Adv. Plant Sci. Env. (2026) 3: 1-9

Review

Advances in Plant Science and Environment

Brassinosteroid Signaling and Its Protective Role Against Heavy Metal-Induced Phytotoxicity

Haiyu Wang1†, Yunxin Zhao1†, Jiale Yan, Yuhao Fu, Jiayao Wang, Wenwu Zhang*, Jun Dai*

https://doi.org/xx.xxxxx/xxxxx

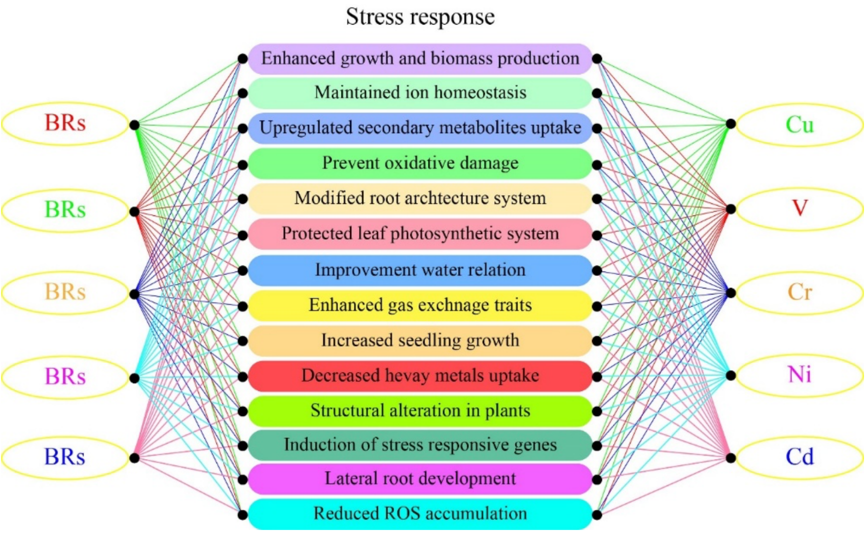
Highlights

- Heavy metals toxicity adversely damage plant biomass production.
- Heavy metals significantly impaired leaf photosynthetic mechanism in plants.
- Brassinosteroids potentially improved plant growth and heavy metals stress tolerance in plants.

Cite this article as: Wang H., Zhao Y., 2026. Brassinosteroid Signaling and Its Protective Role Against Heavy Metal-Induced Phytotoxicity. Advances in Plant Science and Environment 3, 1-9. https://doi.org/XXXXXXX/XXXXX

Article Info.
Received: 11 January 2026
Accepted: 12 March 2026

Graphical Abstract



Abstract

Rapid industrialization and urbanization have led to the widespread presence of heavy metals (HMs) in the environment. The environment is disrupted by the assimilation of these metals into the food chain. Elevated concentrations of HMs in the environment disrupt the normal functioning of diverse physiological and biochemical systems in plants. Plant growth regulators have effectively counteracted the detrimental impact of metal exposure on plant growth. Brassinosteroids (BRs) are a novel plant hormone that exhibit substantial growth-promoting effects. BRs have the ability to enhance plant responses to abiotic stressors, including HMs toxicity. BR application positively regulates seedling growth and development, proline accumulation, protects the photosynthetic system, upregulates secondary metabolite production, maintains redox homeostasis, and balances mineral homeostasis. Importantly, BRs effectively decreased the metal accumulation and enhanced mineral nutrient accumulation from root to shoot. Plants exposed to HMs and treated with BRs activate their antioxidant defense system and decrease the concentration of toxic elements. This may be attributed to the capacity of BRs to enhance cell membrane permeability and interact with membrane-bound proteins. This review systematically summarizes the core mechanisms underlying BR-mediated mitigation of HM stress. Specifically, we highlight three principal mechanisms: the activation of the antioxidant defense system to scavenge reactive oxygen species (ROS) and maintain redox homeostasis; the regulation of metal transport and partitioning, restricting HM accumulation in sensitive tissues while promoting essential nutrient uptake; and the protection of photosynthetic machinery and ultrastructure. Furthermore, we discuss the crosstalk between BR signaling and other hormonal pathways. This review aims to provide a theoretical basis for the application of BRs in remediation strategies for HM-contaminated soils.

Keywords: Signaling molecule, Photosynthesis, Metals toxicity, Brassinosteroids, Enzymes activity

1. Introduction

Abiotic stressors induce metabolic distress, physiological disturbances, generation of toxic substances, rupturing of membranes, resulting in negative effects on seed germination and plant yield (Jaiswal et al., 2018; Godoy et al., 2021; Muhammad et al., 2024). Plants require specific concentrations of certain heavy metals (HMs), such as cobalt (Co), copper (Cu), zinc (Zn), manganese (Mn), iron (Fe), nickel (Ni), and molybdenum (Mo), for optimal development. Nevertheless, when these concentrations exceed the ideal range, these turn out to be noxious for plants (Ramezani et al., 2021). However, certain HMs such as arsenic (As), cadmium (Cd), lead (Pb), chromium (Cr), aluminum (Al), and mercury (Hg) are highly hazardous to plants and are not necessary for plant growth (Chibuike and Obiora, 2014). Excessive HM accumulation disrupts cellular homeostasis by inducing oxidative stress, inhibiting enzymatic activities, and impairing essential metabolic processes like photosynthesis and respiration (Haider et al., 2021). Various HMs may replace vital elements found in plant cells, resulting in deficits in nutrients as well as decreased nutrient content (Muhammad et al., 2024). HM cytotoxicity can also have an impact on the nutrient content of plants (Wani et al., 2007; Abou Fayssal et al., 2024). Several management strategies can be used to lessen HMs buildup in plants (Asati et al., 2016; Pratush et al., 2018; Naz et al., 2022; Alengebawy et al., 2021). Phytohormones have been identified as crucial regulators of plant adaptive responses to HM stress. Among these, brassinosteroids (BRs) have garnered significant attention due to their dual role in promoting growth and enhancing stress tolerance (Bali et al., 2019). However, while the physiological benefits of BRs are well-documented, the underlying signaling mechanisms and their interaction with metal transport networks remain to be fully elucidated (Yadav, 2010). This review aims to bridge this gap by providing a comprehensive analysis of the physiological and molecular mechanisms through which BRs mitigate HM toxicity, with a specific focus on antioxidant regulation, metal transport modulation, and signal transduction pathways (Fig. 1).

The overproduction of toxic chemicals in peroxisomes, mitochondria, and chloroplasts is the most significant adverse impact of HM toxicities in plants. This produces oxidative damage and unanticipated implications for the plant's essential metabolic processes (Jamal et al., 2013; Chen and Su, 2018). HMs toxicity causes plants to close their stomata, induce the photorespiration pathway, interfere with the antioxidant defense system, accumulate excessive amounts of harmful compounds, and alter their metabolism and electron transport chain (Edelstein and Ben-Hur, 2018). The performance of cellular membranes is damaged through oxidative stress because of HMs' toxicities, which is caused by the peroxidation of membrane lipids (Foyer and Noctor, 2009; Nagajyoti et al., 2010). However, HMs accumulated in crops have the potential to seriously endanger people’s health as well as the whole society by getting into the food chain as well as humans' health, as revealed by Edelstein and Ben-Hur (2018). Table 1 displays the plants' responses to HMs toxicity.

Reduced plant size and fruit quality can be the outcome of oxidative stress in plants caused by HMs accumulation (Fig. 2) (Mahmood et al., 2007; Kumar and Aery, 2016). However, once plants are exposed to HMs, BRs can enhance seed germination and plant yield by adapting phytohormone levels (Arnao and Hernández-Ruiz, 2009). According to Ghorbani et al. (2024), this variation may regulate stomatal closure, enzymatic activities, and improve root morphology, which may decrease HMs consumption and boost tolerance. Once plants are exposed to HMs, BRs boost their synthesis of defense-related enzymes and antioxidants, strengthening their defense mechanisms (Bajguz, 2012). Plant tolerance to HMs stress is increased through decreased oxidative harm to plant compartments and tissues (Varma and Jangra, 2021). Brassinosteroids, a hormone linked to plant response, have been demonstrated to enhance the plant defense system during HMs exposure, resulting in better seed germination and excellent plant size (Ghorbani et al., 2021). BRs have a direct impact on defense and growth in plants, but they also have an indirect influence on plant productivity through depressing the accumulation of HMs in edible plant constituents (Basit et al., 2022). Therefore, it is a viable strategy to reduce HM pollution in crops, so this is a viable approach for polluted soils to attain the maximum productivity (Bajguz, 2011).

BRs are important for many biological and cellular processes, such as xylem segmentation, chlorophyll content, and fruit ripening (Bajguz and Hayat, 2009). Investigations exploring the possible financial benefits of BRs in horticultural crops have been conducted since the 1980s. Confirming structure-activity relationships, the profitable production of active BRs for field and greenhouse research is made possible by the biochemical combination of BR similarities (Rhaman et al., 2020). 24-epibrassinolide (EBR) and 28-homobrassinolide (HBR) have been approved as phytohormones for several crops. Supplementation of BRs may greatly increase production as well as quality in a variety of plant species, according to a comprehensive study on EBR and HBR (Tarkowská and Strnad, 2017). Plants could tolerate environmental stresses under BRs supplementation (Krishna, 2003). Moreover, BRs boost crop yield by improving tolerance against metal toxicities (Baghel et al., 2019).

For sustainable production, the function of BRs in shielding plants from metal toxicities is even more important (Ahammed et al., 2013). The combination of two traits that is growth stimulus as well as stress tolerance, transmitted through BRs for higher crop productivity under HMs toxicities will be very beneficial to farming in the future financially (Sultan and Raza, 2015). Hence, the current review intended to explore the latent of BRs supplementation for the sustainable production of crops subjected to metal toxicities.

2. Brassinosteroids Impact on Plant Performance Under Heavy Metals Toxicity

Research has been done on the formation of metals following the application of BRs in several cultivars of cultivated plants, such as radish (Anuradha and Rao, 2007), mustard (Hayat et al., 2007), and tomato (Hayat et al., 2010). Meanwhile, the current hormone significantly lowers the fascination of several HMs, the lead concentration in a beetroot treated with 24-epibrassinolide (EBL) is reduced by about (50%) as compared with the treatment alone in plants (Khripach et al., 1999). BRs were applied to enhance seed germination under stressful circumstances. The application of BRs to mustard seeds prior to germination and subsequent exposure to copper stress resulted in decreased copper uptake and accumulation, along with enhanced biomass production and shoot formation, as revealed by Sharma et al., (2007). The potential function of BRs is presented in Table 2.

Toxic ion generation was regulated by BRs supplementation to plants, focusing on higher yield. According to prior research, Chlorella vulgaris exposed to both metals and BRs exhibits less metal buildup as compared to cultures that were exposed to metals alone. Following the reduction of metal buildup, BRs promote C. vulgaris growth and development. According to Bajguz (2002), BRs enhance the synthesis of phytochelatins and stop the loss of protein, sugar, and chlorophyll in a metal-exposed C. vulgaris culture. Furthermore, it has been demonstrated that brassinolide encourages mung bean seedling growth when exposed to aluminum toxicity (Abdullahi et al., 2003). Furthermore, under aluminum stress, EBL significantly increases the fresh total biomass (leaves, roots, and shoot weight) as well as the amount of photopigments in mung bean (Ali et al., 2008). Furthermore, it has been revealed that applying 28-homobrassinolide (HBL) to Indian mustard subjected to nickel stress enhances vegetative growth and increases shoot and root lengths under and outside of Ni toxicity (Yusuf et al., 2011). By minimizing impairment to response and O2 developing centers also in regulation of effective electron transport, BRs minimize the harmful consequences of Cd on photochemical paths in rape seed leaf (Janeczko et al., 2005). As shown in Fig. 3, BRs application regulated the physiological and morphological functions in plants.

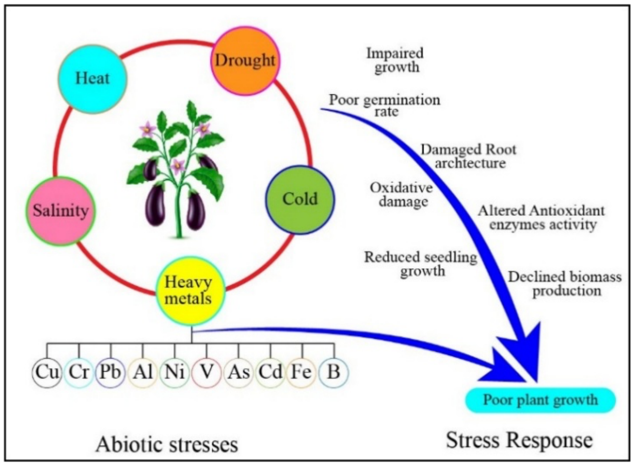


Fig. 1. Abiotic stresses adversely reduce the growth and development of plants.

3. Brassinosteroid Signaling and Molecular Mechanisms under HM Stress

The physiological improvement of HM toxicity by BRs is well documented, understanding the underlying signal transduction mechanisms is crucial to grasping their regulatory role. BRs are perceived by the plasma membrane receptor BRI1 (BRASSINOSTEROID INSENSITIVE 1). When BRs bind to BRI1, it forms a complex with BAK1 (BRI1-ASSOCIATED KINASE 1), which initiates a phosphorylation cascade that ultimately inactivates the negative regulator BIN2 (BRASSINOSTEROID INSENSITIVE 2). This inactivation enables the transcription factors BZR1 (BRASSINAZOLE-RESISTANT 1) and BES1 (BRI1-EMS-SUPPRESSOR 1) to translocate to the nucleus and regulate the expression of downstream target genes (Nie et al., 2022). Under HM stress, this signalling pathway is crucial for coordinating defence responses. For example, recent studies have shown that BZR1/BES1 can bind directly to the promoters of genes that encode antioxidant enzymes (e.g. SOD, CAT and APX) and glutathione S-transferases. This upregulates their expression, which helps to counteract the bursts of reactive oxygen species (ROS) induced by HMs (Mumtaz et al., 2022). Furthermore, BR signalling modulates the expression of metal transporter genes, such as the HM ATPase (HMA) and natural resistance-associated macrophage protein (Nramp) families, facilitating the efflux or vacuolar sequestration of toxic ions (Zhao et al., 2023). This molecular regulation highlights the importance of BRs as key integrators of growth and stress signalling.

4. Beneficial Role Of Brassinosteroids in Mitigation of Cadmium Toxicity

HMs that are known to cause harm even at extremely low concentrations are cadmium (Cd) (Müssig, 2005). It builds up in plants during the growth of edible portions, threatening crop yield and quality. This poses a hazard to the health of people as well as animals (Hasan et al., 2011). By functioning as an antimetabolite with several important metabolites, cadmium is known to induce enzyme inactivation and cause cell damage. Furthermore, different physiological and metabolic systems are altered by Cd (Hayat et al., 2010). Reduced biological yield is the result of all these complex and interlinked processes. Cd seems very dangerous HMs, which may damage plants (Andresen and Kupper, 2013). High amounts of Cd can harm a plant's cellular makeup and respiration, prevent it from growing and developing, and limit absorption and nutrient assimilation (Shanmugaraj et al., 2019). Plants may be exposed to lead poisoning through several different channels, including ingestion from polluted areas, irrigated water, and deposition of air, as recorded by Zulfiqar et al. (2022). After being occupied, Cd may build up in many plant organelles. Plants contain several defense mechanisms against Cd toxicity, including antioxidant defense systems, differentiation, and chelation, as explored by Gallego et al. (2012). However, at high quantities of Cd, these systems can become overburdened and have constraints (Aslam et al. 2023). Based on the growth phase, kind of species, and degree of contact, Cd phytotoxicity revealed different toxic effects on plants (Asgher et al. 2015). Although some plants can store and transport Cd throughout the food network, endangering human health, others have a greater tolerance of the metal than others (Shanmugaraj et al., 2019). Cd toxicity impeded the developmental process of tomato seedlings significantly, as indicated by Hasan et al. (2011); changed the root-building system of tomatoes (Altaf et al., 2022); impeded the levels of photosynthetic pigments (He et al., 2017); changed the functioning of protective enzymes in herbaceous plants (Lin et al., 2014); initiated oxidative stress in Korean perilla (Yang et al., 2022); and boosted Cd buildup in cucumber leaves (Zhang et al., 2002) and watermelon (Shirani Bidabadi et al., 2018).

Plant hormone treatment is the most beneficial and least harmful of the several techniques and technologies developed in recent years for treating Cd-stressed plants (Hasan et al., 2008). BRs have gotten the most attention among the plant hormones (Hayat et al., 2012). Generally, BRs control several physiological functions, including cell separation and enlargement, ATPase movement, and the inhibition of photopigment damage, all of which improve crop growth in stressful environments, as observed by Hasan et al. (2008) and Hayat et al. (2010). BRs alter the permeability of membranes and affect the electrical characteristics of plasma membranes, activating enzymes such as ATPase and as a powerful force for increased nutrient absorption in plant cells by hyperpolarizing the membrane as observed by Zhang et al. (2014). By boosting the buildup of numerous enzymes that can significantly contribute to HM-detoxification, as well as reducing the outflow of electrons within the plant compartments. So, the behavior of seedlings of wheat crop by 24-EBL (0.4 µM) reduced damage more effectively caused by Cd (Allagulova et al. 2015). In metal-stressed plants, BRs promote root growth by activating the mitotic action of meristematic action, which further improves seedling establishment, as reported by two plant researchers, Yusuf et al. (2012) and Allagulova et al. (2015). BR-stimulated prevention of Cd toxicities contributes to maintaining effective photosynthetic electron transport and activating the oxygen-evolving center to reduce damage to photochemical reaction centers, as evaluated by Vázquez et al. (2013) and Asgher et al. (2015). BRs are sprayed on plants against Cd toxicity, the BR signaling pathway is activated, which affects the up-and-down-expression of genes that respond to Cd-induced conditions (Villiers et al. 2012). Similarly, Ahammed et al. (2013) observed elevated levels of antioxidant activities, nutritional level, and photopigments of tomato seedlings co-contaminated with phenanthrene and Cd. Foliar applications of 24-EBL and 28-HBL were found to defense tomato

Table 1. Functions of brassinosteroids in plants under heavy metals toxicity.

BRs functions in plants	References
Regulated seed germination rate, seedling growth	Ali et al. (2008)
Protected photosynthetic system, upregulated pigments content	Ashraf et al. (2019)
Enhanced antioxidant enzymes activity	Baghel et al. (2019)
Balanced redox homeostasis	Bajguz, (2011)
Increased mineral nutrient accumulation	Bhardwaj et al. (2011)
Upregulated proline uptake	Bilikisu et al. (2003)
Decreased HM accumulation	Bajguz (2012)
Increased biomass production and enhanced yield-related parameters	Fariduddin et al. (2014)
Enhanced osmolytes content	Hasan et al. (2008)
Increased secondary metabolites production	Hayat et al. (2007)
Stomatal opening	Hu et al. (2013)
Modified root architecture system	Krishna et al. (2003)
Increased gas exchange related parameters	Madhan et al. (2014)
Upregulated defense related gene expression analysis	Müssig (2005)
Lowered electrolyzed leakage level and malonaldehyde content	Allagulova et al. (2015)
Maintained glycosidase enzymes activity	Bajguz and Hayat (2009)

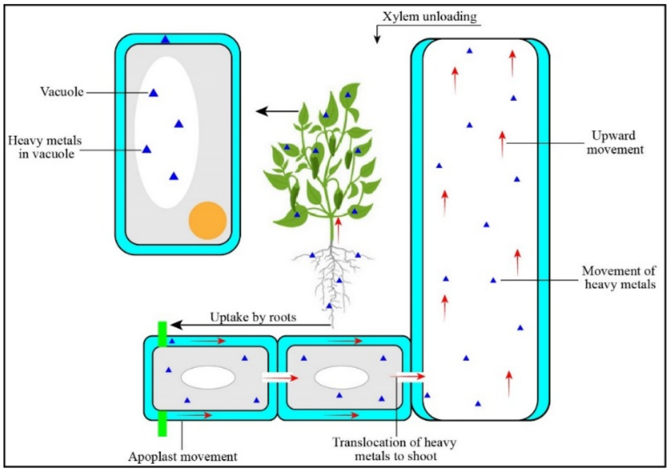


Fig. 2. Heavy metals accumulation and translocation from root to shoot in plants.

Table 2. Plants responses to heavy metals toxicity.

Species	Stress type	Plant response	References
Mung bean	Al	Reduced root length, biomass production, chlorophyll content	Abdullahi et al. (2003)
Saffron	Cd, Ni, Cr	Declined in yield parameters, increased HMs accumulation in leaves	Abou Fayssal et al. (2024)
Tomato	Cd	Impaired photosynthetic activity, increased ROS accumulation and caused oxidative damage	Ahammed et al. (2013)
Radish	Pb	Altered antioxidant enzymes activity, poor plant growth, damage root growth pattern	Anuradha and Rao (2007)
Mustard	Co	Increased cobalt accumulation, causing leaf chlorosis and necrosis, impaired seedling growth	Arora et al. (2012)
Rice	Cr	Ratarded growth traits, increased Cr uptake, altered antioxidant enzymes activity, unbalanced redox homeostasis	Basit et al. (2022)
Wheat	Cd	Impaired seedling growth, chlorophyll content, increased ROS accumulation in leaf	Allagulova et al. (2015)
Tomato	Cd	Increased cadmium accumulation in leaf, damaged root growth	Hayat et al. (2012)
Rice	As	Increased electrolyte leakage, malonaldehyde content, and metals accumulation in leaves	Chen and Su, (2018)
Radish	Cr	Decreased growth attributes, increased Cr accumulation, improved proline uptake, altered antioxidant enzymes activity	Choudhary et al. (2012)
Soybean	Al	Hindered chlorophyll content, impaired gas exchange characteristics, and disturbed photosystem	Dong et al. (2009)
Cucumber	Cu	Disturbed antioxidant enzyme system, altered antioxidant proline activity, increased uptake of copper accumulation	Fariduddin et al. (2013)
Pea	Cr	Unbalanced redox homeostasis, increased Cr accumulation in leaf	Gangwar and Singh (2011)
Tomato	Cd	Impaired photosynthetic machinery, declined chlorophyll content, caused oxidative damage	Hasan et al. (2011)
Radish	Cd	Declined in growth traits, retarded photosynthesis-related parameters	Kapoor et al. (2016)
Mustard	Mn	Increased metals accumulation, decreased mineral nutrient uptake, hindered growth by reducing chlorophyll content	Bhardwaj et al. (2008)

photopigments and osmolytes from Cd toxicities during later growth stages by lessening oxidative harm as exhibited by Hasan et al. (2011). It was discovered that the BR-stimulated higher activity of rubisco, elevated proline levels, and activation of enzymes were linked to the prevention of Cd toxicity. According to reports by Hayat et al. (2012), BRs maintenance of membrane fluidity may be the cause of the increased defense activity in Cd-toxic plants. This enhances the assimilation of minerals such as NO3, which is significantly contributes to NR initiation. When radish seeds were primed with varying concentrations of 24-EBL, Kapoor et al. (2014) observed that in seedlings exposed to Cd toxicity, antioxidative enzymatic properties and photopigments increased with increasing 24-EBL levels. BRs application maintained redox homeostasis, enhanced antioxidant enzyme activity, and reduced oxidative damage in plants (Fig. 4).

5. Crosstalk Of Brassinosteroids, Copper, And Zinc Toxicities In Plants

There are a few reports on the supplementation of BRs to reduce plant toxicity against Cu as well as Zn-exposed plants. 28-HBL fertilization was explored to regulate Cu homeostasis of radish crops subjected to Cu-excessive areas (Fariduddin et al. 2014). Similarly, Yusuf et al. (2014) assessed the interaction between selenium (Se) and 24-EBL in controlling Cu homeostasis in brown mustard seedlings exposed to harmful Cu concentrations. The boosts in proline levels as well as the stimulation of antioxidant machinery, Cu and Se application caused the depollution of Cu toxicities in plants by lessening of toxic substances. So, it has been indicated that applying 24-EBL with Se could be an efficient method of removing excess Cu from contaminated soils. According to these plant researchers, 24-EBL improves cucumber tolerance against Cu stress by regulating photosynthetic machinery and activating antioxidant enzymes (Fariduddin et al. 2013). 24-EBL supplementation has been shown to reduce excess zinc concentration in tomato seedling roots and shoots while simultaneously mitigating phytotoxicity caused by Zn (Li et al. 2016). When 28-HBL was sprayed, it enabled radish seedlings under higher Zn levels to maintain GSH redox homeostasis, which improved defense activities (Ramakrishna and Rao, 2015). It has been stated that GPX uses elevated GSH activity by means of a carrier to eliminate ROS via an ascorbic acid-independent process. Wu et al. (2016) revealed that 24-EBL uses a glutathione-ascorbate-dependent reclamation mechanism to reduce eggplant harmfulness caused by Zn. The results of the study showed that when seedlings are exposed to toxic Zn levels, the expression of genes related to enzymes, which in turn controls the transcriptional level of GSH and AsA regeneration. BRs regulated the antioxidant defense system and balanced redox homeostasis in different plant species under HM toxicity.

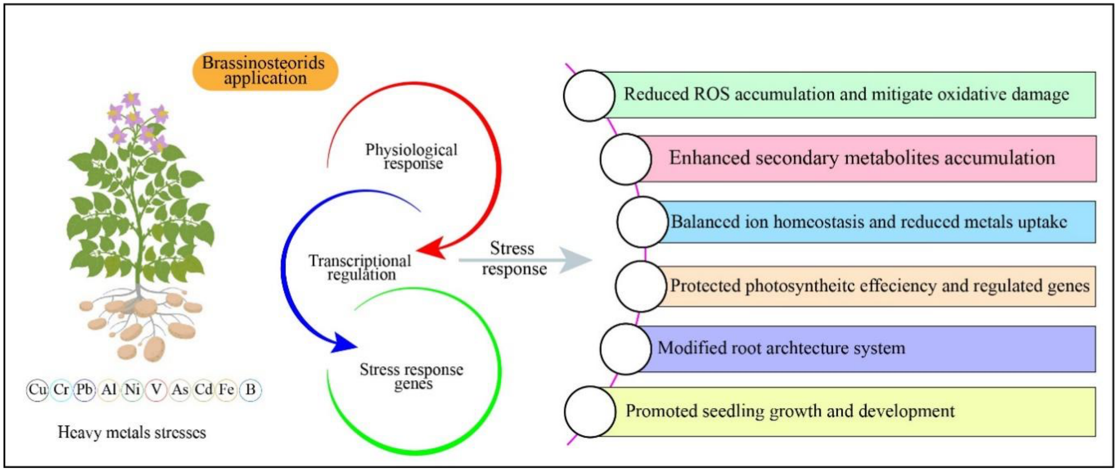


Fig. 3. BRs application regulated physiological responses in plants.

6. Brassinosteroid supplementation against lead toxicity in plants

Applying 20-hydroxyecdysone to C. vulgaris cultures inhibited chlorophyll, sugar, and protein loss, enhanced the production of phytochelatins, and decreased the growth-inhibiting effects of lead (Pb) stress (Bajguz and Godlewska-Zykiewlu, 2004). According to Bajguz (2002), the combination of two levels of Pb and BRs significantly increased the amount of phytochelatins that the C. vulgaris cell produced compared to the Pb-alone culture. Furthermore, the effect of Pb and BRs on C. vulgaris development was perceived to be imperative, focusing on sustainable yield. According to Rady and Osman (2012), tomato plants cultivated in the presence of 100 or 200 mM Pb showed a rise in the capabilities of the antioxidants when exposed to 24-EpiBL. By increasing the activities of antioxidant enzymes, supplementing 24-EpiBL lessened Pb harmfulness and improved radish seedlings growth. This indicates that 24-EpiBL has the ability to scavenge ROS, thereby lessening the oxidative harm induced by Pb levels, as observed by Anuradha and Rao (2007). Similarly, in another study by Swamy et al. (2014), applying 28-Homo-BL to fenugreek seedlings enhanced plant size, canopy, proteins, sugars, and osmolytes by reducing the toxicity of lead.

7. Role of brassinosteroids in mitigating chromium toxicity in plants

Chromium (Cr) contamination is preliminary to extremely affect the atmosphere and poses a significant risk to plant vigor. Additionally, there is a severe apprehension for food safety as well as protection due to the negative impacts of Cr on agricultural farming. Finding a durable remediation approach is, therefore, necessary to remove metal toxicity from the atmosphere. A thorough consideration of Cr accretion, transport, and plant protection systems in crops is imperative for higher yield. Mumtaz et al. (2022) indicated that 24-EBL produced a significant improvement in pepper performance subjected to Cr-induced conditions by regulating antioxidants, osmolytes, and signaling molecules. To preserve the phytochemical and physiological characteristics of radish, the polyamine BR was also applied to reduce Cr stress (Choudhary et al., 2012). Furthermore, under Cr stress conditions, it was revealed that pea seedlings treated with plant hormones showed a decrease in oxidative damage (Gangwar and Singh, 2011). This brief description of phytohormones provides sufficient insight into their capability to reduce Cr toxicity in plants. Therefore, it is necessary to ensure that phytohormones can be effectively used as a potential tactic to avoid Cr harmful effects on plants. By enhancing germination of seeds, photopigments, photosynthesis, and carbohydrates, as well as reducing oxidative damage by limiting the Cr deposit in two varieties of rice exposed to Cr toxicity. However, BRs lessened Cr-induced phytotoxicity in plants as reported by Choudhary et al. (2012). Furthermore, the BRs regulate the ionic assimilation of two cultivars of rice and reduce the Cr-induced oxidative harm by regulating the antioxidant profile of plants. So, earlier findings showed that BRs had the potential to reduce Cr-induced damage in rice seedlings. However, combined treatment is far more effective than single treatment (Basit et al. 2022). BRs potentially performed under different HM stress conditions.

8. Involvement of brassinosteroids to cope with nickel toxicity

Auxin Plants have also been shown to benefit from the protective function of BRs in reducing the harmful impacts of nickel (Ni) toxicity. According to Yusuf et al. (2011), plants supplemented with 28-HBL (0.01 µM) were able to survive Ni toxicity due to their elevated proline levels and improved enzyme and carbonic anhydrase activities. According to Yusuf et al. (2012), soaking radish seeds in 24-EBL solutions greatly enhanced nitrogen in the nodules of Ni-treated plants. This was because the increased activity of carbonic anhydrase, as well as nitrogen reductase led to better quality production. According to a recent study, foliar spraying on radish seedlings with Ni-exceeded oxidative harm also improved nitrogen metabolism and boosted enzyme activity, which led to maximal nodulation and production, as revealed by Yusuf et al. (2014). Because there was less electrolyte leakage, maize seedlings produced through 24-EBL supplementation and exposed to increased Ni toxicity showed great germination as well as seedling size, as indicated by Lukatkin et al. (2013). In recent times, the seedlings of eggplant exposed to Ni, Soares et al. (2016) revealed the protective mechanisms caused by 24-EBL, which revealed better water translocation to apex cells. Moreover, it has been recorded that preharvest supplementation of 24-EBL resulted in higher Ni transportation towards shoots from roots, indicating that BRs boost the formation of organic acids as well as molecules that contribute to Ni transportation through xylem and thereby are involved in the conservation of cellular enlargement, as reported by Hu et al. (2013).

9. Brassinosteroids contribute to aluminum toxicity in plants

Aluminum (Al) toxicity results in stunted growth of plants globally. Moreover, disruption of several metabolic processes also occurs in plants. Excess accumulation of AI in the plant's root zone is toxic because of translocation to other plant parts, including edible parts, because their consumption is toxic to health. According to Silva and Sodek (1997), there is

Table 3. Brassinosteroids regulate various plant physiological, morphological, and molecular functions in plants under heavy metal toxicity.

Species	Stress type	Findings	References
Radish	Cd	Protected photosynthetic system, enhanced antioxidant enzyme system,	Kapoor et al. (2016)
Mustard	Zn	Decreased in metals accumulation, enhanced antioxidant defense system and balanced redox homeostasis	Sharma et al. (2007)
Watermelon	Cd	Increased seedling growth, biomass production, chlorophyll content and reduced cadmium uptake in leaf	Shirani Bidabadi et al. (2018)
Black nightshade	Ni	Lowered electrolyte leakage, enhanced antioxidant enzymes activity, reduced nickel accumulation in leaf	Soares et al. (2016)
Rice	As	Lowered EL and MDA levels, declined in HM uptake in plants	Chen and Su, (2018)
Pigeon pea	Al	Increased soluble protein, antioxidant enzymes activity, chlorophyll content, and balanced ROS homeostasis	Sri et al. (2016)
Maize	Mn	Reduced oxidative damage enhanced antioxidant defense system and protected leaf photosynthesis apparatus	Wang et al. (2009)
Eggplant	Zn	Reduced Zn accumulation, Increased mineral nutrient accumulation, Improved chlorophyll content, enhanced metabolites production	Wu et al. (2016)
Mung bean	B	Increased growth and biomass production, upregulated osmolytes and secondary metabolites production, reduced B uptake in plants	Yusuf et al. (2011)
Pea	Cr	Reduced oxidative damage, lowered EL, upregulated secondary metabolites production	Gangwar and Singh (2011)
Mustard	Co	Decreased HM uptake, maintained redox homeostasis, upregulated antioxidant enzymes system in leaf	Arora et al. (2012)
Tomato	Cd	Resorted photosynthetic capacity, balanced ROS homeostasis and decreased oxidative damage	Ahammed et al. (2013)

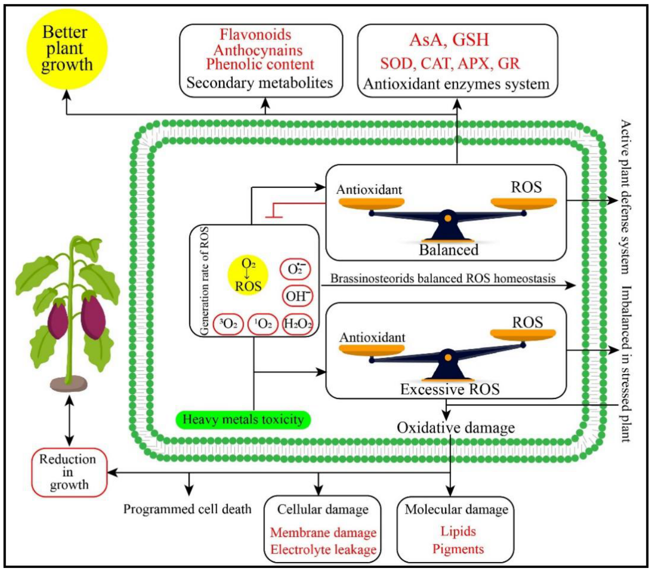


Fig. 4. Brassinosteroids enhance the antioxidant enzymes system and balance redox homeostasis in plants under HMs toxicity.

a suggestion that AI inhibits initially root growth, which further leads to soil compaction and a decline in the uptake of water as well as minerals. 24-EBL supplementing plants produced a reduction in the toxic effect, which was emulated in an improvement in growth, in plants evolving under Al toxicity. Even in the presence of Al toxicity stress, BRs enhancement of root growth translated into an increase in plant growth. Pigeon pea plants growing in an Al-induced soil showed reduced nodulation. Similarly, the 24-EBL fertilization lessened the effect of Al on nodulation. According to Wood et al. (1984), rhizobium multiplication and nodule formation were found to be more vulnerable to excess Al in the symbiotic interaction. Al toxic conditions caused a sharp drop in chlorophyll in pigeon pea plants. It is well known that metal stress both prevents and causes chlorophyll synthesis to happen (Van Assche and Clijsters, 1990). By applying 24-EBL to Cajanus plants, the harmful effects of Al toxicity were mitigated, and photosynthetic pigment levels were significantly raised. By either activating particular genes involved in chlorophyll synthesis or slowing down the degradation of chlorophyll, BRs may be able to stop the loss of photosynthetic pigments (Hayat et al., 2011). However, supplementing EBL to plants under Al toxicity resulted in an increase in all enzyme activity under HMs. EBL has a protective function against Al-induced oxidative damage, as demonstrated by the BRs' modulation of the rise in antioxidative enzyme activity. According to Ashraf et al. (2019), in Cajanus plants, aluminum toxicity increased the buildup of oxidative stress biomarkers in a treatment-dependent manner, suggesting greater membrane peroxidation. The information clearly shows that EBL has a counteracting effect on the cytotoxic impact of Al, as EBL supplementation decreased the oxidative damage in stressed conditions, indicating a decrease in membrane rupturing (Madhan et al., 2014). The capability of 24-EBL to alleviate the oxidative harms caused by AI toxicity was revealed by a strong correlation found between the decline in MDA level in plants fertilized with EBL and cultivating against higher Al concentrations, and increased activity of antioxidants as well as the generation of proline and glycine betaine concentrations (Sri et al., 2016). BRs supplementation to soybeans enhanced their photosynthetic traits when exposed to Al toxicity (Dong and Jiang, 2009). Under Al metal stress, BRs increased seedling enlargement and chlorophyll content, and reduced Al harmfulness in mung bean (Bilikisu et al., 2003). The mung bean performance under Al stress was measured by BRs fertilization and revealed that plant biomass and photosynthetic contents were enhanced to improve the biochemical properties of plants to tolerate stressful conditions. The fertilization of BL was effective for higher seedling performance growing under controlled conditions, as revealed by Abdullahi et al. (2003). Mung bean plants showed higher tolerance against AI toxicities by improving the defense system, photopigments, physiological activities, and osmolyte capabilities, as revealed by previous research by Ali et al. (2008).

10. Brassinosteroids Interplay with Manganese, Cobalt, Arsenic, and Mercury Toxicities

The uptake of manganese (Mn) by brown mustard was modulated by the spray of 28-Homo-BL (Bhardwaj et al., 2008; Bhardwaj et al., 2011). According to Wang et al. (2009), applying EpiBL to maize under Mn stress boosted the events of enzymes, lowered ascorbate, and significantly decreased oxidative damage. They revealed that the improvements in antioxidative potential against Mn stress may have contributed to EpiBL's ameliorative effects on Mn toxicity in maize. When brown mustard was treated with a foliar spray containing 24-EpiBL, the stress caused by CO_2 was reduced, and the number of leaves, shoot length, antioxidative enzyme activity, and protein content all greatly increased (Arora et al., 2012). Similarly, Sharma et al. (2012) revealed that radish performance was improved by regulating the protein content and PPO and GST enzyme activities, hence reducing the oxidative stress by mercury through BRs of a 1.5 mM solution. The harmful effects of Hg on radish plants were eliminated by using 28-Homo-BL, which also increased the protein content and the antioxidant properties, including GST and PPO (Sharma et al., 2014). In a recent study, Kapoor et al. (2014) also found that treating radish plants with 24-EpiBL increased the activities of proteins, antioxidant enzymes, and GSH while lowering the MDH level, hence mitigating the harmful effects of mercury on the plants. Applying 24-EpiBL to 7-day-old radish seedlings demonstrated a beneficial role in mitigating the effects of mercury stress by promoting seedling growth and modifying ionic balance, osmolytes, as well as antioxidants (Kapoor et al., 2016). Arsenic (As) and mercury (Hg) are highly toxic elements that have a significant impact on human health. Research on arsenic-stressed rice revealed that the application of BRs improved growth attributes and reduced arsenic translocation to grains by modulating the expression of aquaporins and phosphorus transporters (Sharma et al., 2021). Regarding Hg toxicity, it was found that BRs alleviate oxidative stress in radishes by enhancing the synthesis of secondary metabolites and osmolytes, which stabilize cellular membranes against Hg-induced damage (Ahammed et al., 2022). BRs application protected the plant photosynthetic apparatus under HM toxicity (Fig. 5).

11. Conclusion and Future Perspectives

BRs are essential phytohormones that control signals to progress plants' ability to tolerate stress. BRs mediate important physiological processes as the main protectors for plants under stressful conditions of HM toxicity. BRs-improved enzymatic activity generation activates the antioxidant machinery, modifying the damaging effects of metal toxicities in plants. Several BR treatment techniques, including foliar spraying, soaking in BR-containing solutions, and seed priming, have been used to assess the exogenous BR fertilization in plants. The beneficial effect of BR fertilization is thought to be influenced by a number of variables, such as the number of BRs, growth phases, different species, and the duration of use. Investigations on the optimization of BR levels as well as time of use in plants are limited, but it is widely recognized that BR-induced growth-promoting movement is simultaneously time- and dose-related. This review emphasizes the vital role of BRs in alleviating HM toxicity in plants by activating antioxidant systems,

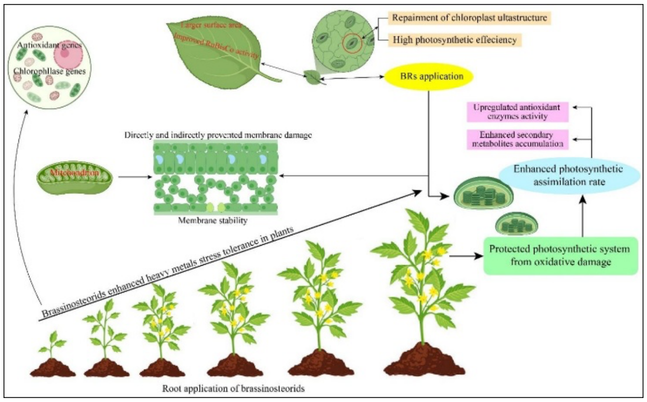


Fig. 5. Brassinosteorids protected the photosynthetic system in plants under heavy metals toxicity.

regulating metal transport and safeguarding photosynthetic machinery. The integration of BR signalling with stress response pathways highlights their potential as biotechnological tools for enhancing crop resilience in contaminated soils. Future research should address the following critical questions. The first concerns hormonal crosstalk. How do BRs interact with other phytohormones, such as ethylene, salicylic acid, and jasmonic acid, to fine-tune the detoxification pathways for specific metals? The second concerns genetic engineering. Can gene-editing technologies be used to optimize BR biosynthesis or signalling components (e.g., BRI1 or BZR1) to generate HM-tolerant crop varieties without growth penalties? The third one is about the potential of phytoremediation. Could BRs be utilised to enhance the efficiency of hyperaccumulator plants in phytoremediation strategies by promoting metal extraction while ensuring the survival of these plants in highly contaminated sites? Addressing these questions will be pivotal for translating fundamental knowledge into practical agricultural applications.

Author Information

Corresponding Author

Wenwu Zhang: College of Biomedicine and Health, Anhui Science and Technology University, Fengyang County, Chuzhou City, 233100, China
Email: zhangww12@ahstu.edu.cn
ORCID: https://orcid.org/0000-0002-9026-3730

Jun Dai: Plant Cell Engineering of Anhui Engineering Technology Research Center, College of Life and Health, West Anhui University, Luan 237012, China.
Email: 346319463@qq.com
ORCID: https://orcid.org/0009-0008-4602-1380
†These authors contributed equally to this work.

Author(s)

Haiyu Wang: Plant Cell Engineering of Anhui Engineering Technology Research Center, College of Life and Health, West Anhui University, Luan 237012, China
ORCID: https://orcid.org/0009-0007-9721-4732

Yunxin Zhao: Plant Cell Engineering of Anhui Engineering Technology Research Center, College of Life and Health, West Anhui University, Luan 237012, China
ORCID: https://orcid.org/0009-0003-2188-0756

Jiale Yan: Plant Cell Engineering of Anhui Engineering Technology Research Center, College of Life and Health, West Anhui University, Luan 237012, China
ORCID: https://orcid.org/0009-0005-7909-8155

Yuhao Fu: Plant Cell Engineering of Anhui Engineering Technology Research Center, College of Life and Health, West Anhui University, Luan 237012, China
ORCID: https://orcid.org/0009-0004-2539-6643

Jiayao Wang: Plant Cell Engineering of Anhui Engineering Technology Research Center, College of Life and Health, West Anhui University, Luan 237012, China
ORCID: https://orcid.org/0009-0007-5219-1397

Author Contributions

HW: formal analysis, funding acquisition, writing–original draft. YZ: formal analysis, writing–original draft. JY: formal analysis, writing–original draft. YF: formal analysis, writing–original draft. JW: formal analysis, funding acquisition, writing–original draft. WZ: supervision, writing, review, and editing. JD: supervision, funding acquisition, resources, writing, review, and editing. All authors read and approved the manuscript.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Data availability

No data was used for the research described in the article.

Additional Information

References

Abdullahi, B.A., Gu, X.G., et al., 2003. Brassinolide amelioration of aluminum toxicity in mung bean seedling growth. Journal of Plant Nutrition 26, 1725–1734. https://doi.org/10.1081/pln-120023278

Abou Fayssal, S., Kumar, P., et al., 2024. Health risk assessment of heavy metals in saffron (*Crocus sativus* L.) cultivated in domestic wastewater and lake water irrigated soils. Heliyon 10, e27138. https://doi.org/10.1016/j.heliyon.2024.e27138

Ahammed, G.J., Choudhary, S.P., et al., 2013. Role of brassinosteroids in alleviation of phenanthrene–cadmium co-contamination-induced photosynthetic inhibition and oxidative stress in tomato. Journal of Experimental Botany 64, 199–213. https://doi.org/10.1093/jxb/ers323

Ahammed, G.J., Wu, M., et al., 2022. Melatonin and brassinosteroid act in concert to mitigate lead toxicity in radish (*Raphanus sativus* L.) seedlings. Environmental and Experimental Botany 196, 104783. https://doi.org/10.1016/j.envexpbot.2022.104783

Alengebawy, A., Abdelkhalek, S.T., et al., 2021. Heavy metals and pesticides toxicity in agricultural soil and plants: ecological risks and human health implications. Toxics 9, 42. https://doi.org/10.3390/toxics9030042

Ali, B., Hasan, S.A., et al., 2008 A role for brassinosteroids in the amelioration of aluminum stress through antioxidant system in mung bean (*Vigna radiata* L. Wilczek). Environmental and Experimental Botany 62, 153–159. https://doi.org/10.1016/j.envexpbot.2007.07.014.

Allagulova, C.R., Maslennikova, D.R., et al., 2015. Influence of 24- epibrassinolide on growth of wheat plants and the content of dehydrins under cadmium stress. Russian Journal of Plant Physiology 62, 465–471. https://doi.org/10.1134/s1021443715040020

Altaf, M.A., Shahid, R., et al., 2022. Melatonin mitigates cadmium toxicity by promoting root architecture and mineral homeostasis of tomato genotypes. Journal of Soil Science and Plant Nutrition 22, 1112–1128. https://doi.org/10.1007/s42729-021-00720-9

Andresen, E., and Kupper, H., 2013. Cadmium toxicity in plants. Cadmium: from toxicity to essentiality, 395-413. https://doi.org/10.1007/978-94-007-5179-8_13

Anuradha, S., and Rao, S.S.R., 2007. Effect of 24-epibrassinolide on the growth and antioxidant enzyme activities in radish seedlings under lead toxicity. Indian Journal of Plant Physiology 12, 396–400. https://www.cabidigitallibrary.org/doi/full/10.5555/20083096897

Arnao, M.B., and Hernández-Ruiz, J., 2009. Chemical stress by different agents affects the melatonin content of barley roots. Journal of Pineal Research 46, 295–299. https://doi.org/10.1111/j.1600-079x.2008.00660.x

Arora, P., Bhardwaj, R, et al., 2012. Effect of 24-epibrassinolide on growth, protein content and antioxidative defense system of *Brassica juncea* L. subjected to cobalt ion toxicity. Acta Physiologia Plantarum 34, 2007–2017. https://doi.org/10.1007/s11738-012-1002-2

Asati, A., Pichhode, M., et al., 2016. Effect of heavy metals on plants: an overview. International Journal of Application or Innovation in Engineering and Management 5, 56-66.

Asgher, M., Khan, M.I., et al., 2015. Minimising toxicity of cadmium in plants—role of plant growth regulators. Protoplasma 252, 399–413. https://doi.org/10.1007/s00709-014-0710-4

Ashraf, S., Dixit, S., et al., 2019. Interactive role of brassinosteroids and calcium ameliorates in response to the aluminium toxicity in plants. International Journal of Trend in Scientific Research and Development 3, 183-203.

Aslam, M.M., Okal, E.J., et al., 2023. Cadmium toxicity impacts plant growth and plant remediation strategies. Plant Growth Regulation 99, 397–412. https://doi.org/10.1007/s10725-022-00917-7

Baghel, M., Nagaraja, A., et al., 2019. Pleiotropic influences of brassinosteroids on fruit crops: a review. Plant Growth Regulation 87, 375-388. https://doi.org/10.1007/s10725-018-0471-8

Bajguz, A., 2011. Brassinosteroids - occurrence and chemical structures in plants. In: Hayat, S., Ahmad, A. (eds) Brassinosteroids: A Class of Plant Hormone. Springer, Dordrecht. pp.1-27. https://doi.org/10.1007/978-94-007-0189-2_1

Bajguz, A., 2012. Origin of Brassinosteroids and Their Role in Oxidative Stress in Plants. In: Khan N, Nazar R, Iqbal N, Anjum N (eds) Phytohormones and Abiotic Stress Tolerance in Plants. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-25829-9_8

Bajguz, A., and Godlewska-Zykiewlu, B., 2004. Protective role of 20-hydroxyecdysone against lead stress in Chlorella vulgaris cultures. Phytochemistry 65, 711–720. https://doi.org/10.1016/j.phytochem.2004.01.015

Bajguz, A., and Hayat, S., 2009. Effects of brassinosteroids on the plant responses to environmental stresses. Plant Physiology and Biochemistry 47, 1-8. https://doi.org/10.1016/j.plaphy.2008.10.002

Bajguz, A., 2002. Brassinosteroids and lead as stimulators of phytochelatins synthesis in Chlorella vulgaris. Journal of Plant Physiology 159, 321–324. https://doi.org/10.1078/0176-1617-00654.

Bali, A.S., Sidhu, G.P.S., et al., 2019. Mitigating cadmium toxicity in plants by phytohormones. cadmium toxicity and tolerance in plants. Academic Press, pp. 375–396. https://doi.org/10.1016/b978-0-12-814864-8.00015-2

Basit, F., Bhat, J.A., et al., 2022. Chromium toxicity induced oxidative damage in two rice cultivars and its mitigation through external supplementation of brassinosteroids and spermine. Chemosphere 302, 134423. https://doi.org/10.1016/j.chemosphere.2022.134423

Bhardwaj, R., Sharma, P., et al., 2008. 28-Homobrassinolide regulated Mn-uptake and growth of *Brass* *ica juncea* L. Canadian Journal of Pure and Applied Sciences 2, 149–154.

Bhardwaj, R., Sharma, P., et al., 2011. Amelioration of Mn toxicity by brassinosteroids in *Brassica juncea* L. International Journal of Environmental Waste Management 8, 114–122. https://doi.org/10.1504/ijewm.2011.040969

Bilikisu, A.A., Xia-gang, G., et al., 2003. Brassinolide amelioration of aluminium toxicity in mung bean. Journal of Plant Nutrition 26, 1725–1735. https://doi.org/10.1081/pln-120023278

Chen, T., and Su, Y., 2018. Uptake by rice seedlings and in-plant degradation of atrazine as influenced by the oxidative stress induced by added arsenic or phosphate deficiency. Human and Ecological Risk Assessment: An International Journal 24, 1550–1564. https://doi.org/10.1080/10807039.2017.1416580

Chibuike, G.U., and Obiora, S.C., 2014. Heavy metal polluted soils: effect on plants and bioremediation methods. Applied and Environmental Soil Science 1, 752708. https://doi.org/10.1155/2014/752708

Choudhary, S.P., Kanwar, M., et al., 2012. Chromium stress mitigation by polyamine-brassinosteroid application involves phytohormonal and physiological Strategies in *Raphanus sativus* L. PLoS ONE 7, e33210. https://doi.org/10.1371/journal.pone.0033210

Dong, D., Li, Y., et al., 2009. Effects of brassinosteroids on photosynthetic characteristics in soybean under aluminum stress. Acta Agronomica Sinica 34, 1673–1678. https://doi.org/10.3724/sp.j.1006.2008.01673

Edelstein, M., and Ben-Hur, M., 2018. Heavy metals and metalloids: sources, risks and strategies to reduce their accumulation in horticultural crops. Scientia Horticulturae 234, 431–444. https://doi.org/10.1016/j.scienta.2017.12.039

Fariduddin, Q., Khalil, R.R., et al., 2013. 24- epibrassinolide regulates photosynthesis, antioxidant enzyme activities and proline content of *Cucumis sativus* under salt and/or copper stress. Environmental Monitoring and Assessment 185, 7845–7856. https://doi.org/10.1007/s10661-013-3139-x

Fariduddin, Q., Yusuf, M., et al., 2014. Brassinosteroids and their role in response of plants to abiotic stresses. Biologia Plantarum 58, 9–17. https://doi.org/10.1007/s10535-013-0374-5

Foyer, C.H., Noctor, G., 2009. Redox regulation in photosynthetic organisms: signaling, acclimation, and practical implications. Antioxidant Redox Signaling 11, 861–905. https://doi.org/10.1089/ars.2008.2177

Gallego, S.M., Pena, L.B., et al., 2012. Unravelling cadmium toxicity and tolerance in plants: insight into regulatory mechanisms. Environmental and Experimental Botany 83, 33–46. https://doi.org/10.1016/j.envexpbot.2012.04.006

Gangwar, S., and Singh, V.P., 2011. Indole acetic acid differently changes growth and nitrogen metabolism in Pisum sativum l. seedlings under chromium (vi) phytotoxicity: implication of oxidative stress. Scientia Horticulturae 129, 321–328. https://doi.org/10.1016/j.scienta.2011.03.026

Ghorbani, A., Emamverdian, A., et al., 2024. Illustrating Recent Development in Melatonin-Heavy Metal Research in Plant. In Melatonin in Plants: A Pleiotropic Molecule for Abiotic Stresses and Pathogen Infection (pp. 95-111). Singapore: Springer Nature Singapore. https://doi.org/10.1007/978-981-99-6741-4_6

Ghorbani, A., Tafteh, M., et al., 2021. Piriformospora indica augments arsenic tolerance in rice (Oryza sativa) by immobilizing arsenic in roots and improving iron translocation to shoots. Ecotoxicology and Environmental Safety 209, 111793. https://doi.org/10.1016/j.ecoenv.2020.111793

Godoy, F., Olivos-Hernández, K., et al., 2021. Abiotic stress in crop species: improving tolerance by applying plant metabolites. Plants 10, 186. https://doi.org/10.3390/plants10020186

Haider, F.U., Liqun, C., et al., 2021. Cadmium toxicity in plants: Impacts and remediation strategies. Ecotoxicology and Environmental Safety 211, 111887. https://doi.org/10.1016/j.ecoenv.2021.111887

Hasan, S.A., Hayat, S., et al., 2011. Brassinosteroids protect photosynthetic machinery against the cadmium induced oxidative stress in two tomato cultivars. Chemosphere 84, 1446–1451. https://doi.org/10.1016/j.chemosphere.2011.04.047

Hasan, S.A., Hayat, S., et al., 2008. 28-Homobrassinolide protects chickpea (*Cicer arietinum*) from cadmium toxicity by stimulating antioxidants. Environmental Pollution 151, 60-66. https://doi.org/10.1016/j.envpol.2007.03.006

Hayat, S., Ali, B., et al., 2007. Brassinosteroid enhanced the level of antioxidants under cadmium stress in *Brassica juncea*. Environmental and Experimental Botany 60, 33–41. https://doi.org/10.1016/j.envexpbot.2006.06.002

Hayat, S., Alyemeni, M.N., et al., 2012. Foliar spray of brassinosteroid enhances yield and quality of *Solanum lycopersicum* under cadmium stress. Saudi Journal of Biological Science 19, 325–330. https://doi.org/10.1016/j.sjbs.2012.03.005

Hayat, S., Hasan, S.A., et al., 2010. Brassinosteroids protect *Lycopersicon esculentum* from cadmium toxicity applied as shotgun approach. Protoplasma 239, 3–14. https://doi.org/10.1007/s00709-009-0075-2

Hayat, S., Yadav, S., et al., 2011. Comparative effect of 28-homobrassinolide and 24-epibrassinolide on the growth, carbonic anhydrase and photosynthetic efficiency of *Lycopersicon esculentum*. Photosynthetica 49, 397-404. http://dx.doi.org/10.1007/s11099-011-0051-x

He, J., Lin, L., et al., 2017. Uniconazole (S-3307) strengthens the growth and cadmium accumulation of accumulator plant *Malachium aquaticum*. International Journal of Phytoremediation 19, 348– 352. https://doi.org/10.1080/15226514.2016.1225287

Hu, W.H., Yan, X.H., et al., 2013. 24-Epibrassinosteroid alleviate drought-induced inhibition of photosynthesis in *Capsicum annuum*. Scientia Horticulturae 150, 232–237. https://doi.org/10.1016/j.scienta.2012.11.012

Jaiswal, A., Verma, A., et al., 2018. Detrimental effects of heavy metals in soil, plants, and aquatic ecosystems and in humans. Journal of Environmental Pathology, Toxicology, and Oncology 37, 183-197. https://doi.org/10.1615/jenvironpatholtoxicoloncol.2018025348

Jamal, Q., Durani, P., et al., 2013. Heavy metals accumulation and their toxic effects. Journal of Bio-Molecular Sciences 1, 27-36.

Janeczko, A., Koscielniak, J., et al., 2005. Protection of winter rape photosystem 2 by 24- epibrassinolide under cadmium stress. Photosynthetica 43, 293–298. https://doi.org/10.1007/s11099-005-0048-4

Kapoor, D., Rattan, A., Gautam, V. and Bhardwaj, R., 2016. Alleviation of cadmium and mercury stress by supplementation of steroid hormone to *Raphanus sativus* seedlings. Proceedings of the National Academy of Sciences, India Section B: Biological Sciences 86, 661-666. http://dx.doi.org/10.1007/s40011-015-0501-5

Kapoor, D., Rattan, A., et al., 2014. 24- epibrassinolide mediated changes in photosynthetic pigments and antioxidative defence system of radish seedlings under cadmium and mercury stress. Journal of Stress Physiology & Biochemistry 10, 110–121. https://www.cabidigitallibrary.org/doi/full/10.5555/20143297580

Khripach, V.A., Zhabinskii, V.N., et al., 1999. Brassinosteroids. A New Class of Plant Hormones. San Diego: Academic Press.

Krishna, P., 2003. Brassinosteroid-mediated stress responses. Journal of Plant Growth Regulation 22, 289-297. https://doi.org/10.1007/s00344-003-0058-z

Kumar, A., and Aery, N.C., 2016. Impact, metabolism, and toxicity of heavy metals in plants. Plant Responses to Xenobiotics, pp.141-176. https://doi.org/10.1007/978-981-10-2860-1_7

Li, M., Ahammed, G.J., et al., 2016. Brassinosteroid ameliorates zinc oxide nanoparticles-induced oxidative stress by improving antioxidant potential and redox homeostasis in tomato seedling. Frontiers in Plant Science 7, 615. https://doi.org/10.3389/fpls.2016.00615

Lin, L., Liao, M.A., et al., 2014. Effects of mulching tolerant plant straw on soil surface on growth and cadmium accumulation of Galinsoga parviflora. PLoS One 9, e114957. https://doi.org/10.1371/journal.pone.0114957

Lukatkin, A.S., Kashtanova, N.N., et al., 2013. Changes in maize seedlings growth and membrane permeability under the effect of epibrassinolide and heavy metals. Russian Agricultural Sciences 39, 307–310. https://doi.org/10.3103/s1068367413040125

Madhan, M., Mahesh, K., et al., 2014. Effect of 24-epibrassinolide on aluminium stress induced inhibition of seed germination and seedling growth of *Cajanus cajan* (L.) Millsp. The International Journal of Multidisciplinary and Current Research 2, 286-290.

Mahmood, T., Islam, K.R., et al., 2007. Toxic effects of heavy metals on early growth and tolerance of cereal crops. Pakistan Journal of Botany 39, 451-462.

Muhammad, H.M.D., Naz, S., et al., 2024. Melatonin in business with abiotic stresses in vegetable crops. Scientia Horticulturae 324, 112594. https://doi.org/10.1016/j.scienta.2023.112594

Mumtaz, M.A., Hao, Y., et al., 2022. Physiological and Transcriptomic Analysis Provide Molecular Insight into 24-Epibrassinolide Mediated Cr(VI)-Toxicity Tolerance in Pepper Plants. Environmental Pollution 306, 119375. https://doi.org/10.1016/j.envpol.2022.119375

Müssig, C., 2005. Brassinosteroid-promoted growth. Plant Biology 7, 110-117. https://doi.org/10.1055/s-2005-837493

Nagajyoti, P.C., Lee, K.D., et al., 2010. Heavy metals, occurrence and toxicity for plants: a review. Environmental Chemistry Letters 8, 199-216. https://doi.org/10.1007/s10311-010-0297-8

Naz, S., Anjum, M.A., et al., 2022. Purification of sewage wastewater though sand column filter for lessening of heavy metals accumulation in lettuce, carrot, and cauliflower. Water 14, 3770. https://doi.org/10.3390/w14223770

Nie, S., Yue, Y., et al., 2022. Advances in the signal transduction and crosstalk of brassinosteroids. Plant Signaling & Behavior 17, 2074450. https://doi.org/10.1080/15592324.2022.2074450

Pratush, A., Kumar, A., et al., 2018. Adverse effect of heavy metals (As, Pb, Hg, and Cr) on health and their bioremediation strategies: a review. International Journal of Microbiology 21, 97-106. https://doi.org/10.1007/s10123-018-0012-3

Rady, M.M., and Osman, A.S., 2012. Response of growth and antioxidative system of heavy metal contaminated tomato plants 24-epibrassinolide. African Journal of Agricultural Research 7, 3249–3254. https://doi.org/10.5897/ajar12.079

Ramakrishna, B., and Rao, S.S., 2015. Foliar application of brassinosteroids alleviates adverse effects of zinc toxicity in radish (*Raphanus sativus* L.) plants. Protoplasma 252, 665–677. https://doi.org/10.1007/s00709-014-0714-0

Ramezani, M., Enayati, M., et al., 2021. A study of different strategical views into heavy metal (oid) removal in the environment. Arabian Journal of Geosciences 14, 1-16. https://doi.org/10.1007/s12517-021-08572-4

Rhaman, M.S., Imran, S., et al., 2020. Seed priming with phytohormones: an effective approach for the mitigation of abiotic stress. Plants 10, 37. https://doi.org/10.3390/plants10010037

Shanmugaraj, B.M., Malla, A., et al., 2019. Cadmium stress and toxicity in plants: an overview. Cadmium Toxicity and Tolerance in Plants, 1-17. https://doi.org/10.1016/b978-0-12-814864-8.00001-2

Sharma, N., Hundal, G.S., et al., 2012. Effect of 24-epibrssinolide on protein content and activities of glutathione – S- transferase and poly phenol oxidase in *Raphanus sativus* L. plants under cadmium and mercury metal stress. Terrestrial & Aquatic Environmental Toxicology 6, 1–7. https://www.cabidigitallibrary.org/doi/full/10.5555/20123302051

Sharma, N., Hundal, G.S., et al., 2014. 28-homobrassinolide alters protein content and activities of glutathione-s-transferase and polyphenol oxidase in *Raphanus sativus* L. Plants under heavy metal stress. Toxicology International 21, 44–50. https://doi.org/10.4103/0971-6580.128792

Sharma, P., Bhardwaj, R., et al., 2007. Effect of 28- homobrassinolide on growth, zinc metal uptake and antioxidative enzyme activities in *Brassica juncea* L. seedlings. Brazilian Journal of Plant Physiology 19, 203–210. https://doi.org/10.1590/s1677-04202007000300004.

Sharma, A., Kapoor, D., et al., 2021. Brassinosteroids: Emerging players in mitigating metal stresses in plants. Plant Growth Regulation, 85, 1-14. https://doi.org/10.1007/s10725-020-00669-7

Shirani Bidabadi, S., Abolghasemi, R., et al., 2018. Grafting of watermelon (*Citrullus lanatus* cv. Mahbubi) onto different squash rootstocks as a means to minimize cadmium toxicity. International Journal of Phytoremediation 20, 730-738. https://doi.org/10.1080/15226514.2017.1413338

Silva, D.M., and Sodek, L., 1997. Effect of Aluminum on Soybean Nodulation and Nodule Activity in a Vertical Split-Root System. Journal of Plant Nutrition 20, 963-974. http://dx.doi.org/10.1080/01904169709365309

Soares, C., de Sousa, A., et al., 2016. Effect of 24-epibrassinolide on ROS content, antioxidant system, lipid peroxidation and Ni uptake in *Solanum nigrum* L. under Ni stress. Environmental and Experimental Botany 122, 115–125. https://doi.org/10.1016/j.envexpbot.2015.09.010

Sri, N.D., Mohan, M.M., et al., 2016. Amelioration of aluminium toxicity in pigeon pea [*Cajanus cajan* (L.) Mill sp.] plant by 24-epibrassinolide. American Journal Plant Science 7, 1618-1628. https://doi.org/10.4236/ajps.2016.712153

Sultan, A., and Raza, A.R. 2015. Steroids: a diverse class of secondary metabolites. Journal of Medicinal Chemistry 5, 310-317. http://dx.doi.org/10.4172/2161-0444.1000279

Swamy, K.N., Vardhini, B.V., et al., 2014. Role of 28-homobrassinolide on growth biochemical parameters of *Trigonella foenu-graecum* L. plants subjected to lead toxicity. International Journal of Multidisciplinary and Current Research, 2, 317-321.

Tarkowská, D., and Strnad, M., 2017. Protocol for Extraction and Isolation of Brassinosteroids from Plant Tissues. In: Russinova E, Caño-Delgado A (eds) Brassinosteroids. Methods in Molecular Biology. Humana Press, New York, NY. https://doi.org/10.1007/978-1-4939-6813-8_1

Van Assche, F., and Clijsters, H., 1990. Effects of metals on enzyme activity in plants. Plant Cell and Environment 13, 195-206. http://dx.doi.org/10.1111/j.1365-3040.1990.tb01304.x

Varma, S., and Jangra, M., 2021. Heavy metals stress and defense strategies in plants: an overview. Journal of Pharmacognosy and Phytochemistry 10, 608-614. https://www.phytojournal.com/archives?year=2021&vol=10&issue=1&ArticleId=13393

Vázquez, M.N., Guerrero, Y.R., et al., 2013. Brassinosteroids and plant responses to heavy metal stress

. an overview. Open Journal of Metal 3, 34–41. https://doi.org/10.4236/ojmetal.2013.32a1005

Villiers, F., Jourdain, A., et al., 2012. Evidence for functional interaction between brassinosteroids and cadmium response in *Arabidopsis thaliana*. Journal of Experimental Botany 63, 1185–1200. https://doi.org/10.1093/jxb/err335

Wang, H.H., Feng, T., et al., 2009. Ameliorative effects of brassinosteroid on excess manganese-induced oxidative stress in *Zea mays* L. leaves. Agriculture Science China 8, 1063–1074. https://doi.org/10.1016/s1671-2927(08)60314-4

Wani, P.A., Khan, M.S., et al., 2007. Impact of heavy metal toxicity on plant growth, symbiosis, seed yield and nitrogen and metal uptake in chickpea. Australian Journal of Experimental and Agriculture 47, 712–720. https://doi.org/10.1071/ea05369

Wood, M., Cooper, J.E., et al., 1984. Soil acidity factor and nodulation of *Trifolium repens*. Plant and Soil 78, 367-379. http://dx.doi.org/10.1007/BF02450370

Wu, X.X., Chen, J.L., et al., 2016. Exogenous 24- epibrassinolide alleviates zinc-induced toxicity in eggplant (*Solanum melongena* L.) seedlings by regulating the glutathione-ascorbate-dependent detoxification pathway. Journal of Horticultural Science & Biotechnology 27, 1–9. https://doi.org/10.1080/14620316.2016.1162030

Yadav, S.K., 2010. Heavy metals toxicity in plants: an overview on the role of glutathione and phytochelatins in heavy metal stress tolerance of plants. South African Journal Botany 76, 167–179. https://doi.org/10.1016/j.sajb.2009.10.007

Yang, X., Li, Y., et al., 2022. Comparative physiological and soil microbial community structural analysis revealed that selenium alleviates cadmium stress in *Perilla frutescens*. Frontiers in Plant Science 13, 1022935. https://doi.org/10.3389/fpls.2022.1022935

Yusuf, M., Fariduddin, Q., et al., 2011. 28-Homobrassinolide mitigates boron induced toxicity through enhanced antioxidant system in *Vigna radiata* plants. Chemosphere 85, 1574–1584. https://doi.org/10.1016/j.chemosphere.2011.08.004.

Yusuf, M., Fariduddin, Q., et al., 2012. 24-Epibrassinolide modulates growth, nodulation, antioxidant system, osmolyte in tolerant and sensitive varieties of *Vigna radiata* under different levels of nickel: a shotgun approach. Plant Physiology and Biochemistry 57, 143–153. https://doi.org/10.1016/j.plaphy.2012.05.004

Yusuf, M., Fariduddin, Q., et al., 2014. Brassinosteroid mediated evaluation of antioxidant system and nitrogen metabolism in two contrasting cultivars of *Vigna radiata* under different levels of nickel. Physiology and Molecular Biology of Plants 20, 449–460. https://doi.org/10.1007/s12298-014-0259-x

Zhang, F., Shi, W., et al., 2002. Response of antioxidative enzymes in cucumber chloroplasts to cadmium toxicity. Journal of Plant Nutrition 26, 1779–1788. https://doi.org/10.1081/pln-120023282

Zhang, Y.P., He, J., et al., 2014. Exogenous 24-epibrassinolide ameliorates high temperature-induced inhibition of growth and photosynthesis in *Cucumis melo*. Biologia Plantarum 58, 311–318. https://doi.org/10.1007/s10535-014-0395-8

Zhao, B., Li, H., et al., 2023. Cross-talk between brassinosteroid signaling and heavy metal stress response. Trends in Plant Science 28, 215-228. https://doi.org/10.1016/j.tplants.2022.10.002

Zulfiqar, U., Ayub, A., et al., 2022. Cadmium toxicity in plants: recent progress on morpho-physiological effects and remediation strategies. Journal of Soil Science and Plant Nutrition 22, 212-269. https://doi.org/10.1007/s42729-021-00645-3