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REVIEW

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Brassinolides signaling pathway: tandem response to plant hormones and regulation under various abiotic stresses

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Abstract

Plant hormones play pivotal roles in stress responses by modulating growth, development, stomatal movement, and the expression of stress-related genes, thereby aiding plants in adapting to and managing various environmental challenges. Each hormone exhibits distinct functions and regulatory mechanisms in stress response, with potential complex interactions among them. Brassinosteroids (BRs) represent a novel hormone that influences the expression of its target genes through a series of phosphorylated cascade reactions involving various transcription factors. This signaling pathway regulates diverse growth and development processes in plants. Additionally, BRs interact with other hormones to modulate physiological development. This review examines BRs biosynthesis and metabolism, elucidates the interactions between BRs and abscisic acid (ABA), jasmonic acid (JA), and gibberellins (GA), and explores their roles in regulating responses to drought, salt, cold, and heat. The review underscores the importance of BRs and other hormonal crosstalk in managing nutrient stress, which is vital for understanding plant growth regulation, enhancing crop stress resistance, advancing biotechnology applications, and furthering plant science research. Future research directions and the potential of BRs production and application to improve plant stress resilience are also discussed in the context of current findings.

Keywords Brassinosteroids, Phytohormone, Abiotic stress, Signaling pathway, Nutrition

Introduction

The growth and development of plants are governed by an intricate network of signaling pathways that enable them to adapt to a dynamic environment (Lu et al. 2024). Plant hormones, functioning as signaling molecules, regulate these processes and enable responses to various stresses through their transport to different plant parts (Cabeza et al. 2024). Increasing evidence highlights that plant responses to external stimuli involve the coordination and integration of these signaling molecules (Brini et al. 2022).

Since the isolation of Brassinosteroids (BRs) in 1979, numerous BRs analogs have been identified, and their roles continue to be elucidated with advances in science and technology (Bashir and John 2023). Initially, research on BRs focused on their effects on endogenous hormonal regulation of physiological processes, such as male sterility and aging, which enhance plant growth and development. Studies have shown that exogenous BRs application significantly boosts stem growth and rooting in pears, while overexpression of *Delta24-sterol reductase 1* (*PcDWF1*) can delay flowering (Sukpitak et al. 2024). Additionally, BRs activate antioxidant enzymes and non-enzymatic defense mechanisms, enhancing resistance to adverse conditions such as drought, cold, heat, salinity, and nutrient deficiencies (Canales et al. 2023). These effects have been confirmed in horticultural crops like *Fragaria*×*ananassa* Duch. and *Vitis vinifera* L. (Khan

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et al. 2023). For example, exogenous 2,4-epibrassinolide (EBR) treatment improves the low-temperature tolerance of *Solanum melongena* L., *Prunus persica* (L.) Batsch, and *Citrus reticulata* Blanco, among others (Emamverdian et al. 2024).

Currently, research on BRs primarily addresses their role in mitigating abiotic stress through exogenous application, with a lack of comprehensive reviews on BRs signal transduction and responses to stress and nutrient deficiencies. This review aims to provide an in-depth examination of the critical functions of brassinolide in plant growth and metabolism. Additionally, the complex molecular mechanisms of BRs biosynthesis, signal transduction, and its interactions with other plant hormones were identified. Additionally, the regulatory mechanisms of BR's response to abiotic stress and nutrient interactions were explored, offering a detailed perspective on the complex network influencing plant physiology.

Biosynthesis of BR

The biosynthesis of BRs begins with the synthetic precursor sterol cycloartenol, which undergoes methylation, reduction, and desaturation to yield the BR-specific precursor canola sterol. Brassterol (CR), a major plant sterol, regulates cell membrane fluidity and serves as a BR-specific biosynthetic precursor. Following C-5 reduction, CR progresses into the late C-22 oxidation pathway (Gholami et al. 2023). In this pathway, CR is initially converted to rape steranol (CN), which is then transformed into brassinosteroid (castasterone, CS), the direct precursor of BL (brassinolide), via two distinct oxidation branches: C-6 early oxidation and C-6 late oxidation, collectively known as the CN-dependent pathway. Alternatively, CR can be hydroxylated at C-22, entering the C-22 early oxidation pathway, also referred to as the CN-independent pathway (Gillani et al. 2022).

Subsequently, CS is converted into BL, a form with enhanced biological activity, through the BRs-specific pathway. The C-22 early oxidation and C-6 late oxidation pathways are considered the principal routes for BL synthesis across various plants. Key enzymes involved in this process include DWARF 4 (DWF4), constitutive photomorphogenesis and dwarf (CPD), DEETIOLATED 2 (DET2), ROTUNDIFOLIA 3 (ROT3), and brassinosteroid-6-oxidase 1/2 (BR6ox1/2) (Zheng et al. 2022).

During BRs biosynthesis, transcription factors (TFs) such as Teosinte branched1/Cycloidea/Proliferating cell factor 1 (TCP1) and beta-hydroxybutyrate 2 (BHB2) enhance DWARF 4 (DWF4) expression. TCP1 directly binds to the *DWF4* promoter, positively regulating its expression (Gao et al. 2015). Additionally, auxin response factors ADP-ribosylation factor 6 (ARF6) and ADP-ribosylation factor 8 (ARF8), along with the ethylene response factor Submergence 1 (SUB1A), can induce *DWF4* expression (Wong et al. 2024). Conversely, the NAC TF MdNAC1 negatively regulates BRs content by inhibiting *constitutive photomorphogenesis and dwarfism* (*MdCPD*) and MdDWARF 4 (MdDWF4) expression (Tanaka et al. 2005). In cotton fibers, the basic helix-loop-helix TF GhFP1 binds to the promoters of BRs biosynthetic genes *Ghconstitutive photomorphogenesis and dwarfism* (*GhCPD*) and *GhDWARF 4* (*GhDWF4*), thereby activating their transcription and increasing BRs levels (Wu et al. 2021) (Fig. 1).

Multiple modifications of BRs

Currently, research has identified several key enzymes and proteins involved in the hydroxylation, glycosylation, sulfonylation, and acylation of BRs.

PHYB ACTIVATION TAGGED SUPPRESSOR 1 (BAS1) is the first enzyme known to participate in BRs metabolism. It inactivates BRs through C-26 hydroxylation, converting castasterone (CS) and BL into hydroxylated derivatives at C-26 (Xiao et al. 2023). This modification likely prevents the BRs side chain from fitting into the binding pocket of the receptor BRI1 (brassinosteroid insensitive 1).

Glycosylation is a key regulatory mechanism for maintaining plant hormone homeostasis, though glycosylation patterns vary among plant species. Research indicates that CS and BL can be glycosylated at C-2, C-3, C-22, and C-23, but the specific enzymes responsible for glycosylation at C-2, C-3, and C-22 of BRs have not yet been identified (Ma et al. 2022).

Bed nucleus of the stria terminalis 3 (BNST3) and BNST4, which are steroid sulfonyltransferases, primarily catalyze the sulfonylation of 24-epicathasterone (24-epiCT). This sulfonylation leads to the loss of biological activity, as these enzymes are specific for 24-epiBR and prefer 24-epiBL as an intermediate, unlike other known enzymes that use CS and BL as substrates (Marsolais et al. 2004). *BNST3* and *BNST4* have been implicated in BRs inactivation; however, genetic evidence supporting the role of sulfotransferases in BRs inactivation is still lacking (Li et al. 2024).

BRASSINOSTEROID INACTIVATOR1/ABNORMAL SHOOT1 (BIA1/ABS1) in *Arabidopsis* is a BAHD acyltransferase that acetylates CS, suggesting its role in BRs homeostasis (Gan et al. 2020). Additionally, BIA2 is a BAHD acyltransferase that inactivates BRs through esterification. ACYLTRANSFERASE1 (BAT1)/DWARF AND ROUND LEAF1 (DRL1) functions as an acyltransferase and may modulate BRs homeostasis by converting BRs intermediates into acylated, inactive forms.

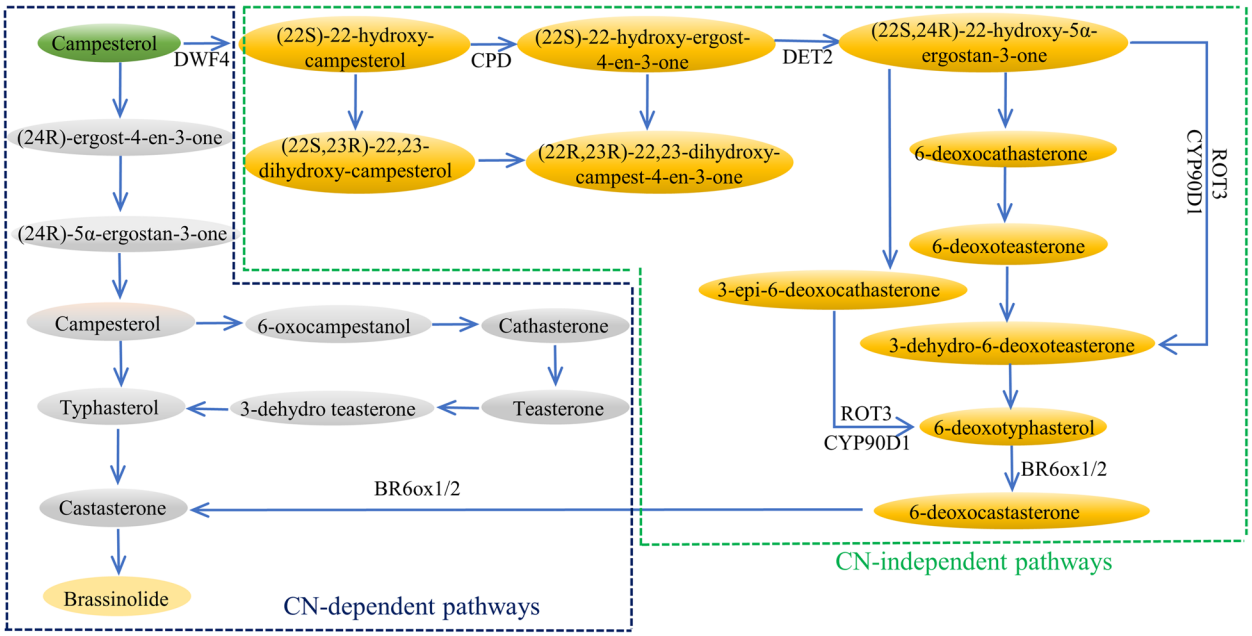


Fig. 1 Biosynthesis of BRs and their sterol biosynthetic precursors in plants. DWF4, DWARF 4; CPD, constitutive photomorphogenesis and dwarf; DET2, DEETIOLATED 2; ROT3, ROTUNDIFOLIA 3; BR6ox1/2, brassinosteroid-6-oxidase 1/2; CYP90D1, cytochrome P450 90D1. In Fig. 1, the yellow font in the green box represents CN-independent pathways, and the gray font in the purple box represents CN-independent pathways

Signal transduction of BR

The well-established model of BRs signaling involves the interaction between BRI1 and BRI1-associated-kinase 1 (BAK1), which initiates a signaling cascade mediated by BR-insensitive-EMS-suppressor 1 (BES1) and brassinazole resistant 1 (BZR1) to regulate BRs-responsive genes (Gao et al. 2015). Brassinosteroid-insensitive 2 (BIN2), a GSK3-like kinase and a key component of BRs signaling, transmits signals from the receptor. In the absence of BR, BIN2 phosphorylates BZR1 and BES1, leading to their loss of DNA-binding activity and subsequent degradation by 14-3-3 proteins in the nucleus (Jiang et al. 2020). BRs binding to BRI1's extracellular domain triggers mutual activation between BRI1 and BAK1. Activated BRI1 then phosphorylates BRI1 substrate kinase 1 (BSK1), which dissociates from the receptor complex and interacts with BRI1-suppressor 1 (BSU1). Additionally, dephosphorylated BIN2 engages with KIB1 (a component of the ubiquitin ligase system), leading to BIN2 ubiquitination and proteasomal degradation. BIN2 can also translocate to the nucleus with BES1 to activate BRs-responsive genes (Gómez-Ocampo et al. 2023). In the presence of BRs, BRI1 binds to BAK1, which stimulates the BRI1 inhibitor 1 (BKI1). This interaction causes BKI1 to dissociate from the BRI1/BKI1 complex, separate from the plasma membrane, and bind to 14-3-3 proteins. Consequently, activated BRI1 transmits BRs signals downstream to BSK and constitutive differential growth 1 (CDG1) (Otani et al. 2022). BSU1, a serine/threonine protein phosphatase, is phosphorylated alongside BSK and CDG1, leading to the dephosphorylation of BIN2. KIB1 inhibits BIN2, preventing its binding to BZR1/BES1 and promoting BIN2 ubiquitination. BZR1/BES1 is then rapidly dephosphorylated by protein phosphatase 2A (PP2A) and translocates to the nucleus, where it collaborates with other TFs to modulate the expression of BRs target genes (Zhu et al. 2023) (Fig. 2).

Interactions of BRs and other hormones in response to stresses

A sophisticated regulatory network emerges from the interplay of various plant hormones, responding to fluctuating environmental factors and collectively governing plant growth and development. The following section provides a detailed analysis of the interactions between BRs and other hormones (Sukpitak et al. 2024).

BRs and abscisic acid (ABA)

ABA plays a pivotal role in plants by regulating growth, development, and stress adaptation in response to environmental changes. While ABA and BRs influence distinct physiological processes, they also exhibit notable interactions and crosstalk. The interaction between BRs and ABA primarily involves the modulation of gene expression and protein activity. For instance, BZR1 binds to the G-box promoter region of the *ABA-Insensitive 5*

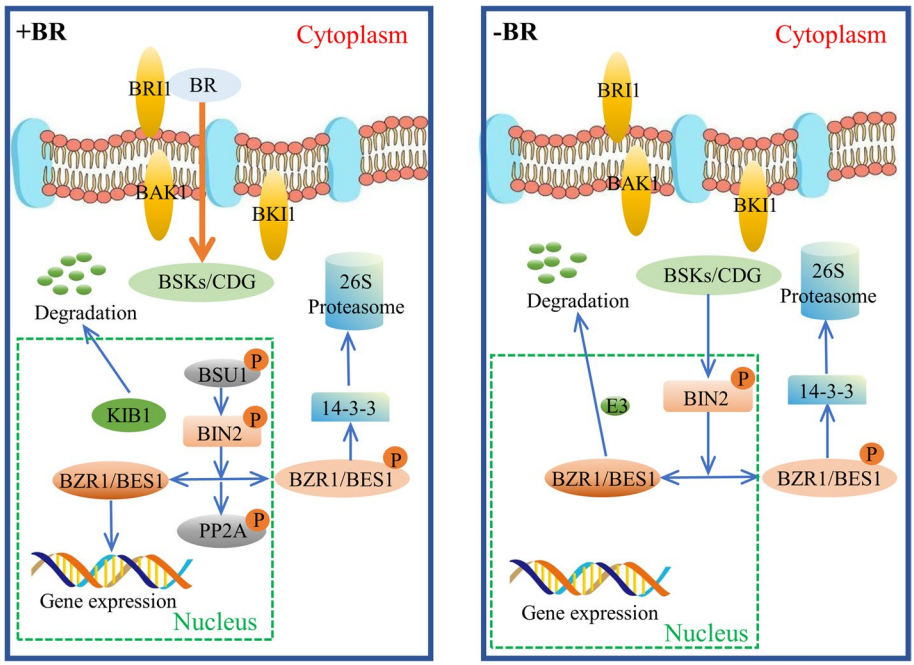


Fig. 2 BRs signal transduction pathway. Upon detecting extracellular BRs signals, BRI1 binds with BAK1 to form a complex. This interaction causes BKI1 to dissociate from the BRI1/BKI1 complex and bind to 14-3-3 proteins. Activated BRI1 transmits BRs signals to BSK1 and CDG1, leading to the phosphorylation of BSK1, CDG1, and BSU1. This phosphorylation prevents BIN2 from binding to BZR1/BES1 and promotes its ubiquitination. Subsequently, BZR1/BES1 is rapidly dephosphorylated by PP2A and collaborates with other TFs in the nucleus to regulate the expression of BR target genes. BRs, Brassinosteroids; BRI1, brassinosteroid insensitive 1; BAK1, BRI1-associated-kinase 1; BKI1, BRI1 inhibitor 1; BSU1, BRI1-suppressor 1; BZR1, brassinazole resistant 1; BES1, BR-insensitive-EMS-suppressor 1; BIN2, brassinosteroid-insensitive 2; BSK, BRI1 substrate kinase 1; PP2A, protein phosphatase 2A; CDG, constitutive differential growth

(*ABI5*) gene, inhibiting the expression of *ABI3* and *ABI5*, which ultimately reduces the stress response (Xu et al. 2023). Conversely, ABA promotes the accumulation of plant U-box 12/13 (PUB12/13), seven in absentia (SINA), and more axillary growth 2 (MAX2) proteins, which target BRI1 or BES1/BZR1 for degradation, thereby downregulating *ABI3* and *ABI5* and inhibiting ABA signaling pathways (Ma et al. 2015). For example, BZR1's interaction with SIRTUIN1 (SRT1) decreases the acetylation and transcriptional activity of histones at the promoters of *MYB transcription factor 13* (*MYB13*) and *basic leucine zipper transcription factor 17* (*bZIP17*), enhancing cold tolerance in *Solanum lycopersicum* (Parrey et al. 2023). Transcriptome analyses indicate that ABA is involved in BRs-induced cold resistance in grapevines (Yang et al. 2016). In rice (*Oryza sativa*), the combined effects of ABA and BRs on growth, physiology, and resistance surpass those of either hormone alone (Kholová et al. 2010; Serratì et al. 2022), highlighting the critical role of their interaction in optimizing plant physiological processes.

Additionally, BRs influence ABA signaling by modulating the phosphorylation of SNF-related protein kinase 2.2 (SnRK2.2), SnRK2.3, and SnRK2.6 (Fan et al. 2024). ABI2 and ABI5, as key regulators of ABA signaling, are integral to the synergistic effects of ABA and BRs (Tang et al. 2022). BIN2 enhances ABA signaling by phosphorylating and stabilizing ABI5. While BES1 interacts with ABI5, this interaction negatively affects ABI5's transcriptional activity, thus impeding ABA signaling. BZR1 also binds to the *ABI5* promoter, reducing its expression and negatively regulating ABA signal transduction. Moreover, BES1 can suppress *ABI3* expression, a positive regulator of *ABI5*, further inhibiting ABA signaling (Ryu et al. 2014).

The interaction between BES1 and ABI5 reduces ABI5's binding to downstream gene promoters, leading to decreased *ABI5* expression and promoting seed germination (Zhao et al. 2019). Overall, these findings emphasize the antagonistic regulation between BRs and ABA signaling pathways, ensuring a balanced response between plant growth and stress adaptation (Fig. 3).

BRs and ethylene

BRs enhance the synthesis and metabolism of endogenous ethylene, which, in turn, mediates the inhibitory effects of BRs. BRs stimulate ethylene biosynthesis by activating genes involved in ethylene production, such as

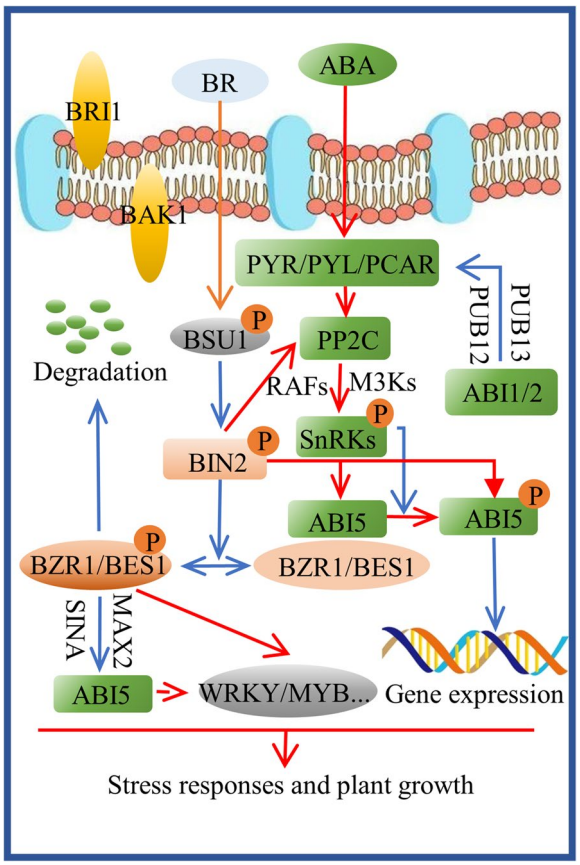


Fig. 3 Crosstalk between BRs and ABA in stress response regulation. ABA receptors (PYR/PYL/RCAR) sense ABA signals, activating SnRKs and promoting their phosphorylation, which enhances the expression of PP2C. Activated SnRKs then phosphorylate ABI5, influencing the transcription of stress response genes. BIN2, a negative regulator of BRs signaling, directly phosphorylates SnRKs and ABI5. ABI5, binding directly to BZR1, inhibits its transcriptional activity, thereby negatively regulating the expression of BRs-responsive genes. BRI1, brassinosteroid insensitive 1; BRs, Brassinosteroids; ABA, abscisic acid; BAK1, BRI1-associated receptor kinase; BSU1, BRI1-suppressor 1; BZR1, brassinazole resistant 1; BES1, BR-insensitive-EMS-suppressor 1; PUB12/13, plant U-box 12/13; SnRK, SNF-related protein kinase; ABI5, ABA-Insensitive 5; MAX2, more axillary growth 2; RAF, rapidly accelerated fibrosarcoma; M3Ks, MAPKK-kinases; SINA, seven in absentia; PP2C, protein phosphatases type 2C; BIN2, brassinosteroid-insensitive 2; PYR/PYL/RCAR, pyrabactin resistance/pyrabactin resistance-like/regulation component of ABA receptors; MYB, myeloblastosis

ACC synthase (*ACS*), and by promoting the degradation of 26S proteasome, thereby facilitating the accumulation of post-transcriptional proteins. For instance, BES1 regulates both *1-aminocyclopropane-1-carboxylate oxidase* (*AtACO2*) expression and endogenous ethylene levels (Hooks et al. 2014). Ethylene and BRs can work synergistically to regulate numerous physiological and biochemical processes in plants. *brassinazole resistant 1* (*SlBZR1*) directly targets genes involved in ethylene and carotenoid biosynthesis, leading to enhanced ethylene production and carotenoid accumulation, which are essential for proper maturation and quality formation. Additionally, ethylene contributes to cucumber seedling tolerance to abiotic stress by participating in BRs-induced alternative oxidases (AOX) activity (Wei et al. 2015). Recent research indicates that BRs-induced growth regulation is mediated by ethylene and hydrogen peroxide, with BRs application enhancing stress tolerance through the ethylene signaling pathway.

BRs and auxin

BRs and auxin also interact to regulate plant growth, development, and stress responses. Genes such as *CPD* and *DWF4*, involved in BRs biosynthesis, are modulated by auxin signaling, illustrating their interconnected roles (Vert et al. 2008). Some studies have demonstrated that Brevis Radix (BRX) positively regulates DWF4 and CPD, highlighting the direct link between auxin signaling and BRs synthesis.

Moreover, BRs and auxin coordinate plant development through interactions between BIN2 and ADP-ribosylation factor 2 (ARF2). BRs may influence the morphological changes in *Nicotiana tabacum* roots under drought stress by regulating auxin signaling upstream (Liu et al. 2023a, b). Additionally, EBR enhances the resistance of Kentucky bluegrass to cadmium and promotes lateral root growth by modulating endogenous auxin and ethylene-related genes (Niu et al. 2023). The interaction between BnaARF8, BnaIAA7s, and BnaBZR1 has been shown to regulate stem elongation in rapeseed (Zheng et al. 2019).

Thus, the interaction between auxin and BRs is essential for orchestrating plant growth and development across physiological, biochemical, and genetic levels, with additional signaling molecules potentially enhancing this regulatory network.

BRs and jasmonic acid (JA)

The interplay between BRs and JA is largely regulated by antimicrobial peptides such as thionine, which mediate their interactions with plant hormones (Lone et al. 2021). Under optimal growth conditions, cytoplasmic JA levels remain low, and the jasmonate-Zim domain (JAZ) proteins inhibit JA signaling by binding to downstream TFs, thus preventing DNA binding.

BRs and JAs exhibit antagonistic interactions by inhibiting each other's biosynthesis and signaling pathways. The expression of BRs is positively correlated with the regulation of JA biosynthesis and signaling genes. In response to cold stress, MdJAZ1 and MdJAZ2 act as repressors of JA signaling, enhancing cold tolerance by

suppressing the transcriptional activation of MdBIM1, which is a activator of C-repeat binding factor 1 (*MdCBF1*). Additionally, these JAZ proteins interact with Interacting MYC-Like Protein1 to prevent the formation of the MdBIM1-MdCBF2 complex, further improving cold stress resilience (An et al. 2023a, b).

Exogenous JA application has been shown to reduce BRs biosynthesis efficacy and alter the expression patterns of *DWF4*, leading to decreased BRs levels (Nguyen et al. 2022). In *Arabidopsis*, BRs mutants exhibit reduced JA-induced anthocyanin accumulation, a trend also seen in wild-type plants treated with brassinoazole, a BRs biosynthesis inhibitor. However, exogenous BRs treatment can mitigate this inhibition. The application of MeJA notably suppresses BR biosynthesis-related genes, decreasing endogenous BRs concentrations while enhancing JA-mediated immunity against root-knot nematodes in rice. Furthermore, the application of either MeJA or 24-epibrassinolide (24-EBL) significantly upregulates the expression of photoperiod-temperature sensitive genic male sterile (*PTSGMS*) genes, which are essential for JA and BRs biosynthesis or signaling, in rice subjected to heat stress (Yang et al. 2021).

BRs and gibberellin (GA)

BRs and GA collaboratively regulate various physiological processes in plants through protein-DNA interactions mediated by BZR1/BES1, with GA deficiency leading to a marked inhibition of BZR1 activity (Retzer et al. 2019). In *Arabidopsis*, the absence of BRs signaling notably impairs GA bioactivity, which is directly linked to changes in GA biosynthesis gene expression. BZR2, a key player in the BRs response pathway, effectively represses the *Ppy*-dormancy-associated MADS-box gene 3 (*PpyDAM3*). Transient overexpression of *PpyBZR2* results in elevated endogenous levels of GA and JA. Specifically, the direct interaction between PpyBZR2 and myelocytomatosis protein2 (PpyMYC2) enhances the transcriptional activation of *GA20 oxidase* genes (*PpyGA20OX1L1* and *PpyGA20OX2L2*), thereby increasing GA_3 content (Wang et al. 2023).

In soybeans, the shade-induced hypocotyl elongation mechanism reveals a synergistic stimulatory effect between auxin and BRs, while gibberellin biosynthesis is significantly repressed by inhibitors targeting Auxin (IAA), GA, and BRs biosynthesis pathways under shading conditions (Jiang et al. 2020). BRs downregulates the transcription of *GA20ox1* and reduces endogenous GA_{20} levels in pea seedlings. High concentrations of exogenous BRs inhibit GA biosynthesis and upregulate the expression of the inactivated gene *GA20ox-3*. This inhibition of GA biosynthesis and concurrent suppression of BR synthesis ultimately leads to growth retardation through a feedback mechanism that reduces endogenous hormone levels (Fig. 4).

Role of BRs in abiotic stress

As plants continue to evolve, their adaptability to environmental changes has markedly improved. BRs, as a novel class of hormones, has been demonstrated to be crucial in numerous physiological and biochemical processes. The subsequent analysis will systematically explore how BRs regulate responses to adverse conditions.

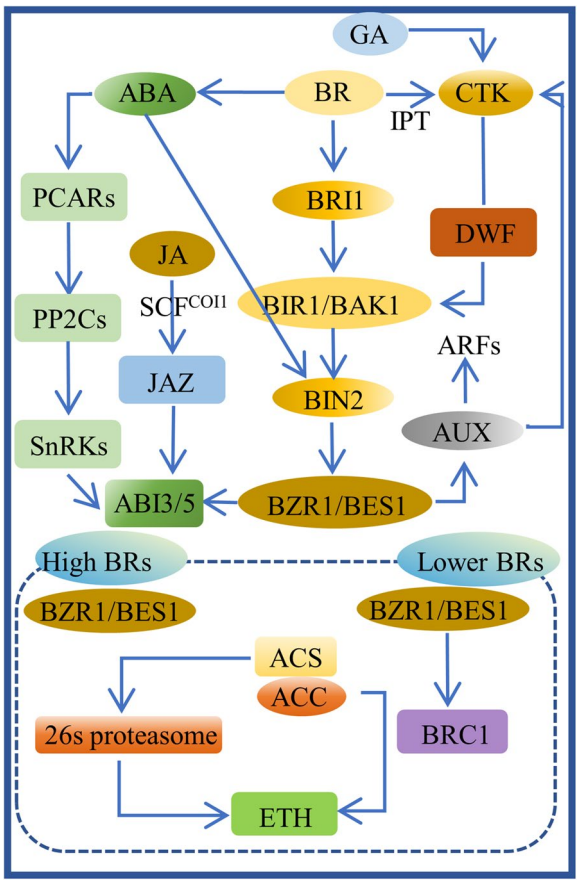


Fig. 4 Interactions between BRs, cytokinin (CTK), auxin (AUX), JA, GA, and ethylene (ETH) biosynthesis pathways. ABA, abscisic acid; JA, jasmonic acid; GA, gibberellins; BRI1, brassinosteroid insensitive 1; BRs, Brassinosteroids; BAK1, BRI1-associated receptor kinase; BSU1, BRI1-suppressor 1; BZR1, brassinazole resistant 1; BES1, BR-insensitive-EMS-suppressor 1; PP2C, protein phosphatases type 2C; BIN2, brassinosteroid-insensitive 2; RCAR, regulation component of ABA receptors; SnRK, SNF-related protein kinase; ABI3/5, ABA-Insensitive 3/5; ACC, 1-aminocyclopropane-1-carboxylate; ACS, ACC synthase; BRC1, BRANCHED1; ARF, auxin response factor; JAZ, jasmonate-Zim domain; IPT, Isopentenyl transferase; SCF^{COI1}, Skp1/Cullin1/F-box protein COI1

Interactions between BRs and other hormones in response to drought and salt stresses

Drought and salt stress induce the generation of reactive oxygen species (ROS) in plants, compromising cell stability and causing damage. In particular, salt stress affects plant ecosystems and growth through ionic toxicity and reduced mineral nutrient absorption and transport, a significant issue in arid and semi-arid regions such as the Loess Plateau in China (Shaban et al. 2023).

Research indicates that exogenous BRs enhance the activity of antioxidant enzymes and elevate non-enzymatic antioxidant levels, thereby mitigating ROS and protecting membrane lipids to maintain membrane integrity (Piskurewicz et al. 2023).

Additionally, BRs help plants withstand adverse conditions by modulating the expression of structural proteins and stress-related genes. For example, BRs induce the transcription of drought response genes like *CBF5* and *dehydration-responsive element binding factors* (*DREBs*), thereby enhancing drought tolerance in rape seedlings. BRs Insensitive Long Hypocotyl 9 (BIL9) not only facilitates plant growth through BRs signaling but also boosts drought resistance by interacting with Homeodomain Glabrous 11 (HDG11). In *Arabidopsis*, the BRs signaling pathway affects taproot development and drought response by repressing the expression of *PLETHORA 1* (*PLT1*) and *PLT2* (Surina et al. 2024). Furthermore, BRs influence plant stress responses through autophagy mediated by BIN2. Specifically, phosphorylated BIN2 activates the expression of the ubiquitin receptor protein dual-specificity protein kinase 2 (DSK2), which interacts with BES1 to facilitate autophagic degradation, thus aiding plant growth and survival under drought stress (Nolan et al. 2017). Exogenous EBR pretreatment has been shown to increase the levels of ABA, GA, auxin, and GA in grapevine (*Vitis vinifera* L.) to combat drought (Zeng et al. 2022). Drought stress relieves ABI1's inhibition of BIN2, activating BIN2 and promoting its phosphorylation to stabilize RESPONSIVE TO DESICCATION 26 (RD26) and enhance drought stress response (Jiang et al. 2019). EBR significantly induces the transcription of key ABA biosynthesis genes, such as *9-cis-epoxycarotenoid dioxygenase 1* (*VviNCED1*), *VviNCED2*, and *zeaxanthin epoxidase* (*VviZEP*), as well as key ABA signaling genes, including *VviSnRK2.6*, *VviPP2C4*, ABF TFs (*VviABF1* and *VviABF2*), under drought conditions. Notably, BZR1 binds strongly to multiple G-box *cis*-acting elements in the *ABI5* promoter, inhibiting *ABI5* expression and thus reducing ABA-dependent drought sensitivity in plants (Yang et al. 2016).

The role of BRs in mitigating salt stress has been established in various horticultural crops, including *Arabidopsis* (Jia et al. 2021a, b) and rice (Onishi et al. 2004). Research consistently shows that exogenous BRs treatment can significantly enhance physiological and biochemical processes in plants under salt stress. This includes improvements in antioxidant enzyme activity, net photosynthetic rate, stomatal conductance, transpiration rate, and chlorophyll content, alongside reductions in Na^+ and Cl^- concentrations in *Arabidopsis*. Additionally, Ubiquitin Coupling Enzyme 32 (UBC32), a key player in endoplasmic reticulum-associated protein degradation, stimulates the BRI1 receptor, thereby regulating the Endoplasmic reticulum (ER)-associated protein degradation signaling cascade to bolster salt stress tolerance (Cui et al. 2012). In tomato, SlBZR1 interacts with multiple proteins, including SlMYB30, SlMYBL2, Phytochrome-interacting factor 4 (SlPIF4), Histone Acetyltransferase 1 (SlHAT1), Waardenburg Syndrome Type 1 (SlWS1), and RELATIVE OF EARLY FLOWERING 6 (SlREF6). Overexpression of *SlBZR1D* enhances salt stress tolerance in *Solanum lycopersicum* L. (Jia et al. 2021a, b). Furthermore, the BRs-biosynthetic gene *BRs-6-oxidase 1* (MdBR6OX1) increases the levels of endogenous compounds such as tyhastero (TY), CS, and BL, thereby improving salt tolerance in apple (Zhang et al. 2024).

ABA modulates salt stress responses by regulating the activity of cell wall receptor kinase FER through the dephosphorylation of ABI2. Concurrently, BRs influences the stability of ACS during ethylene (ETH) synthesis, thereby activating ETH production to help plants withstand adverse conditions.

The role of BRs in DNA methylation regulation related to salt tolerance remains an important area of research, though further studies are needed to fully elucidate this mechanism (Fig. 5).

Interactions between BRs and other hormones in response to cold and heat stresses

Temperature stress induces significant changes in plant morphology, physiology, and biochemical metabolism, leading to modifications in cellular architecture, such as altered cell membrane fluidity and reduced intracellular osmotic potential. As global temperatures rise, agriculture faces increasingly severe challenges. The damage from heat and cold stress manifests as protein denaturation, diminished nucleic acid activity, and toxic substance accumulation (Sheikhi et al. 2023; Sukpitak et al. 2024).

BRs-mediated ROS signaling plays a key role in regulating reduction/oxidation (REDOX) homeostasis under stress conditions. This signaling pathway activates transcriptional regulators that control BRs regulation and stress response genes, ultimately enhancing plant resilience through the production of protective proteins. In response to low temperatures, plants increase the

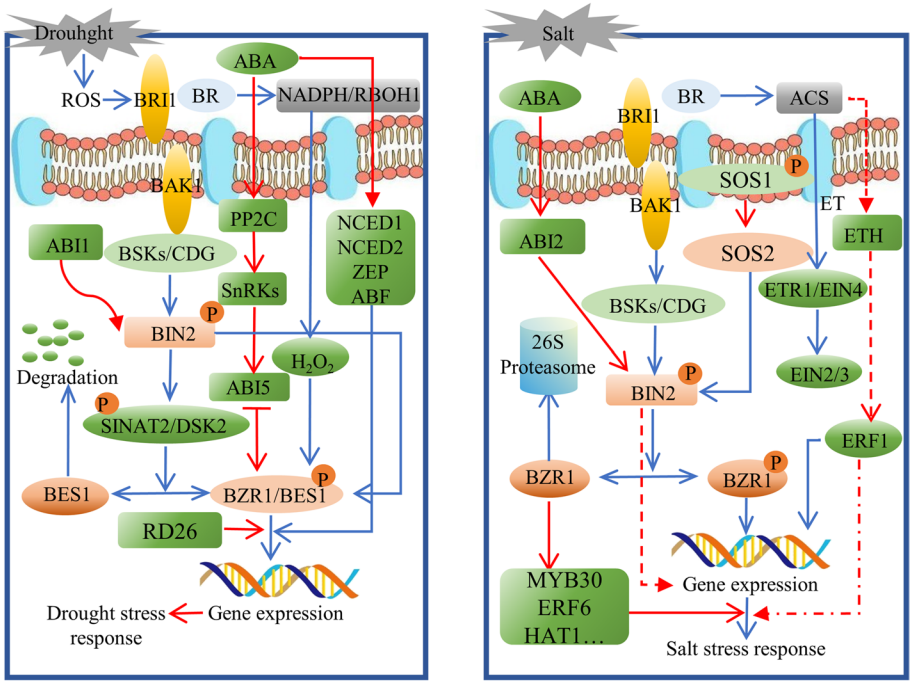


Fig. 5 Regulation of drought and salt stress responses by BRs signaling. Under drought stress, BIN2 promotes its role in drought stress response by phosphorylating RD26. The direct interaction of BIN2 with RD26 and its phosphorylation are required for RD26 to activate drought response genes. In addition, protein phosphatases type 2C (PP2C) ABI1, as a key node connecting upstream stress signal and BIN2 function, inhibits BIN2 kinase activity and plays a role in BR signaling pathway by interacting with and dephosphorylating BIN2 kinase. BR mechanism of response to salt stress through SOS mainly involves the perception and transmission of calcium signal and the activation and phosphorylation of protein kinase. Under salt stress, intracellular calcium signals are sensed by SOS3 and SCaBP8, and interact with protein kinase SOS2 to activate their kinase activity. The activated SOS2 further activates the Na^+/H^+ reverse transporter SOS1, which reduces intracellular Na + toxicity and helps plants resist salt stress by transporting Na^+ to the outside of the cell. Salt stress promotes ABA accumulation, and then activates sucrose non-fermentation-1 associated protein kinase 2 (SnRK2) and clade A-type 2C protein phosphatase (PP2C), which play A key role in mediating the crosstalk between ABA and salt stress signal transduction. BRs, Brassinosteroids; ROS, reactive oxygen species; ABA, abscisic acid; BZR1, brassinazole resistant 1; BRI1, brassinosteroid insensitive 1; BAK1, BRI1-associated-kinase 1; BIN2, brassinosteroid-insensitive 2; BES1, BR-insensitive-EMS-suppressor 1; BSK1, BRI1 substrate kinase 1; CDG1, constitutive differential growth 1; ABI2, ABA Insensitive 2; NADPH, nicotinamide adenine dinucleotide phosphate reduced $NADP^+$; RBOH1, respiratory burst oxidase homolog 1; RD26, RESPONSIVE TO DESICCATION 26; SnRK, SNF-related protein kinase; PP2C, protein phosphatases type 2C; NCED, 9-cis-epoxycarotenoid dioxygenase; ZEP, zeaxanthin epoxidase, SOS1/2, Son of Sevenless 1/2; ERF1/6, ethylene response factor 1/6; ACS, ACC synthase; ETR1, ethylene receptor gene 1; EIN2/3/4, Ethylene insensitive 2/3/4; HAT1, histone acetyltransferases 1; SINAT2, SEVEN IN ABSENTIA 2; DSK2, dual-specificity protein kinase 2; ET, ethylene; ETH, ethylene; MYB30, MYB transcription factor 30. PP2C, protein phosphatases type 2C

transcription levels of *Respiratory burst oxidase homolog 1* (*RBOH1*) and hydrogen peroxide by accumulating BRs and activating *BZR1* expression (Fang et al. 2021). This mechanism has been demonstrated in several horticultural crops, including *Triticum aestivum* L. (Ding et al. 2023), *Solanum lycopersicum* L. (Kim et al. 2020), and *Averrhoa carambola* L. (Duan et al. 2022). Specifically, BRs, whether applied exogenously or produced endogenously, can induce the expression of *RBOH1*, which encodes NADPH oxidase, thereby reducing ROS accumulation in Eucalyptus under adverse conditions (Zhou et al. 2024). Overexpression of BRs biosynthetic genes such as *DWF* or signaling genes like *BZR1* significantly upregulates ABA biosynthetic genes like *NCED1*, increasing ABA levels in tomatoes as a response to low-temperature stress (An et al. 2022). TaBZR1 interacts with the histone acetyltransferase HIGH ALIPHATIC GLUCOSINOLATE 1 (TaHAG1), enhancing histone acetylation and thereby boosting the expression of SAM Transporter 1 (*TaSAMT1*) and modulating the salicylic acid (SA) pathway. This interaction is essential for improving the cold tolerance of wheat (Chu et al. 2024).

BRs are involved in both dependent and independent pathways of *CBF1* activation by inducing the cold-responsive (COR) genes (Kalbfuß et al. 2023; Ding et al. 2023). This involves the accumulation of non-phosphorylated BZR1 and BES1 forms, which promote the transcription of *CBF1* and *CBF2*, central to BR's response to cold stress (Li et al. 2017). The BRs signal regulator MdBIM1 enhances the expression of *MdCBF1* and coordinates with MdCBF2,

thereby boosting the transcription of cold response genes activated by *MdCBF2* and strengthening the plants' cold stress resilience (An et al. 2023a, b). The interaction between BZR1 and reactive oxygen species catalyzes the activation of cold response mechanisms and BRs-mediated *CBF* expression, ultimately increasing the cold tolerance of *Solanum lycopersicum* L. (Fang et al. 2021).

Research on BRs and its interaction with various hormones in stress responses remains a focal point. BZR1, a key regulator in BRs signaling, modulates the transcription of *NCED1*, a gene essential for ABA synthesis, thereby enhancing ABA accumulation and improving tomato plants' resistance to low temperatures (Yueshan et al. 2024). Under cold stress, brassinolide interacts with JA and SA signaling pathways, up-regulating JA and SA-related genes or down-regulating ETH signaling components and ETH response factors to mitigate cold stress. Additionally, exogenous BL significantly boosts heat resistance in ETH, ABA, and JA deficient or insensitive mutants under high-temperature stress (Shakirova et al. 2016). (Fig. 6).

Involvement of BRs in plant response to nitrogen deficiency stress

The equilibrium between nutrient supply and absorption is essential for plant growth, yet fluctuations in external nutrient levels pose significant challenges during plant development. Nitrogen (N), a key nutrient for early plant growth, plays a vital role in promoting nutritional development (Guo et al. 2023). Nitrate and ammonium are the primary forms of nitrogen uptake and utilization in plants. Throughout their growth, plant roots continuously secrete metabolites into the rhizosphere, influencing the oxidation–reduction (REDOX) state and microbial community density, which ultimately affects the nitrate-to-ammonium ratio through self-nitrification (Devi et al. 2022).

Recent research on *Arabidopsis* and rice has elucidated how BRs influence nutrient absorption and plant phenotypes under varying nutrient levels. This research highlights that the synergistic interaction between auxin and BRs signaling significantly enhances root foraging responses and adaptive capacity to nitrogen, thereby facilitating root growth in diverse nitrogen environments (Lorinda et al. 2022). In *Arabidopsis*, natural variation in BSK3 affects nutrient uptake by modulating BSK3 activity under mild nitrogen deficiency (Liu et al. 2023a, b). Genetic analyses reveal that mutations in BAK1 and BSK3 disrupt cell and root development under nitrogen-limited conditions, suggesting that a moderate nitrogen deficit may enhance the transcriptional activity of the BRs receptor BAK1 (Jeon et al. 2024).

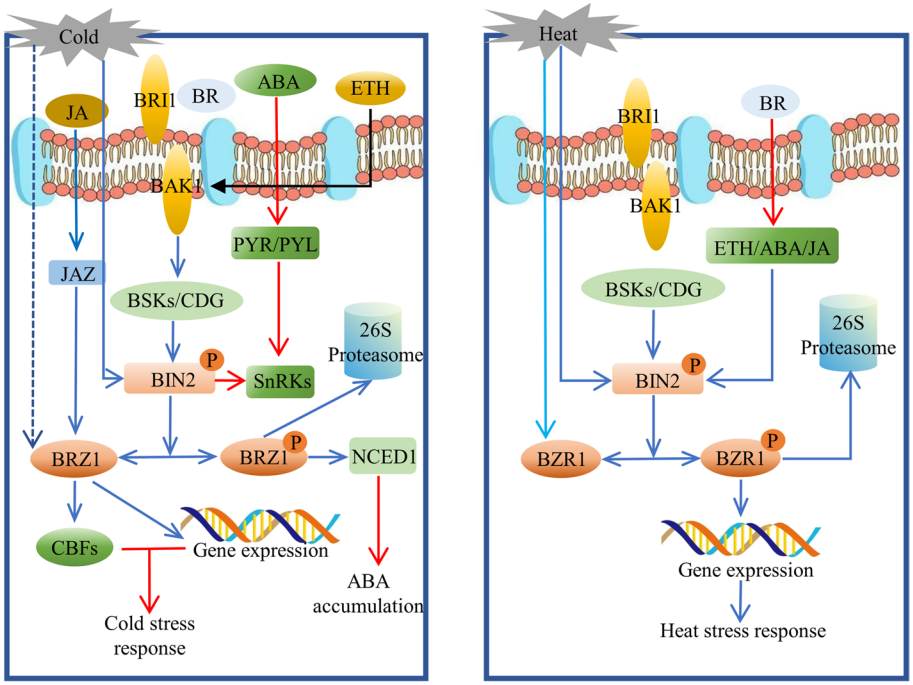


Fig. 6 Regulation of cold and heat stress responses by BRs signaling. BRs, Brassinosteroids; JA, jasmonic acid; BRI1, brassinosteroid insensitive 1; ABA, abscisic acid; ETH, ethylene; BAK1, BRI1-associated-kinase 1; PYR/PYL, pyrabactin resistance/pyrabactin resistance-like; BSK1, BRI1 substrate kinase 1; CDG, constitutive differential growth; JAZ, jasmonate-ZIM domain; BIN2, Brassinosteroid-insensitive 2; SnRK, SNF-related protein kinase; BRZ1, BR-activatedtranscription factor 1; NCED1, 9-cis-epoxycarotenoid dioxygenase 1; CBF, C-repeat binding factor; BZR1, brassinazole resistant 1

Furthermore, even low concentrations of nitrate can markedly induce *BES1* expression in roots, leading to increased accumulation following dephosphorylation. Activated BES1 then inhibits its DNA-binding ability by up-regulating the transcription of lateral organ boundaries domain 37 (LBD37), a negative regulator of nitrogen utilization, thereby controlling nitrogen absorption and utilization (Wang et al. 2023). In tomato, low nitrogen levels also induce the accumulation of dephosphorylated BZR1, which activates the expression of *anti-thymocyte globulin* (*ATG*) and increases the transcription of *DWF1*, a gene associated with BRs biosynthesis. This response enhances nitrogen absorption and represents a common survival strategy for plants under nitrogen deficiency (Jia et al. 2021a, b).

Nitrate transporters (NRTs) and ammonium nitrogen transporters (AMTs) are pivotal for nitrogen uptake and transformation in plants. Studies in model plants like *Arabidopsis* and rice have highlighted their importance.

Recent research has revealed that homolog of brassinosteroid enhanced expression2 interacting with IBH1 (HBI1), activated by the B cell receptor-associated protein (BAP) module at the post-transcriptional level, positively regulates nitrate signaling by modulating ROS homeostasis. HBI1 expression is rapidly induced by the nitrate receptor protein NIN LIKE PROTEIN 7 (NLP7), which accelerates the expression of *catalase 2* (*CAT2*) to clear ROS from plants (Chu et al. 2021). In rice, BRs treatment induces the expression of *OsAMT1* at the transcriptional level. The binding of ABI3/VP1-LIKE 1 (RAVL1) to OsAMT1 is critical in regulating BRs homeostasis and enhancing ammonium uptake by roots (Hussain et al. 2023). Additionally, ethylene and JA signaling pathways collaboratively regulate nitrate redistribution from roots under stress by up-regulating *NRT1*.8 and down-regulating *NRT1*.5.

MicroRNA444 (*miR444*) has been shown to significantly up-regulate the BRs-biosynthesis gene *Bromodomain containing 1* (*OsBRD1*) under ammonium treatment, enhancing BRs biosynthesis (Rubio et al. 2009). Interestingly, some OsMADS-box proteins encoded by miR444 directly bind to the *OsBRD1* promoter and inhibit its transcription in rice (Wang et al. 2024). This suggests that ammonium promotes BRs biosynthesis by inhibiting miR444-BOX proteins, providing a mechanism for ammonium-induced root absorption in rice (Fig. 7).

Response strategies of BRs to phosphorus and *iron* deficiency stress

Phosphorus absorption and utilization are critical factors limiting plant growth and development due to its low solubility, high fixability in soil, and the limited amount available for direct uptake by plant roots (Bashir et al. 2024). Plants primarily respond to phosphorus deficiency through Pi transporters and Pi starvation (PSI) gene induction, such as *Phosphate Starvation Response 1* (*AtPHR1*) and its homologs (*AtPHL1*, *AtPHL2*, and *AtPHL3*), as well as rice *OsPHR1* and its counterparts (*OsPHR2*, *OsPHR3*, and *OsPHR4*) (Sega et al. 2019). These PHRs play vital roles in regulating PSI gene transcription by binding to the *cis*-element GNATATNC (P1BS). Notably, while overexpression of *OsPHR2* leads to excessive Pi accumulation in seedlings, *OsPHR3* overexpression results in a moderate increase in Pi concentration and enhanced tolerance to Pi deficiency under field conditions (Guo et al. 2015). The BRs-regulated core TF BZR1 acts as a "brake", inhibiting the expression of the malic acid transporter *Al-activated malate transporter* (*ALMT1*) gene. This regulation modulates root malic acid secretion under varying phosphorus levels, thereby helping plants balance intracellular carbon source secretion with phosphorus deficiency stress adaptation.

Additionally, CTK is implicated in the regulation of phosphorus hunger response. Phosphorus deficiency reduces the expression of the cytokinin response *1* (*CRE1*) receptor and diminishes BRs and cytokinin concentrations, as demonstrated in rice studies. Furthermore, BRs-mediated ABA may modulate phosphorus-starvation responses by controlling ABI1-type 2C protein phosphatase, which inhibits the expression of certain phosphorus-starvation-induced genes (Müller et al. 2019).

The regulatory mechanisms governing iron and phosphorus nutrients in plants are intricately linked and mutually influential. In *Arabidopsis*, iron toxicity resulting from Pi deficiency can impede root growth. Research indicates that under Pi deficiency, iron accumulates in the root elongation zone, leading to increased expression of BKI1 and decreased expression of *BRI1* (Sukpitak et al. 2024). BRs have been shown to negatively regulate the expression of iron reduction oxidases (*FRO*), *CsFRO1*, and *iron transporter 1* (*IRT1*), as well as the transport of iron from root to stem in *Cucumis sativus* under iron deficiency conditions (Wang et al. 2012).

Iron deficiency suppresses the expression of BRs biosynthesis genes and BRs signaling genes in rice. Conversely, BRs treatment enhances the expression of iron homeostasis-related genes, including *OsIRT1*, *Yellow stripe-like 15* (*OsYSL15*), *OsYSL2*, and *Nicotinamide synthetase1/2* (*OsNAS1/2*) (Sakamoto et al. 2012). This observation has been corroborated in horticultural crops such as rice, *Arabidopsis*, and *Cucumis sativus*. Additionally, exogenous BL can work synergistically with other endogenous hormones, such as indole-3-acetic acid, isopentenyl adenine, and GA_4, to indirectly mitigate

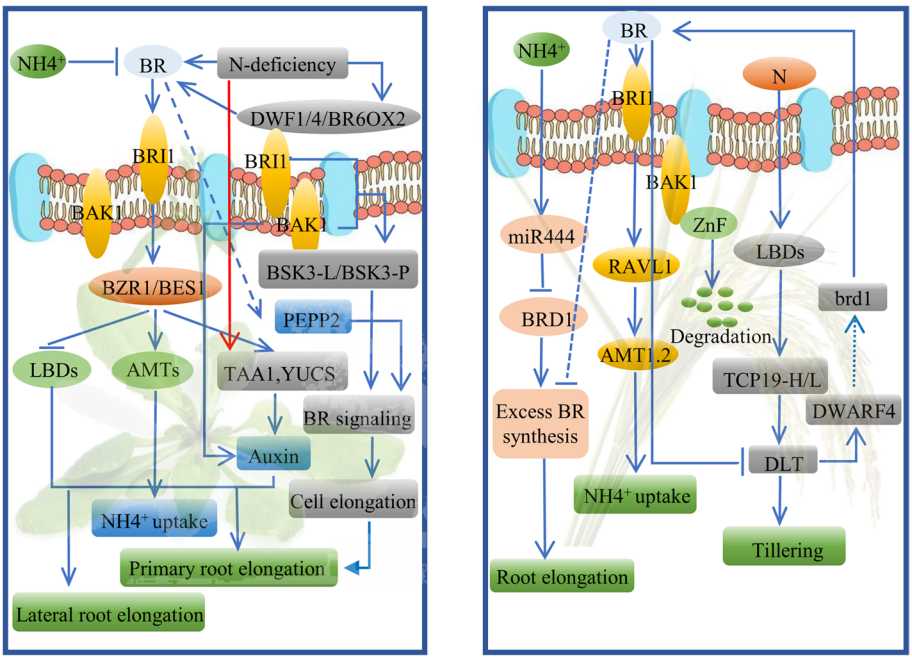


Fig. 7 Regulation of nitrogen response by BRs signaling. In *Arabidopsis*, HBI1 activates BRs signaling to induce reactive oxygen scavenging enzyme CAT2, which prompts NLP7 to translocate to the nucleus and enhance nitrate response and nitrogen foraging. In rice, ammonium treatment induces miR444 accumulation, promotes BRs biosynthesis by reducing the expression levels of *MADS23*, *MADS25*, *MADS27*, *MADS57*, and *MADS61*, and directly binds to the promoter of *BRD1* to reduce its expression. Additionally, BRs stimulates ammonium uptake by upregulating *AMT1.2* through RAVL1.1 and AMT1. BRs, Brassinosteroids; DWF1/4, DWARF 1/4; BR60X2, brassinosteroid-6-oxidase1/2; BRI1, brassinosteroid insensitive 1; BAK1, BRI1-associated-kinase 1; BZR1, brassinazole resistant 1; BES1, BR-insensitive-EMS-suppressor 1; BSK3, BRI1 substrate kinase; PEPP2, reproductive homeobox genes on the X chromosome gene F2; LBDs, lateral organ boundaries domain proteins; AMTs, ammonium nitrogen transporters; TAA1, tryptophan aminotransferase of Arabidopsis 1; YUCS, riboflavin monooxygenase; ZnF, zinc finger; RAVL1, ABI3/VP1-like 1; miR444, MicroRNA444; BRD1, bromodomain containing 1; TCP19, teosinte branched1/cycloidea/proliferating cell factor 19; DLT, DWARF AND LOW-TILLERING; DWARF4, a cytochrome P450 (Cyp450) monooxygenase containing heme and iron

iron deficiency stress in apples (Sun et al. 2022). ETH enhances iron accumulation and uptake by upregulating genes like *ERF95*, *IRT1*, and *FRO2* through ETHYLENE-INSENSITIVE3 (EIN3) mediation. In contrast, BRs negatively regulates FRO activity by interacting with ethylene, thereby influencing the plant's response to iron deficiency (Kurowska and Daszkowska-Golec. 2023). Further investigation is required to elucidate the co-regulation of nutritional stress responses by BRs and other hormones in plants (Fig. 8).

Conclusions and perspectives

To enhance crop production and adapt to environmental changes, researchers are exploring various plant hormones. BRs, discovered for their non-toxicity, rapid absorption, strong penetration, and minimal side effects, have garnered significant interest. They are studied extensively for their roles in seed germination, balanced vegetative and reproductive growth, and responses to external stressors. Despite their potential, many functions and mechanisms of BRs remain incompletely understood.

Recent advances utilizing transcriptome, proteome, and yeast two-hybrid techniques have gradually unveiled the molecular mechanisms, metabolic pathways, and signal transduction processes of BRs synthesis. These insights provide a foundation for leveraging BRs to regulate plant growth and environmental responses. The BRs signal transduction pathway involves several components, including kinases, receptor proteins, and TFs. Specifically, BRs molecules are recognized by the BRI1 and BAK1 complexes on the cell membrane, which activate BZR1 and BES1 through signaling components such as BSK1, BSU1, BIN2, and CDG1. This activation subsequently regulates the expression of BRs-responsive genes. The interaction and regulation of plant growth involve various hormones, with BRs playing key roles. In BRs signaling, BIN2, BZR1, and BAK1 are crucial, while ABI1, ABI5, and SnRK2 in the ABA pathway represent critical nodes mediating the BRs-ABA interaction. Molecular regulation occurs at multiple levels, including transcription, translation, post-translational modification, and protein activity. However, it remains unclear whether other signaling elements and regulatory mechanisms,

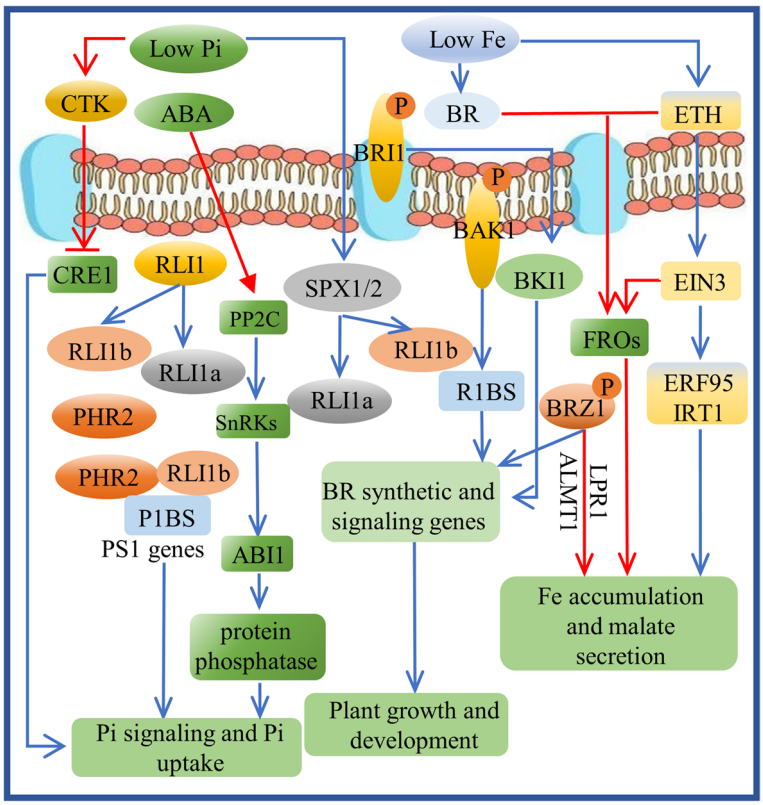


Fig. 8 BRs is involved in plant response to phosphorus and iron deficiency. CTK, cytokinin; ABA, abscisic acid; CRE1, cytokinin response 1; RLI1, REGULATOR OF LEAF INCLINATION 1; PP2C, protein phosphatases type 2C; SPX1/2, SYG1/Pho81/XPR 1/2; SnRK, SNF-related protein kinase; PHR2, Phosphate Starvation Response 2; P1BS, PHR1-binding sequence; PS1, presenilin 1; ABI1, ABA-Insensitive 1; BRs, Brassinosteroids; BRI1, brassinosteroid insensitive 1; ETH, ethylene; BKI1, BRI1 inhibitor 1; EIN3, Ethylene insensitive 3; FROs, iron reduction oxidases; BAK1, BRI1-associated-kinase 1; BRZ1, BR-activatedtranscription factor 1; R1BS, PHR1 Binding Sequence; LPR1, low phosphate root 1; ALMT1, Al-activated malate transporter; ERF95, ethylene response factors 95; IRT1, iron transporter 1

such as ubiquitination modification, are involved in the BRs-ABA interaction. Similarly, BRs may interact with other hormones like ABA, ETH, and JA to manage stress responses to drought, salt, cold, and heat. Elucidating these interactions is essential for constructing a comprehensive BRs regulatory network.

Drought, salt, cold, and nutrient deficiencies represent significant challenges during plant growth and development. BRs play pivotal roles in mediating plant responses to both biotic and abiotic stresses, with BZR1 and BES1 forming the central pathway for BRs activation. Additionally, BRs are vital in regulating plant responses to nitrogen, iron, and phosphorus deficiencies, enhancing nutrient utilization efficiency, and maintaining the dynamic balance of BRs signaling. This positions BRs as a key element for improving crop performance and understanding their role in crop enhancement. However, further research is needed to explore the spatiotemporal and environmental-specific regulation of BRs signaling pathways and biosynthesis, particularly in relation to nutrient balance, transport, and homeostasis in plants.

Currently, most studies on BRs responses to abiotic stress are conducted in controlled greenhouse environments. It is essential to evaluate the effects of BRs on crop yield and quality under field conditions to provide practical insights for agricultural production. Additionally, since crops often face combined stress conditions, investigating the impact of exogenous BRs under simulated multiple stress scenarios is necessary. Such studies will offer valuable theoretical support for its promotion and application in agricultural practices.

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Authors' contributions
YLG and YXW designed the research. XLM and YLG performed the experiments. YLG and ZXZ performed the data analysis and interpretation. YLG and XYW prepared the figures and tables. YLG wrote the manuscript. All authors read, commented on and approved the manuscript.

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Availability of data and materials
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Declarations

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Consent for publication
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