

*Review*

# Mechanisms of Selected Plant Hormones under Heavy Metal Stress

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## Abstract

The present review focuses on the role of auxin (IAA), cytokinins (CKs), ethylene (ET) and abscisic acid (ABA) under heavy metal stress. From the onset of heavy metal stress in plants, cellular levels of ABA tend to increase, leading to the establishment of signal communication and encoding of genes associated with the enzymes involved in antioxidant stress responses. The mechanisms of IAA phytohormones in terms of enhancing plant tolerance to stress mainly comprise developing a link between hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) and auxin homeostasis, which can result in forming a signaling interaction between them. The primary anti-phytotoxicity mechanism of ET in response to heavy metal stress is related to modulating the interaction of ethylene with reactive oxygen species (ROS) signaling, which is reflected in a synergy between induction of ROS and synthesis of 1-aminocyclopropane-1-carboxylic acid (ACC). CKs, particularly when applied exogenously, make a positive contribution to alleviating stress emanating from plant metal exposure. This is achieved by a reduction in ROS levels inside plant cells. Generally, CKs can ameliorate heavy metal stresses via a three-way interaction involving exogenous CK, CK metabolism, and CK signaling. Our aims in this work were to review the major hormonal responses of plants elicited by heavy metal stress.

**Keywords:** abiotic stresses, abscisic acid, auxin, cytokinins, and ethylene

## Introduction

Phytohormones are present in plant tissues either at low or high concentrations but are actively involved as chemical messengers in cellular processes [1]. Plants

encounter many abiotic and biotic environmental stresses during their lifetime. It is important to know how a plant can perceive and transfer these stress signals into its physiological reaction sites to ameliorate abiotic stress such as excess of heavy metals [2]. Additionally, plant hormones act as signaling regulators mediating a link between plant and environmental cues. Hormones as a link of communication can influence internal metabolic processes of the plant via external

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signals. This regulates plant growth and development, especially under stressful conditions [3]. Among phyto-hormones, abscisic acid (ABA) is one of the important hormones that can impact the efficiency and functionality of other hormones [3]. ABA controls and regulates gene expression connected with the signaling molecules involved in stress responses, leading to amelioration of environmental stresses faced by plants, and as a result, it is called a “stress hormone” [4]. ABA acts as a sensor (ABA-Sensor) for perception of external stress factors by plants [5]. Auxins (IAA) is another important phyto-hormone [6-7], which plays an essential role in an array of plant’s basic processes of life including embryogenesis, vascular tissue formation, organ differentiation and is involved in regulating plant defense responses to environmental stress [8]. Cytokinin (CK) participates in cellular function of higher plants in various forms including zeatin, dihydrozeatin and isopentenyladenine [9-10]. There is an inverse relationship between the reduced CK concentration in plant and the accumulation of ABA that can lead to improving plant resistance to stress [11]. Ethylene (ET) as one of the essential phytohormones plays a vital role in plant growth regulation. ET at the appropriate level ( $10 \text{ g L}^{-1}$ ) can modulate seed dormancy and seed germination process [12]. 1-aminocyclopropane-1-carboxylic acid (ACC) has an essential role in ethylene biosynthesis [13]. With the excess of heavy metals in the plant and the onset of oxidative stress, ACC takes on an important role to ameliorate early oxidative stress by forming a link between ACC and glutathione (GSH) [14]. In a study on *Arabidopsis thaliana*, the results revealed that ACC was able to control oxidative stress caused by cadmium by impacting signaling genes and alteration in GSH concentration. This shows that ACC stimulates antioxidant defense mechanisms against heavy metals stress [15]. In general, the impact of excess metals on the induction of ethylene is metal type and concentration dependent. It is reported that Cd, as a toxic nonessential element, has a significant role in stimulating ethylene, raising ethylene levels within plant tissues [16]. Today, with increasing anthropogenic activity, the problem of heavy metal contamination is one of the major concerns for humans. Therefore, it is necessary to introduce and identify determining factors in containing these stressors in plants. In this article, we reviewed the mechanism involved in reducing abiotic stress especially heavy metals by phytohormones in plants based on recent studies.

### Phytohormones and Defense Mechanisms

By impacting accumulation and transfer of metal ions within plant organs and tissues, as well as by stimulating plant antioxidant enzymatic activity, ABA can mitigate heavy metal stress and protect plant cells [17-18]. The root meristems have been known as primary production sites for ABA. Consequently, ABA

can provide initial protection barrier against heavy metal excess in the rhizosphere as plants first come into contact with metal ions in the soil. In a study on *Phragmites* and *Typha*, it was found that Cd-induced ABA accumulation in the plant roots was considerably more conspicuous than the shoots, conferring enhanced tolerance to the metal stress [19]. Therefore, it seems that the enhanced ABA concentration in root has a role in reducing the ion activities of metals. The link between auxin signaling and ROS metabolism is crucial to adjusting plant growth and development under stressful conditions [20].  $\text{H}_2\text{O}_2$  is an important component of ROS that not only affects plant vital processes such as photosynthesis and transpiration but also participates in signal transduction system. The molecular characteristics leading to the effectiveness of  $\text{H}_2\text{O}_2$  in signaling processes include features such as limited reactivity and protracted life duration [21]. Cytokinins (CKs), applied exogenously to plant, can ameliorate heavy metal stress through pathways involving CK metabolism and CK signaling [22]. There is a reverse relationship between the change in levels of ABA and CK where CK and ABA act antagonistically to one another [23], which can result in plant enhanced resistance to stress through increasing apical dominance and regulating stomatal aperture [11]. Additionally, it is reported that ABA and ethylene participate in plant growth and development via both antagonistic and synergistic actions [24]. Ethylene is one of the important stress hormones under adverse environmental conditions [25-26-27]. Aminocyclopropane-1-carboxylic acid synthase (ACC synthase, ACS) is an enzyme that is involved in ethylene biosynthesis. ACC oxidase converts ACC (1-aminocyclopropane-1-carboxylic acid) to ethylene [12]. These processes occur when plants are exposed to different living and non-living stresses [12]. In heavy metal stress conditions, ACC synthase activity increases with rising ACC levels in plants [16-28]. In this condition, the amount of ACC improves plant defense against stress and preserves proteins involved in the activation and transcription of stress-related genes. These genes are responsible for encoding proteins that have protective role in plants in stress conditions [29]. In the following, we refer to the major mechanisms adopted by the four main phytohormone groups to counteract abiotic stresses, in particular, heavy metals.

### The role of IAA in Response to Abiotic Stress

Auxin is known as a signaling molecule with important roles during plant life such as cell division and expansion, embryogenesis, meristem development, maintenance of polarity and tissue and organ development [30-31]. Also, auxin plays an essential role in plant growth and development processes including tropic responses, organ pattern formation, apical dominance and vascular development [31-32]. There are more than four auxin forms in plants, including 1-indole-3-acetic acid (IAA), 2-indole-3-propionic acid

(IPA), 3-indole-3-butyric acid (IBA), 4-chloroindole-3-acetic acid (4-Cl-IAA) and 3-phenylacetic acid (PAA). IAA is the most important auxin, and makes up approximately 1% of auxins in total plant tissue [33]. IAA is a phytohormone (indole-3-acetic acid, IAA) with an important mediatory role in plant growth and development [2]. Also, auxin is an integrator of environmental signals [30]. It is present in nearly all plant parts and organs so that it forms gradients of auxin in plants. This gradient of auxin is predisposed to change depending on plant variables such as plant organ, growth stage and stress type [34]. The pathway of indole-3-pyruvic acid (IpyA) biosynthesis and activities of its associated enzymes can lead to auxin generation in plants [35]. The production and transfer of auxin in plants are facilitated by different auxin transport proteins such as auxin influx protein AUXIN RESISTANT 1 (Aux 1), auxin influx protein AUX 1-LIKE (LAX) and auxin influx protein Pin [34]. The auxin transfer genes are encoded by ATP binding cassette B/P-glycoprotein (ABCB/PGP) families and PIN-FORMED (PIN) membrane proteins [36]. In a study with *Arabidopsis*, it was revealed that *Aux 1* plays an important role as a mediator in (IAA) transportation [37-38-39]. In another study conducted on Cd-stressed rice (*Oryza sativa* L.), OsAUX1 was found to have a pivotal role in the plant response to cadmium, positively affecting the growth and development of the root under the stress condition [40].

### Metal Stress

The signaling role of ROS can improve plant response and adaptation under stress [20]. It is reported that •ROS compounds such as H<sub>2</sub>O<sub>2</sub>, O<sub>2</sub> and OH can contribute to cell elongation via the mediation of auxin [20]. In maize, it is shown that ROS can be beneficial to the auxin-regulated gravitropism [41]. Zhao et al. 2012 investigated the effect of root system exposure to Cd stress in rice seedlings and showed that the root growth was enhanced as a result of H<sub>2</sub>O<sub>2</sub>-stimulated growth through auxin-signaling pathway. [42] Contrary to the high levels of ROS, moderate quantities of ROS can act in collaboration with auxin in environmentally-stressed plant, resulting in cellular homeostasis and stability. [20]. In this regard, ROS can impact the signaling, transport, biosynthesis and metabolism of auxins [21]. Additionally, it is shown that auxin transporter mutant *aux1* confers to enhanced tolerance to arsenic (As(III)) in *Arabidopsis thaliana* by reducing levels of H<sub>2</sub>O<sub>2</sub> via ROS-mediated signaling as opposed to the wild type plant [43]. On the other hand, H<sub>2</sub>O<sub>2</sub> is one of the ROS compounds that can be affected by exogenous auxin [44] where auxin can control H<sub>2</sub>O<sub>2</sub> formation by inducing NADPH oxidase [45], which can consequently influence superoxide production and disrupt the formation of H<sub>2</sub>O<sub>2</sub> [46]. In a study on tomato root, exogenous auxin decreased H<sub>2</sub>O<sub>2</sub> accumulation by prompting antioxidants that are involved in scavenging

H<sub>2</sub>O<sub>2</sub> and other ROS compounds [47]. This has also been observed in a study investigating the impact of auxin signaling mutant, *tirlafb2* in *Arabidopsis* [48]. And also in on wheat (*Triticum aestivum*) in which auxin triggered antioxidant activity [49-50]. Auxin homeostasis is vital to plant growth and development processes. The mechanisms involved in auxin homeostasis include; transport, conjugation degradation, deconjugation reactions and de novo biosynthesis [31]. Auxin biosynthesis is important to auxin homeostasis that occurs in meristematic parts of root tips, young plant aerial organs and in leaves at the edge of leaf mesophyll [21-51]. In auxin biosynthesis, auxin formation (indole-3-acetic acid (IAA) is synthesized from indole by tryptophan pathways including the Trp-independent pathways and the Trp-dependent synthesis [52]. These pathways alternate under stress conditions so that the Trp-independent pathways convert to the Trp-dependent IAA biosynthesis because the Trp-dependent IAA biosynthesis can effectively interact with biotic and abiotic stresses such as pathogens and wounds [31]. Conjugation mechanisms have important implications for plants in terms of transport and storage, as well as the stability of auxin [53]. They are divided into two branches including amide and ester types. In both of these types, the carboxyl group of IAA is attached to the amide-type and the carboxyl group of IAA is linked to the amino acid as an amide bond and an ester type is bound to the carboxyl group of IAA-sugar, which are metabolically involved in auxin biosynthesis [31]. Conjugation mechanism when plant is faced with heavy metal and oxidative stress can be effective in stabilizing auxin against oxidizing IAA [53]. Auxin transport is conducted by passive activity through the phloem from sources to sink sites such as the root to shoot tips. In this process, different pH levels in the apoplast and cytoplasm make important contributions to adjusting this efflux [54]. A reduction in pH level in the apoplast is an important strategy in auxin signaling mechanisms that is attained by the acidity of auxins [21]. Generally, the role of auxin under heavy metals stress can be ascribed to auxin-ROS link, which occurs by the action of special mechanisms involved in auxin homeostasis [21] and is induced by several genes involved in the adjustment of H<sub>2</sub>O<sub>2</sub> levels, the regulation and stimulation of antioxidant enzymes and chlorophyll content status in plants [48]. This needs more consideration in future studies.

### The Tole of Cytokinins (CKs) in Response to Abiotic Stress

Cytokinin (CKs) phytohormones are known as master regulators that play important roles in plant growth and development [55]. They are involved in many physiological processes such as cell expansion and cell division [56-57], nitrogen and phosphorus metabolism [58], water balance maintenance [59], chloroplasts integrity and senescence [60]. CKs are

known to form  $N^6$ -substituted adenine derivatives [61]. They are associated with different hormones such as ABA [61]. CKs reduce seed dormancy while ABA reduces seed germination [23]. There are different forms of cytokinins including: 6-benzyladenine, thidiazuron, 2-isopentenyladenine and kinetin [62]. In roots and apical meristems, free cytokinins are synthesized and transferred to aerial parts with other absorbent materials (mineral elements) through the xylem. Zeatin riboside from is the most abundant CK in xylem exudate [9].

### Metal Stress

CKs are regulatory molecules that can increase plant resistance to heavy metals through varied signaling pathways. It was shown in a study investigating the effect of endogenous CKs on arsenic stress in *Arabidopsis thaliana* where the reduced CK signaling and the CK-synthesizing mutant plants exhibited increased tolerance against arsenic [63]. It is reported that exogenous CK can elevate plant resistance to metal stress [22-63]. The protective role of synthetic cytokinins is attributed to the presence of kinetin group in its molecular structure that can induce plant antioxidant defense system [60]. It is reported that kinetin can ameliorate reactive oxygen species (ROS) [64]. One of the CK mechanisms under heavy metal stress conditions is the alteration of the level of CK. It is reported that with the excess of heavy metals, the amount of CK decreases to improve plant overall efficiency to cope with the stress [61-65]. One of the reasons for the reduced CK content may be the rising accumulation of ABA in stress conditions, which can activate special enzymes involved in CK degradation and preclude the expression of genes responsible for the control of CK biosynthesis [22]. ABA processes such as catabolism, synthesis, transport, and conjugation can influence cytokinin metabolism and change CK concentration in stress conditions [66]. However, the efficiency of CK in the interaction with ROS is concentration-dependent [67]. CK can ameliorate ROS by reducing cellular ROS concentration. This was observed by treating wheat leaves with the synthetic cytokinin 6-benzyladenine (BAP) in dark stress conditions [60]. The genes necessary for CK metabolism can regulate stress in some processes that may lead to a reduction in CK content [68]. Additionally, it has been reported that exogenous CK can ameliorate other various abiotic stress factors. The studies indicate that exposure of drought-stressed maize plants to BAP could improve the crop growth by increasing the chlorophyll content [69]. In another study, by spraying the kinetin on wheat leaves subjected to drought stress, the exogenous CK had positively influenced cellular ion homeostasis and improved membrane injury [70]. However, in transgenic plants, some reports suggest that increasing intensity of abiotic stress may lead to increased CK levels in plants [71]. The mechanism involved is as follows: In response to low water stress, there is an increase in the synthesis

of cytokinin. This leads to changes in plant metabolism that can reduce shoot growth and postpone plant defense activation to preserve plants under restricted water conditions [72-73].

### The Role of Ethylene (ET) in Response to Abiotic Stress

Ethylene (ET) is a gaseous phytohormone that has an essential role in many metabolic and developmental processes of plant including the senescence of flowers, abscission of petals and leaves, as well as fruit ripening. It also acts as a regulatory hormone during plant stress responses [24-74-75]. The rate of ET synthesis increases with enhancement of biotic and abiotic stresses [76]. This increase is associated with decline in plant growth and development, which is the first ET-induced line of response when plant faces environmental stressors [77]. The mechanism of action of ET to ameliorate heavy metal stress is attributable to gene expression that occurs upon the onset of metal-induced stress, leading to the production of increased levels of *ACS* and *ACO* proteins. These two proteins are involved in ethylene biosynthesis. This process increases the generation of ethylene in plants, therefore leading to the protective role of ethylene in plants [76-77]. Many studies confirm the role of heavy metals in inducing the synthesis of these proteins, which has been shown with chromium (Cr) in rice inducing the expression of the genes *ACS1*, *ACS2*, *ACO4*, and *ACO5* [78-79]; with copper (Cu) in potatoes and tobacco inducing the expression of the gene *ACS* [2]; and with Cd in *Arabidopsis thaliana* stimulating the biosynthesis of *ACC* and *ACS6* [77]. Moreover, the *EIN2* genes have an important role in generating ethylene so that these genes are involved in ethylene signaling and transduction pathways. The heavy metal stress can activate ethylene transducer, resulting in enhancement of transcript levels of *EIN2* which is reflected by an increase in the ethylene content in plants. This has been shown in *Arabidopsis* seedlings exposed to lead (Pb), which resulted in the improved plant tolerance to Pb [80]. On the other hand, exogenous *ACC* appears to be effective in enhancing plant heavy metal tolerance by increasing production of ethylene, which per se can raise antioxidant defense levels. *Arabidopsis thaliana* under Cd stress treated with exogenous *ACC* exhibited increased levels of ethylene, leading to enhanced SOD activity and improved root growth [81]. Ethylene has also been found essential for sulfur-mediated alleviation of Cd in mustard [82]. Concomitant induction of ethylene or its precursor *ACC* and chemical compounds such as hydrogen peroxide has been noted under heavy metal stress in various plants such as tomato and chickpea [83-84]. In a study with Cd-stressed potato, a synergistic action between ROS and *ACC* was observed, which was indicative of  $H_2O_2$  and ethylene interplay [85]. It is shown that exogenous  $H_2O_2$  can lead to increased *ACC* production in stress conditions [86]. It is reported that gene expression of

the ethylene receptor has an important role in quenching ROS compounds arising from osmotic stress [87-88]. In a study on *Arabidopsis thaliana*, osmotic and salt stress led to the adjustment of gene expression of the ethylene receptor with the expression of gene ETR1 at both the mRNA and protein levels [89]. In addition, functional potency of mutant plants affects stress. In the *A. thaliana* functional mutant *etr1-7*, there is more potential to ameliorate salt stress than functional mutant *etr1-1*(ethylene insensitivity) [90]. Besides, in another study, a similar result indicated the regulatory impact of ethylene receptor on oxidative stress levels [91]. However, the threshold concentration of ACC is low in plants with the abundance of ACC synthesis. Ethylene appears to play a dual role in plant response to abiotic stresses, which can be interpreted as either alleviatory or aggravating [12-64].

### The Role of Abscisic Acid (ABA) in Response to Abiotic Stress

Abscisic acid (ABA) is a multifunctional phytohormone with vital roles in the plant life cycle [92]. ABA is involved in many physiological and metabolic processes such as stomatal closure, seed dormancy, seed germination and regulates many growth and development processes in plants like fruit ripening and leaf abscission [4]. This molecule is a sesquiterpene, which consists of multi-functional parts [93]. Signaling paths of ABA include PP2C, SnRK2, and PYL/PYL/RCAR, which play an important role in complex ABA regulation [94]. Generally, transduction of ABA signals happens through fourteen genes. These genes include two SnRK2, three PP2C, and nine PYL genes [2]. ABA is a signaling messenger molecule which is indirectly stimulated by plant defense system in response to the generation of ROS [46]. Changes in the amount of ABA content happen through a number of mechanisms, including ABA transport, ABA catabolism and ABA synthesis as well as the reaction with glucose via conjugation and deconjugation mechanisms [3]. ABA synthesis occurs in chloroplasts through two chemical pathways [95] including degradation of the carotenoid violaxanthin and catalysis of neoxanthin into xanthoxin [95-4]. ABA is also synthesized by de novo (de novo biosynthesis in ABA) during the drying process [93], which takes place in plant organs including terminal buds and roots [96]. The ABA conjugation and deconjugation processes has a role in regulating ABA levels and continual modulation of glucose levels. ABA conjugation results in the permanent deactivation of ABA and its vacuolar repository [3]. However, the role of glycosyltransferase genes is considered to be in the production, regulation and storage levels of ABA. This can be attributed to the important role of glycosyltransferase genes in controlling the mechanisms involved in the alteration of ABA levels [97-98]. For many years, researchers thought that mechanisms

involved in ABA transfer were associated with pH gradients in intercellular organs and between symplast and apoplast [99]. However, the recent studies show that AtBCG25 and AtBCG40 transporters have an important role in transferring ABA to sink sites and guard cells, which is the indicative of the role of the AtBCG type in the movement of ABA in cells [100]. This accumulation of ABA and ABA synthesis in guard cells might be a mechanism for regulating stomatal closure during stress [101].

### Metal Stress

ABA can lead to reduced translocation of heavy metals from root to shoot and the accumulation of heavy metals in roots. The oxidative stress triggered by the excess heavy metals causes the amount of ABA concentration in the plant to increase [2], which can play an important role in the stimulation of antioxidants and increasing their protective capacity. This phenomenon has been reported by many studies conducted with different heavy metals on plants such as seaweed species, [102], and rice [103]. In this process, ABA signals activate the expression of genes involved in antioxidant enzymes and non-enzyme activity. In many plant species, ZEP is the gene involved in ABA biosynthesis and ZEP gene expression is higher in leaves than in other parts of plant organs [104] Which has reported in one study on Grapevine (*Vitis vinifera* L.) [105]. The results obtained by a study on rice seedlings indicated that the exogenous levels of ABA decreased Cd uptake by the plant [106]. Exogenous ABA can alter concentration of metal ions within plant body and contribute to metal detoxification by regulating the expression of some key genes involved in metal absorption and transfer. In a study, exogenously applied ABA mitigated zinc toxicity in *Populus×canescens* by reducing the metal uptake and accumulation [107]. This was attributed to the modulation of transcript expression levels responsible for Zn absorption by ABA. On the other hand, ABA is able to alleviate conditions arising from heavy-metal induced dehydration in plants. The excess of heavy metals leads to a disturbance in photosynthetic indexes, a decrease in net photosynthesis and transpiration imbalance [108] and a disruption of ion permeability in guard cells, eventually leading to disturbed water balance throughout the plant [109-110]. Hence, heavy metal stress indirectly induces drought conditions in plants [111]. ABA regulates stomata closure when the plant does not require much CO<sub>2</sub> and when it faces drought stress and cannot afford to lose more water [112]. In these conditions, ABA is produced from roots and transferred to guard cells via xylem sap leading to stomata closure in leaves [111]. The regulation of stomata can preserve water balance and improve drought stress intensity caused by metal toxicity in the plant [112].

Table 1. Ameliorative impacts of phytohormones on different plant species under various heavy metals.

Plant	Metal type	Application of phytohormones	Impact on stress	Response & Mechanism	Reference
Populus × canescens seedlings	Zn	Exogenous abscisic acid (ABA)	+	Reduction of Zn levels with regulation of genes involved in uptake of Zn and plant detoxification	[107]
Tomato mutant	Cd	Abscisic acid (ABA)	+	ABA-regulated responses of cells influence Cd and activation of plant defense system	[113]
Two ecotypes (mining and farmland) of Solanum photeinocarpum	Cd	Exogenous abscisic acid (ABA)	+	Increasing chlorophyll content and biomass – Enhancing the ability of Cd extraction of <i>S. photeinocarpum</i>	[114]
Attractylodes macrocephala	Pb	Exogenous abscisic acid (ABA)	+	Changes in antioxidant activities by low application levels of exogenous ABA may be the reason for the reduction of Pb-induced toxicity in <i>A. macrocephala</i>	[18]
<i>S. cataractae</i>	low-Cu conditions	Auxin	+	Regulatory role of Auxin in cell differentiation of cells	[115]
<i>Arabidopsis thaliana</i>	As	Indole-3-acetic acid (IAA)	+	Auxin transport role in oxidative stress caused by As	[43]
<i>Sunflower (Helianthus annuus L.)</i>	Pb and Zn	Indole-3-acetic acid (IAA)	+	Enhancement of metal phyto-extraction in sunflowers	[116]
<i>Trigonella foenum-graecum L.</i>	Cd	Exogenous indole-3-acetic acid IAA	+	Upregulation of AsA-GSH cycle	[117]
Wheat	Cd	Exogenous indole-3-acetic acid IAA	+	Activation of antioxidant enzyme activities and improving leaf anatomy structure under Cd stress	[49]
Wheat	Cd	Indole-3-acetic acid (IAA)	+	Activation of antioxidant enzymes activities and improving stem anatomy structure under Cd stress in wheat	[118]
Maize seedlings	As	Kinetin (KT)	+	Positive impact on chlorophyll, increasing of antioxidant enzymes activity and reducing lipid peroxidation	[119]
Tomato seedlings	Cd	Kinetin' (KN, 6-furfurylamino purine), Kinetin (KN)	+	Involved in ascorbate-glutathione (Asa-GSH) cycle regulation	[64]
Wheat (Bezostaya and Kutluk cultivars)	Boron	Kinetin (KN)	+	Reduction of oxidative stress by increasing plant antioxidant enzyme activities and defense system	[120]
Pea seedlings	Cr(VI)	Kinetin (KN)	+	KN enhances Cr tolerance by increasing antioxidant activities such as (SOD) (APX) (CAT), (GR) and dehydroascorbate reductase (DHAR)	[121]
Tobacco plant	N-deficiency	Cytokinin	+	Enhancement of cytokine synthesis in transgenic plants	[122]
Mustard ( <i>Brassica juncea L. cv. Varuna</i> )	Cd	Sulfur (S) or ethephon (ethylene source)	+	Stimulation of antioxidant system and enhancement of photosynthesis in the plant expose to Cd stress	[82]
Tobacco plants	Cd	Mediatory role of ethylene synthesis	+	Combination of Cd-NaCl ameliorates Cd stress and improves root growth by the mediatory role of ethylene	[123]
<i>Arabidopsis thaliana</i>	Cd	Mediatory role of ethylene signaling	+	Essential role of ethylene signaling in leaves of <i>A. thaliana</i> in response to early Cd stress, which can moderate Cd concentration	[14]

## Conclusion

ROS produced under various biotic or abiotic stress factors can interact with hormonal signaling pathways. There are four different phytohormones: abscisic acid (ABA), auxin (IAA), cytokinins (CKs), and ethylene (ET), which play vital roles in stress conditions. They contribute to the generation of essential enzymes required for cell protection and preservation of proteins and lipids. ABA acts as a regulator of excessive metal with a role as a signaling molecule. Upon the onset of heavy metal stress in plants, ABA levels start increasing, which leads to establishing a signaling communication and encoding of genes associated with plant antioxidant enzyme and defense systems. In this process, ABA signals activate the expression of genes responsible for the bio-synthesis of plant antioxidant enzymes and non-enzyme components. In addition, ABA, as a signaling messenger molecule, is stimulated by plant defense responses to the generation of ROS. On the other hand, ABA can significantly impede translocation of heavy metal ions from root to shoot, resulting in accumulation of heavy metals in root. The auxin-mediated response to heavy metal stress in plant is related to the reciprocity between  $H_2O_2$  and auxin homeostasis. ROS signaling acts as a mediator in plant growth and development assisted by auxin. ROS signaling can impact signaling, transport, biosynthesis, and metabolism of auxins. Additionally, exogenous auxin can disturb  $H_2O_2$  formation by inducing NADPH oxidase and activating antioxidant defense mechanisms. The enhancement of ethylene production is a warning alarm of a critical situation of stress in the plant. ET biosynthesis and signaling are influenced by the status of nutrients in plants, which in turn is impacted by ROS level. The main mechanism for ET regulation of metal stress is the interaction between ACC, ROS signaling and  $H_2O_2$  production. It seems that there is a relationship in ABA/CK ratio such that with an accumulation of ABA, the level of CKs is reduced. This process leads to increased apical dominance and to positive effects on stomatal aperture and enhanced plant defense resistance. On the other hand, exogenous CK signaling can reduce heavy metals stress by affecting ROS, resulting in decreased ROS production. Generally, CKs can ameliorate heavy metal stresses via some pathways involving exogenous CK, CK metabolism, and CK signaling. Below, Table 1 demonstrates the impact of phytohormones on different plant species subjected to various heavy metals by describing the related mechanisms, which builds an evidence-based argument for the main text. It seems that the phytohormones act as signaling molecules and are in the interaction with redox signaling during metal exposure. This can result in the activation of gene expression involved in plant defense mechanisms. Hence, cross-linked ROS and hormonal signaling networks contribute to increased plant resistance under stress conditions.

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## Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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