Innovations

A Comprehensive Review on Role of Salicylic Acid (SA) Against Lead (Pb) Induced Toxic Responses in Plants

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Abstract: *Lead (Pb) toxicity emerging as a major environmental issue because of its pervasiveness and persistence, which negatively impacts the growth and development of agriculturally important crops. Pb exposure causes serious physiological and biochemical changes in plants, such as oxidative stress, reduced photosynthesis, changed nutrient uptake, stunted growth, impaired metabolism, etc. Although, plants have diverse inherent mechanisms, for example, activation of antioxidant enzymes, phytochelatin synthesis, osmolyte production, etc. to cope with metal toxicity, however they are not sufficient to alleviate the toxicity completely. In order to combat stress induced damages, recently application of various phytohormones and signaling molecules has drawn interest due to their potential to strengthen plant defenses against heavy metal stress. A naturally occurring phenolic compound called salicylic acid (SA) has become one of the most important modulators of plant stress tolerance. SA improves plant resistance to metal stress by modulating various physiological and biochemical reactions. Moreover, SA aids in the control of metal accumulation and transport byregulating ionic homeostasis and modulating antioxidant defense machinery. By keeping all this in mind, the present study addresses the role of SA in eliminating the negative impact of Pb toxicity on plants. Moreover, this review also highlights the interactive role of SA with other phytohormones in negating the impact of diverse abiotic stressors on plants, through sustainable manner.*

Keywords: *Lead, Salicylic Acid, Reactive Oxygen Species, Photosynthesis, Antioxidant, Nutrients*

Introduction

Heavy metals (HMs) are the most common contaminants found in agricultural field, worldwide. Excessive accumulation of HMs not only contaminate the soil but also have an adverse effect on the safety and quality of food (Angon et al., 2024).HMs enters into the field by anthropogenic activities (e.g. industrialization, mining, use of fertilizers, pesticides, etc.) and natural sources (such as volcanic eruption, rock weathering, etc.). HMs such asarsenic (As), Lead (Pb), cadmium (Cd)and nickel (Ni), etc. are the most prevalentmetal ions detected in metal polluted areas (Subasinghe et al., 2022).The majority of HMsare non-biodegradable and therefore, with time their total concentration is building up in soils. Among the different HMs, Pb belonging to group IV of the periodic table, is a potential HM which, ranks 2^{nd} in toxicity as per the substance priority list (ATSDR 2022). It is found naturally in the earth crust with bluish-grey appearance and have various negative effects on growthand metabolism of the plant. The major predominant forms ofPb in soil are lead oxides and hydroxides, lead-metal oxyanion complexes, Pb (II), etc. (Dongre et al., 2021). Moreover, it is also found as a combination with other elementssuch asoxygen ($PbCO_3$), sulphur (PbS, $PbSO_4$), etc.The range of Pb in earth's crust varies from 10 to 30 mg kg^{-1} and in the surface soils, it varies from 10 to 67 mg kg^{-1}(Frank et al., 2019).

Plants majorly take up Pb from the soil through the roots and accumulate it in different plant parts. Moreover, it can also be absorbed by the leaves and thereafter, can be transferred to other arial parts of the plant. By entering into the pants, it leads to the negative impact on morphology, growth, and photosynthetic processes (Sharma et al., 2005). The development and growth of plants are seriously threatened by Pb toxicity. Even in small amounts, it disrupts a number of physiological and biochemical functions in plants. Growing Pb concentrations dramatically reduced seed germination, growth and increased membrane permeability in three sorghum varieties (Osman et al., 2023).Pb toxicity has also been reported to alter the structure of roots which lead to a significant reduction in growth and biomass(Fahr et al., 2013). Pb toxicity impairs the root development which make it difficult for the plant to absorb nutrients and water Moreover, Pb toxicity reduced the root length, biomass, nutrient uptake and overall vegetative growth of Tagetes erecta (Gabash et al.,2023).By decreasing the permeability of cell membranes, Pb also interferes with the plant's ability to absorb and transport water(Raniet al., 2024). Furthermore, by competing for uptake and transport with vital elements including calcium, magnesium, and potassium, Pb results in nutritional imbalances.Deficiencies resulting from this competition further hinder growth and metabolism. Moreover, Pb poisoning increases the generation of reactive oxygen species (ROS), including hydrogen peroxide and superoxide radicals, which leads to oxidative damage to the plants (Mansoor et al., 2023).Various cellular processes are compromised by these ROS because they directly harm proteins, lipids, and nucleic acids. Despite the fact that plants use antioxidant defensemechanisms to fight oxidative stress, extended exposure to Pb cannot overcome the damage caused by ROS and therefore, reduce the growth and productivity of crop plants and leads to cellular damage.

Nowadays, SA a member of the remarkably varied class of plant phenolics, is crucial for controlling plant growth and development of plants**.** SA reduces the vulnerability of plants to environmental stressors by regulating the photosynthetic rate, transpiration rates, stomatal movement, and antioxidant defensesystem. SA increases the net CO2 assimilation rate by improving shoot dry matter (Nazar et al., 2015). Moreover SA reported to enhance the photosynthetic pigments, Osmo protection, membrane stability, carbon metabolism, and antioxidant system in wheat, barley, rice, maize, and tomato (Das et al., 2024).The beneficial impacts of SA on plants' reactions to abiotic stressors, such as ozone and ultraviolet (UV) radiation heat stress, cold and drought, and salt and osmotic stresses have been shown in several studies (Yang et al., 2023). Interestingly, SA plays a crucial role in the plant's immune system under biotic stress circumstances, especially through systemic acquired resistance (SAR). Although, various studies have been conducted in reviewing the impact of SA in plants under diverse abiotic stresses, however, no review is available on unravelling the role of SA under Pb toxicity in different plant species. Therefore, current study will provide an overview on impact of SA in imparting stress tolerance to the plants by modulating various physiological, biological and molecular processes.

Effect of lead (Pb) on plants

Seed germination and growth: Plants majorly take up Pb from the soil through the roots and accumulate it in different plant parts. Moreover, it can also be absorbed by the leaves and thereafter, can be transferred to other arial parts of the plant. By entering into the plants,it leads to the negative impact on morphology, seed germination, growth, and photosynthetic processes. For example, Awan et al. (2015) reported reduced germination index, germination percentage, and plant biomass of rice under Pb toxicity. Similarly, Pb toxicity resulted in shortening of roots and hypocotyl of Lupinus plants and thereby reduced the number of germinating seeds (Wozny et al., 1982).Pb toxicity resulted in reduced root and shoot biomass of cow pea plants due to higher accretion of Pb in respective tissues (Kopittke et al., 2007). Jiang and Liu (2010) correlated the reduced growth of Pb exposed Allium sativum with the alteration in ultrastructure of endoplasmic reticulumand disruption of biological membranes. Zea mays plants displayed reduction in germination percentage, seedling growth, and protein content under Pb stress due to inhibited activities of various vital enzymes (amylase, protease etc)(Hayat et al., 2010).

Similarly in rice endosperm, reported reduced amylase and protease activity under Pb toxicity which led to reduction in seed germination rate (Wang et al., 2020). Exposure of Spartiana alterniflora and Pinus helipensis seeds with Pb displayed reduced germination percentage (Staszak et al., 2020). Pb toxicity delayed the germination trait and reduced the germination ability of seeds in different spices of families Cruciferae, papilionaceae and poaceae.Soil contaminated with Pb toxicity displayed reduced seed germination rate and undesirable morphological traits in Ocimum basilicum (Fattahi et al., 2019).Pb toxicity inhibited the growth of roots and shoots in Zea mays, Triticum aestivum, and Medicago sativa in concentration dependent manner (Vasilachi-Mitoseru etal., 2023). On the same line, exposure of wheat plants with Pb toxicity led to a significant reduction in plant biomass, height and root and shoot growth with greater negative impact on root biomass than the shoots (Kumar et al., 2018). Talha et al. (2023) corelated the negative impact on root growth of maize seedling with increasing dosage of Pb in the rooting media. In the study conducted by Chandrasekhar and Ray (2019) rising lead nitrate levels in the soil had a detrimental effect on the biomass of the roots and shoots of Eclipta prostrata, Scoparia dulcis, and Phyllanthus niruri with lesser impact of Pb stress onEclipta prostratathan the other two species. Overall, the studies highlight that the application of heavy metals including Pb reduced the seed germination, seedling length, growth and overall development of plants in a concentration dependent manner.

Photosynthesis, respiration and nutrient uptake: One of the most important physiological characteristics of plants is photosynthesis, which plays a vital role in growth and productivity of plants. However presence of HM in the rooting medium have detrimental impact on the photosynthetic machinery of plantsas well as its functions, and thereby can reducing the chlorophyll synthesis and inhibit the Calvin cycle either directly or indirectly through blocking the light and dark reactions (Muhammad et al., 2021).When sugar beet plants were exposed with varying concentration of Pb,a significant decline in growth and photosynthetic efficacy was observed by Wu et al. (2021). Various studies have examined the effects of Pb toxicity on chlorophyll fluorescence, growth, photosynthetic pigments, and found adverse effect of the heavy metal on these aspects. For example Ahmad et al. (2008) reported that Pb inhibited the C3 cycle and the electron transport chain, and thereby, prevented the synthesis of vital pigments through altering the ultrastructure of chloroplasts. Additionally, Cencki et al. (2010) reported interference of Pb with other nutrients uptake (Fe, Mn, S) etc. which led to inhibition of photosynthesisin Brassica rapa. L.Pb toxicity inhibited the activity of enzymes involved in nitrate assimilation that is nitrate reductase enzyme, which decreased the nitrogen content in Brassica pekinensis (Xiong et al., 2006) .In a similar way, high Pb concentrations decreased the amount of phosphorous (P) in cabbage, which in turn reduced plant growth and biomass accumulation (Sinha et al., 2006).Pb stress affected mitochondrial activity in S. drummondii leading to reduced cellular respiration rate (Ruley et al., 2006). Kibria et al. (2009) revealed the negative impact of Pb on nutritional status, growth and germination of Amaranthus gangeticus andA. oleracea.Moreover, Pb poisoning interfered with the absorption of nutrients by competing with necessary components, resulting in insufficiencies in iron (Fe), calcium (Ca), and magnesium (Mg). Photosynthetic efficiency of Phaseolus vulgaris was negatively impacted by Pb poisoning, due to decreased photosynthetic pigments, nutrient uptake and limited light absorption (Khalil et al., 2021).Exposure of Leucaena leucocephala to Pb toxicity resulted in alteration of ultrastructure of the chloroplasts and lowering of nutrient uptake which ultimately led to dramatic decrease in the photosynthetic rate (Alkhatib et al.,2019). According to the study of Gupta et al. (2024), Pb poisoning in Zea mays and Oryza sativa hampered photosynthesis by destroying chloroplast structures, altering nutrient uptake (Mg, K, N) interfering stomatal conductance and breaking down chlorophyll pigments.Algethami et al. (2023) reported thatPb and Cd stress in Triticum aestivum reduced chlorophyll content, hampered gas exchange parameter and nutrient acquisition (N, P, K) which had a detrimental effect on photosynthetic efficiency of plants.

Oxidative stress and antioxidant defense: Lipids and proteins in plant cells are the main targets of oxidative damage brought on by ROS (Anjum et al., 2015).For example, Citrus aurantium L. plants grown under Pb enriched soil experienced higher oxidative stress due to increased production of ROS (Giannakoula et al., 2021).Similarly, Sun et al. (2010) reported higher accumulation of H_2O_2 concentrations in roots of Hypnum plumaeforme subjected to Pb stress. Pb toxicity increased the production of H_2O_2 in roots of B. juncea which led to oxidative damage to the plants (Dalyan et al., 2018).Similarly, Huang et al. (2008) reported higher burst of ROS in two different ecotypes of Sedum alferdii under Pb toxicity. Increased ROS and MDA levels were reported by Wang et al. (2012) in Vallisneria natans when exposed to Pb indicating higher level of oxidative stress in metal stressed plant when compared to control. On the same line, elevated level of ROS were reported in Pb stressed Coronopus didymus further indicating the role metal toxicity in inducing oxidative burden on plants (Sidhu et al., 2016).
Plants have a variety of defense mechanisms that work to eliminate ROS before they have a chance to harm delicate components of the cellular machinery. These mechanisms can be easily separated into two categories: enzymatic antioxidants (catalase, superoxide dismutase, glutathione reductase) andnon-enzymicantioxidants (glutathione, ascorbate, carotenoids) etc, which have the ability to nullify the impact of oxidative stress. The antioxidative enzymes GR, GPOX, superoxide dismutase etc. were found to be more upregulated in the roots than leaves of rice plants under Pb toxicity (Verma and Dubey, 2003)**.** Pb toxicity can cause a variety of symptoms, including impaired mitotic division and altered activities of antioxidant enzymes, even at the cellular level (Kang et al., 2009; Kaur et al., 2012).According to Bhatti et al. (2013) under Pb metal stress, levels of chlorophyll a and chlorophyll b significantly decreased in different varieties of wheat.According to Sharma et al. (2023), Pb toxicity in barley raised oxidative stress by increasing lipid peroxidation and ROSlevels and decreasing the activity of antioxidative enzymes; SOD, POD, CAT. Similarly, higher production of ROS were reported in Brassica juncea and Oryza sativa under Pb exposure due to alteration of activity of various antioxidant enzymes which resulted in physiological and cellular damage (Mitra et al., 2020).Khan et al. (2021) reported a significant increase in theproduction of ROS (MDA, H_2O_2, etc.) and decrease in

the activity of antioxidant enzymes such as (CAT) and (SOD) when rice plants were treated with Pb.Overall, Pb toxicity has a negative impact on plant health by impairing Photosynthesis, impeding nutrient uptake, respiration,disrupting the oxidative stress and antioxidant defense system, ultimately compromising overall plant growth and productivity.

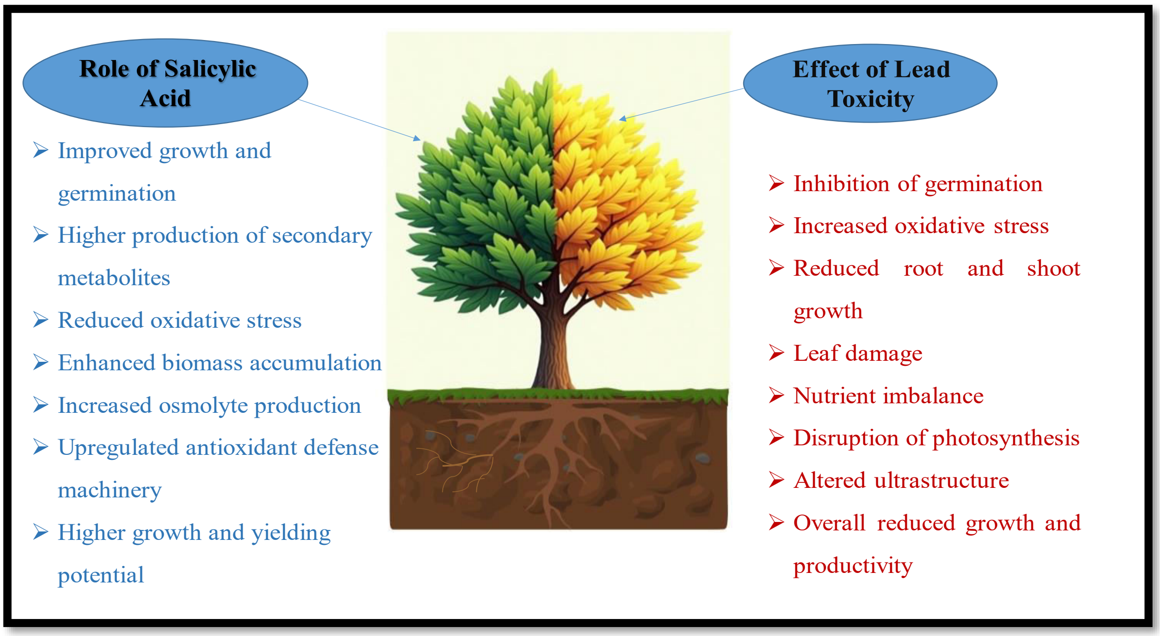

Fig 1:- A schematic presentation of role of SA in alleviating the impact of pb toxicity on plants

Role of SA in mitigation of Pb toxicity

Salicylic acid (SA), is a potential phytohormone that helps the plants to grow under unfavourable environmental conditions (Arif et al., 2020). It regulates various physiological, biochemical and molecular processes which, defend the plants against various stressors (Zulfiqar et al., 2021) (Fig 1). SA has been reported to reduce the effects of various HMs on a variety of crops (Table 1). For example, application of SA improved the root and shoot length of Oryza sativa seedlings when exposed to Pb stress (Jing et al., 2007). Similarly, SA pretreatment enhanced the biomass production, shoot and root growth, and chlorophyll levels in maize plants when exposed to Pb toxicity (Zanganeh et al., 2020). In Brassica napus, SA increased biomass accumulation, preserved water balance, and decreased Pb toxicity by boosting the seedling growth (Jazi et al., 2015). Fontenele et al. (2017) observed a significant improvement in plant height, leaf number, and dry weight whenVigna unguiculatawere treated with SA.

In addition to growth attributes, SA can improve the rubisco activity, stabilize the structure of chloroplast, increased the accumulation of photosynthetic pigments etc. under stressful conditions (Mateo et al., 2006, Hayat et al., 2007). Moreover, SA plays a crucial role in nutrient acquisition, water uptake and maintaining the integrity of the cellular membrane (Khokon et al., 2011). For instance, amendment of maize plants with SA displayed higher photosynthetic efficiency, nutrient uptake and reducedPb accumulation (Gupta et al., 2024). In Vigna unguiculata under Pb stress, exogenous supplementation of SA improved the photosynthetic pigments level, stabilised nutrient intake, and lessened the impact of oxidative stress (Fontenele et al., 2017). Similarly, SA reduced the intensity of oxidative stress by improving the nutritional status (Mn, Ca, Fe) and inhibited the accumulation of Pb in Vallisneria natans (Wang et al., 2011).

Besides, SA decreased the damage caused by oxidative species by increasing the transcription of antioxidant defense genes such asPOD, CAT,SOD in Brassica campestriswhen exposed toPb stress (Hasanuzzaman et al.,2019).Brassica juncea under Pb stress showed increased activity of antioxidant enzymes, including APX, CAT and SOD (Agnihotri et al., 2018). SA treatment reduced the intensity of oxidative stress by improving the antioxidant enzymes activity in Pb stressedBrassica napus(Sharma et al., 2020).When Pb stressed wheat plants were supplied withSA, it acceleratedthe antioxidant defense machinery of stressed plant and prevented them from damage caused by metal toxicity (Chen et al.,2016).SA pre-treatment reduced the generation of oxidative species and increased antioxidant enzymes activity which in turn reduced the oxidative damage to Allium cepa (Kaur et al., 2021). Similarly, SA increased the synthesis of phenolic compounds, organic acids and modulatedantioxidant enzymes activity and thereby reduced the effect of oxidative damage in Brassica juncea exposed to Pb stress (Kholi et al., 2017). On the same way, SA reduced the accumulation of ROS and enhanced the glutathione (GSH) levels as well as the activities of antioxidant enzymes including CAT in Pb-stressed Zea mays plants (Gupta et al., 2024). On the same line, exogenous supplementation of SA reduced the production of ROS in Pb stressed B. campestris plantsby upregulating the antioxidant defensemachineryand thereby, enhanced the growth and productivity (Hasanuzzaman et al., 2019).

SA is well known to enhancethe accumulation of osmolytes (proline, glycine betaine, and soluble sugars), which aid in preserving osmotic balance and maintaining cellular structures. For example, SA application under Pb stress inclined the synthesis of osmolytes (proline, sugar) which imparted metal tolerance to Brassica juncea (Kohli et al., 2018). Exogenous application of SA increased the osmolyte synthesis (proline and soluble sugars) in Pb stressed Faba bean and common bean which helped the plants to maintain cellular homeostasis and thereby mitigated the negative effects of metal stress (Layachi et al., 2023).Similarly, exogenous application of SA to Pb stressedmaize plants displayed improvedtolerance towards metal toxicity by reducing and the level of methylglyoxal, increasing the NOcontent in shoots and roots, and preserving the balance of cysteine and methionine(Zanganeh et al., 2019). Therefore, regulation of ROS detoxification machinery to shield plants from metal-induced damages is another important mechanism underlying SA-regulated metal tolerance in plants (Saleem et al., 2021, Song et al., 2023). All the above studies highlight that SA can activate plant defensemechanisms by upregulating the activity of antioxidant enzymes, maintaining cellular redox homeostasis, and altering the level of transcripts encoding various stress responsive pathways.

Table 1:-Mode of action of SA under heavy metal stress

Sr No.	Host plant	Concentration of salicylic acid	Mode of action of salicylic acid	References
1.	Lycopersicon esculentum	1 mM	Reduced oxidative stress markers, Na level, increased nutrient uptake (Mg, K) and upregulated antioxidant defense machinery	He and Zhu (2008)
2.	Daucus carota	0, 0.5 mmol kg^{-1}	Improved plant biomass, photosynthetic pigment concentration (carotenoids, anthocyanin) and upregulated antioxidant enzymes activity	Eraslan et al. (2007)
3.	Ctenanthesetosa	10^{-6} M	Decreased water loss and upregulated the antioxidant defense mechanism	Kadioglu et al. (2011)
4.	Citrullus lanatus	0, 0.25, 0.50, 0.75 and 1.0 μmol L^{-1}	Increased osmolyte production and reduced membrane damage	Silva et al. (2023)
5.	Helianthus annuus L.	0, 100, 200, 300 mg L^{-1}	Increased leaf SOD and POD activity, growth and photosynthetic capacity	Noreen et al. (2009)
6.	Satureja khuzistanica	100 and 200 mg L^{-1}	Increased growth, essential oil content and yield	Sadeghian et al. (2013)
7.	Lycopersicon esculentum	10^{-7} and10^{-4} M	Reduced oxidative damage and increased antioxidant enzymes activity	Szepesi (2008)
8.	Triticum aestivum	1, 2, 4, 8, and 16 mg L^{-1}	Increased growth, chlorophyll content and activities of various antioxidant enzymes	Wang and Zhang (2017)
9.	Cicer arieitin	0.5 mM	Increased biomass, productivity, higher ROS	Kaur et al. (2022)

	um		scavenging, improved nodulation potential and photosynthetic efficiency	
10.	Medicago sativa	0.1 and 0.5 mM	Increased plant growth and photosynthetic capacity, inhibited catalase activity and prevented the accumulation of polyamines.	Palma et al. (2013)
11.	Vigna radiata	0.5 mM	Increased glycine betaine (GB) accumulation suppressed ethylene formation and enhanced antioxidant defense responses and photosynthetic efficacy	Khan et al. (2014)
12.	Pisum sativum L.	1.0 mM	Increased SOD, APX, CAT activities and lesser production of ROS	Singh et al. (2015)
13.	Hordeum vulgare	500 μM	Enhanced antioxidant defense abilities and photosynthetic efficiency	Habibi (2012)
14.	Pisum sativum L.	0.1 mM	Reduced Pb-induced oxidative stress by improving growth characteristics, photosynthetic pigment contents, and antioxidant enzyme activities	Popova et al. (2011)
15.	Calendula officinalis	0, 1, 2 mM	Increased plant biomass, height, leaf area, no. of flowers and chlorophyll content	Bayat and Neamati (2012)

Crosstalk between SA with phytohormone

SA is a versatile phytohormone that plays a key role in growth and development of plants by coordinating multiple defenseresponses under unfavourable environmental conditions. The conversion points in signal transduction pathways of hormones, have a significant role in regulating the growth and stress responses in plants.Coordination between SA and other phytohormones (auxins, cytokinin, gibberellins, ABA, ethylene, and jasmonates) is acrucial factorthat regulate diverse stress responses in plants facing multiple challenges (Nishiyama et al., 2013).Therefore, it is necessary to comprehend the intricate relationship between pathways of differentphytohormone. SA treatment reduced the negative effects of Pb stress on pepper plants by improving the endogenous H_2S content and modulating ascorbate glutathione pool (Kaya et al., 2023). Moreover, by upregulating the activity of enzymes involved in H_2S biosynthesis, the combined application of SA and H_2S imparted heat tolerance to maize plant (Li et al.,2015).Individual and cumulativeapplication of SA and kinetin improved various physiological and biochemical parameters in Cd-stressed wheat plants (Eydi Asl Shoshtari et al., 2024).On the same line, Cd stressedwheat seedling treated with SA and indole-3-acetic acid displayed synergistic effects of both the phytohormones in term of improved antioxidant enzymes activity and altered ultrastructure of leaf (Agami et al., 2013).Exogenous application of SA reduced the level of ethylene and thereby safeguard the rice plants from detrimental impact of As (Mahajan et al., 2023). A study conducted by Kohli et al. (2018) displayed that individual as well as cumulative application of SA and 24-epibrassinolidedecreased the damaging effects of Pb onBrassica juncea by improving photosynthetic efficiency, nutrient uptake and upregulating the activity of antioxidant enzymes.Additionally, SA and nitric oxide (NO) mitigated the harmful effects of Cd on ryegrass by improving the chlorophyll content, antioxidant enzymes activity and reducing the ROS production (Wang et al., 2013). NajafiKakavand et al., 2018) reported increased osmolytes and carotene accumulation, antioxidant enzymes activity when Ni-stressed Alyssum inflatum were treated with SA and jasmonic acid (JA). Similarly, SA and gibberellic acid reduced metal induced oxidative damage in three different cultivars of Vigna unguiculata (Ahmad et al., 2021). Overall, the studies highlight that coordination between SA signaling and other phytohormones is a crucial factor to mitigate the negative impact of metal stress on various plant species.

Conclusions

Pb toxicity significantly hinders the growth and developmentby disrupting various physiological and metabolic processes in plants. Its buildup in plant tissues endangers food safety in addition to influencing biomass accumulation.Nowadays, application of SA is emerging as a promising approach for increasing the resilience of crop plants, including under metal toxicity. SA has a variety of protective properties, such as the capacity to control physiological functions, modify antioxidant defense systems, and reduce oxidative damage brought on by ROS generated by metal toxicity. Additionally, SA increases nutrient uptake, stabilizes membrane integrity, increases photosynthetic efficiency, and preserves chlorophyll content all of which are essential for sustaining plant vitality. Interestingly, the cumulative application of SA and other phytohormone also proved as an innovative approach in alleviating the detrimental impact of various abiotic stressors. However, the specific report on individual as well as interactive role of SA in negating the effect of Pb stress on agriculturally important crop is scanty and needs further attention.Moreover,very few reports are available on the precise molecular mechanisms underlying SAmediated detoxification processes, which could be a major area of research for the scientists working in the same field.

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