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Role of Brassinosteroids in Alleviating Various Abiotic and Biotic Stresses - A Review

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ABSTRACT

Brassinosteroids (BRs) are a new class of plant hormones with significant growth-promoting influence. BRs were first isolated and characterized from the pollen of *Brassica napus* L. Subsequently they were reported from 44 plants (9 monocots, 28 dicots, 5 gymnosperms, 1 pteridophyte and 1 alga) so far and are regarded probably ubiquitous in plant kingdom. BRs are considered as hormones with pleiotropic effects as they influence various developmental processes like growth, germination of seeds, rhizogenesis, flowering and senescence. BRs also confer resistance to plants against various abiotic stresses. The article reviews the work relating to their effect to alleviate various abiotic and biotic stresses.

Keywords: brassinosteroids, abiotic stresses, temperature stress, water stress, salinity stress, heavy metal stress, biotic stresses

CONTENTS

INTRODUCTION

Brassinosteroids (BRs) are a new type of phytohormones with significant growth promoting influence (Clouse and Sasse 1998; Rao *et al*. 2002; Tanak *et al* 2005; Xia *et al*. 2009a). Sasse (1997) and Bajguz (2009) aptly pointed out that BRs are ubiquitous in the plant kingdom as they were found in all plants tested (9 monocots, 28 dicots, 5 gymnosperms, 1 pteridophyte and 1 alga). But up till now approximately 60 related compounds have been identified (Sasse 1999; Haubrick and Assmann 2006). Dwarf and de-etiolated phenotypes and BR-deficient species of some *Arabidopsis* mutants were rescued by application of BRs (Bishop and Yokota 2001; Zeng *et al*. 2010). Abe (1989) reported that BRs not only increased the yield of sugarcane in the field, but also its tolerance to stresses and diseases, and even decreases to damages caused by herbicides. Even the role of BRs in ethylene production along with auxins and cytokinins in *Arabidopsis thaliana* has been recently reported (Arteca and Arteca 2008). The effect of BRs on the vegetative growth is particularly strong under adverse growing conditions (e.g. suboptimal temperature and salinity) therefore, BRs can be emphatically called as "stress hormones" (Núñez 2003).

The work with BR biosynthetic mutants in *Arabidopsis thaliana* (Li *et al*. 1996) and *Pisum sativum* (Nomura *et al*. 1997) provided strong evidences that BRs are essential for plant growth and development. They play a pivotal role even in the genes expressing the male fertility in *Arabidopsis thaliana* anther and pollen development (Ye *et al*. 2010). The growth inhibition of *Lepidium sativus* (cress) by brassinozole, the specific inhibitor of brassinolide (BL) synthesis was found reverted by the exogenous application of BL indicating the necessity of BRs for plant growth (Asami *et al*. 2000). BRs are plant hormones with pleiotropic effects as they regulate multiple physiological and developmental processes such as growth, seed germination, rhizogenesis, senescence, etc. and also confer resistance to plants against various abiotic stresses (Sasse 1997; Deng *et al*. 2007). Although BRs were initially identified based on their growth promoting activities, subsequent physiological and genetic studies revealed additional functions of BRs in regulating a wide range of processes, including source/sink relationship, seed germination, photosynthesis, senescence, photomorphogenesis, flowering and responses to abiotic and biotic stresses (Deng *et al*. 2007). Even Xia *et al*. (2009b) aptly stated that BRs induce plant tolerance to a wide spectrum of stresses.

BRs are a class of plant poly hydroxyl steroids that are ubiquitously distributed in the plant kingdom. These compounds, when applied to plants, improve their quality and yield. They have been further explored for stress-protective properties in plants against a number of stresses like chilling (Dhaubhadel *et al*. 1999; Liu *et al*. 2009), salt (Ozdemir *et al*. 2004), differential temperature (Mazorra *et al*. 2002), heat (Dhaubhadel *et al*. 2002) and heavy metals (Bajguz 2000; Janeczko *et al*. 2005; Ali *et al*. 2008) and oxidative (Xia *et al*. 2009b) stresses. The influence of BRs

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on the response of the antioxidative enzymes of plants under stress conditions has been studied recently (Cao *et al*. 2005; Hayat *et al*. 2007). The available data shows that the changes induced in the activity of antioxidative enzymes by BRs differed with plant species and stress conditions (Ozdemir *et al*. 2004; Almeida *et al*. 2005; Hayat *et al*. 2007).

Enhancement by BRs to resistance of plants to various environmental stresses has been evaluated with view of finding their practical application in agriculture (Takematsu *et al*. 1983). Greenhouse and field trials have shown that BRs help overcome stresses exerted by low and high temperature, drought and agricultural chemicals (Mandava 1988). Sasse (1991) reported that BRs interact with environmental signals such as light, growth and temperature and stimulate the synthesis of particular proteins. One of the most promising effects of BRs apart from growth stimulation is their ability to confer resistance to plant against various abiotic stresses. Various data provided consistent comments that exogenous BR treatment is effective in stressful rather than optimal conditions. It is not yet confirmed whether endogenous level of BRs in stressed and unstressed plants reflect this and there are many gaps in the knowledge (Sasse 1997; Krishna 2003). Du and Pooviah (2005) also reported that BRs are plant-specific steroid hormones that have an important role in coupling environmental factors, especially light, with plant growth and development, but the role of endogenous BRs changes in response to environmental stimuli is largely unknown. Even molecular analysis of *Arabidopsis* mutants displaying hypocotyl elongation defects in both dark and light revealed that deficiencies in BR biosynthesis and signaling permit de-repression of stress induced genes in light (Salcherk *et al*. 1998). The present paper reviews the amelioration of various abiotic and biotic stresses like high and low temperature, drought, salinity and pathogens by the application of BRs to different crop plants.

BRs AND HIGH TEMPERATURE STRESS

24-Epibrassinolide (24-epiBL) increased the tolerance to high temperature stress in brome grass cell suspension cultures significantly following exposure to high temperature stress and also increased the accumulation of ABA-inducible heat stable proteins (Wilen *et al*. 1995). BRs had a promotive effect on high temperature tolerance in wheat leaves (Kuleava *et al*. 1991) at 40°C and Kuleava *et al.* (1989) contributed about the understanding of the mechanism of the anti-stress activity of BR-influenced protein synthesis in wheat leaves at normal and high temperatures. Kuleava *et al.* (1991) examined the effects of BRs on protein synthesis in wheat leaves under normal and heat shock temperatures and observed that BRs induce *de novo* poly peptide synthesis under normal temperature which corresponds to heat shock proteins. BRs also stimulated the formation heat shock granules in the cytoplasm. BRs also enhanced the photosynthetic rate and nitrate reductase activity and the BRs induced increase in photosynthesis and nitrate reductase activity could be due to the improvement in leaf water balance as indicated by increase in relative water content under stress (Kuleava *et al*. 1991). Dhaubhadel *et al.* (1999) also reported that 24-epiBL increased the basic thermo tolerance of *Brassica napus* and tomato seedlings. The protection of cucumber plants against heat stress after treatment with BRs was observed at high temperature (40^{o}C). However the work conducted by Upadhyaya *et al.* (1991) did not support the hypothesis that BRs confer heat shock tolerance to moth bean where young seedlings of moth bean supplemented with 24-epiBL solutions and exposure to 48°C only led to increased damage like solute leakage and lipid peroxidation. 28-Homobrassinolide (HomoBL) was found to mitigate the heat stress in *in vitro* growth of apical meristems of banana shoots (Nasser 2004). 24-EpiBL treated tomato pollen exhibited higher *in vitro* pollen germination and enhanced tube growth under high temperature stress (Singh and Shono 2003). The physiological and molecular effects of tomato plants treated with 24-epiBL are more tolerant to high temperature than untreated plants (Singh and Shono 2005). An analysis of mitochondrial small heat shock proteins (mt-sHSPs) in tomato leaves by western blotting revealed that mt-sHSPs did not preferentially accumulate in 24-epiBL treated plants at 25°C. However, treatment of plants at 38°C induced much more accumulation of mt-sHSPs in epiBL treated than in untreated plants (Singh and Shono 2005). BRs play a dominant role in the protection of the translational machinery and heat-shock protein synthesis following thermal stress (Dhaubhadel *et al.* 2002). BRs were found to increase the photosynthetic efficiency by enhancing the CO_2 fixation and the antioxidative system activities in *Lycopersicon esculentum* by alleviating the heat stress (Ogweno *et al.* 2008). Winter wheat (*Triticum hybernum*) varieties viz. 'Ebi', 'Estica' and 'Samanta' grown under high temperature stress supplemented with 24-epiBL were found to show reduced negative effect of the monitored stress and increased dry matter content and yields (Hnilicka *et al.* 2007).

BRs AND LOW TEMPERATURE/CHILLING STRESS

In maize (*Zea mays*) seedlings, BRs enhanced the greening of etiolated leaves at low temperature in light, and promoted the growth recovery after chilling treatment (He *et al.* 1991). BR-treated tomato (*Lycopersicon esculentum*) and rice (*Oryza sativa*) plants grew better than control plants under low temperature conditions as under optimal conditions for growth (Kamuro and Takatsuto 1999). A significant influence of BRs on the growth recovery of maize (He *et al*. 1991) and cucumber (Katsumi 1991) seedlings after chilling has also been demonstrated. BRs are involved in increasing tolerance to low temperature stress in brome grass (Wilen *et al*. 1995), chilling resistance in rice seedlings (Wang and Zang 1993) and cold stress tolerance in rice plants during grain filling stage was also reported by Hirai *et al.* (1991). In rice, 24-epiBR treatment reduced electrolyte leakage during chilling at 1-5°C, showed the decrease in the activity of super oxide dismutase, the level of ATP and proline increased and the enhanced resistance was attributed to BR-induced effects on membrane stability and osmoregulation (Wang and Zang 1993). BL and castasterone promoted germination and the early growth of direct sown rice seedlings by promoting the cell elongation under low temperature stress around 15°C and the leaf spraying of BL on rice seedlings at the 4^{th} leaf stage increased the plant height and the fresh weight of the tops and the roots (Fujii and Saka 2002). BRs also alleviated low irradiance stress in rice by increasing the accumulation of chlorophylls and content of soluble proteins (Maibanyse *et al.* 1990). 24-EpiBL broke the bud dormancy of the regenerated bulblets of *Lilium japonicum* under cold temperature stress where, large bulblets pre-treated at 4°C for 10 weeks and cultured on media containing 0.1 and 1 ppm epiBL under light showed 100% leaf emergence (Ohshiro *et al*. 1997). Watanabe *et al.* (1998) experimentally proved that spraying 0.01 ppm of Ts303, a BL analogue before 7 days of flowering promoted fruit set in 15-year-old trees of Japanese persimmon and 12 year old grape old vines and also reported about the reduced defoliation and fruit drop in citrus trees under cold damage. Cuttings of grapes dipped in 0.01 ppm of Ts303 further improved the rooting in grape cuttings under cold stress (Watanabe *et al.* 1998). BL increased the grain ripening of rice plants under low temperature (Hirai *et al*. 1991). Lately a proteomics study also revealed about the ameliorative effect of BRs under chilling stress in mung bean epicotyls (Huang *et al*. 2006).

BRs AND DROUGHT/WATER STRESS

BRs have been suggested to increase the resistance of plants to a variety of stresses, including water stress based on application studies, where exogenously applied bioactive BRs have been shown to improve various aspects of plant growth under water stress conditions (Sairam 1994; Jager *et al.* 2008). Schilling *et al.* (1991) examined the effects of 28-homoBL on sugar beet under drought stress and found an increase of tap root mass under drought stress, and also an increase in sucrose content and sucrose yield was observed, where there was no effect under non-stress conditions. Sairam (1994) observed enhanced soluble protein content, relative water content, nitrate reductase activity, chlorophyll content and photosynthesis under irrigated and moisture stress conditions by treatment with 28-homoBL in two wheat varieties. He also observed improved membrane stability which has beneficial effects like higher leaf area, biomass production, grain yield and yield related parameters. 28-HomoBL application as seed treatment (0.01 and 0.05 ppm) resulted in increased germination, amylase activity and total proteins in 48th old seedling and shoot length in 96th old seedling with and without PEG-6000 induced moisture stress in wheat (Sairam *et al*. 1996). The increase in seed yield was associated with increase in ear number per plant, grain number per ear, 1000-grain weight and harvest index. Treatment with 24-epiBL enhanced the growth of juvenile gram (*Cicer arientium*) plants (Singh *et al.* 1993) and increased the *in situ* relative water content and decreased the stomatal transpiration rate in sorghum (*Sorghum vulgare*) (Xu *et al*. 1994a, 1994b) in conditions of water stress. Semi-dry pretreatment of seeds with epiBL showed promising improvement under drought stress in spring wheat by increased germination rate and improved tissue hydration by reducing the transpiration rate and also increased osmotic pressure of the cell sap as well as the rate of photosynthesis (Prusakava *et al*. 2000). The treatment of BRs to tomato (*Lycopersicon esculentum*) seedlings under water stress resulted in enhanced stomatal conductance and net photosynthetic rate suggesting that the amelioration of the drought stress of tomato seedlings may be due to epiBL-induced inhibition of endogenous ABA (Yuan *et al*. 2010). BR at 12.5 mg^{l-1} increased drought resistance of the drought resistant variety (PAN 6043) and drought sensitive variety (SC 701) of two maize cutivars (Li and van Staden 1998a) and further improved the antioxidative system of the two maize cultivars (Li and van Staden 1998b; Li *et al*. 1998). Foliar application of 0.4 ppm BRs at pre-flowering stage and pod development stage increased oil yield of mustard (*Brassica juncea*) under water deficit conditions (Kumawat *et al.* 1997). DAA-6, a BR analogue exhibited a promotive effect on development of sugarcane (*Saccharum officinarum*) plantlets regenerated from callus subjected to water stress (Gonzalez and Gianza 1997) BRs were found to alleviate water/osmotic stress in seed germination and seedling growth of sorghum (Vardhini and Rao 2003; Vardhini and Rao 2005). This alleviation also resulted in enhanced metabolite contents like soluble proteins and free proline. The effects of BRs on tomato plants grown under water stress recently revealed that BRs considerably alleviated oxidative damage that occurred under drought stress by increasing the activities of antioxidant enzymes [peroxidase (POD: EC 1.11.1.7), catalase (CAT: EC 1.11.1.6), ascorbate peroxidase (APX: EC 1.11.1.11), glutathione reductase (GR: EC 1.6.4.2), and superoxide dismutase (SOD: EC 1.15.1.1)] and changing isoenzymes pattern with higher intensity as well as increases in proline and protein content emphasizing that 24-epiBL may have a role in the mitigation of damage caused by water stress (Behnamnia *et al*. 2009a, 2009b). 24-EpiBL reduced the negative effect of drought stress and increased the dry matter content and yields in winter varieties viz., Ebi, Estica and Samanta (Hnilicka *et al* 2007). BRs further strengthen drought resistance and show favorable effects on plant growth and yield under soil water deficient conditions by increasing the nodulation and phytochrome content in French bean (Upreti and Murti 2004).

BRs AND SALINITY STRESS

The ability of BRs, BL, 24-epiBL and 28-homoBL to counteract the salinity stress induced growth inhibition of ground nut (*Arachis hypogaea* L.) was reported by Vardhini and Rao (1997). BRs not only alleviated the NaCl-induced stress effect, but also further increased the percentage of seed germination and seedling growth in terms of seedling length, fresh weight and dry weight (Vardhini and Rao 1997). 24-EpiBL produced a protective effect on leaf cells ultra structure in leaves placed under saline stress (0.5 M NaCl) and prevented nuclei and chloroplast degradation (Kuleava *et al*. 1991). Improved salt tolerance below 50 mM NaCl after BR treatment was confirmed in rice (Takeuchi 1992). In the case of *Eucalyptus camuldensis*, treatment of seeds with 24-epiBL resulted in increase in seed germination under saline conditions of 50 mM NaCl (Sasse *et al*. 1995). Similarly, 24-epiBL and 28-homoBL were found to alleviate the salinity induced inhibition of germination and seedling growth in rice (Anuradha and Rao 2001) and also improved the photosynthetic pigment levels and nitrate reductase activity (Anuradha and Rao 2003). EpiBL-55 at 0.0001% exhibited anti-stress activity induced by salinity in barley root tip cells by stimulating mitotic activity and growth processes and also reducing the frequency of chromosome aberrations (Khrustaleva *et al.* 1995). EpiBL reduced the salinity induced accumulation of abscisic acid and wheat germ agglutinin about 50% and restored partial growth recovery in the 4-day roots of wheat under 0.3 M salt stress by increasing 2-fold accumulation of lectin (Shakirova and Bezrukova 1998). BL was found to remove the inhibitory effect of salt stress on the growth of rice plants (Hamada 1986). Similarly seed treatment of barley with epiBL and homoBL removed the inhibitory effect of salt stress on the growth of barley (Kulaeva *et al*. 1991; Bokebayeva and Khripach 1993). 28-HomoBL was found to alleviate oxidative stress in salt treated maize plants by acting on the oxidative enzymes like SOD, CAT, GR, APX and POD (Arora *et al.* 2008). The studies of 28-homoBLand 24-epiBL on the growth and antioxidant enzyme activities in rice seedlings under salinity stress demonstrated the ameliorating ability of BRs in scavenging the reactive oxygen species, thereby reducing the oxidative stress induced by NaCl and further enhanced the growth of rice seedlings (Anuradha and Rao 2007). Exogenous application of BRs as foliar spray increased the growth of wheat plants grown under saline stress (Shahabaz and Ashraf 2007). The pretreatment of wheat seedling (*Triticum aestivum* L.) with 24-epiBL on the growth and hormone status of plants under the influence of NaCl clearly exhibited that 24-epiBL increases the cytokinins and decrease abscisic acid (Avalbaev *et al*. 2010). Even the endogenous BRs are positively involved in plants' responses to salt stress in BR-deficient *Arabidopsis* mutants like *det-2-1* and *bin2-1*where the external supplementation of BRs clearly displayed altered salt tolerance and increased the growth and photosynthetic activity (Zeng *et al*. 2010).

BRs AND HEAVY METAL STRESS

Heavy metals have become essential environmental contaminants due to rapid industrialization and urbanization. Increasing levels of heavy metals in the environment affect various physiological and biochemical processes in plants. The toxicity symptoms observed in the presence of excess amounts of heavy metals may be due to interactions at the cellular/molecular level. Recently, the studies on the physiological properties of BRs and their ability to increase resistance in barley plants to the accumulation of heavy metals and radioactive elements was studied by Khripach *et al* (2000). Pre-soaking of tomato seeds with BRs decreased the uptake of zinc and cadmium in tomato fruits (Kripach *et al.* 1999). BRs also reduced lead contents in sugar beet plants (Khripach *et al*. 1999). Toxicity may be due to binding of metals to sulphydryl groups in proteins, thus leading to inhibition of the activity or disruption of the structure (Hall 2002). The ability of BRs to regulate cell membrane permeability and transport of ions has found an agricultural application in the areas polluted with heavy metals.

Earlier reports showed that treatment with 24-epiBL reduced significantly the absorption of heavy metals in barley, sugarbeet, tomato and radish (Khripach *et al.* 1999). Bajguz (2000) reported that 24-epiBL applied at the concentration range of 10^{-6}–10^{-4} M in combination with heavy metals blocked metal accumulation in cells of the alga *Chlorella vulgaris*. The reduction of toxicity by BRs is associated with enhanced levels of soluble proteins and nucleic acids with the increasing activity of ATPase (an enzyme responsible for acid secretion and changes in membrane level) (Bajguz 2002). BRs were found to bind to the membrane proteins and scavenge the reactive oxygen species which are generated by heavy metal toxicity, thereby reducing the membrane destruction that results from AOS-induced oxidative damage (Cao *et al*. 2005). After binding to the membrane proteins BRs may enhance the enzyme and metabolic activities, thus detoxifying heavy metals in plants. It is a proven fact that involvement of BRs helps in lowering the uptake of heavy metals, thus reducing their toxicity in plants.

The anti-stress and immuno modulatory activities of BRs have made them proper candidates for third generation chemicals, which are natural and ecofriendly. The protective effects of BRs have been reported especially under unfavorable low temperature conditions (Takematsu *et al.* 1986). Abdullahi *et al.* (2003) reported that BL stimulated growth in *Phaseolus aurens* (green bean) during aluminum stress. The studies of 24-epiBL on the growth, antioxidant enzyme activities, lipid peroxidation and total glutathione content of rice seedlings subjected to Ni stress was associated with increase in CAT and SOD and decrease in POD activity as well as increase in the glutathione content (Archana *et al.* 2006). Bhardwaj *et al.* (2007) also reported that 28-HomoBL treatment to seedlings of *Zea mays* L. (var. 'Partap-1') grown under Ni stress increased the GR activity.

The effect of 24-epiBL and 28-homoBL on seed germination, seedling growth of radish (*Raphanus sativus* L.) was studied under cadmium and lead toxicity (Anuradha and Rao 2007). BR supplementation alleviated the toxic effect of the two heavy metals and increased the percentage of seed germination and seedling growth in radish. The amelioration of seedling growth by BRs under metal toxicity was associated with enhanced levels of free proline and increased activities of antioxidant enzymes CAT, POD, SOD, ascorbic peroxidase and guaiacol peroxidase.

BRs AND BIOTIC STRESSES

Apart from the regular abiotic stresses BRs even were found to confer resistance to biotic stresses. BRs confer resistance to a broad range of diseases in tobacco and rice (Nakashita *et al*. 2003). BRs also enhanced plant resistance to diseases (Korableva *et al.* 1991; Platonova *et al.* 1993). Roth *et al.* (2000) proved the involvement of BRs in the plant extracts of *Lychnis viscaria* seeds to elicit or mediate the activation of defense mechanism by studying the application BR containing aqueous extracts of *Lychnis viscaria* in concentrations from 0.5-10 mg/L (dry weight of extract) which enhanced the resistance of tobacco, cucumber and tomato to viral and fungal pathogens like powdery mildew, *Phytophthora*, etc. compared to water treated control seeds. Involvement of BRs, time course of POD induction and changes of apoplastic protein patterns revealed by SDS–PAGE indicated an earlier triggering of defense responses after plant–extract treatment and pathogen attack that are probably responsible for increased resistance. BR treatment decreased the level of *Phytophthora infectans* and other diseases of potato plant (Korableva *et al*. 1991; Platonova *et al*. 1993). Khripach *et al.* (1996) reported that foliar spray of BR solutions in doses about 10-20 mg/ha at the beginning of the budding stage was more efficient in reducing the infection of *Phytophthora* and the protective type of BR activity depended upon the method and time of BR application and was connected with the different stimulating points of either the plant or pathogen. EpiBL enhanced resistance of barley plants to leaf diseases induced by mixed fungi (Pshenichnaya *et al*. 1997; Volynets *et al*. 1997b) and this effect was accompanied by an increase in grain yield that was significant even at a dose of 5 mg/ha of epiBL. Churikova and Vladimirova (1997) reported about the protective effect of epiBL against fungi in cucumber plants where epiBL caused an enhancement in yield and increased the activities of certain enzymes like POD and PPO where epiBL was applied twice. First, the seeds were soaked in a 0.1 mg/L solution of epiBL and then the plants were sprayed at a dose of 25 mg/ha in the flowering stage. The ability of BRs to stimulate resistance to various virus infection of potato was reported by Bobrick (1995) and Rodkin *et al.* (1997). Potato starting material, produced from cuttings was cultured in a medium that contained BRs which resulted in significant increase of all the parameters that characterized growth and also exhibited an increase in yield of 56% over control plants.

BR application to crops helps to overcome environmental stresses (Yakota and Takahashi 1986) and increase in crop yields through their growth-promoting and anti-stress effects (Mandava 1988). Recently it has been reported that BRs are playing another unique role like protecting crops from the toxicity of herbicides, fungicides and insecticides in cucumber (Xia *et al.* 2009c). The study of molecular mechanisms by which BRs promote stress tolerance and regulate growth is therefore of considerable importance particularly if these compounds are to be used for practical application in agriculture.

Kamuro and Takatsuto (1999), who were impressed by the ability of BRs to increase resistance of plant against various environmental stresses stated that "*the role of BRs in protecting plants against environmental stresses will be an important research theme for clarifying the mode of action of BRs and may contribute greatly to the usage of BRs in agricultural production*". Future progress in the analysis of *Arabidopsis thaliana* mutants, defective in BR biosynthesis or signaling is expected to give insight into the evolution of steroid hormone regulation in eukaryotes, as well as the mechanisms by which BRs control basic function such as cell elongation, morphogenesis and stress responses (Sczekers and Koncz 1998) and even anther and pollen development (Ye *et al.* 2010).

The growth-promoting and other regulatory properties of BRs in plants are well known (Khripach *et al.* 1999). Further, BRs protect plants from the toxic action of reactive oxygen species either by directly acting on them or indirectly by regulating the enzymatic and non-enzymatic systems of plants. Heavy metals-generated ROS could thus be alleviated by BL treatments (Almeida *et al* 2005; Hayat *et al*. 2007). Application of BRs has been shown to involve the major antioxidative enzymes resulting in increased relative water content, nitrate reductase activity, chlorophyll content, and photosynthesis and membrane stability under various stress conditions (Nunez *et al*. 2003; Ozdemir *et al.* 2004; Janeczko *et al*. 2005; Hayat *et al*. 2007; Kagale *et al.* 2007). These beneficial effects led to higher leaf area, biomass production, grain yield and yield-related parameters in the treated plants. Increased water uptake, membrane stability and higher carbon dioxide and nitrogen assimilation rates under stress seemed to be related to homoBL-induced stress tolerance (Hayat *et al*. 2007; Kagale *et al*. 2007). Lately, Li *et al*. (2009) also emphatically stated that "*Treatment of seedlings with BL may be a useful management tool for afforestation projects in arid and semiarid areas*".

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