Journal of Plant Growth Regulation (2018) 37:1025–1032
https://doi.org/10.1007/s00344-018-9828-5

Interactions of Brassinosteroids with Major Phytohormones: Antagonistic Effects

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Received: 3 March 2018 / Accepted: 25 June 2018 / Published online: 10 July 2018

Abstract

Brassinosteroids (BRs) constitute an important class of signaling molecules capable of executing diverse functions ranging from plant growth, development, reproduction, and even stress tolerance. The recent literature on BRs has discussed these wide ranging roles and potentials of BRs. However, the maintenance of metabolic equivalents in the global context of other phytohormones is largely unknown. In this article, we have highlighted such interactive antagonistic cross-talks between BRs and other phytohormones which are crucial in growth regulation and abiotic stress tolerance. Such competitive interactions with BRs have been observed in the cases of abscisic acid, ethylene, auxin, gibberellins, salicylic acid, and even polyamines during physiological growth or abiotic stresses. The discussion largely presents the unique characters of plant molecular physiology and development regarding BR- and other phytohormone-mediated interactive antagonism.

Keywords Brassinosteroids · Phytohormones · Plant growth regulators · Signaling · Antagonism · Cross-talk · Metabolic homeostasis · Growth and development · Abiotic stress

Introduction

Brassinosteroids (BRs) form a novel group of phytohormones. The members of this family of steroidal hormones contain polyhydroxylated sterol structures (Grove et al. 1979). The name 'brassinosteroids' can be attributed to the initial identification of these compounds in the pollen grains of *Brassica napus*. The first identified BR was named 'brassinolide' (Grove et al. 1979). Previous investigations have validated the potential role of BRs in regulating diverse physiological processes like germination, cell growth and senescence, differentiation of the vascular tissues, floral reproduction, and even abiotic and biotic stress responses (Sharma et al. 2015; Vardhini and Anjum 2015; Tang et al. 2016; Wei and Li 2016; Xia et al. 2014, 2009a, b; Zhang et al. 2008; Bajguz and Hayat 2009).

Biosynthesis of brassinolide (BL) is initiated from the precursor compound, campesterol via recurring reductions, hydroxylations, epimerizations, and oxidations (Fujioka et al. 1998; Fujioka and Yokota 2003). The other major BRs are synthesized via the mevalonic acid-dependent triterpenoid pathway (Chung and Choe 2013). In this pathway, campesterol is modified by enzymes like C-22 hydroxylase dwarf4/CYP90B1 (DWF4) and C-3 hydrogenase constitutive photomorphogenesis and dwarf/CYP90A1 (CPD) (Chung and Choe 2013; Bajguz 2007). The biosynthesis is regulated by controlling the expression of anabolic genes [DWF4, CPD, 5α-reductase: de-etiolated-2 (DET2), C-22 hydroxylase: *rotundifolia*/CYP90C1 (ROT3)] or by reducing the levels of bioactive BR (Guo et al. 2013; Vriet et al. 2013; Clouse 2015). BR-mediated signaling is positively regulated by basic helix-loop-helix (bHLH) transcription factors (TFs) like CESTA and TCP (Poppenberger et al. 2011). Saini et al. (2015) reported that abscisic acid (ABA)-dependent factors like ABA insensitive 3/viviparous1 (ABI3/VP1) and related to ABI3/VP1 (RAV1) positively regulated BR biosynthesis by inducing the expression of *BR insensitive 1* (*BRI1*), the BR receptor in rice. It was found that the plants with mutations in the *BRI1* gene exhibited high accumulation of BRs due to loss of feedback regulation (Sun et al. 2010; Cano-Delgado et al. 2004; Karlova et al. 2006). On association with the co-receptor BRI1 ASSOCIATED RECEPTOR KINASE 1 (BAK1), BRI1 is serially phosphorylated and

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de-phosphorylated (Li et al. 2002; Nam and Li 2002). This promotes BR-mediated signal transduction and regulation of physiologically crucial genes via TFs (Nakamura et al. 2017). Symons et al. (2008) presented important observations regarding BR signaling. They observed that BRs are utilized in close proximity of the synthesizing cells via conjugates and specific transporters. However, the long distance effects of BRs are exerted through extensive cross-talks with multiple phytohormones (Vriet et al. 2013; Gudesblat and Russinova 2011). This article aims at presenting an exhaustive discussion regarding the antagonistic metabolic interactions between BRs and other phytohormones during developmental growth or under various abiotic stress responses. Illustration of the above consequences in this review can be useful for understanding the BR-mediated dynamics in diverse plant physiological responses.

BRs and Plant Growth Regulation

Diverse species ranging from higher plants to the monoplast freshwater algae and brown algae have been reported to produce BRs. In higher plants, the highest BR accumulation was detected in immature seeds, roots, flowers, and pollens. However, shoots and leaves accumulated lower amounts of BRs (Kutschera and Wang 2012; Takatsuto 1994). BRs exhibit autocrine and paracrine functioning. Hence, passive and active intracellular transport are required for the effective mobilization of BRs from the site of synthesis to the cell membrane and early endosomal compartments (Tang et al. 2016). The production of BRs and their receptor-dependent signaling influence cell division and leaf expansion. *Arabidopsis* mutants, constitutive photomorphogenesis and dwarfism (cpd) deficient in BRs exhibited reduced leaf blades and thwarted cell division (Noguchi et al. 1999). Several cyclin-dependent kinase (CDK) encoding genes like *CYCA, CYCB, CYCD3;1, CYCD3;2*, and cyclophilins are regulated by BRs (Fu et al. 2008). Sun et al. (2015) reported the regulatory expression of U-type cyclin CYC U4;1 and glycogen synthase kinase by the TF, BRI1-EMS-SUPPRESSOR 1 (BES1) in rice. This reduces the cellular proliferation in the abaxial sclerenchyma to promote leaf erectness. BRs are involved in regulating diverse physiological parameters like source-sink relationships, germination, photosynthesis, senescence, photomorphogenesis, and flowering (Vardhini and Anjum 2015). Recent data suggest the immense roles of BRs in maintaining meristem size, hair formation, and lateral root growth (Wei and Li 2016). Identifying the involvement of various phytohormones in such BR-mediated growth responses can provide valuable insights into the systemic physiology of plant growth.

BRs and Abiotic Stresses

Abiotic stresses like salinity, drought, temperature, light, and heavy metal toxicity are major agricultural challenges. These edaphic and atmospheric stresses account for a large proportion of global crop losses (Banerjee et al. 2017). The antagonistic cross-interactions between BRs and the growth regulating phytohormones like ABA, ethylene, salicylic acid (SA), auxin, gibberellins, and polyamines can reveal potential molecular targets which can be genetically manipulated to generate tolerance (Vardhini and Anjum 2015). It has been noted that such antagonistic cross-talks actually balance plant growth and survival during abiotic stresses. Accounting for the diverse physiological functions of BRs, this group of phytohormones can be promoted as crucial growth regulators essential for plant development (Divi and Krishna 2009).

Abiotic stresses severely retard plant systemic development by inhibiting the cell cycle and disrupting the cellular architecture. Both control and stress conditions induce the BR-dependent TF, BRASSINAZOLE RESISTANT 1 (BZR1) to maintain normal progression of the cell cycle (Hacham et al. 2011). The R2R3 MYB TF, BRASSINOSTEROIDS AT VASCULAR AND ORGANIZING CENTER (BRAVO) inhibits cellular proliferation of plant stem cells (quiescent center cell). Interaction with BES1 represses the activity of BRAVO and initiates cell division in the root QC (Vilarrasa-Blasi et al. 2014). This mechanism promotes plant longevity and stress adaptation.

Recently, Rao and Dixon (2017) inferred that BRs manipulate cell wall remodeling in members of the Poaceae family during abiotic stresses. Genes encoding cell wall remodeling enzymes, that is, pectin lyase like (PLLs), expansins (EXPs), and xyloglucan endotransglucosylase/hydrolases (XTHs) are induced by BRs (Rao and Dixon 2017). The expression of *EXP*s and *endoglucanases* (*GLU*s) in rice was found to be regulated by BES1 via a cross-talk between phytohormones (Schmidt et al. 2013). Loss of integrity in the *Arabidopsis* cell wall during abiotic stresses is resisted by the stimulation of the BRI1 receptor which up-regulates the expression of genes encoding pectin methyl esterases (PMEs). The cell wall is maintained through an integrated hormonal outplay generated by the interaction of BAK1 and RECEPTOR-LIKE PROTEIN (RPL44) (Wolf et al. 2014).

Some available reports have identified the roles of BRs during abiotic stress responses. Tiwari et al. (2017) proposed active participation of BRs in drought stress responses and tolerance. Overexpression of the BR biosynthetic gene (encoding a cytochrome p450) *CYP85A1* from *Spinacia oleracea* conferred drought tolerance in transgenic tobacco plants (Duan et al. 2017). The transgenics accumulated lower levels of reactive oxygen species (ROS) and malondialdehyde (MDA) along with higher levels of proline and antioxidant enzymes compared to the wild type plants (Duan et al. 2017). In an interesting finding, it was observed that the WRKY TFs, that is, WRKY46, WRKY54, and WRKY70 synchronizes with BES1 to promote BR-induced plant growth by down-regulating the drought stress-induced genes (Chen and Yin 2017). Ahammed et al. (2015) reported significant reduction in photoinhibition in tomato plants exogenously treated with BRs. The plants exhibited increased quantum efficiency of PSII and photochemical quenching coefficient. Inhibition of BR biosynthesis by brassinozole reduced the levels of RuBisCO and other photosynthetic proteins (Xia et al. 2009a). *Vicia faba* plants treated with BRs recorded improved stomatal closure by reducing K^+ uptake in the guard cells (Haubrick et al. 2006). The mitigating roles of BRs in plants exposed to high temperature, low temperature as well as freezing have been observed (Zhang et al. 2013; Janeczko et al. 2011, 2009; Wang et al. 2014). BRs also ameliorate light stress in plants (Vardhini and Anjum 2015). The antioxidant machinery in *Brassica juncea* exposed to zinc (Zn)- and chromium (Cr)-metal stress was activated by the application of 24-epibrassinolide (Arora et al. 2010a, b). Anuradha and Rao (2007a, b) showed the ameliorative effects of 24-epibrassinolide in radish seedlings exposed to lead (Pb) and cadmium (Cd)-mediated heavy metal toxicity.

Compatible solutes like proline, glycine betaine, fructans, myo-inositol, soluble sugars, and so on are essential for the maintenance of cellular equilibria during sub-optimal conditions (Roychoudhury et al. 2015; Roychoudhury and Banerjee 2016). Accumulation of BRs has often been associated with increased cellular content of osmolytes (Kumar et al. 2013). BR accumulation suppresses the phosphorylation activity of the glycogen synthase kinase-3-like kinase, BRASSINOSTEROID INSENSITIVE 2 (BIN2). This maintains the TF, YODA (YDA) in an inactive form leading to the activation of a mitogen-activated protein kinase (MAPK) cascade which negatively regulates the stomatal development (Kim et al. 2012). It was observed that the signaling mutants, *bin-2* and the BR biosynthetic mutants, *det-2* exhibited salt hypersensitivity and suppression of the proline anabolic gene, Δ^1*-pyrroline-5-carboxylate synthase 1* (*P5CS1*) (Zeng et al. 2010).

Cross-Talk Between Brassinosteroids and Other Phytohormones

Phytohormones are the most important signaling mediators in plants. They regulate diverse stress responses by modulating the entire signalosome. BRs are being regarded as a novel class of signaling molecules involved in regulating abiotic stress responses by interacting with multiple conventional phytohormones (Sharma et al. 2017). The underlying section highlights the antagonistic interactions between BR and other phytohormone-mediated signaling.

Antagonistic Interactions Between BRs and ABA

ABA is regarded as the universal stress phytohormone which maintains embryo dormancy during seed maturation (Roychoudhury and Banerjee 2017). Because BRs promote seed germination, their antagonistic interaction with ABA is evident (Hu and Yu 2014). ABA- and BR-mediated co-regulation of several genes have been documented through genetic and physiological studies (Nemhauser et al. 2006; Zhang et al. 2009). Detailed analysis of BR mutants like *det-2* and *bri-1* revealed that BIN2 negatively regulates BR signaling after perceiving ABA-mediated molecular signaling. However, studies in ABA signaling mutants highlighted the participation of PP2C family of Ser/Thr phosphatases, ABI1 and ABI2 in BR signaling (Zhang et al. 2009). These enzymes act downstream of the receptor, BRI1, and upstream of BIN2 to suppress BR signaling (Zhang et al. 2009). Recently, Wang et al. (2018) established that ABI1 and ABI2 interact with BIN2 to dephosphorylate it. Such ABA-mediated regulation inhibits BIN2-induced phosphorylation of BES1 and thus dampens the BR-mediated signaling (Fig. 1). A concise signaling module consisting of PP2Cs-BIN2-SnRK kinases has been highlighted, because BIN2 suffices the feedback regulatory mode to phosphorylate SnRKs. This activates the ABA-dependent signaling and suppresses BR-mediated molecular transduction (Wang et al. 2018).

In another study, it was reported that BIN2 interacts and phosphorylates ABI5. This activates the TF which mediates ABA responses to restrict seed germination (Hu and Yu 2014). Exogenous BR destabilizes the synergistic association between BIN2 and ABI5 and releases the ABA-mediated inhibition of BR signaling (Hu and Yu 2014). Low amounts of BR induce the genes encoding RESPIRATORY BURST OXIDASE HOMOLOG (RBOH) to transiently produce low amounts of hydrogen peroxide (H_2O_2). This equilibrates the cellular redox status by balancing glutathione and also promotes BR-induced stomatal opening. High concentrations of BRs are maintained during stress as a result of which prolonged H_2O_2 production activates ABA-dependent signaling to stimulate stomatal closure (Xia et al. 2014).

A significant correlation between BR and ABA has been observed during heat stress. High accumulations of BRs and HEAT SHOCK PROTEIN 90 (HSP90) were observed in the ABA biosynthetic mutant, *aba1-1* exposed to heat stress (Divi et al. 2010). Up-regulation of the gene encoding BRASSINOSTEROID-SIGNALING KINASE 5 (BSK5)

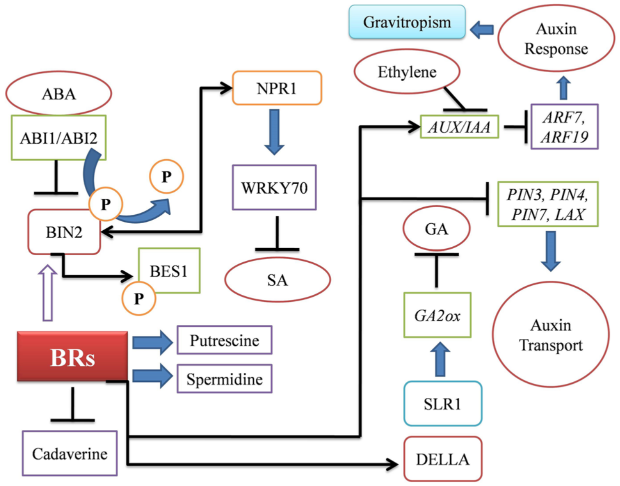

Fig. 1 An overview of some antagonistic cross-talks occurring between BRs and phytohormones. In the presence of ABA, ABI1 and ABI2 dephosphorylate the BR-induced kinase BIN2. As a result, BIN2 remains inactivated and cannot phosphorylate BES1, resulting in suppressed BR-responsive signaling in the presence of ABA. BIN2 also interacts with the pathogenesis receptor, NPR1, which activates the downstream TF, WRKY70 (a negative regulator of SA biosynthesis). BRs suppress multiple *PIN* and *LAX* genes involved in auxin transport. On the contrary, the *AUX/IAA* genes are up-regulated, leading to the elevated expression of *ARF7* and *ARF19*. This promotes auxin-dependent gravitropism which is usually repressed by ethylene. Differential accumulation of PAs has also been observed. BRs inhibit the accumulation of cadaverine and promote putrescine and spermidine synthesis during abiotic stresses. Because PA biosynthesis is positively linked to ABA-dependent transduction, such BR-mediated regulation can be another unidentified tripartite node of BR–ABA–PA signaling

was observed in *Arabidopsis* plants treated with both ABA and BR. BSK5 was found to be a crucial modulator of the ABA signaling pathway, as the *Arabidopsis bsk5* mutants exhibited higher expression of ABA anabolic genes, *ABA3* and *9-cis-epoxycarotenoid dioxygenase 3* (*NCED3*) (Li et al. 2012a, b). The cross-talk between BRs and ABA has also been reported to be regulated by the TF, BZR1 (Yang et al. 2016). The *bzr1-1D Arabidopsis* mutants exhibited less sensitivity to the ABA-induced inhibition on the growth of primary roots. BZR1 also confers ABA hyposensitivity by associating with the G-boxes in the *ABI5* promoter and suppressing *ABI5* gene expression (Yang et al. 2016).

Antagonistic Interactions Between BRs and Ethylene

The gaseous hormone, ethylene, is noted for its roles in fruit ripening and gravitropic reorientations in seedlings. The latter function of ethylene has large implications during desiccation stress (Vandenbussche et al. 2013). BRs on the contrary negatively regulate shoot gravitropism. As a result, the outcome of ethylene and BR interactions influences the auxin signaling genes to control gravitropic responses in shoots (Guo et al. 2008). Unlike BRs, ethylene represses the expression of the *AUX/IAA* genes which negatively regulate auxin signaling. This promotes the expression of *auxin responsive factor 7* (*ARF7*) and *ARF19* (Fig. 1). These genes encode positive regulators of auxin signaling which mediate gravitropic responses in the shoots (Vandenbussche et al. 2013). Similar ethylene-BR antagonism has been observed during root gravitropic responses, where ethylene suppresses the effect and BRs promote it (Buer et al. 2006).

The receptor-like kinase, FERONIA, is quintessential for pollen tube reception and cellular elongation (Deslauriers and Larsen 2010). The *Arabidopsis* knockout mutants of this gene exhibited BR hyposensitivity (Guo et al. 2009). It was reported that the ethylene-dependent growth of hypocotyls in etiolated seedlings was antagonized by FERONIA-mediated BR responses (Deslauriers and Larsen 2010). Interestingly, exogenous application of BRs up-regulated the expression of the ethylene biosynthetic gene, *1-aminocyclopropane-1-carboxylate synthase* (*ACS*) (Muday et al. 2012). Ubiquitination of ACS5, ACS6, and ACS9 by the 26S proteasome was also stalled by BRs (Hansen et al. 2009).

In another report, ethylene and BRs were suggested to antagonistically regulate alternative oxidase (AOX) activity during fruit ripening in *Carica papaya* (Mazorra et al. 2013). The AOX activity is responsive to changes in the electron transport chain (ETC), phytohormone-mediated signals, ROS, and metabolites associated with respiration (Vanlerberghe 2013). The AOX capacity increased both upon the exogenous application of 24-epibrassinolide (epiBR) and even Brz2001 (BR biosynthetic inhibitor). The ethylene emission rate remained constant for the initial 24 h and then decreased on the fifth day of Brz treatment. Application of the ethylene inhibitor, 1-methylcyclopropene (1-MCP) reversed the results obtained by epiBR and Brz treatments without 1-MCP. As a result, papaya fruits treated with 1-MCP and epiBR exhibited suppressed AOX activity, thus highlighting the antagonistic competition occurring between ethylene and BRs (Mazorra et al. 2013). Zhu et al. (2016) identified the interaction between BRs and ethylene in the fruits of tomato plants exposed to salt stress. H_2O_2 was found to mediate the above cross-talk, since application of a ROS scavenger or inhibitor of ROS synthesis significantly blocked BR-induced ethylene production. Under conditions of reduced ethylene production via use of 1-MCP, the BR-induced tolerance to salt stress was reversed (Zhu et al. 2016). This indicates that in tomato plants, ethylene probably acts downstream of BRs to mediate salt stress tolerance.

Antagonistic Interactions Between BRs and Auxin

Plant adaptation and growth during abiotic stresses are mediated via a complex redox signaling module formed by auxin, ROS, antioxidants, glutathione (GSH), and associated proteins. Auxin homeostasis directly regulates plant growth plasticity during responses to stresses like temperature, desiccation, and salinity (Salopek-Sondi et al. 2017). The antagonism between auxin and BRs dictates the development of an exaggerated apical hook in *Arabidopsis* seedlings grown under both light and dark conditions (Grauwe et al. 2005). Exogenous application of BRs suppressed auxin transport and formation of the apical hook (Grauwe et al. 2005; Gruszka et al. 2016). Some of the *pinformed* (*PIN*) genes (*PIN2* and *PIN5b*) associated with auxin transport were up-regulated by heat, cold, and drought stresses, whereas the expression of other *PIN* genes remained suppressed (Saini et al. 2015). BR down-regulated the expression of *PIN3, PIN4, PIN7*, and *like auxin-resistant-1* (*LAX*) genes (Fig. 1). This pointed towards the existence of BR-auxin cross-talk during abiotic stress (Nemhauser et al. 2004). Drought stress in rice down-regulated the expression of all six *YUCCA* genes (encoding rate limiting enzymes in the auxin biosynthetic pathway) except *OsYUCCA4* (Du et al. 2013). Interestingly, cold stress induced *OsYUCCA2, OsYUCCA3, OsYUCCA6*, and *OsYUCCA7*. Again, heat stress strongly up-regulated *OsYUCCA3, OsYUCCA6*, and *OsYUCCA7* genes (Du et al. 2013). The *yucca* rice mutants exhibited altered profile of BR-induced genes which confirmed YUCCA-mediated auxin-BR cross-talk during abiotic stresses.

Proper root growth requires proper co-ordination between auxin and BRs. Elevated levels of auxin and BZR1 are maintained by steady BR catabolism in the *Arabidopsis* roots. This equilibrates the spatio-temporal balance of stem cell dynamics required for optimum root and shoot growth. The genes facilitating the elongation of the transition zone are up-regulated by BZR1 (Chaiwanon and Wang 2015). BR represses *BRAVIS RADIX* (*BRX*) required for root growth, whereas auxin induces the same (Mouchel et al. 2006). Zhang et al. (2014) detected reduced free indole acetic acid (IAA) content in the joints of lamina in rice plants overexpressing *OsARF19* and *OsBRI1*. OsARF19 was also found to bind to the *OsBRI1* promoter and positively regulate its expression. However, in spite of activating BR signaling, excess ARF19 reduced cellular IAA content via a feedback regulation (Zhang et al. 2014).

Antagonistic Interactions Between BRs and Gibberellins

Gibberellic acid (GA) is a crucial growth-promoting hormone which stimulates seed germination and internodal elongation. Abiotic stress conditions usually promote the accumulation of ABA, which in turn suppresses GA biosynthesis. BRs dampen GA-mediated responses by maintaining high cellular concentration of GA inhibitors like DELLA and SLR1 (De Vleesschauwer et al. 2012). As a result, the GA biosynthetic genes, *GA*$_{20}$ *oxidase* (*GA20ox*) and *GA3ox3*, are repressed and the GA catabolic gene, *GA2ox* is induced (De Vleesschauwer et al. 2012) (Fig. 1). Exogenous treatment with high concentration of BRs activated GA2ox-3 and inhibited cell elongation. It has been shown that GAs repress BR biosynthesis via feedback regulation, but activate GA-mediated primary signaling to promote cell elongation (Tong et al. 2014). Internodal cellular elongation promoted by GAs requires BR signaling (Janeczko et al. 2016). The tripartite BR-auxin-GA antagonism has been observed during fiber initiation in cotton plants, *Gossypium hirsutum* (Hu et al. 2011). BR and auxin treatments down-regulated the DELLA gene *GAI1*, whereas GA application induced *GAI1* and *GAI3* during initiation of cotton fibers (Hu et al. 2011). In another study, it was found that the TFs, BZR1 and REPRESSOR OF GAL-3 (RGA) antagonized their mutual transcriptional activities to mediate positive and negative regulation of BR and GA signaling, respectively (Li et al. 2012a, b; Ross 2016).

Antagonistic Interactions Between BRs and Salicylic Acid (SA)

SA, mainly known for its roles in systemic acquired resistance (SAR) during biotic stresses, also participates in abiotic stress responses (Roychoudhury et al. 2016). WRKY70, the major TF acting downstream of the *non-expressor of pathogenesis-related genes 1* (*NPR1*) mediates BR-SA cross-talk (Divi et al. 2010). Interestingly, the *Arabidopsis npr1-1* mutants were highly sensitive to heat stress and also exhibited abnormal expression of the *pathogenesis-related* (*PR*) genes in response to SA application (Larkindale et al. 2005). It has been hypothesized that NPR1 regulates stress tolerance by interacting with BIN2 and BZR1 (Divi et al. 2010) (Fig. 1). The exact type of interaction in this case is not known. WRKY70 negatively regulates SA biosynthesis (Li et al. 2013). Hence, high expression of *NPR1* during stress probably induces BR signaling by repressing SA anabolism.

Interactions Between BRs and Polyamines

Polyamines (PAs) consist of an important class of compatible solutes that maintain the cellular osmoticum in almost all types of abiotic stresses (Banerjee and Roychoudhury 2018). Liu and Moriguchi (2007) suggested the interaction of BRs and PAs in enhancing the systemic tolerance potential. Exogenous application of BRs increased endogenous free PA content and ameliorated Cu stress in *Raphanus sativus* L. cv. ‘Pusa chetki’ seedlings (Choudhary et al. 2010). The antagonistic action of BRs was observed on cadaverine (higher PA) which promotes ROS production. Exogenous application of BRs reduced the endogenous content of cadaverine. However, the content of other PAs like spermidine and putrescine (required for the growth and abiotic stress tolerance in plants) increased significantly after BR treatment (Takahashi and Kakehi 2010) (Fig. 1). Co-application of BR and spermidine promoted tolerance against Cu stress by modulating the ABA and auxin-dependent signaling pathways (Choudhary et al. 2012).

Conclusion

BRs consist of a group of versatile phytohormones which have significantly emerged in the context of the plant signalosome due to diverse functions in developmental growth and stress responses. This minireview concisely illustrates the situation- and stimulus-specific dynamic shifts in the plant metabolome to balance BR-mediated signaling with other phytohormones (Fig. 1). The action of BRs is strictly antagonistic to ABA, the most important stress hormone. Tripartite interactions among BRs, ethylene, and auxin displayed the nodal factors responsible for maintaining plant metabolism under myriad conditions. The roles of GA and SA during abiotic stress are well determined. The antagonistic interactions of these phytohormones with BRs open up a new avenue of studying stress physiology. The involvement of stress regulators like NPR1 and WRKY70 in SA and BR signaling presented a novel interaction of these hormones under both abiotic and biotic stress conditions.

Future Perspectives

Plant signaling in the context of BR-induced responses is still not well deciphered. The synergistic and antagonistic cross-talks of all the phytohormones in a tissue-specific pattern and under each isolated condition need to be documented. PAs are yet to be completely recognized as phytohormones, but their potential role in generating abiotic stress tolerance and proposed cross-talk with BR-mediated signaling during abiotic stress is important. This would facilitate the complete understanding of systemic signaling. The role of epigenetics in phytohormone-BR antagonism is predicted, but largely unknown. Genome-wide epigenetic studies along with next-generation sequencing of the transcriptome under BR-treated conditions can be novel approaches for understanding the overall signaling induced by BRs. Such strategies would also be crucial to sieve out, identify, and validate potential molecular targets that can be genetically altered to confer abiotic stress tolerance in transgenics.

Acknowledgements Financial support from Council of Scientific and Industrial Research (CSIR), Government of India through the research Grant [38(1387)/14/EMR-II] to Dr. Aryadeep Roychoudhury is gratefully acknowledged. The authors thank University Grants Commission, Government of India for providing Junior Research Fellowship to Mr. Aditya Banerjee.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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