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Crosstalk between brassinosteroid signaling and variable nutrient environments

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Brassinosteroid (BR) represents a group of steroid hormones that regulate plant growth and development as well as environmental adaptation. The fluctuation of external nutrient elements is a situation that plants frequently face in the natural environment, in which nitrogen (N) and phosphorus (P) are two of the most critical nutrients restraint of the early growth of plants. As the macronutrients, N and P are highly required by plants, but their availability or solubility in the soil is relatively low. Since iron (Fe) and P always modulate each other's content and function in plants mutually antagonistically, the regulatory mechanisms of Fe and P are inextricably linked. Recently, BR has emerged as a critical regulator in nutrient acquisition and phenotypic plasticity in response to the variable nutrient levels in *Arabidopsis* and rice. Here, we review the current understanding of the crosstalk between BR and the three major nutrients (N, P, and Fe), highlighting how nutrient signaling regulates BR synthesis and signaling to accommodate plant growth and development in *Arabidopsis* and rice.

brassinosteroid, nitrogen, phosphorus, iron, signaling, foraging

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Introduction

Brassinosteroid (BR) represents a class of steroid hormones widely existing in plants, with structural similarity to the steroid hormones in animals and insects. It has attracted more and more attention since its discovery as the sixth phytohormone. Brassinolide (BL), the most bioactive BR in plants and the final product of BR synthesis pathway, was first isolated and purified from the pollen of *Brassica napus* about fifty years ago (Grove et al., 1979; Mitchell et al., 1970). Over the past four decades, a large number of studies have emerged to interpret BR biosynthesis and signaling, especially in the model plants *Arabidopsis* (*Arabidopsis thaliana*) and rice (*Oryza sativa*). To date, BR has been reported to be involved in a variety of biological processes, including cell elongation and division, flowering and senescence, and responses to biotic and abiotic stresses, etc. (Anwar et al., 2018; Vriet et al., 2013).

In addition to phytohormones, soil nutrient status is another critical factor affecting plant growth and development. Nitrogen (N) and phosphorus (P) are two essential macro-

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nutrients required by plants, but inorganic nitrogen (nitrate (NO_3^-) and ammonium (NH_4^+)) and inorganic phosphate (Pi) that can be directly absorbed by plants in the field are very limited (Maathuis, 2009). As another essential mineral nutrient required for plant growth, iron (Fe) usually abundantly exists in the soil in the form of ferric hydroxide. However, due to its low solubility, especially in calcareous soil, plants frequently suffer from low Fe stress (Romera and Alcántara, 2004). The application of chemical fertilizers has dramatically improved the grain yield in cereal crops. Among them, N and P are the two fertilizers with the largest consumption in modern agriculture. Their application was estimated to exceed 1.14 million tons and 0.68 million tons, respectively, in 2018 (Data from International Fertilizer Association: https://www.ifastat.org/databases/plant-nutrition). However, excessive application of fertilizers will not only increase the production cost, but also lead to serious environmental problems, such as water eutrophication, soil degradation, air pollution, etc. Improving the efficiency of plant nutrient usage is the ideal way to cope with these challenges (Hu et al., 2022; Liu et al., 2022c). Therefore, it is essential and urgent to conduct in-depth research on the molecular mechanisms of nutrient utilization.

Plant hormones have a wide range of effects on plant nutrient acquisition and utilization. Conversely, nutrition signaling can also influence the biosynthesis and function implementation of plant hormones (Chen et al., 2022). In recent years, a growing number of studies have shown that BR acts as one of the primary regulators of plant growth and phenotypic changes under nutrient-deficient conditions, including promoting root foraging responses, causing changes in stature, and enhancing the capacity of plants to obtain nutrients. In the case of mild N deficiency, BR biosynthesis and signaling are induced, leading to enhanced cell elongation and finally activating the low N-induced N foraging response in *Arabidopsis* (Jia et al., 2019; Jia et al., 2020). In addition, BR also acts upstream of auxin to stimulate lateral root elongation (Devi et al., 2022; Jia et al., 2021). The phenotypic alterations in rice plants caused by nutrient deficiency are tightly associated with the defects of BR synthesis and signaling (Guo et al., 2022b; Ruan et al., 2018). In general, nutrient starvation signals could manipulate BR signaling or/and BR biosynthesis to activate nutrient acquisition. It should be noted that different nutrients could confer distinctive effects on BR biosynthesis. For instance, low Pi represses while low N induces BR biosynthesis in *Arabidopsis* (Jia et al., 2020; Singh et al., 2014), implying the complexity of nutrient regulation. Here, we overview the crosstalk between BR and three major nutrients (N, P, and Fe) that have been studied in depth in *Arabidopsis* and rice. The information provided here will help us to understand the hormonal regulation of plant architecture changes and nutrient signaling pathways, as well as the balance between plant growth and development and stress responses.

The primary BR signaling pathway

In *Arabidopsis*, BR activates its signaling after being recognized by the plasma membrane-localized receptor BRASSINOSTEROID INSENSITIVE 1 (BRI1) (Li and Chory, 1997; Wang et al., 2001; Yamamuro et al., 2000) and the co-receptor BRI1-ASSOCIATED KINASE 1 (BAK1) (Li et al., 2002; Nam and Li, 2002). Then BRI1 phosphorylates BRASSINSOSTEROID KINASE INHIBITOR 1 (BKI1), leading to its disassociation from BRI1 and further activating the BRI1/BAK1 receptor complex (Wang and Chory, 2006). The signal is then transferred to BR SIGNALING KINASE 1 (BSK1) and CONSTITUTIVE DIFFERENTIAL GROWTH 1 (CDG1) (Kim et al., 2011; Tang et al., 2008), which activate BRI1 SUPPRESSOR 1 (BSU1) phosphatase (Mora-García et al., 2004) (Figure 1). Subsequently, BSU1 inactivates BRASSINOSTEROID INSENSITIVE 2 (BIN2) (Li et al., 2001; Li and Nam, 2002), the key negative regulator of BR signaling, and the dephosphorylated BIN2 is then degraded by the E3 ubiquitin ligase KINK SUPPRESSED IN BZR1-1D (KIB1) (Zhu et al., 2017). As a consequence, BIN2 cannot phosphorylate the transcriptional factors BRASSINAZOLE RESISTANT 1 (BZR1) (He et al., 2002; Wang et al., 2002) and BRI1 EMS SUPPRESSOR 1 (BES1) (Yin et al., 2002). Meanwhile, PROTEIN PHOSPHATASE 2A (PP2A) dephosphorylates BZR1 and BES1 as well as BRI1 (Tang et al., 2011; Wang et al., 2016). The transcriptional factors will then disassociate with 14-3-3 proteins, shuttle from the cytoplasm into the nucleus, where they bind several kinds of *cis*-elements to regulate the expression of BR-related genes, and then initiate BR response (Gampala et al., 2007; Ryu et al., 2007). The stability of BZR1 and BES1 is regulated by multiple E3 ubiquitin ligases, which control their degradation through the 26S proteasome or selective autophagy in response to different environmental, hormonal, and developmental cues. Under dark conditions, CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) E3 ligase degrades the phosphorylated BZR1 (Kim et al., 2014), while under light condition, SINA OF *ARABIDOPSIS THALIANA* (SINAT) E3 ligases mediate the degradation of dephosphorylated BES1 (Yang et al., 2017). MORE AXILLARY GROWTH LOCUS 2 (MAX2), an F-box type ubiquitin E3 ligase known to inhibit shoot branching in strigolactone (SL) signaling, interacts with BES1 and targets it for degradation (Wang et al., 2013). In addition, BZR1 is also degraded by the E3 ubiquitin ligase PLANT U-BOX 40 (PUB40), specifically in roots, but not in shoots (Kim et al., 2021).

In rice, the core BR signaling pathway is conserved with that in *Arabidopsis* (Figure 1). Many key BR signaling

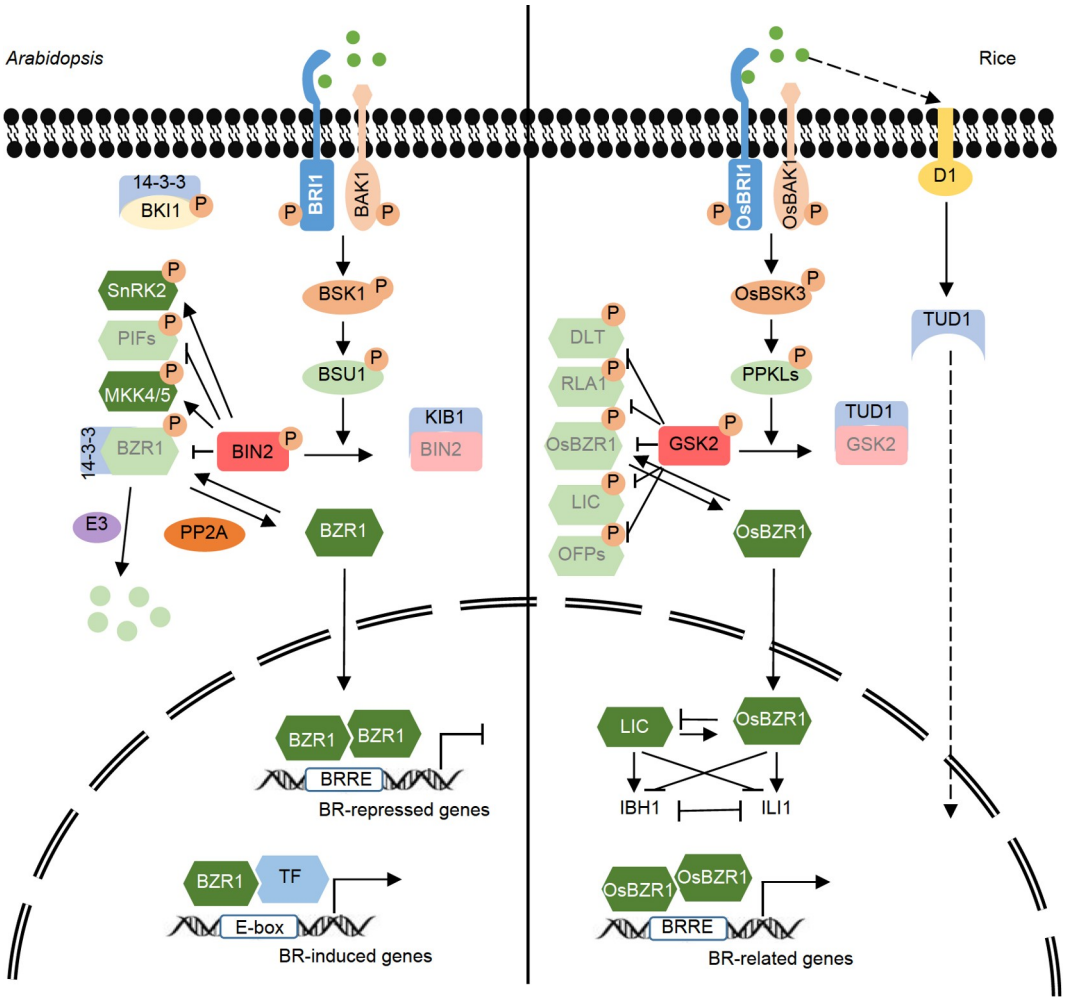

Figure 1 The overview of BR signaling in *Arabidopsis* and rice. The solid and dashed lines indicate direct and indirect actions, respectively. The arrows and bars indicate the promoted and inhibited effects, respectively. The black and gray colors represent the activation and suppression effects on the corresponding proteins, respectively. TF, transcriptional factor. The phosphorylation modification on the proteins (P) that has been demonstrated is indicated by circled P.

components identified in rice, such as OsBRI1, OsBAK1, OsBSK3, GLYCOGEN SYNTHASE KINASE 3 (GSK3)/SHAGGY-LIKE KINASE 2 (GSK2/OsBIN2) and OsBZR1, have the homologous counterparts in *Arabidopsis* (Bai et al., 2007; Li et al., 2009; Tong et al., 2012; Yamamuro et al., 2000; Zhang et al., 2016). Genetic analyses have shown that most of these components, but not all of them, possess similar functions in BR signaling and lead BR to regulate many important agronomic traits in rice, including plant height, leaf angle, and grain size (Tong and Chu, 2018). Similarly, BR is perceived by the OsBRI1-OsBAK1 receptor complex on the plasma membrane (Li et al., 2009; Yamamuro et al., 2000), and then the signal is transferred to OsBSK2 (Yin et al., 2022) and OsBSK3 (Zhang et al., 2016), which will further inhibit GSK2, the homologous protein of BIN2, to de-repress OsBZR1 (Bai et al., 2007; Tong et al., 2012). However, there are at least three steps in rice BR signaling different from that in *Arabidopsis*. First, the roles of some PROTEIN PHOSPHATASE WITH KELCH-LIKE DOMAIN (PPKL)-family members (PPKL1/2/3) in rice are seemingly in opposite to those in *Arabidopsis*, namely BSU1-family proteins (BSU1 and BSL1/2/3). While BSU1 promotes BIN2 degradation to enhance BR signaling in *Arabidopsis* (Mora-García et al., 2004), PPKL1 appears to suppress BR signaling by dephosphorylating and stabilizing OsGSK3 (Gao et al., 2019). Second, while the F-box protein KIB1 is responsible for the ubiquitination and degradation of BIN2 in *Arabidopsis*, a recent study reveals that the U-box ubiquitin ligase TUD1 is responsible for GSK2 degradation in rice (Hu et al., 2013; Liu et al., 2022a; Zhu et al., 2017). Third, downstream of GSK2, a number of distinctive BR signaling components have only been identified in rice, and some of them could also serve as the substrates of GSK2 like DWARF AND LOW-TILLERING (DLT) (Tong et al., 2012; Tong and Chu, 2018) (Figure 1). Since the growth environment of rice is very different from that of *Arabidopsis* in terms of temperature, water, and light, it is understandable that BR signaling pathway in rice is different from that in

Arabidopsis.

As the central BR signaling inhibitors, the GSK3-like kinases, including BIN2 and GSK2, are able to modulate various downstream proteins to regulate different biological processes. Some of them have been demonstrated to be the substrates for the kinase phosphorylation but some not. In *Arabidopsis*, for example, BIN2 phosphorylates BZR1/BES1, SNF1-RELATED KINASE2 (SnRK2), PHYTOCHROME INTERACTING FACTOR 4/5 (PIF4/5), WRKY46/54/70, MITOGEN-ACTIVATED PROTEIN KINASE (MAPK) KINASE 4/5 (MKK4/5), PUB40 (see the review by Nolan et al. (2020)). In rice, many substrates tend to be transcription factors, such as OsBZR1, DLT, REDUCED LEAF ANGLE1 (RLA1)/SMALL ORGAN SIZE1 (SMOS1), OVATE FAMILY PROTEIN 3/8 (OsOFP3/8), and LEAF AND TILLER ANGLE INCREASED CONTROLLER (LIC) (Qiao et al., 2017; Tong et al., 2012; Xiao et al., 2020; Yang et al., 2016; Zhang et al., 2012). These downstream BR signaling components could mediate one or several specific BR responses. For example, DLT tends to regulate leaf angle and plant height, U-TYPE CYCLIN (CYC U4;1) appears to regulate leaf angle, and it seems that OsGRF4 majorly regulates grain size (Che et al., 2015; Duan et al., 2015; Sun et al., 2015; Tong et al., 2009).

As the key transcription factors in BR signaling, BZR-family proteins can bind to promoters of multiple genes to regulate their expression. In *Arabidopsis*, 953 BR-regulated BZR1 target (BRBT) genes were identified by genome microarray assays, and then the BZR1 and BES1 binding motifs were recognized, including BR responsive element (BRRE, CGTGT/CG), G-box (CACGTG), E-box (CATGTG) and GGTCC motif (Sun et al., 2010; Yu et al., 2011). Among them, BRRE and G-box mostly present in promoters of BR-repressed genes targeted by BZR1/BES1 homodimer, whereas E-box mostly exists in promoters of BR-induced genes targeted by heterodimer containing BZR1/BES1 as well as other bHLH transcription factors. In *Arabidopsis*, BRBT genes are found to be involved in many processes, such as BR biosynthesis, cell wall synthesis and modification, chloroplast development, and photomorphogenesis. (reviewed in Wang et al., 2012). Recently, the dinucleotides on either side of the core 5′-NNCGTG-3′ sequence were proposed to impact the binding of BZR1 by affecting DNA flexibility, indicating that indirect contact manipulates the binding between a transcription factor and *cis*-element. DNA affinity purification sequencing (DAP-seq) and microarray data showed that BZR1 tended to bind the core motif, which contained a pyrimidine followed by a purine upstream and downstream, and repressed the expression of target genes (Favero, 2023; Nosaki et al., 2018). So far, a number of genes, including *LIC*, *DLT*, *INCREASE LEAF INCLINATION 1 (ILI1)*, *ILI1 BINDING BASIC HELIX-LOOP-HELIX 1 (IBH1)*, *CYC U4;1*, *BRASSINOSTEROID UPREGULATED 1 (BU1)* and GA synthesis genes, have been reported as the targets of OsBZR1 in rice (Sun et al., 2015; Tanaka et al., 2009; Tong et al., 2012; Tong et al., 2014; Zhang et al., 2009; Zhang et al., 2012). Most of them contain the BZR1/BES1 binding motifs on their promoters; however, there is no clear evidence that OsBZR1 can promote or repress the expression of downstream genes via binding to a specific element in rice. As a pair of antagonistic transcription factors, ILI1 and IBH1 affect leaf inclination by regulating the elongation of lamina joint cells. BR signaling increases *ILI1* and decreases *IBH1* at the transcription level through OsBZR1. In addition to being the target of OsBZR1, LIC binds to the promoters of *ILI1* and *IBH1* and interacts with OsBZR1 to antagonize the regulation of *ILI1*-*IBH1* (Zhang et al., 2012). It will be interesting to explore the biological processes in which BRBT genes participate to deepen the understanding of BR functions in rice.

Crosstalk between N and BR signaling

N is one of the mineral nutrients most demanded by plants and is closely associated with plant growth and crop yield. Nitrate and ammonium are the two primary forms of inorganic N for plants to uptake and utilize, with nitrate predominately existing in oxygen-rich soils while ammonium mostly in flooded environments or acidic soils (Näsholm et al., 2009). The root releases oxygen and secretions into the surrounding environment, thereby altering the redox state of the rhizosphere, the density, and activity of the microbial community, and ultimately changing the proportion of nitrate and ammonium absorbed by the root through nitrification (Sun et al., 2016). Plants absorb nitrate and ammonium primarily through nitrate transporters (NRTs) and ammonium transporters (AMTs), respectively, which have been intensively studied in both *Arabidopsis* and rice (Li et al., 2017).

In addition to serving as a mineral nutrient, nitrate also acts as a signaling molecule to modulate gene expression and activate nutrient utilization. Nitrate is recognized by membrane-localized transceptor (transporter and receptor) CHL1/AtNRT1.1/AtNPF6.3, the dual-affinity nitrate transporter. The affinity of CHL1 is determined by the phosphorylation of threonine (T) residue 101 and is regulated by external nitrate signaling (Ho et al., 2009; Liu and Tsay, 2003). In cells, NIN-LIKE PROTEIN 7 (AtNLP7) is the master transcription factor in nitrate signaling, which is phosphorylated by the subgroup III of Ca^{2+}-SENSOR PROTEIN KINASES (CPKs, including CPK10, CPK30, and CPK32), and the phosphorylation promotes AtNLP7 retention in the nucleus and activates the downstream nitrate responsive genes in *Arabidopsis* (Liu et al., 2017). Very recently, AtNLP7 has also been identified as a nitrate sensor, for it directly binds to

nitrate through its N-terminus (Liu et al., 2022b). In rice, OsNRT1.1B, the functional homolog of CHL1, perceives and transduces nitrate signal by recruiting an E3 ubiquitin ligase, NRT1.1B INTERACTING PROTEIN 1 (NBIP1) on the plasma membrane, which degrades OsSPX4 (named after SYG1 (suppressor of yeast gpa1), PHO81 (CDK inhibitor in yeast PHO pathway), and XPR1 (xenotropic and polytropic retrovirus receptor)) and promotes the nuclear localization of OsNLP3 (Hu et al., 2015; Hu et al., 2019). As the uptake and utilization of nitrate and Pi are synergistically reinforced, the OsNRT1.1B-NBIP1-OsSPX4-OsNLP3 module provides new insight into understanding the mutually beneficial cooperation of nitrate and Pi.

Ammonium is also regarded as a signal molecule, but the signaling mechanism from the sensor to downstream responsive genes is still poorly understood. In *Arabidopsis*, extracellular ammonium is sensed and transported through AtAMTs. Sufficient ammonium triggers the phosphorylation of threonine (T) 460 residue at the C-terminus of AtAMT1;1, leading to a closed state of ammonium channel to prevent ammonium toxicity due to excessive absorption of ammonium (Loqué et al., 2007). The phosphorylation of threonine (T) 452 residue in OsAMT1.2 (relevant to T460 in AtAMT1.1) has also been reported to protect rice from ammonium toxicity (Beier et al., 2018), indicating that the phosphorylating regulation of AMTs is a conserved mechanism between *Arabidopsis* and rice.

Under mild N deficiency, both the primary roots and lateral roots of *Arabidopsis* show enhanced elongation, terming N foraging response (Giehl and von Wiren, 2014). Recently, it was reported that BR is involved in this process. Genome-wide association study (GWAS) of 200 widespread *Arabidopsis* accessions was performed to identify genetic components and search for natural variations responsive to N foraging, and then *BSK3* and auxin biosynthesis gene *YUCCA8* (*YUC8*) were identified as the candidates modulating the growth of primary roots and lateral roots under mild N deficiency (0.55 mmol L^{-1} NH_4NO_3 + KNO_3) (Jia et al., 2019). Analysis of the coding sequences (CDSs) of the candidate genes of 139 re-sequenced accessions suggests that *BSK3* contains a natural variation causing leucine (L) to proline (P) substitution in its protein kinase domain, which is responsible for N foraging response. Furthermore, under low N conditions, those accessions carrying the BSK3-L-allele show longer primary roots than those carrying BSK3-P-allele, possibly due to the higher BR sensitivity conferred by the BSK3-L variant compared with BSK3-P. Since BRI and BAK1 work upstream of BSK3, treatments of *bri1* and *bak1-1* with low N were performed. The result indicates that BAK1 rather than BRI1 regulates root elongation in N foraging response. In addition, N deficiency does not affect the expression of *BRI1* and *BSK3*, but upregulates that of *BAK1* at the transcriptional level. These results suggest that low N activates BAK1 via a BRI1-independent pathway, further activates BSK3 to enhance BR signaling, and finally stimulates root growth by promoting cell elongation (Figure 2A).

BR signaling also acts upstream of auxin to regulate lateral root elongation. The application of brassinozole (BRZ), an inhibitor of BR synthesis, largely represses auxin accumulation in the meristem of the lateral root. Consistently, the auxin synthesis increases in the lateral roots of *bzr1-D*, a mutant with constitutively activated BR signaling (Jia et al., 2021). *YUC8* has been identified as a determinant of N foraging response in lateral roots, it acts redundantly with its homologs *YUC5*, *YUC7* and *TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS 1* (*TAA1*), encoding the other key enzymes in auxin biosynthesis that are upregulated under mild N deficiency. Therefore, the roles of these genes in N foraging response were investigated. Indeed, the study finds that these genes modulate local auxin synthesis in the lateral root meristem, leading to low N-induced lateral root elongation (Jia et al., 2021). Furthermore, N-deficiency directly induces the expression of *YUCs*, resulting in enhanced auxin levels in the apical root meristem, which in turn promotes cell elongation of the lateral roots (Figure 2A). More recently, another study shows that root foraging response under low N (0.05 mmol L^{-1} NH_4NO_3 + 0.05 mmol L^{-1} KNO_3) increases BR-induced auxin translocation and, conversely, high auxin levels inhibit BR signaling via BKI1 (Devi et al., 2022). Under severe N deficiency (continuous growth in 0.3 mmol L^{-1} nitrate), BR still functions in modulating root system architecture (RSA) in *Arabidopsis* (Song et al., 2021). CALMODULIN-LIKE 38 (CML38) and PEP1 RECEPTOR 2 (PEPR2) interact at the cell membrane and negatively regulate root elongation under low nitrate conditions. Furthermore, BL treatment in Col-0 inhibits primary root elongation, which is unaffected in *cml38*, *pepr2*, and *cml38 pepr2* plants. Also, in these mutants, changes in the expression of the BES1 target gene become weaker compared to Col-0 after BL treatment, indicating that CML38 and PEPR2 play positive roles in BR signaling. Low nitrate has been shown to promote BR signaling due to more significant inhibition of primary root elongation under low-nitrate versus high-nitrate conditions. However, in *cml38*, *pepr2*, and *cml38 pepr2* plants, no inhibitions of primary root growth are observed under low-nitrate or high-nitrate conditions, suggesting that CML38 and PEPR2 play key roles in low-nitrate-promoted BR signaling (Song et al., 2021). In conclusion, different N nutritional conditions could confer variable effects on BR signaling to modulate root length.

Ammonium, when supplied as the sole N source (1 mmol L^{-1} NH_4SO_4), inhibits BR signaling; whereas nitrate, when supplied as the sole N source (10 mmol L^{-1} or 0.3 mmol L^{-1} KNO_3), promotes BR signaling (Devi et al., 2022; Song et al., 2021). In comparison to N foraging re-

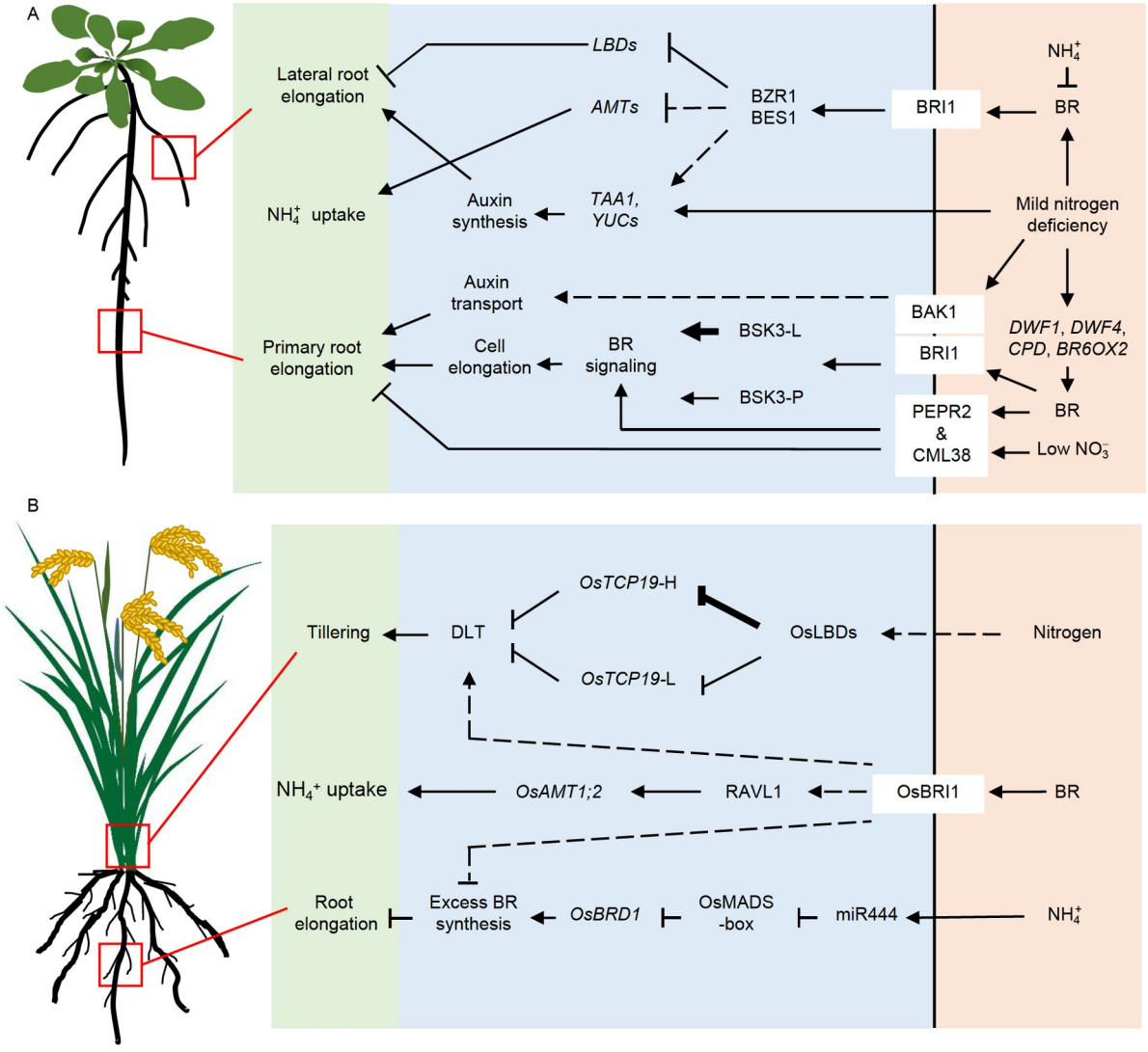

Figure 2 Crosstalk between BR and variable N nutrient in *Arabidopsis* and rice. A, *Arabidopsis*. B, Rice. The solid and dashed lines indicate direct and indirect actions, respectively. The arrows and bars indicate the promoted and inhibited effects, respectively. The bold line indicates a relatively stronger effect. Orange areas represent external signals, blue areas represent molecular mechanisms, and green areas represent outputs.

sponses under mild N deficiency (0.55 mmol L^{-1} NH_4NO_3 + KNO_3), growing under continuously low nitrate conditions (0.3 mmol L^{-1} KNO_3) inhibits primary root elongation in *Arabidopsis* (Figure 2A). These studies suggest that BR stands in a more upstream position to receive different nutrient signals and regulate RSA in *Arabidopsis*. Since the initiation of primary roots and lateral roots of dicots occurs at different embryonic stages, how plants distinguish these nutritional signals, leading to the development of either primary roots or lateral roots, requires further investigation.

Notably, in addition to regulating BR signaling, transcriptomic data reveal that N concentration also regulates the expression of several BR biosynthesis genes, such as *DWARF1* (*DWF1*), *DWARF3*/*CONSTITUTIVE PHOTOMORPHOGENIC DWARF* (*DWF3*/*CPD*), *DWARF4* (*DWF4*) and *BRASSINOSTEROID-6-OXIDASE 2* (*BR6OX2*), and mild N-deficiency induces the expression of *DWF1*, *CPD*, *DWF4*, and *BR6OX2* (Jia et al., 2020). Furthermore, BRZ treatment strongly prevents the elongation of the primary roots and lateral roots under low-N conditions, and N foraging response of the roots is significantly repressed in *dwf1*, *cpd*, and *dwf4* mutants (Jia et al., 2020), suggesting that enhanced root elongation under low N depends on BR synthesis in *Arabidopsis*. On the other hand, BR signaling also directly regulates the expression of *AMTs* to influence ammonium uptake in *Arabidopsis*. BL treatment inhibits the expression of *AMT1*;*1*, *AMT1*;*2*, and *AMT1*;*3*, thus enhancing cellular ammonium content in *Arabidopsis* roots (Zhao et al., 2016). Although BES1 interrupts the repression of ammonium-mediated *AMT1* expression, it has been shown that BES1 fails to bind to the E-box of *AMT1* promoter directly. Very recently, it is shown that BES1 is

involved in low N-induced lateral root elongation, which is promoted in *bes1-D*, the gain-of-function mutant of *BES1*, but is inhibited in *bes1* (Chai et al., 2022). This is consistent with the finding that mild N deficiency promotes BR signaling to regulate the N foraging response positively. Further studies suggest that low N treatment significantly enhances both the transcriptional level and dephosphorylated level of BES1 in *Arabidopsis* root. Moreover, BES1 directly binds to the promoters of *LATERAL ORGAN BOUNDARIES DOMAIN 37 (LBD37)*/*LBD38*/*LBD39*, the repressors in the nitrate signaling pathway that are induced by N treatment, to suppress their expression, thereby releasing the inhibition of *AtLBD37* on lateral root growth (Figure 2A).

Besides root length, tiller number is also a significant factor responsive to N in rice. As a positive regulator of BR signaling pathway promoting tillering in rice, DLT is involved in tillering response to N (TRN). GWAS of 110 rice accessions has identified OsTCP19 as a candidate regulator of TRN (Liu et al., 2021). A 29-bp indel (insertion-deletion) polymorphism in the promoter of *OsTCP19* leads to the variation of TRN in different rice accessions. The varieties carrying the 29-bp (*OsTCP19*-L) usually have relatively low TRN, whereas those lack of the 29-bp (*OsTCP19*-H) generally show high TRN. The presence of 29-bp inhibits the binding of OsLBD37/OsLBD39 to *OsTCP19* promoter and alleviates their repressive effect on *OsTCP19* expression, leading to enhanced expression of *OsTCP19* and, therefore, low TRN. To decipher the regulation of rice tillering by *OsTCP19*, RNA-sequencing analysis was performed using wild-type (ZH11) and *OsTCP19*-overexpressing plants to identify the downstream target genes of OsTCP19. Among 304 differentially expressed genes (DEGs), *DLT* was noticed due to its simultaneous response to N treatment and regulation of rice tillering in BR signaling. Notably, besides reduced tillering, *OsTCP19*-overexpressing plants exhibit other BR-deficient phenotypes, such as decreased plant height, panicle length, and erect leaves. Further studies reveal that OsTCP19 directly binds to *DLT* promoter and suppresses its expression to regulate tillering in rice (Figure 2B). Importantly, the expression of *OsTCP19* is strongly correlated with the global soil N-content distribution. The varieties carrying *OsTCP19*-H allele, which is highly retained from wild rice, mainly distribute in N-poor regions and are almost absent in N-rich regions. This study not only elucidates the molecular mechanism by which N affects tillering through manipulating BR signaling, but also exemplifies how to exploit superior alleles from wild rice resources.

GRAIN SIZE ON CHROMOSOME 2 (GS2)/GRAIN-LENGTH-ASSOCIATED QTL (GL2)/GROWTH-REGULATING FACTOR 4 (GRF4) and SMOS1/RLA1/NITROGEN-MEDIATED TILLER GROWTH RESPONSE 5 (NGR5), two components of BR signaling pathway, were recently found to be involved in N-mediated grain yield improvement (Li et al., 2018; Wu et al., 2020). However, the studies on both transcriptional factors have not touched on the roles of BR but suggested the roles of gibberellin signaling in regulating N utilization efficiency. Coincidently, all three N-related regulators, including DLT, GRF4, and SMOS1/RLA1, could be GSK2 substrates (Che et al., 2015; Qiao et al., 2017; Tong et al., 2012). In addition, GRF4 can interact with DELLA protein to regulate gibberellin signaling (Li et al., 2018), and DLT can directly interact with SMOS1 to integrate BR and auxin response (Hirano et al., 2017). Moreover, BR promotes GA to regulate plant height (Tong et al., 2014). These studies imply different phytohormones' complex roles in N-mediated plant development. In *Arabidopsis*, N affects shoot branching depending on signaling pathways of phytohormones such as auxin and cytokinin, while little is known about BR in this process (Vega et al., 2019). Although the function of BR on shoot branching in *Arabidopsis* was well documented previously (Hu et al., 2020a; Hu et al., 2020b; Wang et al., 2013), direct evidence about BR in N-regulated branching in *Arabidopsis* is still missing. Further studies on whether and how BR regulates N-dependent branching would be attractive.

Consistent with the N foraging response in *Arabidopsis*, a high concentration of ammonium, when supplied as the sole N source, inhibits the elongation of the primary roots and lateral roots. In rice, BR biosynthesis is responsible for ammonium-triggered root growth inhibition. Ammonium-cultured rice seedlings show both increased leaf inclination and shortened root length, which could be weakened by BRZ treatment (Jiao et al., 2020). Pure ammonium treatment is also accompanied by the accumulation of microRNA444 (miR444), which enhances BR biosynthesis by upregulating the expression of *OsBRD1*, one of the BR biosynthetic genes. Further studies find that several OsMADS-box proteins (OsMADS23, OsMADS25, OsMADS27, OsMADS57, and OsMADS61), encoded by the target genes of miR444, directly bind to the *OsBRD1* promoter and repress its transcription. These results reveal a signaling cascade that ammonium induces miR444 to promote BR biosynthesis through de-repressing the inhibitory effect of OsMADS-box proteins on *OsBRD1* transcription, providing a possible explanation for the ammonium-induced root shortening in rice (Figure 2B).

While ammonium modulates RSA by affecting BR biosynthesis in rice, BR also regulates ammonium uptake and homeostasis. BR treatment induces the expression of *OsAMT1*;*1* and *OsAMT1*;*2* at the transcription level (Xuan et al., 2017). In addition, *RELATED TO ABI3*/*VP1-LIKE 1* (*RAVL1*), a transcription factor involved in BR homeostasis, activates *OsAMT1*;*2* via directly binding to the E-box motifs on *OsAMT1*;*2* promoter, which promotes the uptake of ammonium in rice roots (Je et al., 2010; Xuan et al., 2017).

Intriguingly, the upregulation of *OsAMTs* by BR in rice is contrary to the inhibition of *AtAMTs* by BR in *Arabidopsis*. The reason might be due to the fact that different nutritional conditions were utilized in different experiments, i.e., distilled water was used for growing the rice plants, whereas the nutrient medium containing nitrate as the sole N source was used for growing the *Arabidopsis* plants. This possibility implies that BR signaling could acutely respond to different nutrient signals, which in turn differentially regulates plant growth and development. The underlying molecular mechanism is worth to be further explored. Given that AMTs are able to undergo phosphorylating modifications (Loqué et al., 2007) and phosphorylation is one of the key event in BR signaling, it will be interesting to investigate the post-transcriptional modifications of the BR signaling components on AMTs.

Crosstalk between Pi, Fe, and BR signaling

P is a massive element necessary for plant growth. Due to the low solubility and high fixation of Pi in soil, effective Pi that could be directly taken up by plant roots is less than 10%, including soluble inorganic Pi: $H_2PO_4^-$ and HPO_4^{2-}, mainly $H_2PO_4^-$ (Maathuis, 2009; Shen et al., 2011). This means that Pi is one of the major limiting factors for plant growth. To survive in a Pi-limited environment, plants have evolved sophisticated mechanisms in response to Pi deficiency to acquire and remobilize Pi to maintain Pi homeostasis. This signaling network is called Pi starvation response (PSR), which is engaged by Pi transporters and Pi starvation-induced (PSI) genes (Chiou and Lin, 2011; Wu et al., 2013). In this network, the MYB-CC family proteins, including PHOSPHATE STARVATION RESPONSE 1 (AtPHR1)/PHR-LIKE 1 (AtPHL1)/AtPHL2/AtPHL3 in *Arabidopsis* and OsPHR1/OsPHR2/OsPHR3/OsPHR4 in rice, work as the key transcription factors. They can bind to the *cis*-elements termed PHR1-binding sequence (P1BS) distributed in the promoters of PSI genes and upregulate their expression. Among them, AtPHR1 and OsPHR2 are the central regulators in *Arabidopsis* and rice, respectively, because they have broader expression patterns and stronger binding affinity to target genes (Guo et al., 2015). The SPX domain-containing proteins (SPXs) are essential in regulating Pi signaling in plants (Secco et al., 2012; Zhou et al., 2015). It has been reported that AtSPX1 and AtSPX2 in *Arabidopsis* and OsSPX1, OsSPX2, and OsSPX4 in rice, as negative regulators in PSR, interact with AtPHR1 and OsPHR2 to inhibit their transcription activities in a Pi-dependent manner (Lv et al., 2014; Puga et al., 2014; Wang et al., 2014).

To adapt to the Pi-deficient conditions, plants undergo various morphological changes, including the changes of RSA in *Arabidopsis*. As Pi is mainly present in the upper layer of soil, RSA changes from deep to shallow, with gradually shortened primary roots but increased number and density of lateral roots and root hairs (Lopez-Bucio et al., 2002; López-Arredondo et al., 2014). This process is inhibited in *bzr1-D*, suggesting that the constitutive activation of *BZR1* causes RSA insensitivity to Pi levels, which results in unaltered root systems in Pi-harsh environments (Singh et al., 2014). On the contrary, the reduction of BR levels promotes the response of the roots to a low Pi environment. Anthocyanin accumulation and enhanced acid phosphatases (APase) activity, the additional physiological responses caused by Pi deficiency, are also interrupted in *bzr1-D* (Singh et al., 2014). However, the expression of PSI genes and Pi content are undistinguishable between the mutant and wild type plants, implying that the perception of Pi is normal in *bzr1-D*. Nevertheless, low Pi results in the reduction of BR synthesis gene (*DWF4*, *BROX2*, *CPD*) expression and 28-norCS (an active BR precursor) content, leading to the reduction of nucleus/cytoplasmic ratio of BZR1/BES1, and ultimately inhibiting BR-mediated primary root growth in *Arabidopsis* (Singh et al., 2014). A ubiquitin E3 ligase PUB40 degrades BZR1 in the roots. a *pub39 pub40 pub41* triple mutant (*pub39* and *pub41* are homozygous to *pub40*) shows decreased root sensitivity to Pi starvation due to the increase of BZR1 protein level (Kim et al., 2021). To cope with Pi deficiency, plants secret malate to dissolve insoluble oxides such as Fe-P, enhancing Pi availability (Lambers et al., 2015). Low Pi condition enhances the translocation of AtSTOP1 to the nucleus, which activates *ALUMINUM-ACTIVATED MALATE TRANSPORTER 1* (*AtALMT1*) expression and promotes malate efflux (Balzergue et al., 2017; Godon et al., 2019). Very recently, reduced malate secretion in the roots of *bzr1-D* mutant plants was thought to be responsible for the insensitivity to Pi starvation. Exogenous addition of malate led to the rescue of the phenotype of *bzr1-D* (insensitive to low phosphorus), indicating that AtBZR1 represses *AtALMT1* expression and malate secretion (Liu et al., 2023). Although Pi deficiency did not result in shorter root length in rice, the mechanism by which OsBZR1 inhibits *OsALMT1* expression and malate secretion was proved to be conserved in rice (Liu et al., 2023). Taken together, these studies clearly show that BZR1 is involved in regulating RSA adaption to low Pi, especially in inhibiting the elongation of primary roots in *Arabidopsis*.

Pi and Fe always lead to antagonistic physiological effects in plants, such as the content, root length, and leaf color, which has attracted extensive attention. Under Pi-deprived condition, the elongation of *Arabidopsis* primary roots is inhibited, which may be due to the Fe toxicity caused by Pi-deficiency; when the Fe concentration decreases, the inhibition is significantly relieved, even without increasing Pi concentration (Hirsch et al., 2006; Ward et al., 2008). However, Fe deficiency promotes the accumulation of Pi and

total P in rice shoots and roots (Saenchai et al., 2016; Zheng et al., 2009). Very recently, it was reported that HEMERYTHRIN MOTIF-CONTAINING REALLY INTERESTING NEW GENE-AND ZINC-FINGER PROTEINS (HRZs), an E3 ligase that is induced by high Fe level and negatively regulates Fe acquisition under Fe-sufficient condition, interacts with and degrades OsPHR2 in rice, which reveals the molecular mechanism of the antagonistic effect between Pi and Fe (Guo et al., 2022a; Kobayashi et al., 2013). BR has also been reported to regulate the crosstalk between Pi and Fe:Pi starvation induces Fe accumulation in the elongating zone of the roots, and the accumulation of Fe promotes *BKI1* expression, which suppresses BRI1 and then inhibits root elongation in *Arabidopsis* (Singh et al., 2018). RNA sequencing analysis of *bzr1-D* roots identified *LOW PHOSPHATE ROOT 1 (LPR1)* as a target gene of BZR1 (Singh et al., 2018). LPR1 and LPR2 function as ferroxidases, converting Fe^{2+} to Fe^{3+}, which is a key step for plants to absorb and utilize Fe (Müller et al., 2015; Wang et al., 2019). The *lpr1* and *lpr1 lpr2* mutants show enhanced primary root length compared with Col-0 plants under Pi deficiency, due to the reduction of apoplastic Fe accumulation in root elongation and differentiation zones (Liu et al., 2023; Müller et al., 2015; Wang et al., 2019). Fe accumulation due to constitutive overexpression of *LPR1* in *bzr1-D* mutant plants restored the insensitivity of RSA to low Pi (Singh et al., 2018). This indicates that BR affects root elongation under low-Pi conditions through repressing *LPR1* by BZR1. Fe deficiency also inhibits the expression of BR biosynthesis genes (*OsD2* and *OsDWARF*) and BR signaling gene (*OsBRI1*) in rice (Wang et al., 2015) (Figure 3). Moreover, under low-Fe conditions, BR treatment is able to enhance the expression of Fe-homeostasis-related genes, such as *Fe^{2+} TRANSPORTER (OsIRT1)*, *YELLOW-STRIPE LIKE (OsYSL15)*, *OsYSL2*, *NICOTIANAMINE SYNTHASE (OsNAS1)* and *OsNAS2*. However, this effect appears to only occur in the shoots, not in the roots. Applying BR intensifies the Fe-deficient symptoms, including decreased chlorophyll concentration and suppressed plant growth (Wang et al., 2015). These results indicate that BR may be required for Fe translocation from roots to shoots, but the potential mechanisms remain unclear.

As a monocotyledonous plant, rice has evolved a RSA different from *Arabidopsis*. Rice responds to a Pi-deficient environment mainly by increasing the angle of adventitious roots and the number of root hairs (Huang and Zhang, 2020). The RSA of rice depends on Pi levels, Pi-deficiency duration, and rice varieties (Negi et al., 2016). In addition to root growth, rice shows decreased plant height, poor tillering, dark green leaves, and reduced leaf angle under Pi deficiency (Mghase et al., 2011). These symptoms are very similar to those in BR-deficient mutants, consistent with the finding in *Arabidopsis* that low Pi inhibits BR synthesis to manipulate RSA (Singh et al., 2014). Recently, REGULATOR OF LEAF INCLINATION 1a (RLI1a) was reported to be responsible for the reduced leaf angle caused by low Pi. The alternative splicing of *RLI1* produces two protein isoforms in rice: RLI1a and RLI1b. RLI1a contains MYB domain only, and RLI1b contains both MYB and coiled-coil domains. RLI1a directly binds to R1BS (RLI1 binding sequence, NNATNC) on the promoters of BR biosynthetic genes (Os*D11*, *OsDWF4*) and signaling genes (Os*BZR1*, *OsBU1*), activates their expression and thus BR biosynthesis and signaling, and finally leads to a loose shoot architecture (Guo et al., 2022b). Os*BU1* and *BU1-LIKE 1 COMPLEX1* (Os*BC1)* are BASIC HELIX-LOOP-HELIX (bHLH) transcription factors, they promote lamina joint cell elongation to enhance leaf angle (Jang et al., 2017; Tanaka et al., 2009). Under low Pi condition, RLI1a is directly inhibited at the protein level by Pi defciency and OsSPX1/OsSPX2. This inhibition weakens the activation of Os*BU1* and Os*BC1* by RLI1a, suppresses the elongation of lamina joint cells, and results in a compact plant shoot architecture (Ruan et al., 2018). By contrast, RLI1b has a significantly lower binding strength to R1BS and almost has no impact on BR biosynthesis and signaling; therefore, RLI1b-overexpressing plants have unaltered shoot architecture. As MYB-CC family proteins, both RLI1a and RLI1b interact with OsSPX1/2, as OsPHR2 does, to regulate Pi starvation and Pi homeostasis in rice (Figure 3). So far, most studies focus on Pi regulation of BR synthesis or signaling in modulating RSA and plant shoot architecture in rice. Whether and how BR affects and regulates Pi signaling and Pi homeostasis in crop plants remain largely unclear.

Conclusion and future perspective

Unlike animals with the ability to move freely, plants survive by changing their phenotypes to adapt to adverse environments. Nutritional deficiency is one of the most common dilemmas that plants have to face, and they have evolved distinct strategies for various nutrient signals. Recent studies have demonstrated the roles of BR in regulating this process. Both the synthesis and signaling of BR are activated under mild N deficiency to promote root elongation in *Arabidopsis*, which ensures plants to gain more N by increasing the available space (Figure 2A). Root elongation is inhibited in both *Arabidopsis* and rice when ammonium is supplied as the sole N source (Figure 2), and BR plays a role in this process, as ammonium induces BR biosynthesis while excess BR inhibits root elongation. This could be explained by the dose- and tissue-dependent effects of BR on root growth, which is supported by the findings that a low concentration of BR applied exogenously can promote root elongation, whereas a high concentration of BR inhibits root elongation in rice

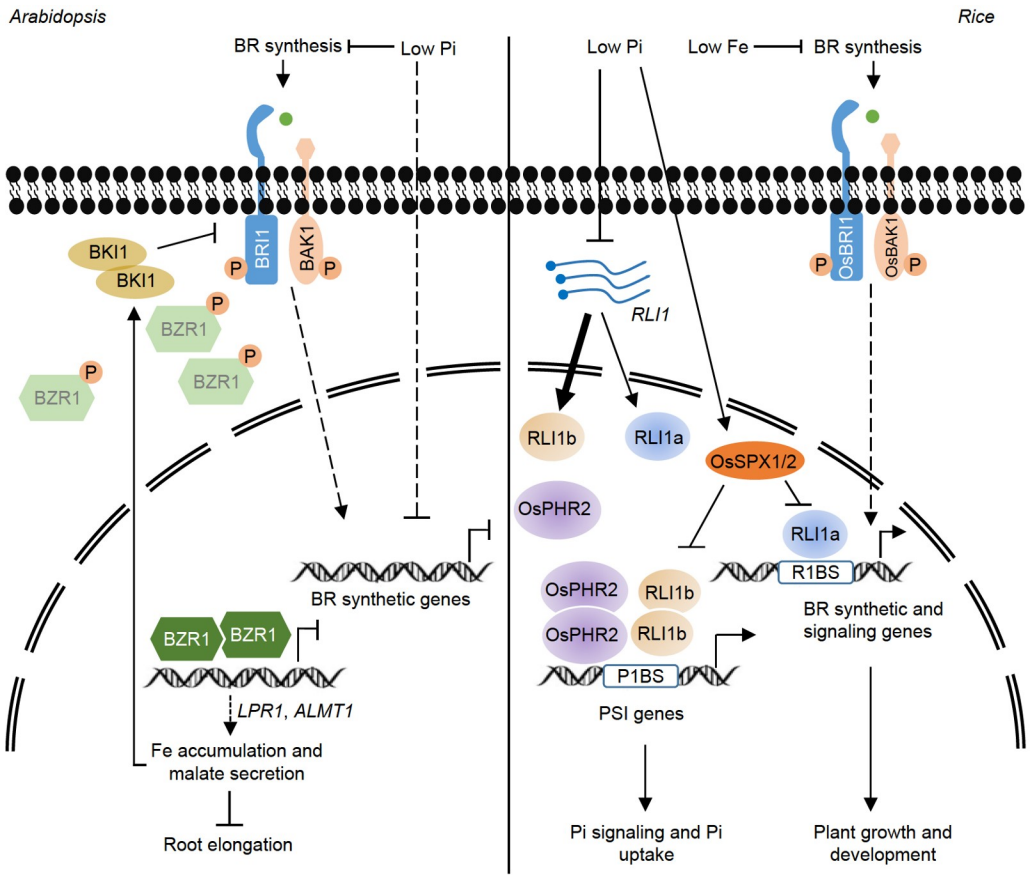

Figure 3 Crosstalk between BR, and Pi and Fe in *Arabidopsis* and rice. Involvement of BR in plant responses to low Pi and low Fe conditions. The solid and dashed lines indicate direct and indirect action, respectively. The arrows and bars indicate the promoted and inhibited effects, respectively. The bold line indicates the relatively strong effect.

(Tong et al., 2014). In *Arabidopsis*, BR biosynthesis and signaling are repressed under low Pi conditions, and more BZR1 remains in the cytoplasm. Thus the inhibitory effect of BZR1 on LPR1 is released and Fe accumulates in roots, which ultimately suppresses the primary root elongation (Figure 3). BR also plays a vital role in regulating yield-related traits in rice, such as tillering and leaf inclination. As an essential regulator of rice tillering as well as BR signaling, *DLT* can be targeted and inhibited by OsTCP19, which is repressed by N and holds a natural variation controlling TRN (Figure 2B). BR biosynthesis and signaling also determine the changes in rice phenotypes under low Pi conditions. RLI1a directly activates BR synthesis and signaling genes, and the inhibited expression of *RLI1a* under Pi deficiency leads to decreased BR synthesis and signaling, and thus a compact plant architecture (Figure 3). There is a tightly antagonistic relationship between Fe and Pi, which may be achieved partly through the modulation of BR signaling. In contrast to low Pi, which inhibits BR signaling, low Fe promotes BR signaling through the de-repression of BKI1—a negative regulator of BR signaling. Taken together, BR plays a vital role in plant responses to variable nutrient environments.

The key role of BR signaling in tackling nutrient deficiency offers new insights into achieving the goal of increasing food production with fewer fertilizers. By modifying key components of BR or nutrient signaling pathways, it is possible to construct and cultivate nutrient-efficient plants with deeper root systems, enhanced tillering, reduced leaf angle for dense planting, etc., to achieve higher yields with fewer inputs. With the development of the economy and the loss of resources, the demand for micronutrients such as Fe, zinc, and magnesium is also significant for the normal functioning of the human body. However, there are limited studies on the absorption and transportation of micronutrients regulated by BR in rice, a staple food crop. The researches we summarize here will provide valuable references and useful resources for further work in these aspects.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

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