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REVIEW ARTICLE: BRASSINOSTEROIDS MEDIATED PLANT RESPONSES TO HEAVY METAL STRESS

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Abstract

Being sessile organisms, plants confronts several abiotic factors such as drought, salinity, heavy metal, extreme temperatures etc. Among these, heavy metal stress is adverse factor because their excessive release from industrial wastes severely affects plant growth, ultimately results in poor food quality and yield therefore, improving food superiority against stress conditions is important to fulfill the growing world population food requirement. In this context, the usage of brassinosteroids (BRs) have gained an imperative appearance in the field of plant systems because they appear beneficial in mitigating various environmental stresses including heavy metal stress. BRs, naturally occurring plant steroidal hormones which regulate various morphological, biochemical, physiological and molecular assets of the plants with great biological activity. BRs beneficial in mitigating heavy metals stress in plants by improving plant growth, photosynthetic functioning, nutrients balance, also by diminishing the generation of reactive oxygen species (ROS) by stimulating the antioxidative and non-enzymatic antioxidants and improved the amount of osmo-proctectants and soluble proteins. This review mainly provides an insight into BRs mediated alleviation of plant morphological, biochemical and physiological assets under heavy metal stress.

Key words: Brassinosteroids, biological, biochemical, physiological.

Introduction

Soil and H_2O polluted with heavy metals due to anthropogenic activities has become a major threat to plants in recent times and their high exposure to plants affects plant growth, productivity and also altered the sustainability of agricultural production (Bhat *et al.,* 2019). Heavy metals contaminated soil causes ecological trouble and menace flora and fauna because of their potential toxicity and high persistence (do Nascimento and Xing, 2006; Adrees *et al.,* 2015). Heavy metal stress disrupts plant functioning by altering the cellular activities of proteins, lipids, nucleic acids and cellular apparatuses of thylakoid membranes (Kim *et al.,* 2014). Level of heavy metal toxicity based on metal bioavailability, their uptake, transport, bioaccumulation, storage, immobilization and also depends upon plants avoidance and tolerance strategies (Rajewska *et al.,* 2016). Plants have several protective strategies to cope with heavy metal stress detoxification, phytoremediation of metals, stimulation of plant antioxidant defense system, and chelation (Vamerali *et al.,* 2010; Zhang *et al.,* 2013; Zhou *et al.,* 2013). Some 2^0 metabolites and some plant hormones like auxin, abscisic acid, ethylene, jasmonic acid and plant steroids are also useful in alleviating metal toxicity (Sharma *et al.,* 2016).

Among steroids, BRs are a group of polyhydroxylated plant steroid hormones which shows varied functions in almost all phases of the plant course of life, regulating activities such as cell division, cell expansion, seed germination, etiolation, stomata movement, flowering, senescence and fertility and hence, regarded as vital governors of various phases of growth (Duran and Zipfel, 2015). They are found in minute concentrations in almost every part of the plant like seeds, roots, shoots, leaves, pollen, fruits, flower buds and vascular cambium (Bajguz and Piotrowska-Niczyporuk, 2014). BRs not only coordinate various plant morphogenetic and physiological assets but also aids in decreasing adverse effects caused by various stress factors. Heavy metal stress results in

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generation of plethora of ROS such as superoxide ($O2^{\cdot -}$), hydrogen peroxide (H_2O_2) and hydroxyl ion ($OH^{.}$) radicals (Marschner, 1995) which alters membrane integrity through lipid peroxidation and also disturbs the cellular metabolism, however BRs supplementation mitigate metal toxicity by improving functioning of various components of antioxidants system, increasing metabolic functioning (Shahzad *et al.,* 2018), improved level of soluble proteins and macromolecules (Ramakrishna and Rao, 2012; Madhan *et al.,* 2014).

Brassinosteroids signaling in plants

BRs are cell-surface receptors of leucine-rich motif receptor kinases BRASSINOSTEROID INSENSITIVE 1 (BRI1), that coordinates with co-receptor BRI1 ASSOCIATED RECEPTOR KINASE 1 (BAK1) and go through phosphorylation and dephosphorylations to transmit signal towards the nucleus and regulate gene expression of different physiological functions (Belkhadir and Jaillais, 2015; Fig. 1). Recombinant cytoplasmic domains of BRI1 and BAK1 auto-phosphorylate not only serine and threonine, but also auto-phosphorylate tyrosine, signifying that these kinases are dual-specific in function (Oh *et al.,* 2009). Another protein, BKI1 (BRI1 kinase inhibitor 1) functions as a negative regulator in BR signaling (Wang and Chory, 2006) which block the downstream BR signaling by preventing the association of BRI1 with BAK1 and other BRI1 substrates (Li and Jin, 2007). BR association with receptor BRI1 stimulates a signal cascade for instance BRI1 autophosphorylation in its C-terminal end, association of BRI1 with another LRR-RLK, BAK1 and dissociation of BKI1 (Wang and Chory, 2006), which possibly increases signaling outcome through reciprocal BRI1 transphosphorylation (Wang *et al.,* 2008). Three homologous plasma membrane bound BR-signaling kinases *i.e.* BSK1, BSK2, and BSK3 were found in plants which acts as the substrates for BRI1 kinase (Tang *et al.,* 2008) and these BSKs are vigorously included in prompting BR signaling downstream of BRI1 (Ashraf *et al.,* 2010). If there is fault in BRs biosynthesis or BRs mediated signaling, then aberrations were observed in the growth and physiology of plants (Ahanger *et al.,* 2020).

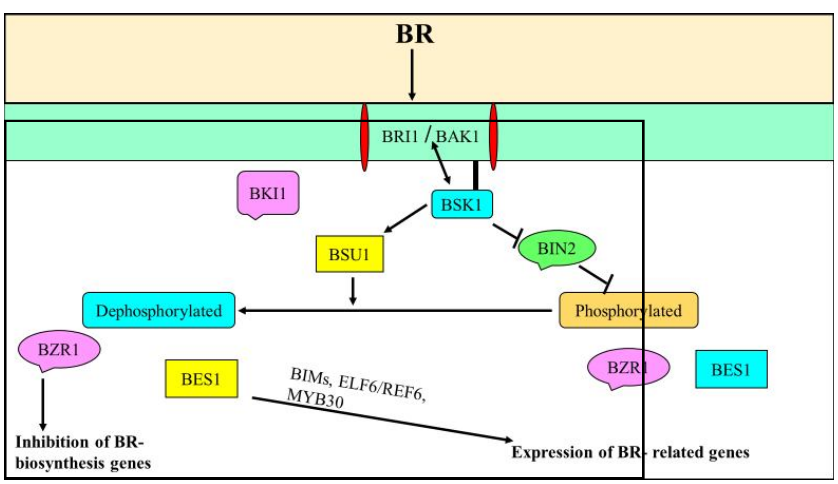

Fig. 1: Diagrammatic representation of Brassinosteroids signaling in plants (modified after Ashraf *et al.,* 2010).

Brassinosteroids induced mechanism to alleviate heavy metal stress in plants

BRs and plant growth

Certain heavy metals like Cu, Zn at low amounts needed by plants for their growth and maintenance which turn toxic to them at high concentrations whereas, some of the nonessential metals (Cd, Hg, Cr etc.) become toxic even at very low concentrations and alters normal growth process of plants. For instance, wheat plants show reduced root and shoot growth under low levels of Cd (Ahmad *et al.,* 2012). BRs are found to have a positive influence on the plant morphology and their exogenous application improves growth parameters such as plant architecture, biomass, leaf expansion, hypocotyl or shoot elongation, seed development, yield and quality. 24-EBL improved heavy metal induced impairment of growth by adopting multiple mechanisms such as regulating cell division and expansion by activating related genes (Hu *et al.,* 2000; Catterou *et al.,* 2001); reducing metal uptake and biosorbing heavy metals via ion exchange and formation of phytochelatins under metal stress (Bajguz, 2002). Presoaking of *Brassica juncea* seeds in 24-EBR alleviate Co induced toxicity by enhancing germination percentage, root and stem length (Sharma and Bhardwaj, 2007) whereas homo-brassinolide treatment to *Brassica juncea* escalates root and stem length, area of leaves as well as the plant biomass under Cu induced stress (Fariduddin, 2009).

BRs and photosynthesis

Heavy metal induced toxicity affects photosynthesis which is the most important metabolic process in plants by damaging the chloroplast, its membranes, photosynthetic enzymes, PS II, chlorophyll content, ultimately lessening the photosynthetic efficiency. BRs improved chlorophyll and carotenoid content and membrane stability via activation of CHLASE gene (chlorophyllase enzyme) and PSY gene (phytoene synthase) respectively under Pb stress in *Brassica juncea* and Cd stress in *Raphanus sativus* (Farriddudin *et al.,* 2003;

Anuradha and Rao, 2009; Kohli *et al.,* 2017). BRs also uplift CO_2 assimilation rate by activation of Rubisco through regulating RCA (Rubisco activase) gene mediated carboxylation capacity and other C3 cycle enzymes like those associated with regeneration of Rubisco by maintaining cellular redox status in *Cucumis sativus* (Yu *et al.,* 2004; Xia *et al.,* 2009). Cu toxicity effects on electron transport chains catalyzed by with or without involvement of PS II get alleviated by treatment with EBR in *Brassica juncea* along with enhancement of stomatal conductance and transpiration rate (Bali *et al.,* 2016). Maintenance of organization of grana and thylakoids in chloroplasts of *Nicotiana tabacum* upon EBR foliar spray reverses the effects of chloroplast damage under chromium stress (Ahammed *et al.,* 2020).

BRs and antioxidant defense system & osmolytes accumulation

Plants contains several defense apparatuses to stand against heavy metal stress such as stimulation of intricate metabolic processes including antioxidant defense system which scavenges ROS generation (Vardhini and Anjum, 2015), therefore plant hormones such as BRs activate plant antioxidant system against metal toxicity (Ramakrishna and Rao, 2012; Kapoor *et al.,* 2014). BRs decreased the metal uptake because of its capability to maintain ions uptake into plant cells (Fariduddin *et al.,* 2014) and also suppressed the ROS induced lipids degradation and improved antioxidative enzymes activities under metal stress (Soares *et al.,* 2016). EBL alleviated antimony (Sb) toxicity by reducing malondialdehyde (MDA) amount and enhancing antioxidative enzymes action of superoxide dismutase (SOD), POD and catalase (CAT) in *Arabidopsis* (Wu *et al.,* 2019) and reason for enhanced metal tolerance by EBL is because of activation of gene expression of antioxidants genes (Sharma *et al.,* 2016) and their ability to block metal uptake by plants (Sharma and Bhardwaj, 2007). Application of 24-EBR improved the Zn induced toxicity in soybean plants by elevating the functioning of SOD, ascorbate peroxidase (APX) and peroxidase (POX), CAT enzymes (dos Santos *et al.,* 2020).

Plant osmolytes beneficial in protecting the cellular components from different abiotic and biotic stresses (Giri, 2011), assist the plants to sustain severe osmotic stress (Singh *et al.,* 2015) and diminishes level of ROS formation (Alia *et al.,* 1993). 24-EBL application under Cu and Cr stress enhanced the proline content in *Raphanus sativus* (Choudhary *et al.,* 2010; Sharma *et al.,* 2011) and this improved level of proline is due to the increased expression of proline biosynthetic genes (Lalotra *et al.,* 2017). 24-EBL improved the proline amount against Ni stress however, this escalation in proline amount is because of the activation of D^1 pyrroline- 5-carboxylate synthase which is associated with proline synthesis under stressed conditions in *Raphanus sativus* (Sharma *et al.,* 2011). Glycine betaine (GB) is helpful in protecting photosynthetic associated components and enzymes that are crucial for e^- transport in the thylakoid membrane under stress conditions (Park *et al.,* 2007). 24-EBL increased the synthesis of proline and GB in Hg treated chickpea plants which further resulted in improved plant growth, optimal regulation of photosynthetic machinery and formation of photo-assimilates (Ahmad *et al.,* 2018). This BRs induced GB synthesis is because of increased activity of the betaine aldehyde dehydrogenase (BADH) enzyme (Rattan *et al.,* 2014).

BRs and mineral nutrients

Adequate quantity of indispensable plant nutrients is essential for optimal plant functioning and therefore higher ion influx results in improved photosynthetic functioning, efficiency of CO_2 conductivity and increased potential of light and dark reactions (Talaat and Shawky, 2013). Heavy metals suppress the mineral nutrients uptake by blocking their active uptake, competition, lipid peroxidation of root membrane or by causing damage to the proteins (Siedlecka, 1995). BRs causes alterations in membrane integrity and affect membrane potential to stimulate ATPase, which ultimately elevates nutrient absorption in plant tissues due to hyperpolarization of membrane (Zhang *et al.,* 2014). Application of 24-EBL enhanced the uptake of Mg, Ca, Zn, iron and this beneficial character of 24-EBL is due to its influence on the action of transport proteins (Song *et al.,* 2016). 24-EBL escalates the content of Na^+ and K^+ in *Raphanus sativus* under Hg stress showing that BRs helpful in maintaining plant cell membrane permeability and ions transport against metal stress circumstances (Kapoor *et al.,* 2016). BRs alleviated cadmium induced toxicity in *Pisum sativum* by increasing uptake of Ca, P, K, S, Mg macronutrients which further resulted in higher plant physiological activity (Jan *et al.,* 2018). Cd being toxic metal decreased the nitrogen level by disrupting the cellular metabolism and membrane permeability but application of EBL increased the N content in chickpea (Wani *et al.,* 2017).

Conclusion

Heavy metals badly affect plant morphology and yield by the production of excessive ROS which alters cellular metabolism by disrupting various macromolecules, which ultimately lead to apoptosis. BRs are among the most useful plant hormones that play crucial function in improving plant metabolism, productivity and plant responses to stress conditions. BRs mitigates metal toxicity by enhancing plant water uptake, N_2 assimilation rate, amount of chlorophyll and photosynthetic activity, maintains membrane integrity by reducing lipid peroxidation and MDA content, enhanced functioning of antioxidative enzymes and non-enzymatic antioxidants. Heavy metal toxicity is major threat to the environment, therefore care and requirement to reestablish environment original state, pressurized human beings to discover novel and substitute technologies to protect the environment. Phytoremediation is an inexpensive, efficient and promising strategy to solve this ecological problem and therefore, use of BRs is beneficial to plants and the supplementation of such plant hormones in phytoremediation is a useful practice of modern times study.

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