

Innovations

Salicylic Acid: A Potential Metal Stress Attenuator in Legumes Plants

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Abstract: Heavy metals (HMs) have a negative impact on growth and development of plants, especially legumes, which are essential for the world's food security. Presence of HM alters the growth and metabolism of plants by inhibiting photosynthesis, decreasing vegetative growth, decreasing seed germination, and nutrient uptake, etc. Plants have some inherent defense mechanisms for example, osmolyte accumulation, antioxidant defence machinery, production of secondary compounds, etc. to cope with these environmental constraints, however, under severe stressed conditions these strategies are not sufficient. Recently, application of exogenous stress ameliorators such as phytohormones, signaling molecules, etc, have emerged as potential tools that can alleviate the detrimental effects of HM stress on plants. Among diverse phytohormones, salicylic acid (SA) is known to play important role in growth and development of plants by modulating various physiological and metabolic attributes. By keeping this in mind, the current review is highlighting the various physiological, biochemical and molecular role of SA in mitigating the effect of HM stress on legumes. This review also summarises the latest findings on the exogenous application of SA could be a better approach for the sustainable agricultural practices in contaminated soils.

Keywords: Antioxidants, growth, heavy metal, legume, phytohormone, salicylic acid, ROS.

Introduction:

Among the various abiotic stressors, heavy metals (HMs) are a major growing threat to the growth and development of the plants. HMs can be defined as'' elements having atomic number greater than 20 and density higher than 5 grams per square centimetre (Mishra et al., 2018). HMs pose a serious threat to the plants due to their capacity to form bonds with various functional groups present in biomolecules such as carboxylic acid, amino, or sulphur-containing groups (Li et al., 2022). HMs are naturally present in soil due to the processes

involved in the soil formation that break down parent resources. The other major sources of HMs are coal mining, waste combustion, steel processing, excessive and unregulated use of fungicides, bactericides, electroplating processes, fertilizer application, etc. (Mackie et al., 2012; Sardar et al., 2013). Increased buildup of HMs in agricultural soils poses significant challenges for growth and productivity of agriculturally important crops particularly in legumes, which are vital for global food security (Rajput et al., 2024).

Plants are sensitive to the HM ions due to their negative impact on various physiological and metabolic processes (Ghori et al., 2019). Legumes, including beans, peas, lentils, and chickpeas, are more susceptible to HMs because exposure to these metals can impede their growth, yield, and nutritional value. Moreover, High levels of HMs can affect the soil characteristics, such as modulation of soil enzymatic activity, microbial growth, nutrient availability, etc. which directly hampers the plants growth (Bisht and Garg, 2022). Disruption of physiological processes like photosynthesis and water absorption, oxidative stress, nutritional imbalance, and interference with enzyme activity are the main causes of metal toxicity in plants (Bhaduri and Fulekar, 2012; Maleki et al., 2017). Furthermore, changes in the composition of important proteins or the replacement of an essential elements by HMs, results in photosystem inactivation, chlorosis, stunted development, and browning of roots (Gohre and Paszkowski, 2006). The absorption of vital nutrients including calcium, magnesium, potassium, and phosphorus is hampered by the presence of HMs which, further results in reduced growth and productivity of crop plants (Jaiswal et al., 2022).

Under harsh conditions, plants have created a plethora of intricate signaling mechanisms to ensure normal growth and development (Paul and Roychoudhury, 2019). Plants possess inherent tolerance mechanisms to deal with HM stress, which involve a variety of cellular and molecular processes. Metal ions in the cytosol are chelated through phytochelatins and metallothioneins before being compartmentalised in vacuoles (Hasan et al., 2017). Additionally, in order to retain functional proteomes under metal stress, plants use repair mechanisms for stress-damaged proteins and eliminate or degrade proteins that are unable to recover their native conformations (Chaudhary et al., 2019). Interestingly, the activation of enzymatic and non-enzymatic antioxidant systems, as well as a number of signaling pathways including non-protein messengers, calcium ions, kinases, phosphatases, etc., are additional detoxification mechanisms that plants have evolved (Kumar and Trivedi, 2018). Moreover, under stressed conditions plants accumulate osmolytes, which include sugars (fructans, sucrose, trehalose), quaternary ammonium compounds (glycine betaine), amino acids (alanine, arginine, and proline), and sugar alcohol (inositol, mannitol), etc. (Ejaz et al., 2020). Through the direct or indirect scavenging of reactive oxygen species (ROS), the growth of antioxidant bioactive compounds, or the induction of antioxidant enzymatic activity, osmolytes reduce the adverse effects of oxidative stress (Shivashankara et al., 2016). However, under severe metal toxicity, this

balance shifts towards an overabundance of ROS. Therefore, there is a dire need to innovate some strategies which can favour the plants under unfavourable environmental circumstances, in a sustainable manner.

Plant phenolic compounds are among the most abundant and vital defensive substances which, play vital roles in alleviating the detrimental effects of abiotic stressors (Kumar et al., 2023; Kumari et al., 2025). Among the various phenolic compounds, SA is a naturally occurring phenol having the ability to enhance plant resilience against various abiotic stressors. SA regulates various key physiological processes in plants, including nitrogen metabolism, photosynthesis, metabolism, osmolytes synthesis, plant water relations etc. (Naza et al., 2011; Miura and Tada, 2014), and thereby, improve the growth and productivity of crop plants. Moreover, it helps to activate antioxidant defense system, in plants which mitigates the level of oxidative stress caused by ROS generated in response to metal exposure (Hasanuzzaman et al., 2020). By scavenging these harmful compounds, SA reduces cellular damage and promotes better survival under stressed conditions. Moreover, SA help the plants to cope with different types of stress by interacting with various functional and signaling molecules involved in complex stress response (Emamverdian et al., 2020). Overall, SA could be act as a potential stress attenuator in negating the detrimental impact of abiotic stressors on plants, including HMs.

Legumes are plants that belong to the Fabaceae, is one of the largest family of plants including 700 genera and 20,000 species. They have the ability to form symbiotic associations with nitrogen-fixing bacterium, Rhizobium, giving them the intrinsic ability to grow in nitrogen-depleted soils and making them suitable crops for land reclamation and economic development (Delić et al., 2016). They are an excellent source of plant-based protein and are rich in dietary fibre, vitamins and mineral which, assists digestion, regulates blood sugar levels, boosts immunity and maintain overall health of human beings (Slavin, 2013; Giller et al., 2009). A part from this, legumes have the potential to improve soil structure and increase organic matter, which benefits overall health of the soil. They are also an important crop in crop rotation systems, which maintain agricultural productivity over the time (Meena and Lal, 2018). However, in the present scenario, the growth and productivity of legumes are declining due to various environmental constraints, especially the HM stress, which is a serious concern.

By focusing on these factors, the current work provides a comprehensive compilation of data about how SA contributes to the development of stress tolerance in legumes against HM stress. Furthermore, this review's objective is to provide an overview of the most recent developments on the exogenous administration of SA in regulating the morphological, physiological, and molecular responses of stressed legume plants.

Effect of Metal toxicity on legumes

Germination, growth and yield

HM toxicity leads to delay in germination of seeds, seedling emergence, and reduction in growth and productivity of plants by interfering with nutrient as well as water uptake and photosynthesis. Additionally, it hinders reproductive processes, which lowers seed yield, pod growth, and flower formation (Kumar, 2021). Jalali et al. (2018), observed that Cuscutta significantly decreased the germination percentage in *Vicia faba*, *V. sativa*, *Medicago truncatula* and *Trigonella foenum-graecum*. In *Lotus corniculatus*, aluminium (Al) toxicity led to inhibition of root elongation plant growth and thereby, resulting in a lower yield (Navascués et al., 2012). According to the study, conducted by Bishnoi et al. (1993) chromium stress significantly decreased the germination rates, seedling growth, and ultimate yield in pea plants. Similarly, presence HM in the rooting medium negatively impacted the seed germination, development, and yield of chickpea (Naz et al., 2015). The reason being HM toxicity resulted in poor establishment of seedlings due to harmful impact on various physiological functions like root formation and nutrient uptake, which resulted in stunted plant growth and a markedly lower yield. Chromium (VI) toxicity significantly reduced the number of pods and seed weight, which in turn decreased yield by preventing seedling emergence, root and shoot development, and biomass accumulation in chickpea plants (Singh et al., 2020). Mungbean plants exposed to mercury displayed dramatic decrease in seedling growth, seed germination and overall yield (Muhammad et al., 2015).

Photosynthesis and nutrient uptake

HM toxicity disturbs photosynthesis by lowering chlorophyll levels and disrupting the photosynthetic system, as well as impeding the uptake of critical nutrients such as nitrogen, phosphorus, magnesium, calcium, etc. For instance, Cd toxicity lowered the chlorophyll concentration and degraded photosynthetic efficiency in soybean (*Glycine max*), by interfering with the uptake of important nutrients (Xue et al., 2014). Similarly, exposure of chickpea plants to the Lead (Pb) toxicity reduced chlorophyll production, impaired stomatal function, and inhibited calcium as well as magnesium uptake. (Vaishnani et al., 2022). In lentil (*Lens culinaris*), arsenic (As) poisoning impaired the photosynthetic system and lowered the nitrogen and sulphur uptake, thereby, impacting overall growth and development of plants (Kumar, 2021). When exposed to Al stress, pea (*Pisum sativum*) plants displayed reduced chlorophyll content and disturbed nutrient uptake, especially for calcium and phosphorus (Ansari et al., 2023). Furthermore, Cr exposure reduced photosynthetic efficiency and inhibited the uptake of iron and nitrogen in blackgram which, thereby hampered the plant growth (Rath and Das, 2021). When mungbean plants exposed to nickel (Ni) and cadmium (Cd) stress, lowered photosynthetic efficiency, disturbed photosystem, and decreased the amount of chlorophyll were reported by Aqeel et al. (2021). Furthermore, Cd

and Ni hindered the absorption of vital nutrients such as potassium, phosphorus, and nitrogen, which further hindered the plant growth. According to Beri and Sharma (2016) Ni toxicity decreased the photosynthetic efficiency of *Lens culinaris* (lentil) leaves by reducing chlorophyll content and nutrients uptake. On the same line, Elkelish et al. (2024) discovered that chromium treated *Vigna radiata* (mung bean) plants displayed a significant decline in photosynthesis and nutrient uptake.

Respiration and water status

Heavy metal poisoning interferes with respiration by decreasing mitochondrial activity and limiting energy output. It also has an impact on water status of plants by causing root damage and modifying water intake. According to Sanchez-Pardo and Zornoza (2014), under copper (Cu) toxicity, *Glycine max* and *Lupinus albus* showed higher respiration rates, speeding metabolism and depleting energy resources. Moreover, Cu stress also harmed the roots, decreased water uptake and thereby, resulting in poor water stress of plants. HM toxicity in legumes such as *Medicago sativa* (alfalfa), *Pisum sativum* (pea), *Vicia faba* (broad bean), and *Glycine max* (soybean) frequently resulted in increased respiration rates and lowered water stress, which caused metabolic inefficiency and dehydration (Ahmad and Athar, 2002). Al toxicity affected the respiration rate in *Lotus corniculatus* by interfering with mitochondrial activity, which in turn decreased the synthesis of ATP (Navascués et al., 2012). The study also revealed that exposure of plants to aluminium had a detrimental effect on water status and resulting in dehydration of tissues, which lowered turgor pressure and impacted the overall health of the plants. According to the study conducted by Aqeel et al. (2021), respiration process adversely affected by Cd and Ni poisoning, which thereby, disrupted the energy metabolism in mungbean. In addition, water status of plants suffered from decreased water absorption and retention, which resulted in dehydration and reduced turgor pressure.

Oxidative damage

By causing oxidative stress, HMs like As, Cd, and Pb have a negative impact on legumes. They lead to the generation of reactive oxygen species (ROS) by upsetting the equilibrium of cellular antioxidants. This overabundance of ROS harmed DNA, proteins, and lipids, which hindered cellular processes (Ercal et al., 2001). For instance, Navascués et al. (2012) reported that Al toxicity resulted in oxidative damage to *Lotus corniculatus*, due to overproduction of ROS, which resulted in DNA damage, protein deterioration, and lipid peroxidation. Chickpea (*Cicer arietinum* L.) plants treated with vanadium toxicity displayed increased level of ROS which hindered the ability of plants to grow and reproduce (Imtiaz et al., 2018). According to Singh et al. (2020), chickpea (*Cicer arietinum* L.) plant suffered severe oxidative damage as a result of chromium (VI) poisoning. The production of ROS as a result of chromium exposure caused damage to lipids,

proteins, and DNA, among other biological components. According to the study conducted by Muhammad et al. (2015), mercury enhanced accretion of ROS in mungbean, creating oxidative stress that damaged cellular components like proteins, lipids, and DNA and hindered plant development and function. Similarly, copper toxicity caused oxidative burden in *Glycine max* and *Lupinus albus* plants by increasing the generation of ROS, which caused lipid peroxidation and protein breakdown (Sanchez-Pardo and Zornoza, 2014). According to Talukdar (2013), *Phaseolus vulgaris* experienced higher oxidative stress as a result of As exposure due to excessive generation of ROS such as hydrogen peroxide and superoxide radicals.

Rhizobial Symbiosis

The process of conversion of free atmospheric nitrogen into a form that could be available for the plants is known as nitrogen fixation. It is mostly done by nitrogen-fixing bacteria, some of which interact with legumes. Soil fertility and plant growth depend on this mechanism. The presence of HMs in the rooting (Cu, Cr, Co, Cd, Ni, Pb) affects the nodulation potential and nitrogen fixing efficiency of leguminous crops (Haddad et al., 2020). For example, Cd and Pb stress had a negative impact on nitrogen fixation, which led to a notable decrease in nitrogenase activity, nodule number as well as dry weight and leghemoglobin content in Pigeon pea (Bisht and Garg, 2024). Higher Ni concentration in the soil impaired nitrogen fixation in lentil (*Lens culinaris*) plants by impairing the nodule development (Saad et al., 2016). On the same line, *Medicago truncatula*, nitrogen fixation ability decreased in nodules of Hg-sensitive strains of rhizobium whereas, Hg-tolerant *Ensifer medicae* remains unaffected (Arregui et al., 2021). Excessive concentration of Ni in soil damaged root nodules, increased oxidative stress, and impaired the plant's capacity to absorb and use nitrogen properly in *Vigna unguiculata* (Mendes et al., 2023). HMs (Cd, Pb, and Ni) reduced the nitrogen fixation in common beans by lowering nitrogen content and nodule density with Cd had the most negative impact than the others (Wael et al., 2015). The availability of HMs such as Zinc (Zn), Pb, and Cd caused reduction in growth of pea plant due to impaired rhizobial symbiosis (Wani et al., 2008).

The mechanism of SA biosynthesis

Biosynthetic Pathway

Salicylic acid (SA) is a crucial phytohormone important plant hormone that influences plant defence mechanisms and stress responses. The two main routes for the production of SA in plants are the isochorismate pathway and the phenylalanine ammonia-lyase (PAL) (Figure 1). The first step in SA biosynthesis is when ICS (isochorismate synthase) transforms chorismate into isochorismate (IC). The next step involved the conjugation of IC with amino acids, which is catalysed by PBS3 (*avrPphB SUSCEPTIBLE3*). It helps in isochorismate-9-glutamate, which

can either spontaneously degrade to SA or to be transformed by EPS1 to SA (Torrens-Spence et al., 2019; Rekhter et al., 2019). SA accumulation during pathogen infection depends on the EDS5(ENHANCED DISEASE SUSCEPTIBILITY 5) protein, which moves IC from the plastid to the cytoplasm (Nawrath et al., 2002).

Another step in biosynthesis of SA involved the phenylalanine (Phe), pathway in which Phe is changed into trans-cinnamic acid (tCA) by phenylalanine ammonia-lyase (PAL). Secondary tyrosine ammonia-lyase (TAL) activity is also demonstrated by certain PAL enzymes (Cass et al., 2015; Barros et al., 2016). Plant genomes include numerous copies of the PAL gene, which exhibits tissue-specific variation in expression (Reichert et al., 2009). AIM1 (abnormal inflorescence meristem 1) a multifunctional protein involved in fatty acid metabolism, catalyses the conversion of tCA (trans-cinnamic acid) to benzoic acid (BA) (Arent et al., 2010). A benzoic acid 2 hydroxylase, most likely a P450 monooxygenase, is thought to catalyse the last step, which is the conversion of BA to SA (Leon et al., 1995).

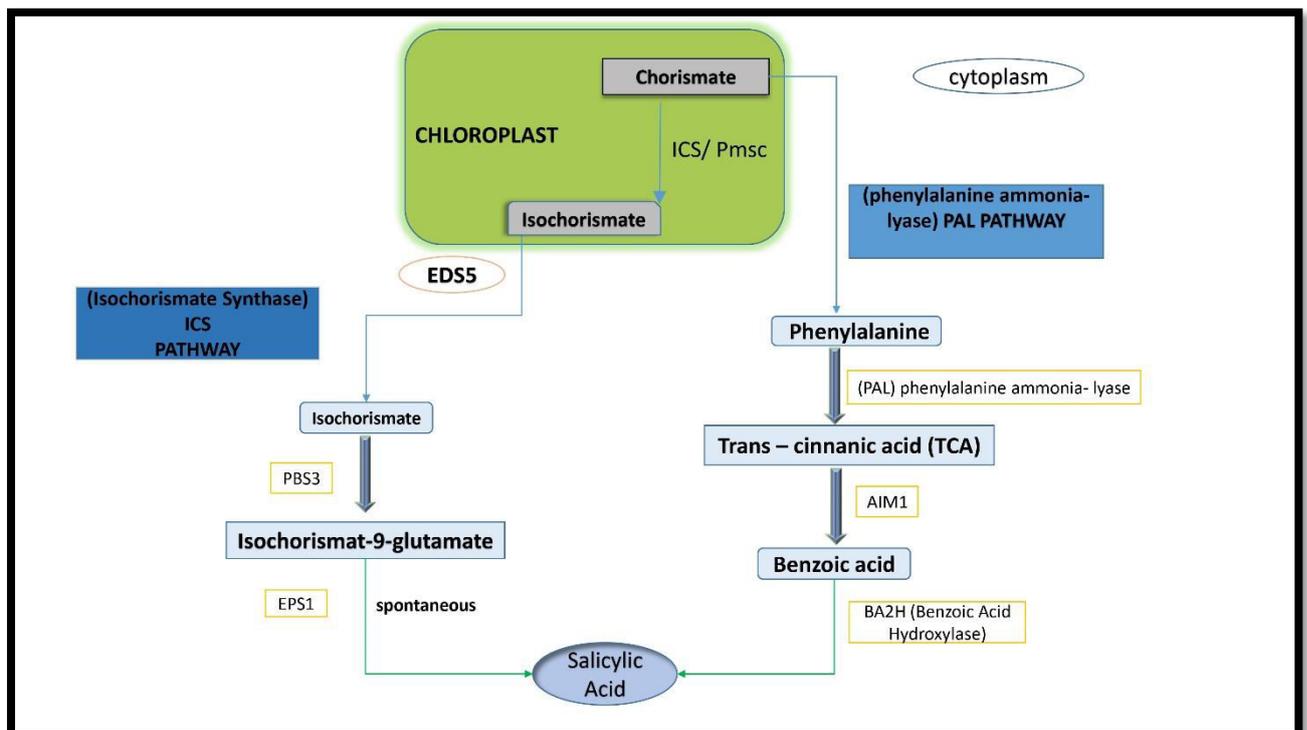


Figure 1: A schematic presentation of SA biosynthesis in plants

Role of SA under HM stress

Effect on growth, yield, nutrient uptake and photosynthesis

SA helps plants to grow better under metal stressed conditions by improving nutrient uptake, boosting photosynthesis, and supporting overall growth (Sharma et al., 2020; Khan et al., 2015). For instance, Ansari et al. (2023) reported that SA

treated pea plants when exposed to Al toxicity, displayed improved growth, photosynthesis efficacy and nutrient uptake (Mg, P). Foliar applications of SA improved morphological, biochemical, and yield parameters in pea plants when grown under Cd and Cu stressed environment (Zahra et al., 2024). Similarly, Gupta et al. (2017) reported improved seed germination and seedling growth when metal stressed (Zn and Pd) soybean plants were supplemented with SA. Exogenous application of SA improved the root growth and shoot growth and yielding potential of bean plants by reducing the uptake of Cd^{2+} (Wael et al., 2015). On the same line SA promoted the growth of metal stressed (Ni, Cd), chickpea plants by reducing the metal uptake and improving the nutrient accumulation (Khan and Bano, 2018). Boron (B) stressed pea plants when amended with SA displayed increased growth, chlorophyll and carotenoid contents (Oliveira et al., 2022). SA improved nutrient intake and photosynthetic efficiency by decreasing the accumulation of HM (Cd) in pea plants (Saleem et al., 2024). Moreover, SA enhanced the photosynthetic rate, water use efficiency, stomatal conductance and CO_2 fixation in chickpea plants when exposed to Cd toxicity (Alyemeni et al., 2014). Under Pb stress, SA treatment increased seedling length and germination percentage, number of pods, seed weight, and total yield of common bean, indicating that SA has a beneficial effect in reducing Pb toxicity and improving plant productivity (Zengin, 2014). SA enhanced the biomass production and pod formation by reducing the negative effects of lead exposure, thus enhancing seed germination, plant growth, and yield of common beans (Qader and Abdul, 2020). Interestingly, SA boosted the growth of Cd stressed chickpea plants by improving nodulation potential in terms of (nodule no. and nodule biomass) indicating positive role of SA in rhizobial symbiosis (Hayat et al., 2014).

Osmotic homeostasis

Osmolytes play critical roles in plant responses to various abiotic stressors. Osmolytes, such as proline, soluble sugar, amino acid etc. serve to maintain cellular activities during stressed environment. For example, according to Barket Ali (2017), mung bean plants exposed to Al toxicity displayed increased buildup of osmoprotectants like proline and free amino acids, which helped to maintain osmotic equilibrium and increased stress tolerance when treated with SA. According to Khalil et al. (2021), when *Phaseolus vulgaris* exposed to HMs (nickel and lead) a significant improvement of osmolytes (proline and protein content) was reported in plants supplemented with SA. SA improved the synthesis of osmolytes (total soluble sugar, proline and protein content) in two different varieties of pea plants when exposed to HMs stress (Cu, Cd) (Zahra et al., 2024). Application of SA significantly enhanced the proline level in Cd stressed common Bean which assisted the plants in managing with stress and water balance (Wael et al., 2015). In common beans (*Phaseolus vulgaris* L.), SA treatment enhanced the accumulation of osmolytes like proline and soluble sugars, helping the plant to

preserve osmotic balance and reducing the negative impacts of Pb stress (Qader and Abdul, 2020). Similarly, under Pb stress SA promoted the synthesis of soluble sugars and proline in faba beans, leading to osmotic balance and protecting cells from oxidative damage (Layachi and Kechrid, 2023).

Antioxidant Defense Mechanism

To cope up with unfavourable environmental conditions plants contain an inherent defense machinery that is antioxidant defense system, which includes both enzymatic antioxidants and non-enzymatic antioxidants for removal and detoxification of ROS (Dhiman et al., 2022). Various studies have discovered the role of SA in strengthening the antioxidant defense mechanism of the plants. For instance, Boron stressed pea plants displayed a significant improvement in SOD, CAT, APX, GSH, GPOX, and GR activity when treated with SA (Oliveira et al., 2020). Similarly, when Cd stressed soybean plants supplemented with SA they displayed increase in activities of various antioxidant enzymes which helped the plants to detoxify the ROS (Dhiman et al., 2022). Roychoudhury et al. (2016) reported that SA treated mung bean seedlings under Cd stress displayed increased activity of antioxidant enzymes (CAT, POD and SOD) and lowered the levels of malondialdehyde and hydrogen peroxide. By boosting the antioxidant defence systems, SA assisted the pea plants in fending off oxidative stress brought on by Al toxicity (Ansari et al., 2023). According to Gupta et al. (2017), application of SA improved the antioxidant enzyme activity and crop productivity of soybean by reducing the negative effects of Pb and Zn stress. Application of SA to Cd stressed *Phaseolus vulgaris* L. displayed reduction in the level of polyphenols, flavonoids, and tannins, especially in roots and cotyledons, indicating the role of SA in regulating defence responses in plants (Hediji et al., 2021). SA treatment enhanced POD, SOD, and APX activities in soybeans and reduced the intensity of oxidative damage by lowering the level of H₂O₂ under Al toxicity (Liu et al., 2017). SA enhanced the antioxidant enzyme activity in leaves and roots of peanut (*Arachis hypogaea* L.) under iron deficiency and thereby, decreased the level of harmful compounds like MDA, H₂O₂, and O₂^{•-} (Dong et al., 2016). Moreover, spraying of Chickpea plants with SA significantly enhanced the proline content, antioxidant enzyme activity and yield when subjected to Cd stress (Alyemeni et al., 2014). Interestingly, under mercury (Hg) stress, SA improved the proline content and upregulated the activity of enzymatic (APX, GR, and SOD) and non-enzymatic antioxidants (Glutathione and Ascorbate) (Arregui et al., 2021). Moreover, Pretreatment of mung bean seedling with SA improved the osmolytes level such as sugars, proline and activity of antioxidant enzymes (CAT, SOD, APX, and GPX) under Cd stress (Roychoudhury et al., 2016). Overall, SA has a crucial role in ameliorating the detrimental impact of various HMs on legumes by modulating various physiological and biochemical attributes (Table 1).

Table 1. Role of SA in mitigating the impact of HM stress on legumes

| Heavy metal | Concentration of Heavy metal | Host Plant | Concentration of SA | Mode of action of SA | Reference |
|-------------|--|-----------------------|--|--|-----------------------|
| Cd | 0, 25, 50, or 100 mg Kg ⁻¹ | Cicer arietinum | 10 ⁻⁵ M | Improved growth, nodulation parameter, and activity of enzymes involved in nitrogen assimilation | Hayat et al. (2014) |
| Cd | 0, 0.25, or 0.50 mM | Phaseolus vulgaris L. | 1.0 mM | Increased chlorophyll content and growth, decreased oxidative stress, and increased antioxidant enzymes activity | Wael et al. (2015) |
| Cd | 0.5, 1.0, 2.0 and 5.0 μM | Pisum sativum L. | 500 μM | Increased photosynthesis and growth of parameters | Popova et al. (2008) |
| Cd | 0, 5, 10 and 15 mg Cd kg ⁻¹ | Vigna radiata L. | 0, 10 ⁻⁶ and 10 ⁻³ M | Enhanced plant growth, antioxidant enzyme activities and protein content | Imran et al. (2021) |
| Cd | 200 μM | Glycine max L. | 0.5 mM | Improved root and shoot development, soluble carbohydrate content, and upregulated antioxidant defence | Marefat et al. (2012) |

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|----|--------------------------|-------------------------------|------------------------|--|---------------------------|
| Cd | 0.5, 1.0, 2.0 and 5.0 mM | <i>Pisum sativum</i> L. | 500 mM | Improved biomass, chlorophyll content and rate of CO ₂ fixation | Popova et al. (2009) |
| Pb | 100, 150, and 200 mM | <i>Vigna unguiculata</i> L. | 0.05, 0.08, and 0.1 mM | Increased seed germination, root and shoot biomass, antioxidant enzymes activity and protein content | Kasim et al. (2014) |
| Pb | 0, 5, 10 ppm | <i>Phaseolus vulgaris</i> L. | 0,100,200,400 ppm | Improved vegetative growth, yield, and nutritional value | Abdul and Qader (2021) |
| Pb | 0.25 mg/L | <i>Pisum sativum</i> L. | 10 ⁻⁴ M | Enhanced height and growth parameters | Ratushnyak et al. (2012) |
| Zn | 0, 25, 50, 75 mg/L | <i>Vigna radiata</i> | 0, 50, 100, 200 mg/L | Improved uptake of nutrients, photosynthesis and yield | Ali et al. (2013) |
| Ni | 0.75, 1.5 and 3 mM/L | <i>Cicer arietinum</i> L. | 1 mM/L | Improved Proline accumulation, reduced oxidative and increased photosynthetic efficiency | Çanakci and Dursun (2011) |
| Fe | 250 ppm | <i>Pisum sativum</i> L. | 250 μM | Higher growth, photosynthetic pigments, soluble sugars and nutrient acquisition | Naseer et al. (2022) |
| B | 0.001-600 μg/ml | <i>Phaseolus aureus</i> Roxb. | 10 ⁻⁴ M | Reduced MDA accumulation, lipoxygenase | Muhammad and Shaheed |

| | | | | | |
|----|----------------------------------|---------------------|-----------------------|---|---------------------------|
| | | | | activity and higher proline content | (2012) |
| As | 0 or 50 mg kg ⁻¹ soil | Vigna radiata | 0, 0.25, 0.5 and 1 mM | Improved growth, metal tolerance and antioxidant enzymes activity | Sadeghipour et al. (2021) |
| Fe | 100 μM | Arachis hypogaea L. | 50, 100, and 250 μM | Enhanced plant growth and restored nutrient uptake | Kong et al. (2014) |

Molecular mechanisms

SA is widely known phytohormone which can improve the growth and developments of plants by modulating various physiological, biochemical and molecular response. Various studies have shown that SA can modulate the expression of stress responsible genes at transcript level in various plant species. However, very few reports are there on the specific role of SA in modulating the expression of stress responsive genes in legumes under HM stress. A study conducted by Liu et al. (2017) reported that SA had a beneficial effect in modulating the expression of antioxidant defence gene - GmNPR1 which, imparted Al tolerance to soybean plants. Similarly, under Cd stress, application of SA induced the expression of MsHO1 gene (Haem Oxygenase-1) in Medicago sativa which, reduced the accretion of ROS and upregulate the antioxidant enzyme activity, and thereby, improved the resilience of plants toward metal stress (Cui et al., 2012). Interestingly, SA has been reported to improve the freezing resistance in Medicago sativa by upregulating the genes involved in MAPK signalling and the NPR1-dependent pathway; NPR1, WRKY, TGA, PR1, and TRxh (Wang et al., 2023). In addition to legumes, Zhanganah et al. (2018), revealed that application of SA altered the level of transcripts and coding methionine biosynthesis (including 1-aminocyclopropane-1-carboxylate synthase (ZmACS6); S-adenosylmethionine synthase (ZmSAMD) which, played a significant role in lead tolerance in maize plants, indicating the potential role of SA in non-legume species. By significantly up-regulating the key genes CYP71AV1, artemisinic aldehyde Δ¹¹(13), amorpha-4,11-diene synthase (ADS) and aldehyde dehydrogenase 1 (ALDH1) double-bond reductase (DBR2) in Artemisia annua, SA significantly improved the content of secondary metabolite that is artemisinin and thereby, imparted As stress tolerance (Kumari et al., 2018). SA treatment significantly enhanced the expression of antioxidant enzymes StAPX, StSOD and StSABP2 (SA biosynthesis) in Cd-stressed potato plants (Li et al., 2019). Moreover, SA amendment decreased the uptake of Cd in spinach shoots by modulating the expression of genes (SoHMA3-like, SoNramp3.2-like, and

SoNramp6) involved in Cd uptake (Tang et al., 2024). SA pretreatment significantly upregulated the expression OsCuZnSOD1, OsCATB, and OsGLY1 genes in rice plants and thereby, enhanced antioxidant defense and glyoxalase activity leading to improved vanadium stress tolerance (Altaf et al., 2022). In lettuce, SA treatment improved Cd stress tolerance by upregulating the expression of HMA3, HMA4 and SAMT genes (Tang et al., 2023)

Conclusions

Heavy metal (HM) stress negatively affects the growth and development of legumes by affecting the photosynthesis, nutrient and water uptake, oxidative damage, rhizobium symbiosis and thereby, ultimately impacting the yield. Fortunately, SA has emerged as a promising candidate for alleviating the detrimental effects of HM stress on legumes. Extensive research has demonstrated that SA possesses the remarkable ability to enhance plant growth, nutrient uptake, photosynthesis, osmotic homeostasis, antioxidant defense. Overall, application of SA could be a potential sustainable technique to alleviate the detrimental impact of abiotic stressors on agriculturally important crops, especially in legume. Although various studies are available at physiological and biochemical level, however the work of SA on the molecular aspects, especially in legumes, are scanty which, needs further attention.

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