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CROSSTALK BETWEEN SALICYLIC ACID AND GIBBERELLIC ACID TO MODULATE PLANT RESPONSES OVER METAL STRESS: A MOLECULAR APPROACH

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ABSTRACT

Heavy metal stress is one of the most critical abiotic challenges limiting plant growth, productivity and ecological sustainability, as excessive accumulation of toxic metals such as cadmium, lead, arsenic, mercury, nickel, and copper disrupts nutrient homeostasis, impairs photosynthesis and nitrogen metabolism, damages cellular structures, and induces oxidative stress through excessive reactive oxygen species (ROS) generation. To cope, plants employ a wide range of defense strategies, including antioxidant enzyme activation, osmolyte accumulation, and synthesis of metal-chelating peptides, while phytohormones play a pivotal role in fine-tuning the growth-defense balance. This review highlights the roles of salicylic acid (SA) and gibberellic acid (GA) and their crosstalk in modulating plant adaptation to heavy metal stress. SA primarily acts as a defence signal by enhancing antioxidant activity, stabilizing chloroplast function, maintaining ion homeostasis, stimulating phytochelatin and metallothionein synthesis, whereas GA functions as a growth recovery regulator by promoting mitotic activity, cell elongation, osmotic adjustment and photosynthetic efficiency under different stress. Crosstalk between SA and GA involves synergistic and antagonistic interactions mediated through NPR-dependent redox signaling and DELLA protein-regulated GA pathways allowing plants to dynamically balance growth and defence depending on stress severity and recovery. Exogenous applications of SA and GA either individually or in combination have revealed potential in alleviating from arsenic, cadmium, lead and several other heavy metals toxicity across different crop species. By bridging mechanistic insights with applied strategies this review emphasizes the importance of SA-GA interplay in advancing phytoremediation, crop improvement and sustainable agriculture in metal-contaminated environments.

***Keywords*:** Metal stress; Salicylic acid (SA); Gibberellic acid (GA); Phytohormone signaling; Hormonal crosstalk

Introduction

Plant stress occurs when external or internal factors disrupt normal growth and metabolism, leading to reduced productivity. It is classified into abiotic stress (drought, salinity, temperature extremes, heavy metals, nutrient deficiencies etc.) and biotic stress (pathogens, pests, herbivores etc.). Such stresses affect key processes like photosynthesis, nutrient uptake and hormonal balance (Olayinka *et al.*, 2021). To cope, plants activate defense mechanisms including antioxidants, osmolyte accumulation, stress-responsive genes, and hormonal crosstalk. Understanding these responses is essential for developing stress-tolerant crops and achieving sustainable agriculture.

Heavy metal stress is a major environmental concern that adversely affects plant growth, yield and overall ecosystem stability (Angon *et al.*, 2024). The accumulation of toxic metals such as cadmium, lead, arsenic, mercury, nickel and copper, often introduced through industrial emissions, mining operations, excessive use of agrochemicals and contaminated irrigation water. (Alengebawy *et al.*, 2021). Although certain metals serve as essential micronutrients in trace amounts, their excessive accumulation disrupts nutrient homeostasis, impairs membrane integrity, inhibits enzyme activities and promotes excessive generation of reactive oxygen species (ROS). This oxidative imbalance leads to damage of vital biomolecules including lipids, proteins and nucleic acids, ultimately compromising plant health and productivity. (Mansoor *et al.,* 2023, Rahman *et al.,* 2024). Photosynthesis and nitrogen metabolism are highly sensitive to heavy metal toxicity often showing declines in chlorophyll biosynthesis, photosystem II efficiency, stomatal conductance and nitrate reductase activity (Rahman *et al.,* 2023). In response, plants employ a range of defense strategies, including the activation of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), the synthesis of metal-chelating peptides like phytochelatins, metallothioneins and the accumulation of osmoprotectants like proline and glycine betaine, which help stabilize cellular structures and maintain metabolic functions under stress (Riyazuddin *et al.,* 2021).

A central mechanism by which plants modulate their defense responses is through the action of phytohormones. These naturally occurring organic compounds also referred to as plant growth regulators which exert profound effects on plant growth, development, and environmental adaptability even at minute concentrations (El Sabagh *et al.,* 2022, Das *et al.,* 2025). Phytohormones control crucial physiological processes including cell division, elongation and differentiation thereby shaping plant architecture, organogenesis and reproductive development (Chakraborty *et al.,* 2025). The major categories of phytohormones are auxins, gibberellins, cytokinins, abscisic acid, ethylene, salicylic acid and jasmonates etc. which possess distinct functions but often operate in a highly interconnected manner to coordinate growth and stress responses (Zhao *et al.,* 2022). Among them, salicylic acid and gibberellins is a most essential growth regulator involved in both development and stress tolerance.

Salicylic acid (SA) is a fundamental phytohormone that regulates various physiological and developmental processes in plants such as flowering, stomatal closure, osmolyte metabolism, photosynthesis, fruit quality improvement, water balance and activation of antioxidant defences (Song *et al.,* 2023). Under heavy metal toxicity, SA plays a key role in assisting photosynthetic efficacy by regulate stomatal conductance, preserving chloroplast ultrastructure and regulating critical photosynthetic enzymes such as ribulose-1,5-bisphosphate carboxylase oxygenase (RuBisCO) and carbonic anhydrase (Nazar *et al.,* 2015, Ahmad *et al.,* 2019). As a phenolic signaling molecule, SA enables plants to sense metal-induced toxicity and initiate protective metabolic and physiological responses to maintain growth and survival (Kaya *et al.,* 2023). On the other hand, Gibberellins (GAs) are a group of tetracyclic diterpenoid carboxylic acid phytohormones which play important roles in regulating plant growth and development by control critical physiological processes (Urbanová *et al.,* 2012). Beyond that GAs crucial role like as seed germination, flowering, fruit ripening, leaf expansion and suppression of trichome formation etc. It is also act as highly potent growth regulators to recover plant life during stress conditions (Feng *et al.,* 2025; Vishal, & Kumar, 2018). GAs also modulates source-sink dynamics by influencing assimilate production and translocation through adjustments in source and sink development, resource allocation and photosynthetic efficiency. At the cellular level, GAs helps maintain structural integrity and support continuous mitotic activity (Iqbal *et al.,* 2011). Additionally, GAs can enhance plant detoxification capacity under heavy metal stress by activating antioxidant defense systems, inducing catalase synthesis and promoting phytochelatin accumulation (Alharby *et al.*, 2021).

Crosstalk between SA and GAs involves both synergistic and antagonistic interactions depending on stress severity and tissue specificity (Ohri *et al.,* 2015). GA signaling mediated mostly through the degradation of DELLA proteins and promotes growth-related gene expression (Ito *et al.,* 2018). However, under stress DELLA proteins may interact with SA-responsive transcription factors to shift priorities from growth to defence (Li *et al.,* 2019). Conversely SA can regulate GA biosynthesis or signal transduction to balance growth and stress adaptation, down regulating GA activity during acute stress to conserve resources or synergizing with GA during recovery to accelerate repair and regrowth (Emamverdian *et al.,* 2020). This review highlights the roles of gibberellic acid (GA) and salicylic acid (SA), with particular emphasis on their crosstalk and underlying molecular mechanisms in modulating plant responses to Heavy metal stress.

Salicylic Acid Signaling Pathways: Regulating Plant Adaptation under Metal Stress

Salicylic acid (SA) is a plant hormone which plays important role in modulating plant growth and enhancing tolerance to various environmental stresses. Under stress, SA modulates the synthesis of specific stress-related proteins, improves chlorophyll fluorescence efficiency, regulates transpiration, suppresses ethylene biosynthesis and strengthens resistance against diverse pathogenic infections (Song *et al.,* 2023). Various studies have observed the SA capacity to alleviate heavy metal toxicity in various plant species including mercury (Hg) stress in *Medicago sativa* (Zhou *et al.*, 2009), lead (Pb) stress in pea and Indian mustard (Ghani *et al.,* 2015, Boroumand *et al.,* 2011) and cadmium (Cd) stress in maize (Gondor *et al.,* 2016). As biochemical modulator, SA provides to heavy metal tolerance by mitigating the harmful impacts of reactive oxygen species (ROS) through their disintegration by compartmentalizing metal ions within specific cellular structures (Khan *et al.,* 2015). Exogenous SA application has been shown to activate antioxidant defence systems thereby decrease ROS accumulation in wheat under Cd stress (Agami *et al.,* 2013). SA treatment increased catalase (CAT) and superoxide dismutase (SOD) activities, while in *Linum usitatissimum* exposed to Cd, SA enhanced H_2O_2 detoxifying enzymes, effectively preventing Cd-induced oxidative damage (Haider *et al.,* 2021). Exogenous application of salicylic acid (SA) has been shown to mitigate the damaging effects of cadmium (Cd) on plant cells, highlighting the involvement of SA in complex signaling networks that regulate plant responses to heavy metal stress. SA may function as an iron-chelating agent or act directly as a scavenger of hydroxyl radicals thereby reducing metal toxicity through enhanced antioxidant enzyme activity (Wang *et al.,* 2021). Additionally, proline accumulation often stimulated under stress-contributes to osmotic adjustment and activation of antioxidant defences, further complementing SA's protective role (Hosseinifard *et al.,* 2021). Oxidative stress induced by reactive oxygen species (ROS), and excessive H_2O_2 leads to hydroxyl radical formation, disrupting plant metabolism, low SA concentrations can activate antioxidant enzymes, enhance defense mechanisms and reduce oxidative damage (Jomova *et al.,* 2023). Numerous studies have confirmed that exogenous SA enhances ROS scavenging through increased antioxidant activity under heavy metal stress. However, some reports indicate that SA may reduce catalase (CAT) activity while elevating peroxidase activity, a response linked to the accumulation of H_2O_2 acting as a secondary messenger to trigger defense-related signaling pathways (Herrera-Vásquez *et al.,* 2015). Physiologically, SA influences growth parameters under metal stress for instance, Cd exposure typically reduces the shoot-to-root ratio, but low SA concentrations have been shown to restore or even increase this ratio by elevating chlorophyll content. These effects-reported in multiple plant species-underscore SA's role in preserving photosynthetic capacity and supporting growth under heavy metal stress (Luo *et al.,* 2022).

Salicylic acid (SA) plays a significant role in regulating plant growth and stress responses by influencing cell division and expansion particularly in meristematic tissues, which enhances radicle development, shoot elongation and root growth (Li *et al.,* 2022). Under salt stress, SA has been shown to mitigate adverse effects by reducing Na^+ and Cl^- accumulation and facilitating K^+ transport through modulation of biomolecular structures (Talebi & Haghighatnia 2024). In rice, SA improves seed germination and seedling growth under Pb^{2+} and Hg^{2+} stress. Its regulatory role extends to mineral nutrient uptake, distribution and homeostasis, helping maintain membrane integrity and supporting growth under heavy metal stress (Parameswaran *et al.,* 2021). However the effects of SA are dose-, species- and application-method dependent; while moderate concentrations enhance tolerance, excessive levels can trigger ROS accumulation, particularly H_2O_2, causing oxidative stress. For example, in *Arabidopsis thaliana*, SA promoted ROS generation in photosynthetic tissues under salt and osmotic stress. SA's protective action against heavy metal toxicity operates through four primary mechanisms: activation of antioxidant defense systems, stimulation of osmolyte accumulation, enhancement of metal-chelating compound synthesis and modulation of secondary metabolism (Liu *et al.,* 2022). In the antioxidant pathway, SA functions as a signaling molecule in systemic acquired resistance (SAR), triggering redox-mediated activation of defense-related genes including those regulated by NPR1, NPR3 and NPR4, which also serve as SA receptors (Mishra *et al.,* 2024). SA biosynthesis occurs via two major routes: the phenylalanine pathway-where phenylalanine ammonia-lyase (PAL) and cinnamate-4-hydroxylase drive phenylpropanoid metabolism and the isochorismate pathway in chloroplasts, catalyzed by isochorismate synthase and isochorismate pyruvate lyase. SA also enhances the synthesis of phytochelatins (PCs), metallothioneins (MTs) and metal-binding proteins crucial for detoxification, by promoting sulfur and glutathione assimilation (Chen *et al.,* 2009). In the osmolyte-mediated response, SA interacts with compounds such as glycine betaine, proline and soluble sugars to preserve osmotic balance, membrane integrity and enzyme activity under stress. Proline biosynthesis, regulated by salicylic acid (SA) through key enzymes like pyrroline-5-carboxylate reductase and γ-glutamyl kinase, which plays an important role in protecting plants by scavenging reactive oxygen species (ROS) and stabilizing cellular structures. SA also promotes the accumulation of secondary metabolites-such as phenolics, flavonoids, alkaloids and coumarins which contribute to stress tolerance. Examples include increased PAL activity and total soluble phenols in *Matricaria chamomilla* under Cd and Ni stress, and elevated protocatechuic acid in *Scenedesmus quadricauda* under Cu stress (Sharma *et al.*, 2019). In photosynthesis regulation, SA enhances photosynthetic indices by increasing pigment content, Rubisco activity and chloroplast structural integrity while reducing PSII damage and maintaining redox homeostasis. These effects improve CO_2 assimilation, electron transport, and ROS-scavenging enzyme activities, ultimately enhancing tolerance to heavy metal and other abiotic stresses (Ogunsiji *et al.*, 2023).

Gibberellic Acid Signaling Pathways Regulating Plant Adaptation under Metal Stress

Gibberellins (GAs), commonly occurring in the bioactive forms GA_1 and GA_3, are tetracyclic diterpenoid carboxylic acids. Although many GA forms are not biologically active as plant growth regulators, a few play pivotal roles in plant growth and development (Urbanová *et al.*, 2011). These active gibberellins are involved in key physiological processes such as flower and fruit development, stem elongation, leaf expansion, trichome initiation and the regulation of critical growth cycles including transitions between developmental phases (Yamaguchi *et al.*, 2007). Gibberellins (GAs) influence plant osmotic responses, as demonstrated in *Arabidopsis thaliana*. GA signaling operates through multiple components, including the F-box protein GID2/SLEEPY1 (SLY1), the GID1 receptor and transcriptional regulation mediated by DELLA proteins. In this pathway, GAs first binds to the GID1 receptor, triggering interactions with DELLA proteins, which act as negative regulators of GA signaling. The GA-GID1-DELLA complex formation marks the initiation of DELLA protein degradation via the 26S proteasome. This degradation process is facilitated by the interaction between DELLA proteins and the F-box protein GID2/SLY1, ultimately enabling downstream GA responses (Harberd *et al.*, 2009, Gao *et al.*, 2020). Gibberellin (GA) biosynthesis begins in plastids, where trans-geranyl diphosphate is produced via the methylerythritol phosphate pathway. This intermediate is subsequently oxidized by 2-oxoglutarate-dependent dioxygenases and cytochrome P450 monooxygenases within the plastids and endoplasmic reticulum. The dioxygenases involved in GA biosynthesis are encoded by specific genes, notably *GA20ox* (GA 20-oxidase), *GA3ox* (GA 3-oxidase) and *GA2ox* (GA 2-oxidase). Among these, *GA2ox* plays a key role in modulating plant responses to abiotic stress. It is generally hypothesized that abiotic stress reduces GA content through the upregulation of *GA2ox* genes however, some studies have also reported a down-regulatory effect of these genes under stress conditions (Sun *et al.*, 2009, Gupta *et al.*, 2013). In terms of GA signal transduction, one of the most important components identified is DELLA, a nuclear protein belonging to the GRAS transcription factor family. DELLA proteins act as suppressors of GA signaling, thereby modulating GA-dependent developmental and stress-response pathways. The role of gibberellins (GAs) in regulating plant growth under various abiotic stresses is largely mediated by DELLA proteins (Davière *et al.*, 2016, Zhao *et al.*, 2013). In *Arabidopsis thaliana*, exogenous GA application has been linked to the accumulation of DELLA proteins under salt stress, suggesting a functional relationship between DELLA activity and stress adaptation. This highlights the critical role of DELLA in enhancing plant tolerance to adverse environmental conditions. Supporting evidence comes from transgenic *pRGA:GFP-RGA* lines, where expression of the GFP-RGA fusion protein under high salt stress resulted in increased GFP-RGA signal intensity, indicating DELLA stabilization in response to stress (Qin *et al.*, 2014). DELLA-mediated transcriptional regulation plays a role in activating the plant antioxidant defense system in *Arabidopsis thaliana* reported by Achard *et al.* (2008). This suggests that DELLA responses under stress are linked to reduced reactive oxygen species (ROS) accumulation, thereby delaying ROS-induced cell death in stressed plants. In addition to modulating antioxidant defenses, DELLA proteins influence key cellular processes such as cell expansion and proliferation. Evidence from *A. thaliana* shows that DELLA activity and cell number can significantly decrease even in wild-type plants however, under stress, DELLA enhances the expression of cell cycle inhibitory proteins, including SIAMESE (SIM) and Kip-related protein 2 (KRP2). This inhibition of cell cycle progression is thought to be an adaptive strategy that enhances cell survival during stress. Despite these insights, the precise molecular mechanisms underlying DELLA-mediated stress responses remain poorly understood (Claeys *et al.*, 2012). In certain studies, gibberellins (particularly GA_3) have been shown to mitigate the detrimental effects of cadmium (Cd) and lead (Pb) on the yield and biochemical processes of *Vicia faba*. GA_3 application enhanced mitotic activity as reflected by increased cell division indices and stimulated various biochemical and metabolic processes under Cd and Pb stress, ultimately improving seedling growth and overall yield (Mansour *et al.,* 2005, Ahmad *et al.,* 2021). In perivious reports, GA_3 bioactivity was found to decrease in plants exposed to copper (Cu) which was associated with improved plant growth. The findings suggest that GA biosynthesis and signaling play a critical role in alleviating heavy metal-induced stress and promoting plant development under such adverse conditions (Zhu *et al.,* 2012). It has been shown that the GA_3 increase endogenous amino acid levels in plants, which can influence key metabolic processes including the regulation of membrane permeability, enzyme activities, osmolyte accumulation and ion uptake. These changes collectively contribute to enhanced plant tolerance to abiotic stress. Furthermore, GAs can improve photosynthetic capacity and nitrogen fixation. Assessing the effects of GAs on photosynthesis under stress, is a crucial aspect of understanding their role in cellular detoxification (Kang *et al.,* 2017, Laghari *et al.,* 2025). For example, exogenous GA_3 application in soybean has been reported to enhance photosynthetic traits such as stomatal conductance, net photosynthetic rate, photosynthetic oxygen evolution and carboxylation efficiency (Yuan *et al.,* 2001). Similarly, in wheat seeds, GA_3 treatment increased net photosynthetic rate, water-use efficiency, transpiration rate and stomatal conductance, demonstrating its potential to improve photosynthetic performance under adverse environmental conditions (Ashraf *et al.,* 2002, Iqbal *et al.,* 2013). In maize subjected to high salinity, GA application has been shown to enhance chlorophyll and proline accumulation, along with increasing the activity of enzymes involved in reactive oxygen species (ROS) scavenging. This improvement is associated with the activity of key enzymes regulating photosynthetic carbon fixation, such as ribulose-1, 5-bisphosphate carboxylase (RuBPCase) (Tuna *et al.,* 2008, Gururani *et al.,* 2008). Similarly, in soybean under cadmium (Cd) stress, GAs was found to increase growth rate, chlorophyll content and net CO_2 assimilation rate (Ghorbanli *et al.,* 2000).

Crosstalk between Salicylic acid (SA) and Gibberellic acid (GA) plays a crucial role in modulating plant adaptive responses to heavy metal stress

Several researches have well documented the interaction between gibberellins (GAs) and salicylic acid (SA) under both normal and stress conditions (Alonso-Ramírez *et al.,* 2009, Khan *et al.,* 2012) Both hormones play important roles in regulating different plant responses, including the stimulation of proteins involved in pathogenesis (Song *et al.,* 2023). Significantly, GA and SA can work synergistically to enhance plant defence mechanisms under abiotic stress (Kaya *et al.,* 2023). SA contributes to stress tolerance by increasing antioxidant enzyme activities and reducing lipid peroxidation (Yang *et al.,* 2023). In *Arabidopsis* seedlings exposed to salt stress, SA application improved seed germination, enhanced antioxidant capacity and strengthened overall stress resilience (Rajjou *et al.,* 2006). Similar results observed in tomato by Jahan *et al.,* 2019 for heat tolerant. Under challenging environmental conditions, GA and SA can act together, with GA-induced gene expression supporting the activation of defense pathways and ultimately improving plant resistance to abiotic stress (Emamverdian *et al.,* 2020). Various studies have shown that the *FaGASA4* transgenic line of *Arabidopsis* exhibits significantly greater resistance to abiotic stresses, including oxidative and salt stress (Alonso-Ramírez *et al.,* 2009). In an experiment, inoculating *Arabidopsis* seeds with 50 μM GA_3 for 24 hours led to a two fold increase in SA levels compared with seeds incubated in water and with wild-type plants. This response was associated with the enhanced expression of NPR1 (Nonexpressor of Pathogenesis-Related Genes 1) and ICS1 (Isochorismate Synthase 1), key genes involved in SA biosynthesis and perception. The over expression of *FaGASA4* likely upregulates these genes, thereby boosting SA content during seed germination relative to wild-type counterparts. Exogenous application of GA_3 can stimulate the biosynthesis of salicylic acid (SA) and the resulting increase in SA levels enhances the plant's defence responses against abiotic stress. In *FaGASA4* transgenic seedlings grown in GA_3-supplemented medium, the ICS1and NPR1 genes-key regulators of SA biosynthesis and signaling are activated, helping to mitigate the adverse effects of abiotic stress on seed germination. This illustrates that the GA-SA interaction can alleviate abiotic stress by inducing SA biosynthesis and enhancing stress tolerance, by a process mediated through GA-SA intermediate genes (Seyfferth *et al.,* 2014, Emamverdian *et al.,* 2020). Furthermore, the enzyme isocitrate lyase, essential for lipid metabolism during seed germination, is influenced by SA in *Arabidopsis thaliana* (Eastmond & Graham 2001, Rajjou *et al.,* 2006). Notably, GA_3 treatment increases endogenous SA levels through GA-induced overexpression of the *GASA4* gene. This suggests that gibberellins not only stimulate isocitrate lyase gene expression indirectly via SA biosynthesis but also regulate SA's downstream action. Overall, these findings indicate that GA plays a critical role in promoting seed germination and growth under abiotic stress with its effects tightly regulated through crosstalk with SA (Alonso-Ramírez *et al.*, 2009). The interaction between salicylic acid (SA) and gibberellic acid (GA) plays a significant role in mitigating abiotic stress. This interaction enhances SA biosynthesis, which in turn strengthens plant tolerance to adverse environmental conditions. The process is regulated by GA-SA responsive intermediate genes which illustrated in Figure 1.

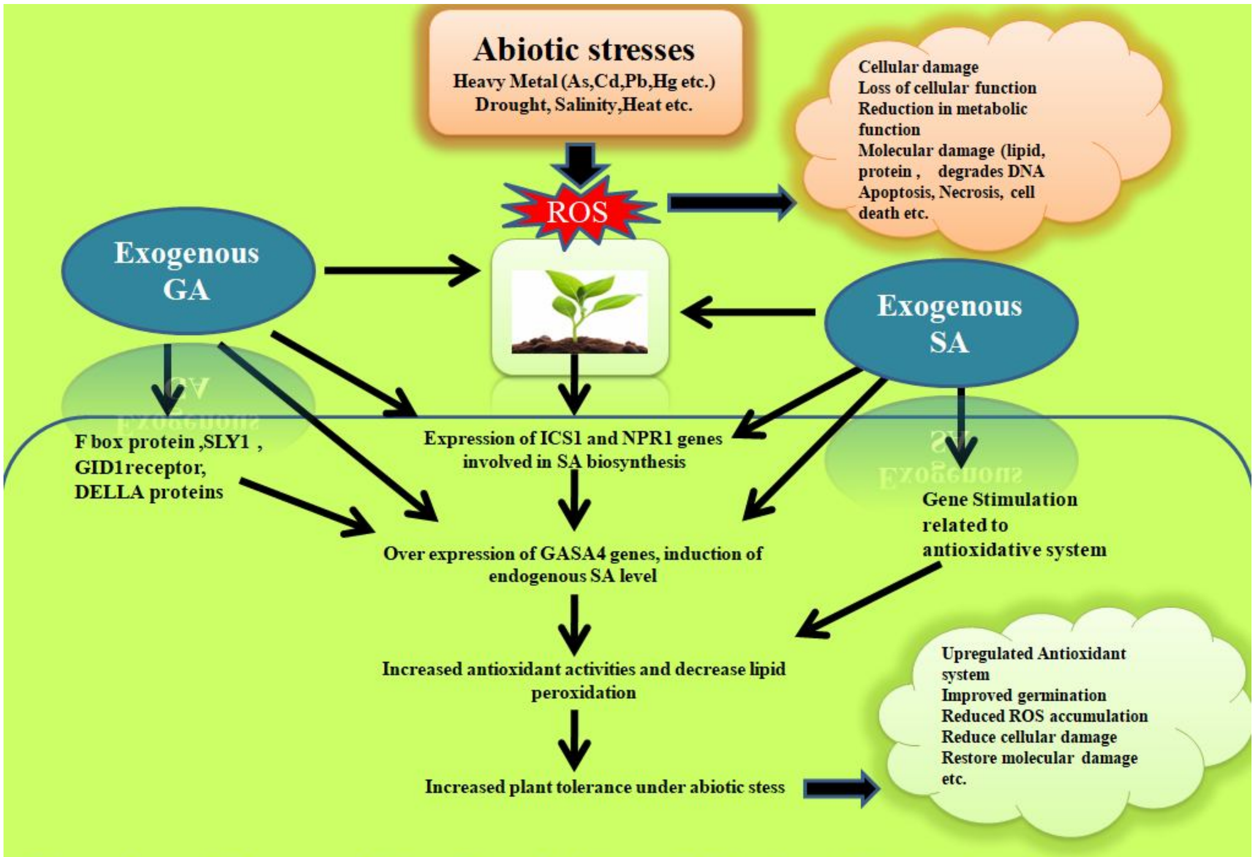

Fig. 1: Crosstalk between Gibberellic acid (GA) and Salicylic acid (SA) under Abiotic stress

Conclusion

Heavy metal stress represents one of the most severe abiotic challenges for plants which leading to impaired growth, photosynthesis, nutrient imbalance, oxidative damage and reduced productivity. To cope with such toxicity plants activate a range of defence mechanisms, many of which are tightly regulated by phytohormones. Among phytohormones salicylic acid (SA) and gibberellic acid (GA) emerge as two critical regulators of plant adaptation. SA plays a central role in initiating defence responses by enhancing antioxidant activity, stabilizing chloroplast function, regulating ion homeostasis and stimulating the synthesis of metal-binding compounds such as phytochelatins and metallothioneins whereas GA primarily acts as a growth recovery regulator by maintaining mitotic activity, promoting cell elongation, enhancing photosynthetic performance and supporting osmotic adjustment under different stress. Importantly, their crosstalk provides a fine balance between growth and defence, enabling plants to both withstand toxicity and restore normal development once stress subsides. At the molecular level, this interplay involves SA-mediated signaling through NPR1 and redox-sensitive pathways and GA signaling via DELLA protein degradation with synergistic or antagonistic interactions between these pathways helping plants dynamically allocates resources depending on stress severity and recovery stage. Exogenous applications of SA and GA as well as their combined use have shown promise in enhancing plant tolerance to cadmium, lead, copper and other heavy metals across multiple crop species. Overall, understanding SA-GA crosstalk deepens our knowledge of plant stress biology and opens avenues for biotechnological and agronomic strategies aimed at developing stress-resilient crops.

Future perspectives

Despite significant advances in understanding the individual roles of salicylic acid (SA) and gibberellic acid (GA) in plant stress physiology, knowledge of their crosstalk under heavy metal stress remains limited. The molecular mechanisms through which SA and GA regulate antioxidant defense, photosynthesis, nutrient balance and metal detoxification are still unclear, particularly their integration with ROS metabolism and secondary metabolite pathways. Future research should emphasize integrative omics approaches to unravel SA-GA signaling networks, identification of key transcription factors mediating their interaction and application of genome-editing tools such as CRISPR-Cas9 to enhance stress resilience. In addition, exploring exogenous applications of SA and GA, alone or in synergy with nanoparticles and other bio-stimulants, offers promising eco-friendly strategies for phytoremediation. Field-level validation is essential to translate laboratory findings into sustainable crop improvement. Advancing knowledge on SA-GA crosstalk will facilitate the development of metal-tolerant, high-yielding crops, contributing to food security and ecological restoration.

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