seed germination and reduced oxidative damage by improving the activity of SOD, POD, and CAT (Zhang et al. 2007). Moreover, exogenously (foliar) sourced EBL (10^{-8} M) has been reported to enhance the polyamine (putrescine, 10^{-3} M)-induced NaCl tolerance (100 mM) in *Cucumis sativus* by mediating quick elimination of ROS and the accumulation of osmolytes (Fariduddin et al. 2014). A number of key enzymes of different metabolic processes are also believed to be inhibited in salt-stressed plants, but their inhibited activity can be effectively recovered by the exogenous application of BRs. For example, salt stress can hamper nitrogen metabolism by inhibiting the activity of key nitrogen metabolizing enzymes including nitrate reductase that mediates the first and rate limiting step in

nitrogen metabolism (Ahanger and Agarwal 2017). The activity of nitrate reductase is impeded by salt-induced restriction of nitrate uptake and xylem loading having a direct impact on its transport to shoot tissues (Cerezo et al. 1997). For example, in *Cicer arietinum* the activities of some key enzymes of N metabolism were reported to be decreased due to saline stress, but exogenously applied EBL improved nitrogen metabolism by improving the nitrogen fixing and mobilizing capacity by increasing the number of nodules and associated biochemical attributes including nitrogenase activity and leghemoglobin content (Ali et al. 2007). In another study with *Vigna radiata*, application of HBL improved nitrate reductase activity and the nitrogen content with a concomitant enhancement in carbonic anhydrase activity and photosynthetic efficiency under salt stress (Hayat et al. 2010).

BRs are also known to regulate a variety of genes involved in some key metabolic processes in plants exposed to saline stress. For example, EBL application enhanced the expression of stress-responsive genes and the *OsBR1* conferred stress tolerance in *Oryza sativa* (Sharma et al. 2013). In another study with *Arabidopsis thaliana*, application of EBL enhanced the expression of phytohormone marker genes and it rescued the ethylene-insensitive *ein2* mutant and the ABA-deficient *aba-1* mutants of *Arabidopsis* from salt stress, suggesting that BRs share transcriptional targets with other hormones (Divi et al. 2010). Further they suggested that the master regulator of salicylic acid-mediated defense genes—the redox-sensitive protein NPR1 (NON-EXPRESSOR OF PATHOGENESIS-RELATED GENES1)—has a critical role in EBL-mediated salt tolerance. In another study with wheat, application of EBL (0.4 nM and 0.4 mM) induced enhancement in the synthesis of wheat germ agglutinin (WGA). WGA is a classical lectin that belongs to the *rab* gene family and its expression is controlled by endogenous ABA levels; however, experiments with EBL have shown the ABA-independent control of WGA expression in *Triticum aestivum* imparting enhanced salt tolerance (Shakirova and Bezrukova 1998; Shakirova et al. 2002). Over-expression of sterol glycosyl transferases (WsSGTL1) from *Withania somnifera* increased salt tolerance of *Arabidopsis thaliana* by enhancing expression of genes coding antioxidant, salt sequestration pathways, LEA proteins, and photosynthetic system (Mishra et al. 2013).

From the above-reported studies, it is evident that exogenously applied BRs can effectively mitigate the salt-induced adverse effects on crop growth and metabolic processes by improving the activities of key enzymes, the antioxidative defense mechanism, and expression of a number of genes involved in some key metabolic processes behind salt tolerance.

Metal/Metalloid Stress

In the contemporary era, metal(loid)-induced growth inhibition has become a subject of great concern for sustainable agricultural productivity. With continuous addition of highly metal-polluted industrial effluents, sewage waste and sludge, agricultural toxic chemicals, and garbage dumping, productive agricultural soils are converted into unproductive lands, thereby affecting crop growth adversely. Once taken up by the plant system, metal(loid)s restrict growth by interfering with the membrane structure, enzyme activity, and transport, distribution, and metabolism of mineral elements (Ahmad et al. 2011, 2015, 2016a, b, 2018a). In addition, the most toxic effect of metal(loid)s is the free radical-induced oxidative stress causing genotoxic stress by triggering the formation of exocyclic DNA/RNA adducts, which have been reported to alter the cellular redox homeostasis leading to restriction in the electron transport (Asgher et al. 2014; Khan et al. 2015; Ahmad et al. 2010, 2018a). Metal(loid)s once taken by plants can be deleterious for humans as well. Plants have a remarkable ability to withstand metal-induced changes to some extent by the induction/regulation of several indigenously existing tolerance mechanisms (Ahmad et al. 2015). Use of BRs for averting metal(loid)s-induced oxidative stress has been under intense research for many years, and the results of the research reported so far favor strongly the use of exogenous BR for metal(loid)s stress amelioration. For example, Hayat et al. (2007) demonstrated Cd-induced oxidative stress amelioration in *Brassica juncea* by foliar application of 0.01 μM HBL through enhancement in the activity of antioxidant enzymes and the contents of some key osmolytes. Cadmium is known to affect photosynthesis by (a) down-regulating the activity of chlorophyll synthesizing enzymes and such a negative effect of Cd has been attributed to Cd-induced inactivation of the sulfhydryl site of proteins (Ernst 1980), and (b) by down-regulating the expression of the Rubisco protein (Asgher et al. 2014). However, a significant role of exogenous BR in assuaging the metal(loid)-induced growth inhibition has been reported time and again. For example, enhancement in RWC and membrane stability due to EBL application was evident due to increased activity of antioxidant enzymes and the accumulation of osmolytes in *Raphanus sativus* (Anuradha and Rao 2007; Sharma et al. 2010; Ramakrishna and Rao 2015), *Phaseolus vulgaris* (Rady 2011), *Solanum lycopersicum* (Hayat et al. 2012), *Brassica juncea* (Kanwar and Poonam Bhardwaj 2015), and *Oryza sativa* (Sharma et al. 2016). In radish (*Raphanus sativus*), treatment of EBL for 8 h significantly neutralized the Cd- and Hg-induced oxidative stress by causing considerable elevation in the activity

of antioxidant enzymes including SOD, CAT, polyphenol oxidase (PPO), glutathione-S-transferase (GST) and the enzymes of the ascorbate–glutathione pathway (ascorbate peroxidase, APX; dehydroascorbate reductase, DHAR; monodehydroascorbate reductase, MDHAR; glutathione reductase, GR), and the accumulation of flavonoid content (Kapoor et al. 2014). They also observed that the EBL-induced antioxidative defense system protected photosynthetic pigments from the individual as well as combined effects of these metals. HBL and EBL application has been reported to nullify the adverse effects of Cd on the photosynthetic attributes and the antioxidant machinery in *Cicer arietinum* (Hasan et al. 2008) and tomato cultivars (Hasan et al. 2011). A study by Arora et al. (2010a, b) showed a strong growth-promoting effect of exogenously applied EBL on *Brassica juncea* exposed to chromium (Cr) stress and at all concentrations of EBL applied stimulated growth by up-regulating the activities of the enzymes of the ascorbate–glutathione pathway. In *Raphanus sativus*, Choudhary et al. (2011) reported that exogenous application of EBL suppressed Cr-induced oxidative damage by enhancing the activity of SOD, GR, and APX and the accumulation of GSH and AsA leading to photo-protection by maintaining the cellular redox and osmotic balance. In addition, supplementation of EBL triggered the synthesis of indole-3-acetic acid (IAA), polyamines (putrescine and cadaverine), and phytochelatin, thereby mediating better signaling events and the subsequent chelation under Cr stress. They also reported the growth-promoting interactive role of EBL and polyamine (spermidine), which was reflected in enhancement in the accumulation of secondary metabolites and the non-enzymatic components of antioxidants leading to improved free radical scavenging potential (measured as DPPH radical scavenging). Treatment of BRs (BL; EBL; castasterone, CS; 24-epicastasterone, ECS; 28-homoCS) to *Chlorella vulgaris* enhanced the synthesis of phytochelatin (Bajguz 2002). Fariduddin et al. (2009) showed that soaking *Brassica juncea* with HBL (10^{-10} , 10^{-8} , and 10^{-6} M) for 8 h significantly improved growth and photosynthetic parameters under copper (50, 100, and 150 mg kg⁻¹ sand) stress by enhancing SOD, POD, and CAT activity, thereby reducing the formation of H₂O₂-induced lipid peroxides together with improved nitrate reductase activity and proline accumulation. They also observed that HBL at 10^{-8} M proved to be most effective in imparting tolerance in *Brassica juncea* to externally added copper. Exogenous application of EBL (10^{-6} M) to *Vigna radiata* cultivars with contrasting nickel (Ni) stress tolerance was shown to improve the nitrogen-fixing attributes (number of nodules, leghemoglobin content, etc.) and the nitrogen metabolism by mediating improvement in the synthesis of osmolytes and the activities of SOD, CAT, and POD, hence resulting in improved yield and biomass

productivity (Yusuf et al. 2012, 2014). Application of EBL to Ni-stressed *Solanum nigrum* enhanced the growth by causing a significant enhancement in relative content of Rubisco, proline, ascorbate acid (AsA) and the activities of SOD and APX accompanied with the decline in the generation of superoxide, H₂O₂ and MDA (Soares et al. 2016). They also reported EBL-induced post-translational level regulation of antioxidant enzymes. Application of EBL protected chickpea from Hg-induced oxidative damage and nutrient uptake by up-regulating the antioxidant system and osmolyte accumulation (Ahmad et al. 2018a, b).

Zinc stress was mitigated in *Brassica juncea* by EBL treatment (10⁻⁷, 10⁻⁹, 10⁻¹¹ M), which improved the antioxidant defense system and restricted uptake and accumulation of excess Zn in plant tissues (Sharma et al. 2007). In another study, supplementation of EBL to Zn (0.5, 1.0, 1.5, and 2.0 mM)-treated *Brassica juncea* ameliorated oxidative stress and growth inhibition by mediating up-regulation of ROS scavenging system including SOD, CAT, and enzymatic and non-enzymatic components of the ascorbate–glutathione cycle (Arora et al. 2010). Ramakrishna and Rao (2015) have demonstrated that foliar application of EBL and HBL at the concentrations of 0.5, 1.0, or 2.0 μM effectively alleviated the deleterious effects of zinc toxicity on *Raphanus sativus* primarily by protecting the membranes by reducing the production of ROS and stabilizing the protein structures by reducing the formation of protein oxidative products, carbonyls. Moreover, both BRs improved RWC by triggering the synthesis of osmolytes like proline, thereby providing protection to nitrate reductase activity. Supplementation of EBL (5 nM) to tomato seedlings raised on Murashige and Skoog medium supplemented with ZnO nanoparticles (0, 10, 20, 50, and 100 mg/L) exhibited reduced oxidative damage due to enhanced activity and expression of SOD, CAT, APX, and GR isozymes, and the contents of AsA and GSH, thereby protecting the cellular redox homeostasis (Li et al. 2016). It shall be noted here that the exact mechanisms underlying BR-induced growth regulation under metal(loid) stress is largely unknown. Understanding the possible genetic controls regulating BR-mediated changes and tolerance potential needs more research.

Temperature Extremes

Climate change is being widely witnessed in the current era resulting in considerable fluctuation in the mean temperatures. Both high and low (cold and chilling) temperatures are potential environmental factors affecting both physiological and biochemical aspects of metabolism, and such changes are regulated at the molecular as well as genetic levels (Kazemi-Shahandashti et al. 2014; Siboza et al. 2014; Hatfield and Prueger 2015; Calzadilla et al. 2016).

However, BR application has been reported to benefit crop plants by enhancing the efficiency of growth mediating key metabolic pathways. Exogenous application of BR has been widely reported to mitigate the adverse effects of high (Zhou et al. 2004; Ogwenno et al. 2008; Hayat et al. 2010; Mazorra et al. 2011; Sahni et al. 2016; Yadava et al. 2016) and low (Janeczko et al. 2007; Liu et al. 2009; Aghdam et al. 2012; Aghdam and Mohammadkhani 2014; Calzadilla et al. 2016) temperature regimes to considerable extent in different crops by regulating a variety of metabolic processes. Both high and low temperatures can effectively retard plant growth but the effects of low and high temperatures differ considerably in plants. Also, plant responses to high and low temperatures vary significantly. For example, low temperature particularly below freezing can freeze the cells, thereby causing a marked disruption in uptake and translocation of both water and nutrients. However, the ameliorative effect of BRs has been assessed in different crops exposed to low temperature stress. For example, in a fruit crop, grapevines, application of BR was reported to reduce the cold-induced ion leakage by maintaining membrane integrity through improvement in antioxidant and osmoregulatory components (Xi et al. 2013). In *Cucumis sativus*, foliar spray of HBL (10⁻⁸ or 10⁻⁶ M) mediated growth enhancement under chilling stress (10/8 °C, 5/3 °C) by improving the activities of antioxidant enzymes (SOD, CAT, and POD), thereby providing protection to the photosynthetic system from the ROS-induced oxidative damage (Fariduddin et al. 2011). Such BR-induced growth enhancement was well correlated with enhancement in the activities of nitrate reductase, carbonic anhydrase and the accumulation of proline, and the quantum yield of PSII. Pepper fruit supplied with BR (5, 10, and 15 μM) and stored for 18 days at 3 °C had reduced electrolyte leakage, lipid peroxidation with a concomitant increment in the activities of antioxidant enzymes like POD, APX, and GR, as well as enhanced chlorophyll and AsA levels (Wang et al. 2012). Experiments with tomato have inferred that supply of BR (3 and 6 μM) enhanced the chilling tolerance (1 °C) by elevating antioxidant metabolism and osmolyte accumulation together with up-regulating phenylalanine ammonia lyase activity leading to improved phenol accumulation, thereby reducing electrolyte leakage and lipid peroxidation (Aghdam et al. 2012). Exogenous application of EBL (0.1 mg L⁻¹) to *Cucumis sativus* subjected to chilling under low light increased the activity of ROS neutralizing antioxidant system imparting quick recovery after the stress release (Hu et al. 2010). They also evidenced that EBL application proved significantly protective for the photosynthetic system by restricting the production of ROS including superoxide and H₂O₂. Pectin methylesterases (PMEs) are considered among key cell wall enzymes having beneficial roles in plant tolerance against chilling and/or freezing and BRs regulate the expression of PME in chilling-stressed *Arabidopsis*

(Qu et al. 2011). Exogenous application of BR activated Calvin cycle enzymes and antioxidant enzymes leading to improved photosynthesis through the alleviation of chilling-induced photo-oxidative damage (Jiang et al. 2013). Treatment of EBL (3 and 6 μM) to stored tomato fruits at 1 °C for 21 days resulted in reduced chilling injury by causing a decline in electrolyte leakage and lipid peroxidation leading to maintained membrane integrity by down-regulating the activities of phospholipase-D and lipoxygenase (Aghdam and Mohammadkhani 2014). However, despite having such a plethora of literature available, no research work has been published depicting the role of BRs in regulation of cold-responsive genes. Thus, future research in this direction could be worthwhile.

Like for cold stress, assessment of the influence of BRs on high-temperature mitigation has also been under intensive research with different crops. For example, banana plants when exposed to high (34 °C) temperature showed a marked necrosis, but the application of the trihydroxylated spirotane analogue of BR significantly enhanced growth by improving the accumulation of proline and the photosynthetic efficiency (Gonzalez-Olmedo et al. 2005). In Indica rice, Cao and Zhao (2008) demonstrated that exogenous application of BR (0.005 mg L^{-1} foliar spray) mitigated the deleterious impact of high temperature (38/30 °C) in two cultivars differing in stress tolerance by improving the expression of antioxidant isozymes resulting in enhanced antioxidant protection and reduced lipid peroxidation. In another study with tomato, in three lines, that is, BR-deficient mutant, BR-insensitive mutant, and a line over-expressing the BR-biosynthesis gene, exogenous application of EBL (1 μM) under heat stress (40 °C) was correlated with reduced lipid peroxidation and membrane leakage more in the BR-deficient mutant as compared to that in BR-insensitive mutant. However, in the cultivar over-expressing the BR-biosynthesis gene, exogenously sourced BR did not show a significant benefit evidencing the active involvement of endogenously produced BR in heat stress amelioration and growth promotion (Mazorra et al. 2011). This means if the endogenous concentration of BR is high, then exogenously supplied BR may not be effective in promoting growth. However, in contrast in another study with tomato, exogenous application of EBL protected photosynthetic efficiency of tomato plants from heat stress (40/30 °C for 8 days) by improving photosynthetic electron transport and carboxylation efficiency of Rubisco concomitant with reduction in lipid peroxidation and production of high amounts of H_2O_2 which was well correlated with increased activity of antioxidant enzymes like SOD, CAT, POD, and APX (Ogwenio et al. 2008). In the same crop, Ogwenio et al. (2010) reported that treatment of EBL protected the photosynthetic system in detached leaf tissues from mild light intensity (400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF) at 28 °C by preventing the photoinhibition and increasing

the quantum yield by stimulating the antioxidant system. In another crop, *Vigna radiata*, exogenous application of HBL enhanced membrane stability and leaf water potential by increasing the activities of antioxidant enzymes and accumulation of proline (Hayat et al. 2010). In *Ficus concinna*, foliar spray of EBL (0.25 μM) mitigated the high (40 °C) and moderate (35 °C) temperature-induced oxidative damage by elevating the activities of antioxidant enzymes (SOD, CAT, APX, GR, MDHAR, DHAR, and GST), the glyoxylase system, and the synthesis of GSH and AsA leading to maintenance of redox homeostasis, thereby causing a significant reduction in lipid peroxidation (Jin et al. 2015). Recently, it has been demonstrated that over-expressing the BR biosynthetic gene *DWF4* in *Brassica napus* imparted high temperature (40 °C) and dehydration stress tolerance, and these transgenic lines maintained higher yield and biomass accumulation. In heat-stressed (30/40 °C) *Oryza sativa* L. var Pathum Thani 1, Thussaganpanit et al. (2015) reported that exogenous application of EBL and the BR-mimic compound, 7,8-dihydro-8 α -20-hydroxyecdysone (DHECH), at the flowering (reproductive) stage protected the photosynthetic system by improving water use efficiency, stomatal conductance, and the quantum yield of PSII, and EBL- and DHECH-treated plants showed higher synthesis of free sugars, starch, and yield.

Heat shock proteins have been widely studied in plants because of their potential role in high-temperature tolerance. However, in view of some reports it is evident that BRs can promote the expression of heat shock proteins in heat-stressed plants. For example, exogenously supplied EBL improved growth of *Brassica napus* and tomato seedlings by enhancing the expression of heat shock proteins (hsp) including hsp100, hsp90, hsp70 and the low molecular weight hsps under thermal stress (Dhaubhadel et al. 1999). Involvement of EBL in protection of the hsp-translational machinery during heat stress has been suggested via EBL-mediated increase in the number of several translation initiation and elongation factors in spite of having a negative correlation with mRNA levels leading to improved basic thermotolerance after the stress release (Dhaubhadel et al. 2002). Such EBL-induced increase in the expression levels of hsps during recovery triggers rapid resumption of cellular protein synthetic machinery after heat stress exposure, hence enhancing the survival rates. Singh and Shono (2005) reported that foliar application of EBL (5 μM) induced the expression of mitochondrial-small hsp (Mt-shsp) more at 38 °C as compared to that at 25 °C causing a significant improvement in photosynthesis, pollen germination, and pollen tube growth with prevention of pollen bursting, indicating an important role of EBL in reproduction and yield. In *Cucumis sativus*, manipulating BR synthesis through a chemical genetics approach affected tolerance to photo-oxidative, cold stresses and cucumber mosaic virus,

and treatment of BR optimized the H_2O_2 levels inducing the expression of both regulatory (RBOH, MAPK1, and MAPK3) and stress defensive and antioxidant genes (Xia et al. 2009). However, the exact mechanisms mediating tolerance to extreme temperatures are still being investigated and experimental evidence is needed to consolidate the protective role of BR whether it is regulated independently or in combination with the stress-triggered mechanisms. An investigation of the possible link between the expression of temperature responsive genes and endogenous BR levels in model crops can lead to identification, enhancement, and better understanding of the tolerance mechanisms controlling plant growth.

Nutrient Stress

Optimal availability of mineral nutrients is believed to regulate growth by mediating changes at physiological, biochemical, and molecular levels (Ahanger et al. 2015, 2016, 2017a), and deficiency of essential inorganic nutrients affects growth adversely. Although phytohormones including BRs cannot replace nutrients in regulating the physiological and biochemical aspects of plant metabolism, they can compensate the need for nutrients to some extent. For example, foliar application of EBL caused a significant enhancement in the uptake of potassium and calcium, thereby enabling *Triticum aestivum* cultivars S-24 and MH-97 to counteract salt stress by maintaining the K/Na ratio (Janeczko et al. 2010). In addition, exogenous application of EBL (foliar and soaking) increased uptake of potassium, magnesium, and calcium, and reduced sodium and iron in wheat (Janeczko et al. 2010). In *Cucumis sativus* L., cv. 'Jinyou No. 4' adverse effects of excess calcium [80 mM $Ca(NO_3)_2$] on the uptake of important mineral elements, like potassium, phosphorous, magnesium, and manganese, were mitigated by foliar spray of EBL (0.01 M). EBL-treated plants maintained a higher K^+/Na^+ ratio and improved activity of Ca^{2+} -ATPase, which mediated extrusion of excess Ca^{2+} from the cells to prevent toxicity (Yuan et al. 2015a, b). Song et al. (2016) demonstrated that application of EBL to *Arachis hypogea* mitigated the Fe-deficiency-induced oxidative stress by up-regulating the activity of nitrate reductase, the antioxidant system, and the accumulation of osmolytes, thereby reducing the production of ROS including superoxide and H_2O_2 . An enhancement in the activity of H^+ , and Ca^{2+} ATPase and ferric(III)-chelate reductase (FCR) was also noticed in EBL-treated plants, and such EBL-induced increase in FCR activity mediated improved uptake of Fe(II) ions across the root plasma membrane under Fe-deficient conditions (Song et al. 2016). In *Arabidopsis*, Zhao et al. (2016) demonstrated that treatment of BR reduced ammonium

toxicity by down-regulating the expression of *ammonium transporter-1* (AMT1) expression in roots, which was confirmed by its reversion using the BR receptor BRI1 mutant *bri1-5*. The expression of AMT1 transporters (AMT1;1, AMT1;2, AMT1;3) is directly regulated by BR signaling transcription factor, BES1, and NH_4^+ -mediated repression of AMT1 transporters was observed to suppress in a gain-of-function in ammonium-sensitive BES1 mutant (*bes1-D*). Further, by supplying exogenous glutamine, they confirmed that NH_4^+ -mediated suppression of AMT1 was induced by nitrogen metabolites rather than NH_4^+ reflecting the activation of BES1 causing inhibition of the NH_4^+ -mediated induction of GS/GOGAT. They concluded that BR-induced regulation of nitrogen uptake and assimilation occurs *via* the BR signaling pathway. 14-3-3 proteins are believed to regulate many cellular processes by binding to phosphorylated proteins and hence assist in plant nutrient signaling and hence can modulate nutrient metabolic pathways (Shin et al. 2011). This protein has been reported to control the nuclear location of key transcription factors BZR1/BZR2 involved in BR-mediated signaling via its interaction with cell-surface receptors (BRI1 and BAK1) and a GSK3 kinase (BIN2) in transgenic *Arabidopsis* (Gampala et al. 2007). Therefore, integrating the transgenic approach with the efficient uptake and compartmentation of beneficial mineral ions shall be a fruitful future exercise for biofortification in essential food crops. Additionally, the exclusion and sequestration of toxic ions can be achieved by visiting the role of BR in transport proteins involved therein.

Interplay Between BRs and Other Phytohormones, and the Underlying Signaling Events

For displaying regulated and continuous growth patterns, a controlled, integrated, and regulated coordination forms a preminent part, of which the interaction between phytohormones forms an essential part. Like other phytohormones, BRs perform various important functions by interacting with other phytohormones including auxins, ABA, cytokinins, ethylene, gibberellic acid, polyamines, SA, and jasmonic acid (Bajguz and Hayat 2009; Saini et al. 2015). Such coordination between BRs and other phytohormones is regulated by several intriguing networking mechanisms including transcription and protein–protein interaction. Studies carried out so far have provided evidence about the underlying interactions between BRs and other phytohormones, and several studies have shown antagonistic as well as synergistic roles of BRs with other hormones.

Auxins

Several aspects of growth have been observed to be under regulated interaction between BRs and auxins; however, the actual mechanisms are still illusive (Maharjan et al. 2011; Saini et al. 2013, 2015; Liu et al. 2014; Ma et al. 2016). For example, in *Arabidopsis*, Mouchel et al. (2006) have demonstrated that auxin-induced root growth is regulated by *BRAVIS RADIX (BRX)* which they observed to be dependent on the threshold BR level. This *BRX* phenotype results due to root-specific deficiency of BRs and affects expression of other genes. However, such inhibition can be restored by exogenous treatment of BRs. Moreover, BR treatment rescued the *brx* phenotype fully or partially at the embryonic and post-embryonic stages, respectively. Exogenous application of auxins has been reported to promote the BR synthesis gene *DWF4* (Maharjan and Choe 2011). Interestingly, positive regulation of *DWF4* and *CPD* by *BRX* (Tanaka et al. 2005) has been reported, thereby demonstrating a direct linkage of auxin signaling with BR synthesis (Mouchel et al. 2006; Chung et al. 2011). Zhang et al. (2014) have demonstrated the synergistic role of BR and auxins in leaf lamina inclination. They reported that over-expression of *OsGH3.5* and *OsARF19* exhibited reduced free auxin content when lamina joint tissues were analyzed, altering the lamina inclination. *OsBRI1* has been reported to be up-regulated under the positive regulation imparted by binding of *OsARF19* to its promoter, and finally *OsBRI1* activates the expression of *OsBZR1*, and subsequently the downstream signaling genes affect the lamina inclination (Zhang et al. 2014). Chaiwanon and Wang (2015) have reported an antagonistic interaction of auxins and BRs in *Arabidopsis*. Such interaction was reported to be linked by the *BZR1* transcription factor and the optimal expression of *BZR1* was dependent on BR catabolism, auxin biosynthesis, and BR-mediated signaling leading to activation of genes in the elongation zone concomitant with the repression in the quiescent center. Such spatio-temporal gene expression is regulated in a totally opposite way by auxins. IAA and BR regulate the dwarfism in autotetraploid apple (*Malus × domestica*) by up-regulating the expression of microRNA390 which contrary to diploids maintained shorter vertical length of cortical parenchyma cells. The dwarf phenotype in autotetraploid apple plants has been suggested due to the miR390 accumulation following genome doubling, and inducing up-regulated expression of trans-acting short-interfering RNA 3 (*MdTAS3*) which imparts down-regulation of *MdARF3*. This has been suggested to disturb the IAA and BR-mediated signal transduction pathway (Ma et al. 2016).

The phytochrome-mediated induction of shade avoidance syndrome in *Arabidopsis thaliana* has been reported to be under direct regulation of auxin/BR responses in the petiole and further evidence has been provided by using

auxin-deficient (*doc1/big*) and BR-deficient (*rot3/cyp90c1*) mutants indicating that auxin and BR contribute equally for a normal petiole elongation response to the shade stimulus (Kozuka et al. 2010). Therefore, interactions between auxins and BRs are emerging as key regulators in the major growth and developmental processes being implicated at physiological, biochemical, and genetic levels. However, studying the involvement of other molecules in such interactions can be useful in categorizing them as independent or dependent regulatory crosstalk.

Gibberellic Acid

BRs regulate biosynthesis of gibberellins (GA) and it has been evidenced that BR-regulated transcription factor *BES1* regulates GA biosynthesis by binding to the promoters. *Arabidopsis thaliana* deficient in BR signaling has been posited to exhibit severe impairment in the synthesis of bioactive GA which has been directly correlated with altered GA biosynthetic gene expression (Unterholzner et al. 2015). Quite strong evidence showing the involvement of BRs in GA-mediated growth regulation under normal as well as stressful conditions is available. For example, in rice while studying the interactive role of BRs and GA against the root oomycete *Pythium graminicola*, De Vleeschauwer et al. (2012) demonstrated the BR–GA antagonistic interaction in which *P. graminicola* made use of BRs as virulence factors taking over the rice BR machinery to counteract the disease. Using inhibitors of GA (uniconazole) and BR (brassinazole) synthesis, they demonstrated suppression of SA-mediated defenses by BRs occurs downstream of SA biosynthesis, but upstream of *NPR1* and *OsWRKY45*, the master defense regulators. However, exogenously supplied BR enhanced GA-controlled immunity by interfering with GA metabolism ensuing oblique stabilization of protein and the central GA repressor, *DELLA* and *SLENDER RICE1 (SLR1)*, respectively, indicating that the BR pathway is co-opted by *Pythium graminicola* to tempt antagonistic effect of SA- and GA-mediated defenses. The findings of Tong et al. (2014) have shown that an unknown mechanism underlying BR–GA crosstalk becomes operative depending on tissues and hormone levels. They reported that under physiological conditions, BR promotes cell elongation by inducing the synthesis of GA through up-regulating the expression of GA biosynthesis genes *D18/GA3ox-2* in rice and consequently *d18*, and loss-of-function GA-signaling mutant exhibited decreased BR sensitivity. Exogenously supplied high concentrations of BR suppressed GA biosynthesis by up-regulating the expression of inactivation gene *GA2ox-3* concomitant with repression of BR synthesis, thereby causing growth retardation by reducing endogenous hormone levels. They suggested that GA inhibits BR biosynthesis and signaling through a feedback mechanism. Direct signaling

crosstalk between BR and GA results from the interaction between BZR1/BES1 and DELLAs—key transcriptional regulators of BR and GA signaling pathways, leading to controlled cell elongation in *Arabidopsis*. Such elongations occur after DELLA proteins affect protein stability leading to inhibition of the transcriptional activity of BZR1 and GA releases DELLA-mediated inhibition of BZR1 thereby inducing cell elongation (Li et al. 2012a, b; Li and He 2013).

Cytokinins

Cytokinins (CK) are another broad group of phytohormones involved in regulating a myriad of plant developmental and metabolic processes. Recent research has evidenced its crosstalk with other growth hormones either through direct interaction for eliciting a common growth response or imparting indirect interactive effect reflecting the role of other phytohormones. For example, Bao et al. (2004) reported the indirect crosstalk of CK–BR in regulating lateral root development by modulating the transport of auxins in which BR over-expresses the efflux carrier of auxins including the PIN gene. Bajguz and Piotrowska-Niczyporuk (2013, 2014) have reported the interactive effect of BR and CK on the growth and metabolite accumulation in *Chlorella vulgaris* and also observed a concentration-dependent increase due to application of BR and CK with a maximal positive obvious impact when BR and CK were supplemented together compared to their individual involvement, depicting the synergistic operation of BRs and CK activities. They also observed a positive influence of BR–CK interaction on auxin levels. BR has been reported to maintain the levels of CK in wheat (Yuldashev et al. 2012). Peleg et al. (2011) have reported that transgenic rice over-expressing the isopentenyltransferase (IPT) gene driven by P(SARK), a stress and maturation-induced promoter, resulted in enhanced synthesis of CK, and IPT-overexpressing plants were observed to exhibit increased water stress tolerance by displaying enhanced expression of BR-related genes including those implicated in the synthesis (*DWF4*, *DWF5*, *HYD1*) and signaling (*BRI1*, *BZR1*, *BAK1*, *SERK1*, *BRH1*). BR–CK crosstalk was observed to show a positive influence on the yield by modifying the source/sink relationships. Interaction of BRs with CK have been evidenced to regulate the CK-deficiency-induced excess root growth which is under direct influence of the CYTOKININ OXIDASE/DEHYDROGENASE-3 (*CKX3*) controlled by root-specific *PYK10* promoter (Vercruyssen et al. 2011). Plants harboring *PYK10-CKX3* exhibited higher leaf and root growth, and such synergism in growth enhancement was reported due to the ectopic expression of *CKX3* and BRASSINOSTEROID INSENSITIVE-1, indicating crosstalk between CK and BR (Vercruyssen et al. 2011). Transcriptomic analysis of *Gerbera hybrida* has revealed the involvement of CK in the

BR-mediated petal growth (Huang et al. 2017). Further studies employing gain/loss-of-function procedures can assist in unraveling the exact targets for enhancing the growth promoting signaling crosstalk between BR and CKs.

Abscisic Acid

ABA is known as an inhibitor of germination and a major factor of causing seed dormancy throughout the embryo maturation. In contrast, BRs are known to promote germination depicting the antagonistic interaction between ABA and BRs (Hu and Yu 2014). Such regulation of ABA-mediated growth inhibition by BR is regulated by the interaction of glycogen synthase kinase 3-like kinase BRASSINOSTEROID INSENSITIVE2 (*BIN2*; a critical repressor of BR signaling) with ABSCISIC ACID INSENSITIVE5 (*ABI5*; a bZIP transcription factor) in *Arabidopsis*. Furthermore, genetic analysis has revealed that the ABA-hypersensitive phenotype of *BIN2*-overexpressing plants requires *ABI5*, which is phosphorylated and stabilized by *BIN2* in the presence of ABA, mediates ABA responses during seed germination and contrarily the exogenous sourced EBL inhibited the *BIN2*-induced regulation of *ABI5* by repressing the *BIN2-ABI5* cascade for antagonizing the ABA-mediated growth inhibition in plants (Hu and Yu 2014). Zhang et al. (2009) have also evidenced the involvement of *BIN2* in ABA signaling in *det2-1* and *bri1* mutants of BR synthesis and signaling. However, while analyzing the ABA signaling mutants *ABI1* and *ABI2*, PP2C family serine/threonine phosphatases were observed to be the major regulators of BR signaling in addition to *BIN2*. These ABA signaling components act downstream and upstream of *BRI1* and *BIN2* receptors, respectively (Zhang et al. 2009). In another study, growth regulation by BRs has been reported due to the activation of the BRASSINAZOLE-RESISTANT 1 (*BZR1*) family transcription factor, mediating partial crosstalk between BRs and ABA signaling (Yang et al. 2016). They have also reported that the *bzr1-1D* dominant mutant exhibited enhanced BR signaling and less sensitivity to ABA-induced primary root growth inhibition by suppressing the expression of the major ABA signaling component *ABI5* by binding of *BRZ1* strongly with several G-box *cis*-elements in the promoter of *ABI5*. However, the accurate underlying mechanisms are largely unknown. Recently, *KIB1* has been identified as an F-box E3 ubiquitin ligase and believed to be an active player in BR signaling after inhibiting *BIN2* by blocking its access to substrate (*BZR1*) through dephosphorylation-triggered degradation (Zhu et al. 2017).

BR regulated positively the stress responses in the ABA-deficient *aba1-1* mutant of *Arabidopsis* leading to elevated thermo and salt tolerance (Divi et al. 2010). BR induces rapid and transient production of H_2O_2 and expression of NADPH oxidase and *RBOH1* genes triggering generation of

ABA in ABA biosynthetic mutants (*notabilis*; *not*), thereby leading to enhanced tolerance to cold and paraquat-induced oxidative damage (Zhou et al. 2014).

Ethylene

Like interactions with other phytohormones, more or less similar interactions in a different way are depicted between BRs and ethylene for growth regulation. For example, while studying the role of BRs and ethylene in regulation of gravitropism, it was found that auxins are involved in signaling (Vandenbussche et al. 2013). They reported the involvement of BRs in activation of *AUX/IAA* gene, causing a negative regulation of auxin signaling by inactivating the auxin response factors, ARF7 and ARF19 (the positive regulators of auxin signaling), resulting in inhibition of shoot gravitropism, which is however regulated positively by ethylene by down-regulating *AUX/IAA* and up-regulating ARF7 and ARF19. However, during root gravitropism an antagonistic regulatory role of BRs and ethylene has been reported (Buer et al. 2006; Vandenbussche et al. 2013). Moreover, exogenous BR treatment enhanced the synthesis of ethylene by enhancing the activity of the 1-aminocyclopropane-1-carboxylate synthase gene (Muday et al. 2012) and also preventing ubiquitination of ACS proteins (including ACS5, ACS6, ACS9) by 26S proteasome, thereby providing stability to ACS proteins depicting the BR-induced post-translational regulation. Further involvement of BRs in sharing crosstalk with ethylene-mediated defense responses has been confirmed by its involvement in attenuating the ethylene-induced xylanase (Eix), an effective elicitor of plant defense responses after silencing BAK1. The receptors for Eix belonging to the leucine-rich receptor-like protein (RLP) group and bearing signals for receptor-mediated endocytosis with the ability to bind Eix include LeEix1 and LeEix2; however, only LeEix2 has been recognized for its key role in inducing the defensive responses. Application of Eix is believed to induce heterodimerization of LeEix1 with LeEix2 resulting in considerable reduction in Eix-triggered internalization and signaling. However, in BAK1-silenced plants, LeEix1 no longer attenuated the plant responses to Eix indicating the interaction between BRs and ethylene (Bar et al. 2010). Over-expression of the BR transcription factor brassinazole-resistant 1 (BZR1) has been reported to mediate BR signaling leading to regulation of many specific developmental processes like fruit ripening and the accumulation of carotenoids, sugars, and ascorbic acid, thereby improving the nutritional quality of ethylene-insensitive tomato in addition to the up-regulation of SIGLK2 involved in chloroplast development (Liu et al. 2014). Growth regulation induced by BRs is also controlled by the co-ordinated effect of ethylene and H₂O₂ with application of BR triggering ethylene signaling pathways leading to greater stress

tolerance contrary to this silencing ethylene signaling that inhibited BR-mediated salt tolerance (Zhu et al. 2016). Further analysis confirmed the involvement of H₂O₂ in overall crosstalk between BR and ethylene. As already pointed out, it is not clear whether it is dependent or independent of ROS, and therefore further studies are needed to make final confirmation.

Jasmonic Acid

BRs have been reported to interact (antagonistic or synergistic) with jasmonic acid (JA) for developmental regulation during normal as well as stress conditions. For instance, Kitanaaga et al. (2006) reported enhancement in endogenous levels of JA by BR application reflecting synergistic crosstalk of JA and BR in enhancing the expression of antimicrobial peptide coding thionin genes. BRs negatively regulate JA signaling in root growth inhibition. In *Arabidopsis thaliana*, F-box protein CORONATINE INSENSITIVE1 (COI1) plays a central role in JA signaling and partially suppressing COI1 mutants (*psc1*) has been demonstrated as a leaky mutation of DWARF4 (*DWF4*) encoding a key enzyme involved in BR biosynthesis thereby inhibiting root growth. JA-induced root growth inhibition is due to COI1-dependent JA-mediated down-regulation of DWF4 located downstream of COI1 in the JA signaling pathway (Ren et al. 2009). In tomato while studying the role of JA and BRs in framing an interactive defense against the insect *Spodoptera frugiperda* and pest *Tuta absoluta*, it was confirmed that BRs and JA affect the trichome density and allelochemical content in opposite fashion with increased pubescence, zingiberene biosynthesis, and expression of the proteinase inhibitor in the BR-deficient mutant *dpy* compared to the JA-insensitive *jail-1* mutant which displayed an opposite trend, causing enhanced creation of defensive traits. Additionally, experiments with the double mutant, *dpy* × *jail-1* revealed that *jail-1* is epistatic to *dpy* indicating the action of BR upstream of the JA signaling. This study has confirmed the negative regulation of JA-induced anti-herbivory by BR (Campos et al. 2009). BR mutants in *Arabidopsis* exhibited reduced JA-mediated anthocyanin accumulation and similar evidence has been claimed in wild type treated with the BR biosynthetic inhibitor, brassinazole, and exogenous BR reversed this effect significantly. Such effects have been attributed to down-regulation of 'late' anthocyanin biosynthesis genes like DFR, LDOX, and UF3GT and the Myb/bHLH transcription factors like PAP1, PAP2, and GL3 which form key components of the WD-repeat/Myb/bHLH transcriptional complexes implemented in regulation of 'late' anthocyanin biosynthesis genes (Peng et al. 2011). Therefore, it needs to be clarified whether it is negative or positive crosstalk that dominates in plants in response to different stresses and developmental transitions.

Salicylic Acid

Salicylic acid has been reported to mediate the expression of a master regulator of systemic acquired resistance usually promoted through expression or induction of pathogenesis-related genes—*non-expressor of pathogenesis-related genes-1* (*NPR1* also called *NIMI*), and in *Arabidopsis* it has been reported that *NPR1* is active only after induction of SA (Maier et al. 2011). Mutants defective in the *NPR1* gene are sensitive to stresses (Clarke et al. 2009). Divi et al. (2010) demonstrated that EBL triggers the *NPR1* gene expression to mediate the SA-induced defense against salt and thermal stress depicting EBL–SA interaction. However, EBL mediates induction of PATHOGENESIS-RELATED 1 (*PR1*) genes independent of SA. They further reported that BR shares transcriptional targets with other hormones. Not many reports are available pertaining to the transcriptomic and molecular genetic approaches for unraveling the BR–SA-mediated stress tolerance. Thus, future research work in this direction can be meaningful.

Conclusion and Future Prospects

From the present review, it can be concluded that BRs are effectively involved in diverse metabolic processes. BRs can regulate processes including photosynthesis, antioxidant metabolism, osmotic regulation, nitrogen metabolism, and plant–water relations under normal and stressful conditions, but limited information is available within the existing literature on how BR-induced regulation of these plant processes varies from species to species with BR application. From the past two decades, much progress has been made in identifying and characterizing the biosynthetic and metabolizing enzymes of BRs. However, research work regarding the interactive role of BRs with other phytohormones is currently being intensively executed for making the elusive interactive events clear which is expected to add to the current understanding of the BR-induced growth regulation mechanisms. In addition, much work is to be done in identifying the receptors involved in BR signaling while regulating the metabolic processes from germination to senescence. Identification and characterization of key genes regulating the hormonal crosstalk and the underlying signaling also need to be explored. Involvement of transcription factors in integrating the beneficial crosstalk of BR with multiple phytohormones and the subsequent identification of gene and gene products posing a negative regulatory effect on growth need clarification. Knocking out such growth inhibitory regulating gene products shall be a way forward in understating and improving plant growth. In addition, optimizing the endogenous levels of phytohormones for maximizing the

stress-responsive crosstalk mechanisms between multiple hormones needs attention.

Compliance with Ethical Standards

Conflict of interest The authors declare that no conflict exists among the authors.

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