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REVIEW PAPER

Roles of brassinosteroids in plant growth and abiotic stress response

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Abstract

Brassinosteroids (BRs) are widely used class of natural steroidal plant hormones. BRs take part in the regulation of growth and development of plants, maintaining BRs homeostasis, and allowing adaptation to environmental changes through the life cycle. They also play an important role in abiotic stress responses such as drought, salinity, high temperature, low temperature and heavy metal stresses. Through the signal transduction pathway, BRs interact with a variety of transcription factors via a series of phosphorylation cascades to regulate the expression of BR target genes. Thus, they regulate the various growth and development processes of plants. BRs crosstalk with different hormones to regulate plant physiology and development. This review primarily introduces the signaling pathways of BRs, their role in regulating plant growth and development, abiotic stresses, and their interaction with other plant hormones at the transcriptional and post-transcriptional levels. Our review of this topic will provide a complete reference for the study and utilization of BRs in the future.

Keywords Brassinosteroids (BRs) · Plant growth and development · Signaling crosstalk · Stress response

Introduction

Plant hormones are many molecules signals which produced by plants. These molecules can be transported to various locations throughout the plant, and they play an essential role in regulating plant growth and development (Lee et al. 2019). Current research suggests that plant hormones may be the initiating factor for the expression of resistance genes. Adverse conditions change the balance of source hormones in plants, leading to changes in metabolic pathways, which may be the result of the activation and expression of resistance genes (Wang 2010).

Brassinosteroids (BRs) are important plant hormones, which are involved in the regulation of plant growth and development, and in general, a certain concentration of BRs can increase crop yield, crop quality, and also play an important role in improving crop stress resistance. Brassinolide, a plant growth-promoting steroid, was isolated from *Brassica napus* pollen in 1979 (Grove et al. 1979). In 1998, at the 13th Annual Meeting of International Plant Growth Substances, it was confirmed as the sixth class of plant hormones. The five classes previously known plant hormones are auxin (IAA), gibberellin (GA) and cytokinin (CTK), abscisic acid (ABA) and ethylene (ETH) (Clouse and Sasse 1998). To date, this class of phytohormones is represented by more than 70 compounds, which have been isolated or detected from more than 100 plant species, from algae to angiosperms, revealing their ubiquitous distribution throughout the plant kingdom (Zullo and Adam 2002). These steroidal compounds occur in free form and conjugated to sugars and fatty acids (Bajguz and Hayat 2009). They are structurally similar to animal and insect steroids (Sasse 2003) and are primarily distributed in most organs of plants, such as pollen, stem apex growth point and ungerminated seeds. BR perception occurs at membrane-localized receptors, and downstream cytosolic regulators transducer BR-mediated signals to the nucleus where they activate the transcription of BR-responsive genes that drive cellular growth (Belkhadir and Jaillais 2015). They interact with other hormones to regulate adaptation to abiotic stresses, such as drought, temperature changes, and salinity. Exogenous application of BR to plants

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can effectively promote plant growth and improve crop yield, and increase abiotic stresses tolerance of plants (Divi and Krishna 2009). Many detailed studies have been conducted on the involvement of BRs in plant growth and development and the expression of resistance genes under adverse conditions. In this review, we introduce the signaling pathways of BRs, their role in regulating plant response to abiotic stresses, and their interaction with other plant hormones.

Brassinosteroids (BRs) signal transduction pathway

In the process of signal transduction (Fig. 1), BR receptor (BRASSINOSTEROID INSENSITIVE 1, BRI1), a receptor kinase rich in leucine repeat sequence (Li and Chory 1997), recognizes the BR signal through the extracellular domain. It induces phosphorylation at multiple sites (Wang et al. 2005). Activated BRI1 binds to the BRI1-associated receptor kinase (BAK1), to form a complex. Self-or-trans-phosphorylation of the C terminal of BRI1 enhances the activity of the receptor kinase, increases the affinity of BRI1 to BAK1 (Nam and Li 2002) and induces a phosphorylation cascade (Wang et al. 2005, 2008). Their activation stimulates the separation of the BRI1 kinase inhibitor 1 (BKI1), which is detached from the complex of BRI1 and BKI1 (Wang and Chory 2006), and the detached BKI1 is phosphorylated, separated from the plasma membrane, and bound to 14-3-3 protein (Bai et al. 2007; Jin and Dai 2014). After activation, BRI1 will transmit BR signal to the downstream of the two kinds of protein signaling kinases (BSKs) and constitutive differential growth protein 1 (CDG1) (Kim et al. 2011; Tang et al. 2008). When BRI1 phosphorylates BSKs and CDG1, BSU1 will subsequently be phosphorylated. BSU1 is a serine/threonine protein phosphatase with the N-terminal kelch-repeat domain, which leads to BIN2 dephosphorylation. BIN2 is restrained by KIB1 (KIK SUPPRESSED IN BZR1-1D), which prevents the association of BINs with BZR1/BES1 and facilitates its ubiquitination (Zhu et al. 2017). BZR1/BES1 is rapidly dephosphorylated by PP2A (PHOSPHATASE 2A) and enters the nucleus. In cooperation with other transcription factors, BZR1/BES1

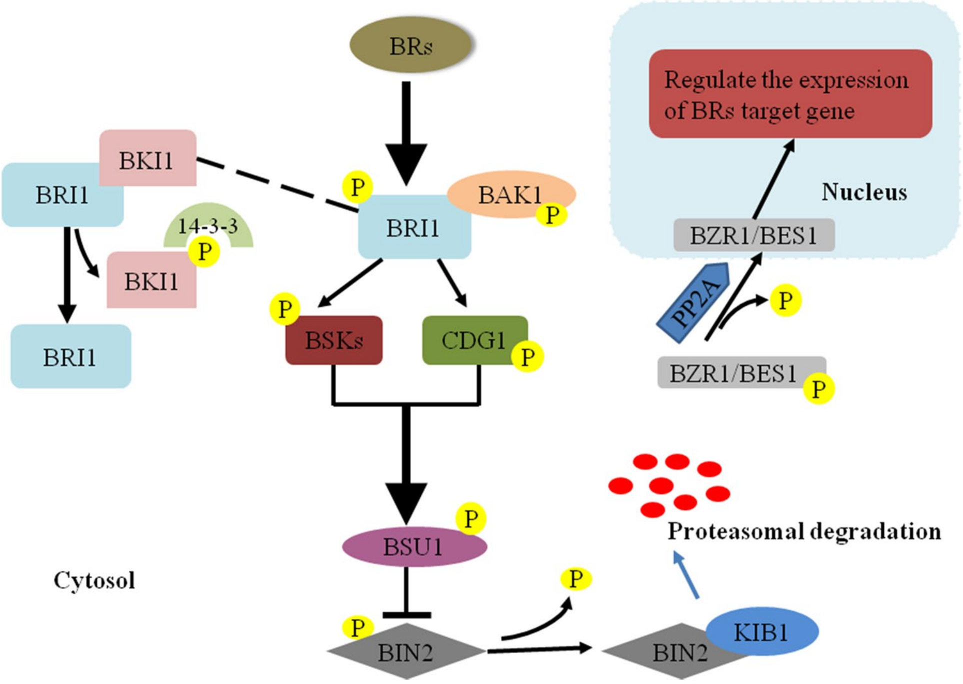

Fig. 1 Model of the signaling pathway of brassinosteroids (BRs) in *Arabidopsis*. In the presence of BRs, BRI1 (BRASSINOSTEROID INSENSITIVE 1) senses BRs signal through its extracellular domain, BRI1 binds to the BAK1 (BRI1-ASSOCIATED RECEPTOR KINASE 1), to form a complex and their activation stimulates BKI1, the inhibitor of BRI1, which is dissociated from the BRI1/BKI1 compounds, phosphorylated, separated from the plasma membrane, and bound to the 14-3-3 protein. After activation, BRI1 will transmit BRs signal to the downstream of the BSKs (BR-SIGNALING KINASE 1) and CDG1 (CONSTITUTIVE DIFFERENTIAL GROWTH 1). When BSKs and CDG1 are phosphorylated by BRI1, BSU1 (BRI1 SUPPRESSOR 1) will be subsequently phosphorylated. BSU1 is a serine/threonine protein phosphatase with the N-terminal kelch-repeat domain, which leads to BIN2 (BRASSINOSTEROID INSENSITIVE 2) dephosphorylation. BIN2 is restrained by KIB1 (KINK SUPPRESSED IN BZR1-1D), which prevents the association of BINs with BZR1/BES1 and facilitates its ubiquitination. BZR1/BES1 is rapidly dephosphorylated by PP2A (PHOSPHATASE 2A) and enters the nucleus. In collaboration with other transcription factors, BZR1/BES1 regulates the expression of BRs target genes

regulates the expression of the BR target genes and closely regulates various growth and development processes in plants (Wei and Li 2011). Li et al. (2020b) found a bHLH transcription factor BES1 directly involved in regulating the expression of auxin signal components SHY2 and PIN7 in the transformation region of the root. In addition, BRs and CKs antagonistically regulate the development of root meristem, which provides a theoretical basis for further research on the molecular mechanism of BRs involved in the regulation of root development (Li et al. 2020b).

Role of BRs in plant growth and development

BRs are a kind of steroid hormones that is widely present in the plant kingdom. These steroids have a unique biological effect on growth and development in plants (Trevisan et al. 2020; Mao et al. 2017). In the study of leaf inclination in rice, the typical phenotype of the dwarf mutant *d2* was that the upright leaf angle or left inclination, significantly reduced, and could be restored to its normal shape by exogenous BRs treatment (Hu et al. 2019). EBL (2,4-epibrassinolide) can also provide defense against various biotic and abiotic stresses as a type of brassinosteroids. EBL treatment of apricot fruit significantly inhibited the production rate of superoxide anion. It also reduced the content of malondialdehyde (MDA), the permeability of cell membranes, the incidence of disease, and significantly inhibited the expansion of the diameter of apricot fruit plaque (Shi et al. 2019). Transmission electron microscopy revealed that EBL treatment could maintain the structural integrity of organelles such as mitochondria and chloroplasts in apricot fruit during storage. EBL also plays an important role in response to heavy metal stress. Lead accumulation directly affects cell metabolism, leading to damage of the antioxidant enzyme defense system and free radical toxicity. Soares et al. (2020) found that the use of BRs reversed the effect of lead stress on seed germination and seedling growth of *Brassica juncea* (L.) Czern. & Coss. Especially 10^{-8} M EBL could increase the activity of superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and other antioxidant enzymes, thus overcoming the toxic effect of lead (Soares et al. 2020). Recently, scientists have made new advances about BRs in influencing plant growth and development. Zhang et al. (2020) used mass spectrometry analysis (LC/MS/MS), yeast hybrid (Y2H), double fluorescent complementary (BiFC), and the CRISPR/Cas9 experiments to provide more direct evidence for BAK1 mediated light signaling and improve the activity of catalase (CAT), which reduced the hydrogen peroxide (H_2O_2) levels and inhibited the growth of plants (Zhang et al. 2020). Li et al. (2020a) found that the starch in stomata of wild-type plants degraded rapidly in light, while in stomata of BRs-deficient and insensitive mutants, starch was enriched in large quantities and could not be degraded in light, making stomata unable to open normally. It is concluded that BRs promote starch degradation in guard cells and thereby promote stomatal opening through its interdependence with H_2O_2. This theory provides strong experimental support for the starch-sugar hypothesis (Li et al. 2020a). Wang et al. (2020a) found BRs play an important role in the process of etiolated seedlings in *Arabidopsis thaliana*, BRs mutant *det2-1* (*de-etiolated2*) relative to the wild type, containing excessive protochlorophyllide, the gain-of function mutant *bzr1-1D* (*brassinazole-resistant 1-1D*) suppressed the protochlorophyllide accumulation of *det2-1*, thereby promoting greening of etiolated seedlings. However, BRs-deletion and BRs-insensitive mutants grew in darkness for 4–8 days, and after exposure to light for 2 days, the green turning ability of seedlings was significantly lower than that of wild-type. Further analysis showed that BZR1, the Phytochrome-Interacting Factors 4 (PIF4) and GROWTH REGULATING FACTOR 7 (GRF7) coordinated the expression of genes encoding key enzymes in chlorophyll biosynthesis, and thus promoted the etiolated seedlings to become green (Wang et al. 2020a).

In plants, each hormone does not exist independently, and their role in plant growth and development cannot be viewed in isolation. BRs play an essential role in plant development but not independently. A complex network of plant hormones is formed by BRs interacting with other plant hormones to regulate the growth and development (Xu 2019). BRs control the biosynthesis of ETH mainly by regulating the enzyme activity necessary for the synthesis of ACS (ac-synthase enzyme) and ACO (ac-oxidase enzyme) (Hansen et al. 2009). The high content of BRs can reduce the activity of the main transcription factor BZR1/BES1 in the BR signaling pathway, improve the stability of ACC and ACS, prevent degradation by 26S proteasome, and activate the biosynthesis of ETH. However, the lower content of BRs increased the activity of BZR1/BES1, promoted the binding of BZR1/BES1 with ACS and ACC (1-aminocyclopropane-1-carboxylic acid) promoter regions, and prevented transcription, thus inhibiting the biosynthesis activity of ETH (Peres et al. 2019). In addition, exogenously applied BRs can promote fruit ripening. In *Solanum lycopersicum* culture, BRs can raise lycopene levels and reduce chlorophyll levels. *LePSY1* and *LeGLK2* are key regulators of lycopene biosynthesis and chloroplast development, respectively. After BRs treatment, *LePSY1* expression was significantly higher than that of the control group, while *LeGLK2* expression was significantly lower than that of the control group. However, *LePSY1* expression treated with BRZ (a brassinosteroid biosynthesis inhibitor) was slightly lower than that of the control group, and *LeGLK2* expression decreased somewhat (Zhu et al. 2015), which indicates that BRs are involved in ETH-mediated fruit ripening.

It has been observed that BRs and ABA present antagonistic effects. ABA decreased the activity of the BRs signaling pathway by upregulation of *BIN2* (BRASSINOSTEROID-INSENSITIVE 2), a negative regulator of the BRs signaling pathway. During plant growth and development, BRs inhibited ABA action by down-regulating the expression of PP2C (PROTEIN PHOSPHATASE 2C) family (Zhang et al. 2009). PP2C is a positive regulator of ABA signaling. ABA can also inhibit the CK signaling pathway by up-regulating the activity of CK oxidases/ dehydrogenases, leading to the inactivation of CK (Nishiyama et al. 2011). Other experiments have shown that BR-CK cross-talk may lead to changes in the source/sink relationship (Roitsch and Ehness 2000), increasing food yield, and enhancing tolerance to stress. CK up-regulates genes related to BR biosynthesis (*DFW4*) (Sahni et al. 2016; Li et al. 2018) and genes related to signaling pathways (*BRI1*, *BAK1*). BRs promote the biosynthesis of CK by up-regulating the activity of IPT (ISOPENTENYLTRANSFERASE). In a variety of bioassays representing diverse species, BRs have been shown to synergistically promote cell elongation when supplied with AUX (Mandava 1988). BRs has been shown to regulate the expression of *PIN* genes, which encode a vital component of auxin polar transport (Goda et al. 2004; Nemhauser et al. 2004; Nakamura et al. 2004). BRs and AUX signaling pathways converge at the level of transcriptional regulation of target genes with common regulatory elements: AUX regulates signal transduction via the ubiquitin ligase SCF^{TIR1}, AUX/IAA protein is degraded by proteasome through interaction with TIR1, and this relieves the repressive effects of AUX/IAAs on ARFs and resumes transcriptional regulation (Halliday 2004) (Fig. 2).

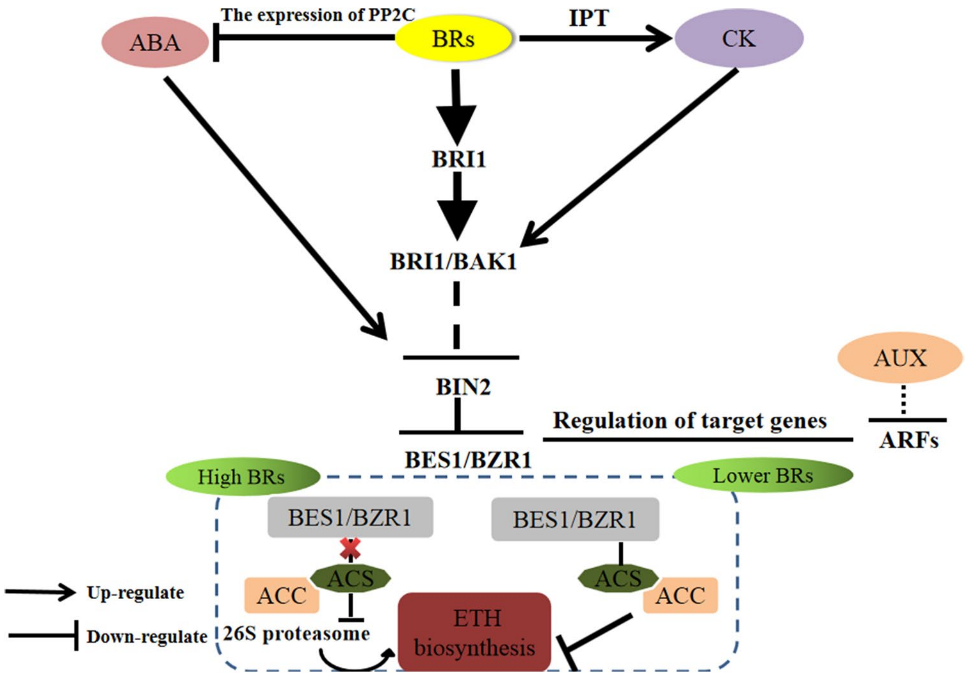

Fig. 2 A putative interplay between brassinosteroids (BRs), abscisic acid (ABA), cytokinin (CK), auxin (AUX) and ETH biosynthesis. ABA decreased the activity of BRs signaling pathway by upregulation of BIN2 (BRASSINOSTEROID-INSENSITIVE 2), a negative regulator of BRs signaling pathway. While during plant growth and development, BRs inhibited ABA action by down-regulating the expression of PP2C (PROTEIN PHOSPHATASE 2C) family, PP2C is a positive regulator of ABA signaling. CK up-regulates genes related to signaling pathways (*BRI1*, *BAK1*). And BRs promotes the biosynthesis of CK by up-regulating the activity of IPT (ISOPENTENYLTRANSFERASES). In addition, BRs and AUX signaling pathways converge at the level of transcriptional regulation of target genes with common regulatory elements. The effect of BRs on ETH biosynthesis is influenced by dose. The high content of BRs can reduce the activity of the main transcription factor BZR1/BES1 in the BRs signaling pathway, improve the stability of ACC (1-aminocyclopropane-1-carboxylic acid) and ACS (ACC synthase), prevent degradation by 26S proteasome, and then activate the biosynthesis of ETH. However, the lower content of BRs increased the activity of BZR1/BES1, promoted the binding of BZR1/BES1 with ACS and ACC promoter regions, and prevented transcription, thus inhibiting the biosynthesis activity of ETH

Application of brassinosteroid (BRs) in plant drought response

Drought stress is one of the main adverse factors affecting plant growth and metabolism (Todaka et al. 2015; Liu et al. 2012; Song and Wang 2015; Niether et al. 2020). It can destroy the enzyme system, lead to stomatal closure, reduce water content, decrease seed germination potential, and significantly diminish the length of roots and stems (Guo et al. 2018b; You et al. 2019). Severe drought stress will lead to plant death. Studies have shown that the application of exogenous substances can improve the growth conditions of plants to some extent (Liu and Chan 2015). The use of BRs can alleviate the damage caused by drought stress (Wang et al. 2019c). EBR processing has been shown to enhance the survival rate of *Brassica napus* and *Solanum lycopersicum* seedlings under drought condition. BR application can also increase the expression of related genes induced by drought stress (Kagale et al. 2007). Superoxide dismutase (SOD) is the primary active antioxidant substance in plant cells, which can convert O_2^- into H_2O_2 (Liu et al. 2017) and produce a defense response. Under drought conditions, BRs can improve soybean photosynthetic efficiency, cell water potential, soluble sugar, proline content, SOD activity, and reduce MDA content and leaf electrical permeability to promote plant growth (Zhang et al. 2008). Osmotic stress caused by drought can also obstruct the normal absorption of water by plant cells and affects the physiological functions of plants. Studies have shown that after treatment with BRs, water content and water potential increased, improving the viability of plants under low water potential (Yuan et al. 2010). These results have also been observed in sugar-beet plants under drought stress. A reduction of taproot weight was related to the degree of stress for the beets. After treatment with BRs, the application of BRs completely compensated for the decrease in biomass caused by mild drought stress. Increased biomass can lead to increased acid invertase activity in young leaves. This increase in acid invertase activity may provide more assimilative materials for plants (Schilling et al. 1991). EBR could increase the survival rate of *Arabidopsis thaliana* and *Brassica napus* seedlings subjected to drought stress (Krishna 2003), and significantly alleviated water stress and increased the RWC and PN of *Solanum lycopersicum* seedlings. EBR application also significantly increased ABA concentration and the activities of antioxidant enzymes, while it decreased the contents of H_2O_2 and MDA in tomato seedlings (Schilling et al. 1991).

Effect of brassinosteroid (BRs) on plant salt resistance

At present, more than 800 million hectares of land in the world is affected by salt, accounting for approximately 6% of the world's total land area (Munns 2005). Salinization is an important abiotic stress factor that severely affects crop production in many places, especially in arid and semi-arid regions. Salt stress can lead to many detrimental outcomes for plant and ecosystem health and function. Salt stress can affect plant growth in many aspects, such as photosynthesis (Feng et al. 2014; Kalaji et al. 2016; Sui et al. 2015; Li et al. 2012b; Zhang et al. 2010; Yan et al. 2013), rapid accumulation of reactive oxygen species (Wang et al. 2019b), stomatal conductance (Gs), intercellular CO_2 concentration (Ci) (Sui and Han 2014), seed germination rate (Song et al. 2017; Zhou et al. 2016; Guo et al. 2012, 2015, 2018a; Wang et al. 2015a; Xu et al. 2016; Liu et al. 2018; Zhang et al. 2015), cell membrane permeability (Li et al. 2012a; Song et al. 2016), biomolecular macromolecules, ion toxicity (Han et al. 2010; Feng et al. 2015; Zhao et al. 2010), and even osmotic stress (Tang et al. 2015). In particular, excessive salt concentration will reduce the water available in plants, cause cell dehydration, and threaten plant survival (Nxele et al. 2017). The application of hormones is an effective way to improve salt stress (Nimir et al. 2014). BRs play a significant role in plant salt response (Tanveer et al. 2018). BRs can be exogenously applied via at least three different techniques: seed treatment, root treatment, and foliar spray. Seed treatment and foliar spray are the most common of these methods (Ashraf et al. 2010). As an essential compatible solute, proline is involved in maintaining REDOX balance, ROS detoxification, and protecting protein structure (Han et al. 2014). It was established that BRs could promote the accumulation of proline and thus improve the activity of antioxidant enzymes by using chickpeas and mung beans as model organisms (Hayat et al. 2010).

In addition, to determine the roles of BR in stress tolerance, *SlBRI1-, SlBAK1-* and *SlDWARF*-silenced *Solanum lycopersicum* plants were challenged with salt stress. The *Solanum lycopersicum* were treated with 200 mM NaCl for 3 weeks and found that the plants grown under salt stress and pretreated with BRs presented better growth phenotype than plants pretreated with water alone (Zhu et al. 2016). Therefore, BRs could enhance the tolerance of *Solanum lycopersicum* seedlings with high salinity. In rice, pre-soaking seeds with NaCl and BRs (EBL or HBL) can alleviate the inhibition of salt on seed germination and seedling growth (Anuradha and Rao 2001). In barley plants grown under salt stress, it was determined that the application of BRs could significantly reduce salt-induced damage to nuclei and chloroplasts through the rooting medium (Kulaeva et al. 1991). By applying EBL to the leaves of two wheat varieties with different salt tolerance, Shahbaz and his colleagues (2008) found that the antioxidant systems of both types were affected. The activity of SOD, CAT and POD all increased under salt stress (Shahbaz et al. 2008). BRs play an important role in the regulation of salt tolerance in plants, but not in all cases. Liu et al. (2020) found that EBL (24-epibrassinolide) can promote putrescine (Put) transformation to triamine spermidine (Spd) and tetraamine spermine (Spm), so as to significantly improve the germination rate of rape seeds under salt stress. When the salt concentration is lower than 150 mM, the demand for BRs decreases and the same EBL concentration may be in an excessive state. Under this condition, EBL will promote the oxidative metabolism of Put and produce a large amount of H_2O_2, thus reducing the germination rate under salt stress. They defined this phenomenon as hormonal stress-level-dependent biphasic effects (SLDB). Therefore, the study put forward a new view that appropriately raise the level of BR or enhance BR signalling to improve plant salt resistance, either excessive or insufficient BR will have an adverse effect on the plant's salt tolerance (Liu et al. 2020).

Effects of brassinosteroid (BRs) on plant temperature response

Temperature is one of the leading environmental factors affecting plant growth. When plants are exposed to non-freezing temperatures below 12 °C for a period of time, and beyond the critical period, a physiological dysfunction known as "low- temperature damage" will occur (Seydpour and Sayyari 2015). Low-temperature stress usually leads to changes in plant morphology, physiology, biochemical metabolism, and cell structure (Krishna et al. 2017; Ma et al. 2018). Low-temperature stress can decrease plant growth, lead to photo-inhibition (Sui 2015; Zhuang et al. 2019). Sub-optimal temperatures can also cause leaf necrosis, discoloration, abnormal plant maturation, lipid cell membrane destruction (Cheng et al. 2014), blocked thylakoid electron transfer, increased MDA content, and increased relative conductivity (Chen et al. 2013). The accumulation of MDA can reflect the degree of cell membrane damage to a certain extent, and its accumulation rate can reflect the scavenging ability of free radicals of plants. Under adverse conditions, reactive oxygen species (ROS) will be produced in large quantities, breaking the balance and accumulating to a harmful degree, which will cause serious damage to the growth and development of plants. Plants have enzymes that can remove reactive oxygen species and free radicals (Li et al. 2010), such as SOD and POD. When applying BRs to KJD6 and KY131 at the rice booting stage, it was found that BRs could significantly improve SOD and POD activity, increase soluble sugar, soluble protein content, and reduce MDA content. Thus, low-temperature stress was alleviated. Grain number and seed setting rate were also mediated. The 1000-grain weight per panicle was increased, which maintained grain yield (Wang et al. 2020b). Thus, the application of BRs is an effective way to alleviate the plant cold stress response. Photosynthesis is the primary process of plant growth and organic matter accumulation. Low-temperatures often cause severe damage to the ultrastructure of chloroplasts by producing the following structural changes: chloroplast expansion, thylakoid decomposition, and a decrease in the number and volume of starch grains. Meanwhile, osmiophilic particles increase, forming the outer network vesicles, and the inner and outer membrane separation is visible (Yang et al. 2017; Li et al. 2016). Yang et al. (2013) showed that after 24-h treatment at low temperature, the inner and outer chloroplast membranes were almost completely separated in WT and the structure was distorted (Yang et al. 2013). Chl*a*, chl*b* and chl*a* + *b* contents were significantly decreased. Sun et al. (2019b) showed that under low-temperature conditions, the SPAD (Chlorophyll meter) value of the two selected maize varieties increased after spraying three different mass concentrations (T1, T2 and T3) of BRs (Sun et al. 2019b). With the increase of spraying concentration, the SPAD value of seedlings increased first and then decreased. In addition, MDA content and relative conductivity decreased.

High-temperature stress can also cause severe damage to physiological metabolism and growth and development of plants (Zhuang et al. 2020; Sun et al. 2019a; Wang et al. 2010, 2015b, 2019a). Heat damage to plants includes direct damage and indirect damage. Direct damage mainly manifests in protein denaturation, while indirect damage includes blocked photosynthesis of leaves, metabolic starvation, accumulation of toxic substances such as ethanol acetaldehyde, accelerated protein degradation, and reduced biological activity of nucleic acid (Zhang et al. 2018). Using heat-sensitive rice IR36 as the material, Chen et al. (2019) found that under the condition of 40 °C, the application of EBL could increase the expression of sucrose transporter genes *OsSUT1*, *OsSUT2* and *OsSUT4* in young ears, and reduce the content of superoxide anion, thus reducing the damage to the cell membrane (Chen et al. 2019).

Conclusions and opinions

As sessile living beings, plants have developed complex mechanisms during their evolution, with phytohormones playing crucial regulatory roles. These plant hormones are widely distributed in a variety of plants and are involved in the regulation of plant growth and the development of various stages. Currently, BRs have attracted increasing attention from phytologists and are believed to play a critical role in the growth and development of plants and stress alleviation. It is generally thought that BRs conduct a phosphorylation cascade reaction with transcription factors through the signal transduction pathway, transmitting BR-mediated signals to the nucleus, activating the transcription of BR-responsive genes in the nucleus, and thus driving cell growth. In addition, a large number of studies have shown that BRs can crosstalk with ABA, ETH and other plant hormones to jointly regulate various abiotic stresses. However, the mechanism of its biosynthesis has not been sufficiently studied; at present, the technology used to synthesize BRs artificially is very limited. Therefore, with the development of biotechnology, the production of cheap and efficient BRs will likely become a hot research topic.

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Author contributions SL, HZ and LL prepared the manuscript. NS and FW revised the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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