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Review

Research Progress in Soybean by Phytohormone Modulation and Metal Chelation over the Past Decade

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Abstract: Phytohormones have been acknowledged as an eco-friendly and alternative source for plant growth promotion and abiotic stress tolerance. Heavy metal stress has attained considerable attention worldwide because of its serious effects. Globally, it is a major cause of crop yield loss. Soybean is an important legume crop that continuously faces environmental stress, such as heavy metal stress. The application of plant growth regulators, such as phytohormones, enhances plant tolerance toward heavy metals. Phytohormones augment the interaction with plants. They improve plant productivity under stress due to the potential of phytostabilization. They are capable of enhancing metal stress tolerance by reducing oxidation stress. In the present review, an attempt has been made to summarize the role of phytohormones in metal chelation in a model plant, soybean. The results suggest that among the phytohormones, ABA, JA, SA ET, GA, and IAA are synergistic with metal chelation, whereas cytokinins are antagonistic. The application of phytohormones and corresponding microbes enhances the production of glutathione (GSH), which enhances metal tolerance by metal sequestration.

Keywords: phytohormones; growth regulator; soybean; heavy metal stress; abiotic stress

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1. Introduction

The agricultural industry is currently facing a dual challenge: environmental stress and an increasing global population. Environmental stress poses a constant threat to agricultural productivity, leading to potential reductions of up to 70% [1,2]. Various environmental factors contribute to these alarming levels of stress, including heavy metals, heat, drought, salinity, chilling, and UV radiation. The proliferation of heavy metal pollution in the environment has become more pronounced in recent years due to escalating human activity and rapid urbanization, posing a threat to all forms of life [3,4]. The detrimental effects of heavy metal toxicity on ecosystems, crops, and human health have become a global concern, affecting millions of hectares of cultivable land worldwide [5]. Heavy metal (HM) stress, categorized as an abiotic stress, presents a persistent challenge to agricultural practices and significantly reduces the yield of vital crops, such as rice [6], maize [7], millet [8], wheat [9], and soybean [10]. HMs are characterized by their high density, with a density exceeding 5 g/cm^3, and they possess relatively higher osmotic weight. Although certain essential heavy metals, such as zinc (Zn), copper (Cu), cobalt (Co), nickel (Ni), molybdenum (Mo), and manganese (Mn), play crucial roles in plant metabolic and developmental pathways when present in low concentrations, elevated levels of these metals in soil have detrimental effects on plant physiology, metabolomics, and biochemical processes. Consequently, such elevated concentrations impede growth and production and ultimately lead to a decreased overall crop yield [11,12].

The presence of heavy metals in soil can arise from either natural occurrences or human activities. Natural causes include factors such as geological processes and the weathering of rocks. On the other hand, anthropogenic sources contribute to elevated levels of heavy metals in soil and encompass various activities, such as the excessive use of pesticides and chemical fertilizers, smelting, mining operations, emissions from automobiles, leather tanning, municipal waste disposal, the dyeing and processing of textiles, and manufacturing processes [13,14]. Moreover, heavy metal stress in the ecological system can also be caused by natural disasters, such as forest fires and earthquakes. In many industrialized countries, the widespread use of agrochemicals, such as pesticides, and the utilization of untreated irrigation water have significantly contributed to heavy metal pollution, which in turn affects agriculture and the food chain. These pollutants find their way into farmlands, get absorbed by plants, and accumulate within the food web [15,16]. Additionally, human activities and natural processes, such as the formation of land surfaces, have led to increased deposits and concentrations of heavy metals in the soil, reaching toxic levels for plants [17]. The impact of heavy metal stress on the entire food chain and human health has garnered significant attention in recent years, posing threats to food and energy security [18]. It is now recognized as a major hazardous pollutant, surpassing even pesticides in terms of its serious implications [19,20]. Figure 1 shows the causes of heavy metal stress in plants.

Figure 1. A holistic review of various causes of heavy metal stress in plants.

Soybean (*Glycine max*) is globally recognized as one of the most significant commercial crops. Despite the continuous increase in soybean production, the presence of heavy metal stress adversely affects plant productivity [21,22]. Soybean plants grown in heavy-metal-contaminated soils also undergo stunted development due to metabolic changes [23]. The disruption of nutrient absorption, decline in photosynthetic activity, suppression of electron flow, reduction in carbon dioxide (CO_2) sequestration, chloroplast disruption, free-radical-mediated damage, and the industrial production of toxic by-products are examples of the potentially negative consequences of heavy metal stress on plants [24–28].

Plants exhibit diverse responses when faced with heavy metal stress. They employ various strategies, including modifying their HM uptake and transport, employing chelation or compartmentalization mechanisms, inducing structural changes in different plant parts, regulating water balance, enhancing antioxidant defenses, and activating metal ion transporters. To combat the toxic effects of HMs in contaminated soil and water, numerous biological and chemical techniques have been employed. In recent times, there has been a growing interest in utilizing phytohormones as an environmentally friendly approach to enhance HM stress tolerance in plants [29,30]. Phytohormones serve as signaling molecules that orchestrate a wide range of crucial physiological processes in plants. They also play a significant role in enabling higher plants to withstand HM stress [31].

Numerous studies have been conducted to explore the bioremediation of heavy metal toxicity in plants. However, there remains a knowledge gap regarding the response of soybeans to heavy metal stress. Additionally, limited information is available regarding the uptake of heavy metals by soybeans [32]. Given that soybeans are a significant global crop with economic importance, it is crucial to investigate the uptake of metals by this crop and to explore eco-friendly phytoremediation techniques. Furthermore, the increased use of inorganic chemicals in agriculture has raised concerns about food safety for human consumption, as well as social and environmental considerations [33,34]. This review aims to provide the latest information on the response of soybean plants to HM stress and highlight the importance of phytohormones in conferring resistance to heavy metals. Relevant articles were carefully selected and reviewed, with comprehensive searches conducted in electronic databases using keywords, such as "heavy metals," "phytohormones", and "soybean". This study included all available data until 2023, and excluded non-English articles and conference papers.

2. Pro-Oxidant and Reactive Oxygen Species

Pro-oxidants are molecules that have the potential to initiate oxidative stress by triggering the DNA and protein of the cells. These molecules act as signaling molecules to enhance stress in the plant cells. However, plants try to minimize their stress levels via activation of the intrinsic antioxidant system. If the hemostasis between pro-oxidant and antioxidant molecules fails, then reactive oxygen species are rapidly generated [35,36].

Reactive oxygen species (ROS) and their derivatives are among the free radicals that rapidly accumulate whenever a plant is subjected to heavy metal stress [37,38]. These ROS include oxide, peroxide, singlet oxygen, and superoxide. The accumulation of these ROS results in a disturbance in the hemostasis of the cell, triggering damage to various cellular organelles and biomolecules, such as mitochondria, golgi bodies, proteins, and DNA [11,39]. Moreover, oxidative stress causes downregulation of the non-cyclic transport of ATP. Additionally, plants elevate their stress levels, which increases the likelihood of damaging the molecular structure of the plant cells [40,41].

However, plant triggers can cope with the series of events needed to reprogram cellular events to mitigate heavy metal stress [42]. For example, activation of the TCA cycle through the mitogen-activated protein kinase (MAPK) pathway, the production of secondary metabolites and phytohormones, activation of intrinsic antioxidant pathways such as antioxidant enzymes (SOD, APX, and glutathione reductase (GSH)), and phenolic compounds or the expression of some genes up to an optimum level of stress [3,43,44]. These involve the programming and reprogramming of cellular events. Plants attempt to cope with metal stress; however, they are unable to reprogram the events due to continuous stress. Plant cells show some symptoms of heavy metal stress, such as chlorosis, inhibition of enzymatic metabolism, inhibition of growth, or sometimes death of the plant cells [40,45]. The entire mechanism is shown in Figure 2. Moreover, it is crucial to alleviate metal stress because it causes genotoxicity. There is a rise in the buildup of ROS when the plant is exposed to heavy metal stress. ROS cause the deformation of essential proteins by directly attacking the thiol groups. As a result, the bases are deleted and modifications to the genes and dimers cause chromosomal abnormalities.

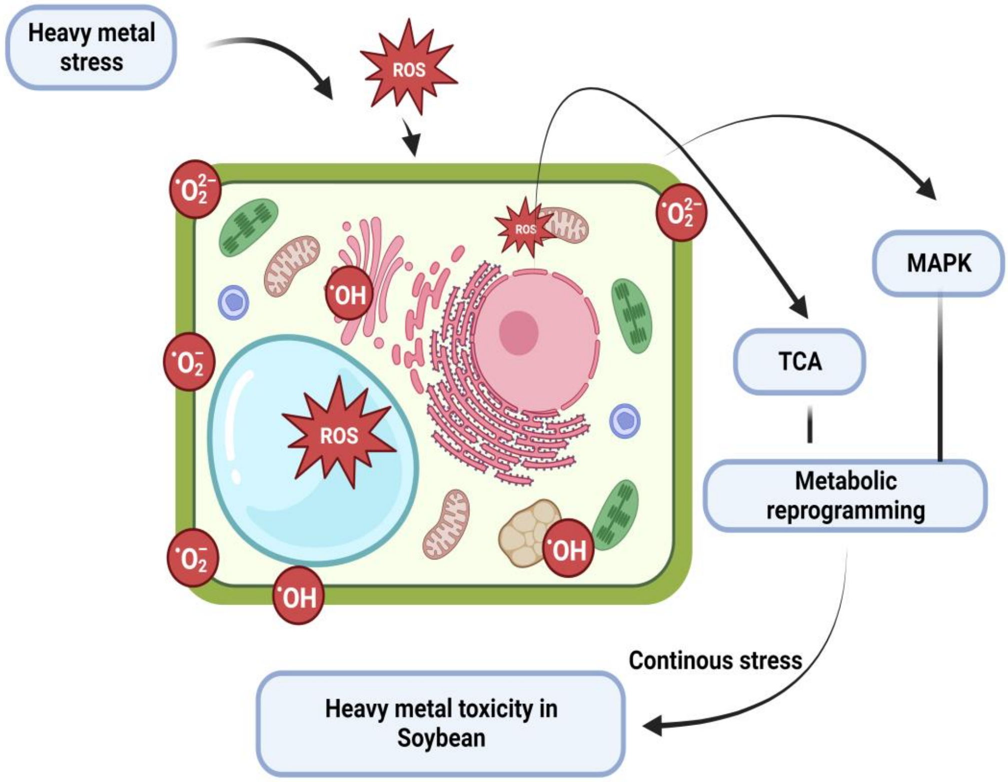

Figure 2. A schematic representation of heavy metal stress producing oxidation stress through the production of ROS.

3. Phytohormones in Heavy Metal Tolerance

In response to heavy metal stress, the antioxidant defense system is activated. Furthermore, if the antioxidant defense system fails to cope with the stress, the plant alters its endogenous phytohormone levels, including ABA, JA, and SA levels. These hormones are important for cross-talk between the stress elevation pathways. They have a complex signaling pathway. The primary signaling pathway for the activation of phytohormones is SCF (SKIP-CULLIN-F-BOX) [46,47].

Phytohormones are crucial for carrying out biological processes and are important growth regulators in plants. In response to environmental stresses, many plant species use a variety of distinct defense systems. Several studies suggest that phytohormones are essential for stress mitigation [48–50]. Furthermore, phytohormones have gained attention because they are important in stress alleviation. Exogenous phytohormone treatment has been shown in numerous studies to reduce stress in a variety of plant species [51–53]. Phytohormones may increase a plant's resistance to the damaging effects of heavy metals by activating a wide variety of molecules that are involved in regulation and signaling [8]. Phytohormones are well-known for the functions they play in controlling nutrient absorption through roots, since they enhance nutrient source–sink interactions, root phenotypes, and the symbiotic connection between plants and rhizobacteria [48,49]. They not only provide systemic growth, but also give protection to plants by providing them with systemic tolerance [54,55].

Phytohormones are chemical messengers that increase plant tolerance to metal stress, enabling the plants to continue growing despite adversity [49]. Metals in the soil are taken up by the tips of the roots and are then transported up the plant through vascular bundles to the tissues of the shoots [50]. Auxin and cytokinin are examples of phytohormones that regulate the development of shoots and roots and enhance the uptake of nutrients and heavy metals by plants [56]. Further studies have highlighted the contribution of ethylene in the development of dense root hairs that facilitate the rapid absorption of minerals and metals within plants [57]. Contrarily, certain microorganisms that produce phytohormones, such as indole acetic acid (IAA), result in the physiological modification of plant root exudates, enhancing nutrient mobility and active metal absorption [58,59].

Abscisic acid (ABA) is a derivative of sesquiterpenoid. It improves a plant's ability to tolerate heavy metals and plays a significant part in the regulatory network that controls antioxidant-related activities [53,54]. As a direct consequence of stress, there is an immediate and significant rise in the amount of ABA. It acts as a signaling molecule, causing the inhibition of growth or germination and arresting the mounting stress. It also has an integrative role in transmitting stress response signals downstream [60,61]. Various studies show that it exhibits an adaptive response to abiotic stress. Moreover, upon exposure to stress, there is rapid accumulation of ABA and its responsive gene. A study conducted on soybeans demonstrated the upregulation of expression levels of $NCED_3$ of up to 74% following the application of Cd and Pb [62]. Similarly, in 2022, a study showed that exposing plants to arsenic toxicity resulted in the upregulation of endogenous phytohormones and their responsive genes. Endogenous ABA levels increased from 9000 to 80,000 $pmol^{-1}$ in the dry weight of the plant sample [63]. The findings of the genetic research revealed the overexpression of the genes GmbZIP and GmPYL1, which are involved in the accumulation of the ABA signaling pathway containing the Pyrabactin Resistance1/PYR-like/Regulatory Components of ABA Receptors. Upon attachment to the PYL, the negative directive of ABA is reduced, leading to the activation of the element binding factors of ABA, which are referred to as AREB/ABFs. They are called transcription factors (TFs), and they are a kind of basic leucine zipper (bZIP). These transcription factors are located in the promoter regions of target genes, and they look for ABA response elements. It has been shown that the GmPYL1 and GmbZIP1 genes of soybean plants include ABA-responsive elements that are capable of being triggered either by the administration of ABA or through the induction of any form of abiotic stress [8,57,58].

Furthermore, the exogenous applications of ABA and ABA-producing microbes [64] are found to tolerate cadmium [65–67], nickel [64], and chromium [68,69] via the activation of antioxidant molecules. Similarly, auxin also minimizes the determinable effect of heavy metal stress by activating the intrinsic antioxidant system and reducing oxidative stress [70–72]. Exogenous applications of auxin and auxin-producing microbes also trigger activation of antioxidant enzymatic molecules (such as the production of CAT, APX, and SOD) and non-enzymatic molecules (such as GSH) [73,74]. Moreover, aluminum toxicity in soybean plants revealed that auxin is involved in the remediation of heavy metals via induced citrate exudation through the upregulation of GmMATE [75]. Similarly, the application of plant growth-promoting rhizobacteria (PGPRs) enhanced the level of auxin, ultimately increasing the cellular processes in plants that augment metal resistance and stress tolerance. A study conducted by [76] showed that the application of LHL06 enhanced transcriptomic responses and metal stress, and there was overexpression of GmMATE1, which also enhanced the auxin levels seen in the soybean plant. This suggests that auxin also plays an important role in enhancing metal tolerance [76]. Auxin is an important plant hormone that regulates various metabolic and cellular processes and aids in stress mitigation via a reduction in oxidative stress [70,73,77]. In a similar study, cadmium stress was mitigated via the inoculation of rhizobacteria, and the application of these microbes enhanced the levels of auxin, which also contributed to metal tolerance [78].

Moreover, gibberellins also enhance metal tolerance in various plant species. Gibberellin (GA) is a precursor of diterpenoid. It promotes the antioxidant defense system of plants and tolerates stress levels. Treatment with gibberellins and gibberellin-producing microbes enhances heavy metal tolerance by producing an enzymatic and non-enzymatic antioxidant defense system [79–81]. Various studies indicate that the application of gibberellins or GA-producing microbes also helps to mitigate stress. A study conducted in

South Korea showed that the inoculation of GA-producing fungal endophytes is a promising approach to achieve sustainable agronomy [82]. Gibberellins have a synergetic effect on soybean plant growth and productivity. GA is involved in a wide range of biological processes. Studies have shown that a reduction in GA levels leads to a reduction in plant growth [83]. In another study, nickel toxicity was reduced with the application of gibberellins [84]. The priming of phytohormones, including GA, has been found to reduce the negative effects of metalloids, including Pb, which induce stress in soybeans [85].

Recently, brassinosteroids (BRs) have gained popularity among researchers due to their involvement in a wide range of metabolic reactions [68,86]. Brassinosteroids are steroids in nature that can induce the activation of antioxidant molecules [87]. Various studies support the hypothesis that the exogenous application of BRs enhances heavy metal tolerance via the activation of different antioxidant molecules [87–89]. Furthermore, a study was conducted on chromium toxicity in soybeans by applying brassinosteroids. The results revealed that the application of BRs improved metal tolerance by adapting the mechanism of translocation [90]. Several studies support that BRs have great potential in mitigating heavy metal stress [87,91].

Interestingly, jasmonate and salicylic acid are also essential phytohormones that regulate biological processes in plants and lead to stress mitigation; however, they work antagonistically [92,93]. Several scientific studies support the exogenous application of JA [94,95] and salicylic acid [96,97]. Studies have also confirmed that the inoculation of JA- and SA-producing microbes mitigates heavy metal stress in various plants, such as soybean [98–100]. Salicylic acid is an important phytohormone that regulates metabolic processes in plants. The application of stress leads to a reduction in salicylic acid. It enhances systemic resistance in plants by inducing and provoking the antioxidant defense system. SA also improves metal tolerance in plants. Furthermore, three independent studies conducted on soybeans under cadmium stress showed that salicylic acid is involved in stress tolerance. The mechanism of action of stress alleviation involves activation of the intrinsic antioxidant system and, ultimately, the reduction of oxidative stress [101–103]. Another study was conducted on germination metrics under zinc stress. The results revealed that the application of salicylic acid improved the germination rate index and enhanced the early seedling characteristics [104]. It has also been reported that the application of salicylic acid confers aluminum toxicity in soybeans. Soybeans enhance immunity and promote the overall general health of the plant [105–107]. Jasmonate is another important hormone that enhances stress tolerance in plants. The rapid accumulation of JA has been observed when plants are subjected to heavy metal stress. Furthermore, ABA and JA are synergistic with each other. In addition, three independent studies reported that methyl jasmonate enhances cadmium stress tolerance in soybeans. Cadmium is a toxic metal that has an adverse effect on plant growth. Jasmonic acid mitigates the adverse effects of cadmium [108–110].

4. Metal Chelation and Activation of Phytohormones

Metal chelation is an essential mechanism of action by which a plant responds to heavy metal tolerance. Chelation is a process that involves the binding of ions and molecules with metal ions. It comprises the formation of distinct coordinating bonds between a polydentate (multi-bonded) ligand and a single central metal atom [31,111,112]. These ligands are termed chelators, chelating agents, or sequestering agents. Furthermore, metal chelators are an essential mechanism of action by which the plant shows heavy metal tolerance [113,114]. Several biomolecules act as chelators, such as organic acids, secondary metabolites, and proteins. Interestingly, chlorophyll acts as a natural chelator. It has a magnesium-binding ligand that chelates with the metals. Thus, the plant can tolerate heavy metal stress up to a certain threshold [115–117]. Further, chelators can be activated through exposure to HM stress. For example, re-exposure of the plant to heavy metal stress results in the activation of plant hormones. The activation of plant hormones in response to heavy metal stress has been observed to be remarkably significant [56,118]. For example, in response to heavy metal stress, the phytohormones ABA, JA, and SA rapidly accumulate in the model soybean plant, acting as metal chelators and tolerating stress [23,76,82]. Furthermore, the phytochelatin biosynthesis pathway leads to the production of phytochelatin compounds, specifically PC2–PC11. These are oligomers of GSH, and this pathway is directly related to the availability of cysteine and the production of GSH [53,68].

Furthermore, the production of GSH in competition with cysteine and the assimilation of sulfate leads to metal sequestration. This leads to reprogrammed cell events, including the production of phytohormones (such as ABA, JA, SA, GA, and ET) in response to heavy metal stress. It shows positive synergic regulation in response to heavy metal stress, whereas cytokines and polyamines show an antagonistic effect on phytochelatin and the production of GSH [20,119,120]. Glutathione (GSH), a tripeptide, is the most prevalent low molecular weight thiol in all eukaryotes with mitochondria, including plants. GSH is engaged in a variety of cellular functions in plants, including ROS defense, heavy metal sequestration, and xenobiotic detoxification. GSH is also involved in the regulation of developmental processes, such as cell division and flowering. Furthermore, GSH is a key form for the transport and storage of reduced sulfur. GSH is produced in two ATP-dependent processes in which glutamylcysteine synthetase (GSH1, E.C. 6.3.2.2) catalyzes the creation of a peptide bond between the carboxyl group of glutamate and the carboxyl group of cysteine [121,122].

Moreover, when a plant is subjected to heavy metal stress, there is an increased accumulation of ROS, which leads to a transient increase in ABA levels. The ABA level also augments the increase in metal tolerance by enhancing phytochelatin production [41,123]. ABA is an important phytohormone that is involved in various plant biological functions, i.e., the activation of O-acetyl serine lyases, which ultimately causes the production of cysteine biosynthesis [124,125]. A study reported that on exposure to heavy metal stress in soybeans, there is an increase in ABA, which ultimately causes an increase in the production of cysteine, and a marked increase in the production of GSH results in metal chelation [126]. Jasmonate is also an important phytohormone involved in the important physiological processes of plant growth and stress mitigation. Various studies support the hypothesis that jasmonate protects the soybean in polluted metal soil and helps the plant grow under stress conditions [92,127]. Under heavy metal stress, the inoculation of beneficial microbes produced a significant amount of JA following ABA, which enhanced the production of GSH and enhanced metal chelation [76]. Salicylic acid (SA) is an important phytohormone that is gaining attention because of its protective role in a plant’s response to stress conditions. Salicylic acid is activated in plants in response to heavy metal stress. Along with beneficial microbe inoculation, it also enhances salicylic acid production. *Sphingomas* LK11 enhances metal tolerance by mitigating the effect of chromium and improving plant growth. A study found that it enhanced the production of GSH [76]. IAA is an essential phytohormone that brings out important metabolic processes in various plant species. IAA is not only responsible for carrying out physio-metabolic processes, but it also plays a significant role in stress mitigation. Various studies have shown that the activation of IAA causes stress inhibition by promoting cell growth. It has a positive synergetic response toward heavy metal stress [128,129]. Cytokinins and polyamines are also important phytohormones. Studies have revealed that it has an antagonistic effect on the production of GSH and phytochelatin production. Several studies investigating the model plant soybean show that it has a negative synergetic effect on metal chelation [47]. Figure 3 shows the biosynthesis pathway of phytochelatin from its common precursors.

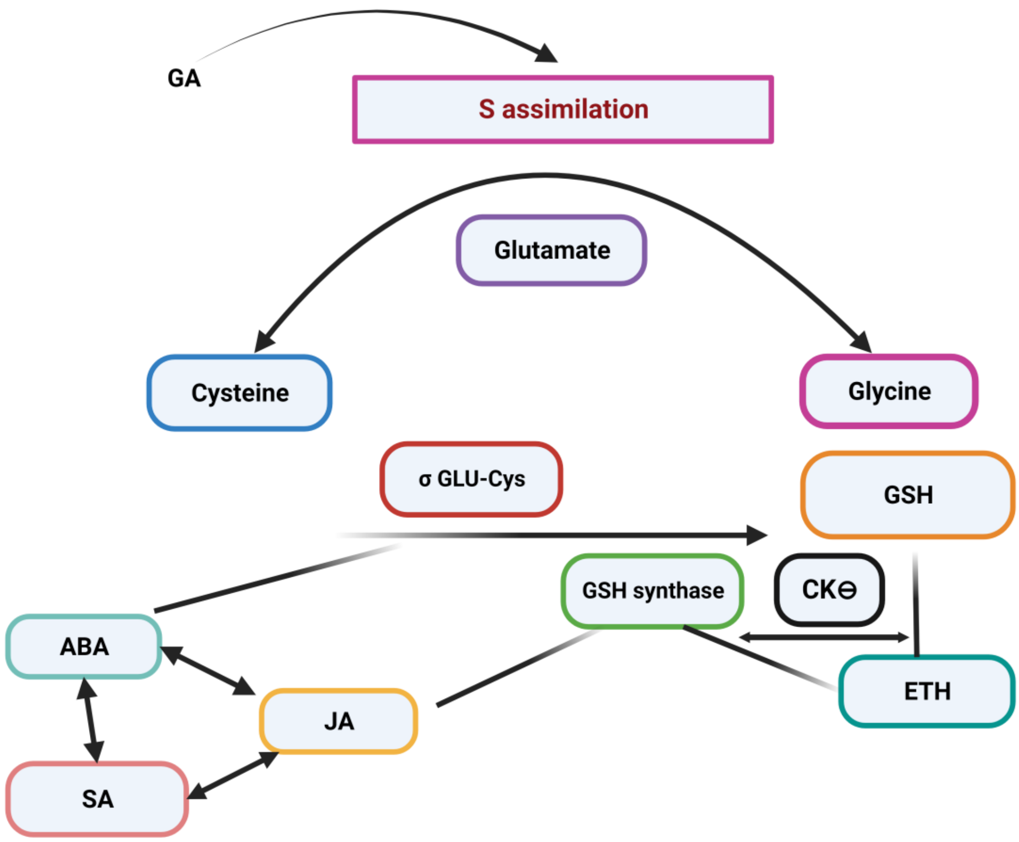

Figure 3. Biosynthesis and activation of phytochelatin from the common precursors of glutamate, glycine, and cysteine.

HM toxicity exerts an adverse effect on soybean growth [130]. The present study demonstrated that the application of phytohormones not only improves plant growth but also enhances metal tolerance. The present study demonstrated the significant potential of phytohormones in promoting the growth and physiology of soybeans (*Glycine max*) under conditions of extreme heavy-metal-contaminated soil. Additionally, this study depicted the synergetic interaction of phytohormones in reducing metal uptake in host plants and remediating soil. In the present study, various phytohormones exhibited marked potential against HM toxicity. Furthermore, improved soybean growth proved to be a vital source of biofertilizer for sustainable agriculture. The phytohormones conferred tolerance to increasing levels of metal phytotoxicity by reducing the level of metal toxicity in soybean roots and shoots. They enhanced metal tolerance by facilitating the distribution of metals in plant cells via the induction of hormonal and antioxidant regulation. Thus, the association between phytohormones and their producing microbes (bacteria and fungi) may represent a promising strategy for achieving profitable nontoxic crop production. The application of phytohormones improved plant productivity by inhibiting the uptake and translocation of metals, by enhancing the uptake of essential nutrients, and by modulating ATPase regulation [131,132]. This approach further improved the oxidative stress induced by the metals. Further studies on larger scales are required to explore the synergetic potential of phytohormones.

5. Conclusions

Plants are sessile by nature; hence, they face constant environmental stress, including heavy metal stress, which is due to several biotic and abiotic causes. Despite the tremendous increase in the production of soybeans, soybeans are threatened by heavy metal stress. Phytohormones and phytohormone-producing microbes are essential for phytostabilization and mitigating heavy metal stress. The present review suggests that phytohormones mitigate heavy metal stress via activation of the antioxidant defense system, including the production of GSH. Among the phytohormones, ABA, JA, SA, and ET have a synergetic effect, whereas cytokinin has an antagonistic effect.

6. Future Prospects

The present study is significant since it greatly interests the researcher to do more research on phytohormones because they alleviate abiotic stress. In addition, they do not have hazardous effects and are environmentally friendly. The present study gave the direction that more studies should be conducted on the application of phytohormones in stress mitigation.

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