Roles of phytohormones in mitigating abiotic stress in plants induced by metal(loid)s As, Cd, Cr, Hg, and Pb

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Roles of phytohormones in mitigating abiotic stress in plants induced by metal(loid)s As, Cd, Cr, Hg, and Pb

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ABSTRACT

Phytohormones, including auxin, abscisic acid, gibberellic acid, ethylene, cytokinin, brassinosteroids, salicylic acid, and jasmonic acid, provide beneficial effects for plants against metal(loid) toxicity. However, their mechanisms in alleviating metal(loid) toxicity in plants have not been fully understood. Here, we summarize phytohormone-mediated detoxification mechanisms of metal(loid)s in plants, including As, Cd, Cr, Hg, and Pb. First, we discussed the functions of phytohormones on plant growth and nutrient uptake, and the effects of metal(loid)s on plant growth and hormone contents. We then discussed the underlying mechanisms of selected phytohormones in alleviating metal(loid) toxicity in plants. Those phytohormones protect plants against metal(loid) toxicity mainly by enhancing plant growth, increasing antioxidant capacity, promoting cell wall synthesis and nutrient uptake, and decreasing metal(loid) accumulation. This review highlights the beneficial roles of phytohormones in reducing plant metal(loid) uptake and in enhancing crop yields, which helps to improve crop production and food safety.
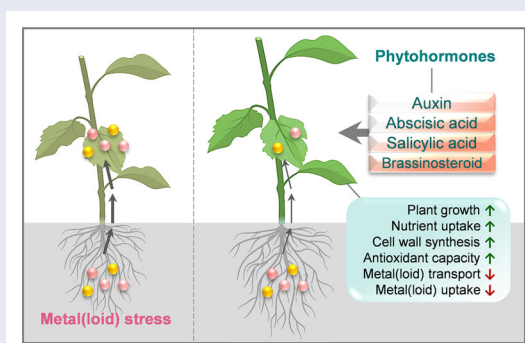
1. Introduction

Toxic metal(loid)s including As, Cd, Cr, Hg, and Pb are non-essential for plant growth and can be toxic to plants (Bandara et al., 2020). They are often present in contaminated soils, causing adverse health effects on humans (Balali-Mood et al., 2021). Their contamination in the environment mainly results from industrial and agricultural activities, while the main natural sources include rock weathering and volcano eruption (da Silva et al., 2020). Among the five metal(loid)s, As and Cr are present in soils mostly as oxyanions while Cd, Hg, and Pb as cations. In soils, As is mainly present as arsenate (AsV) and arsenite (AsIII) (Tang & Zhao, 2021) whereas Cr exists as oxidized CrVI and reduced CrIII (de Oliveira et al., 2015). Among the three cationic metals,

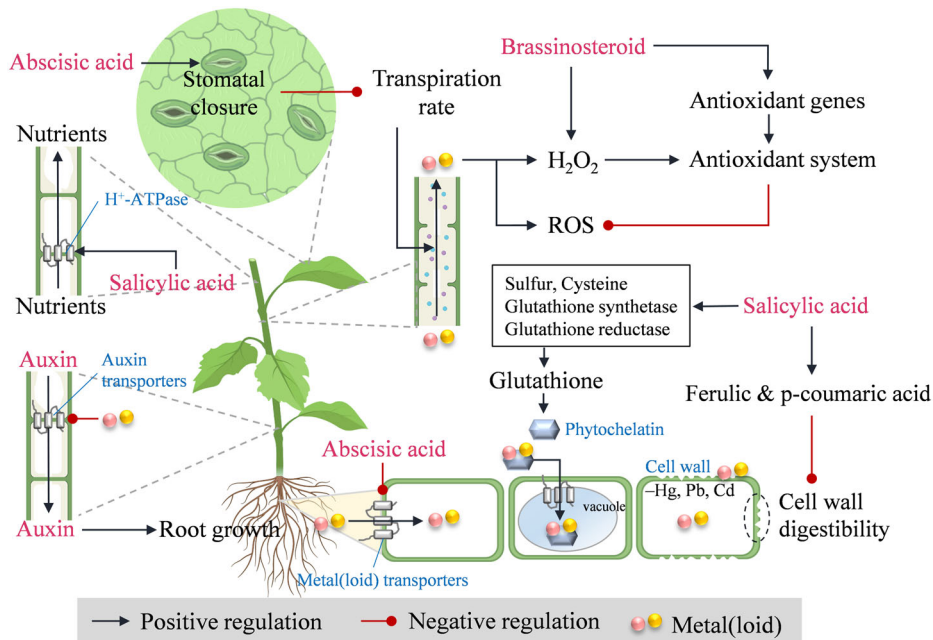**Figure 1.** Strategies of different phytohormones in alleviating metal(loid) toxicity in plants.

Cd is the most mobile and can be readily taken up by plants and translocated to different tissues (Rasafi et al., 2022).

Abiotic stress is defined as the negative impacts of non-living factors on living organisms in the environment (Ben-Ari & Lavi, 2012). Plants cope with metal(loid)-induced abiotic stress by altering the levels of their phytohormones. For example, under abiotic stress, root cells can stimulate rapid synthesis of phytohormones (Zhang et al., 2020), which changes root morphology, nutrient absorption, and expression of metal transporters (Rasafi et al., 2022). Further, plant growth and development are also regulated by phytohormones. For example, the application of hormones decreases metal accumulation in plants (Verma et al., 2020). As such, the application of phytohormones can be used to help plants to grow better under abiotic stress (Sytar et al., 2019), which is important to improve crop production.

Phytohormones are trace secondary metabolites in plants, which play important roles in regulating plant growth and development as well as against metal(loid) stress (Ruzicka et al., 2009). Classical plant hormones include auxin, abscisic acid, gibberellic acid, ethylene, cytokinin, brassinosteroids, salicylic acid, and jasmonic acid (Li et al., 2020), which regulate plant defensive responses under abiotic stress. They all play important roles in controlling metal(loid) stress in plants through regulating cell division, nutrient metabolism, antioxidant system, and metal(loid) uptake.

This review aims to discuss the functions and the associated mechanisms of phytohormones in enhancing plant growth and reducing its abiotic stress (Figure 1; Table 1). This review may provide a theoretical basis and guidance to mitigate metal(loid)-induced abiotic stress by adopting different practical approaches to improve crop production and food safety.

2. Functions of phytohormones on plant growth and nutrient uptake

The functions of different phytohormones in plant growth and development have been reviewed (Jiang & Asami, 2018; Santner & Estelle, 2009). However, the interactions of different hormones and their effects on nutrient uptake in plants need further research, which is the basis for plant adaptation to abiotic stress. Important phytohormones can be grouped into growth-promoting

Table 1. Effects of different phytohormones in alleviating metal(loid)-stress in plants.

Hormone types	Hormone levels	As levels	Plant species	Major changes in plants	References
Auxin (IAA)	2 μM	10 μM AsV	*Oryza sativa*	↑ Plant growth ↓ Plant As	He et al. (2022)
	3 μM	150 μM AsIII	*Oryza sativa*	↑ Plant growth, chlorophyll	Pandey and Gupta (2015)
	5 μM	300 μM AsV	*Brassica juncea*	↑ Plant growth	Srivastava et al. (2013)
Brassinosteroid (24-Epibrassinolide)	0.5 μM	75 μM AsIII	*Glycine max*	↑ Plant growth, membrane stability, gene expression of CAT ↓ Plant As, MDA	Chandrakar et al. (2017)
	0.5 and 0.75 μM	50 and 100 μM AsV	*Triticum aestivum*	↑ Pn, chlorophyll, POD, SOD, CAT, APX ↓ Plant As, H_2O_2, MDA	Maghsoudi et al. (2020)
Methyl jasmonate	0.25 μM	25 μM AsIII	*Oryza sativa*	↑ Plant growth, chlorophyll, antioxidant enzyme ↓ MDA, Plant As, AsIII uptake and translocation genes	Verma et al. (2020)
Cytokinin (Kinetin)	0.4 $\sim$ 7.0 μM	6 μM AsV	*Zea mays*	↑ Plant growth, chlorophyll, SOD, POD, CAT ↓ MDA	H. J. Wang et al. (2015)
	Transgenic Cytokinin-deficient	5 μM AsV	*Arabidopsis thaliana*, and *Nicotiana tabacum*	↑ Plant As, PC, GSH	Mohan et al. (2016)
Salicylic acid	0.5 and 1 mM	50 and 100 μM AsV	*Triticum aestivum*	↑ Chlorophyll, photosynthesis, SOD, POD, CAT, APX ↓ Plant As, MDA, H_2O_2	Maghsoudi et al. (2020)
	40 μM	25 μM AsIII	*Oryza sativa*	↑ Plant growth, chlorophyll, GR, root Ca, shoot Fe ↓ H_2O_2, SOD, CAT, APX, GPX, shoot As; root Fe transport gene	Singh et al. (2017)
	500 μM	100 μM AsV	*Zea mays*	↑ Plant growth, chlorophyll a + b, F_v/F_m, CAT, POD, GSH, AsA, GSH/GSSG, APX, GR ↓ Plant As, MDA, H_2O_2, SOD, GSSG	Kaya et al. (2020)
Abscisic acid	10 μM	25 and 50 μM AsIII	*Oryza sativa*	↑ Plant growth, GR, GPX, GSH/GSSG, PC, SOD, CAT, APX ↓ Plant As, H_2O_2, O_2^-	Saha et al. (2021)
		Cd levels			
Auxin (NAA)	0.05 μM	50 μM	*Arabidopsis thaliana*	↑ Root Cd, Cd in cell wall ↓ Shoot Cd, Cd membrane transporters expression	Zhu et al. (2013)
Brassinosteroid (24-Epibrassinolide)	0.1 μM	500 μM	*Vigna unguiculata*	↑ Plant growth, Ca, Mg, Mn, Fe, Cu, Zn content, F_v/F_m, Pn, chlorophyll, carotenoids ↓ Plant Cd, O_2^-, H_2O_2, MDA	Santos et al. (2018)

(continued)

Table 1. Continued.

Hormone types	Hormone levels	As levels	Plant species	Major changes in plants	References
	5 μM	1 mM	Phaseolus vulgaris	↑ Plant growth, chlorophyll, carotenoids, SOD, CAT ↓ Plant Cd	Rady (2011)
	0.1 μM	1.3 mM	Pisum sativum	↑ Plant growth, chlorophyll, carotenoids,F_v/F_m, Pn, SOD, CAT, APX, GR, AsA, GSH, Mg, Ca, K, P, S ↓ H_2O_2, MDA, Plant Cd	Jan et al. (2018)
Cytokinin (Kinetin)	50 μM	100 μM	Vigna angularis	↑ Plant growth, chlorophyll, carotenoids, Pn, SOD, CAT, APX, GR, AsA, GSH, N and K ↓ Plant Cd, O_2^-, H_2O_2, lipoxygenase activity, lipid peroxidation	Ahanger et al. (2020)
Salicylic acid	50 μM	1 mM	Triticum aestivum	↑ Plant growth, IAA, CTK ↓ Plant Cd, MDA, ABA	Shakirova et al. (2016)
	100 μM	10 μM	Solanum lycopersicum	↑ Cell wall synthesis, Cd distribution ratio in cellulose and lignin ↓ Plant Cd	Jia et al. (2021)
	100 μM	200 μM	Arachis hypogaea	↑ Cd content in cell wall, Plant growth, chlorophyll, SOD, POD, CAT, AsA, GSH, Pn, K, Ca, Mg, Fe ↓ Plant Cd, MDA, O_2^-, H_2O_2,	Xu et al. (2015)
	100 μM	25 μM	Oryza sativa	↑ Plant growth, chlorophyll ↓ H_2O_2, O_2^-, MDA, CAT, Plant Cd	Majumdar et al. (2020)
	100 μM	89 μM	Oryza sativa	↑ Plant growth, SOD, POD, CAT ↓ Plant Cd, H_2O_2	F. Wang et al. (2021)
	100 μM	53 μM	Glycine max	↑ Plant Fe, Mg, Ca; Cd; chlorophyll ↓ Root K	Drazic and Mihailovic (2005)
	200 μM	500 μM	Oryza sativa	↑ Plant growth, chlorophyll, carotenoids, GSH, AsA, SOD, CAT ↓ Plant Cd, H_2O_2, MDA	Mostofa et al. (2019)
	100 μM	267-1068 μM	Mentha piperita	↑ Plant growth, chlorophyll, F_v/F_m, SOD, POD, GR, GSH ↓ Plant Cd	Ahmad et al. (2018)
	10 μM	223-893μM	Cicer arietinum	↑ Plant growth, nitrogen fixation and assimilation	Hayat et al. (2014)
Abscisic acid	0.5 μM	10 μM	Arabidopsis thaliana	↑ Plant growth, Fe ↓ Plant Cd, Cd transporter IRT1	Fan et al. (2014)
	2-10 μM	500-1500 μM	Oryza sativa	↑ Chlorophyll ↓ Plant Cd, transpiration rate	Hsu and Kao (2003)

(continued)

Table 1. Continued.

Hormone types	Hormone levels	As levels	Plant species	Major changes in plants	References
		Cr levels			
Brassinosteroid (24-Epibrassinolide)	10^{-9} M	1.2 mM CrVI	*Raphanus sativus*	↑ Plant growth, IAA, GSH, AsA, SOD, PC, chlorophyll, carotenoids, F_v/F_m ↓ ABA, CAT, GR, MDA, O_2^-, H_2O_2, Plant Cr	Choudhary et al. (2012)
	0.01-1 μM,	0.5 mM Cr	*Oryza sativa*	↑ Plant growth, SOD, CAT, AsA, GR, APX, antioxidant genes ↓ MDA, H_2O_2, Plant Cr	Sharma et al. (2016)
	0.01 μM	100 μM Cr	*Oryza sativa*	↑ Plant growth, photosynthesis, SOD, POD, CAT, APX ↓ MDA, H_2O_2	Basit et al. (2022)
		Hg levels			
Salicylic acid	50 μM	50 μM Hg (HgCl$_2$)	*Melissa officinalis*	↑ Plant growth, chlorophyll synthase gene, chlorophyll, antioxidant activities ↓ MDA	Safari et al. (2019)
		Pb levels			
Auxin (IAA)	0.01 μM	100 μM	*Acutodesmus obliquus*	↑ Auxin, CTK, GA_3, GSH, PCS ↓ ABA	Piotrowska-Niczyporuk et al. (2020)
Brassinosteroid (24-Epibrassinolide)	100 nM	200 μM	*Oryza sativa*	↑ Plant growth, chlorophyll, *Pn*, SOD, CAT, APX, K, Ca, Mg, Mn, Cu, Zn ↓ Plant Pb, MDA, O_2^-, H_2O_2	Guedes et al. (2021)
Jasmonic acid	0.01, 1, and 100 nM	0.25, 0.50, and 0.75 mM	*Lycopersicon esculentum*	↑ Plant growth, chlorophyll, carotenoids, *Pn*, AsA, GSH, APX, GR ↓ Plant Pb, H_2O_2	Bali et al. (2018)
Cytokinin	0.01 μM trans-zeatin, or 0.1 μM Kinetin	100 μM	*Acutodesmus obliquus*	↑ Auxin, CTK, and GA_3; GSH ↓ ABA, PC	Piotrowska-Niczyporuk et al. (2020)

Abbreviations: SOD: superoxide dismutase; CAT: catalase; POD: peroxidase; MDA: malondialdehyde; *Pn*: net photosynthetic rate; APX: ascorbate peroxidase; PC: phytochelatin; PCS: phytochelatin synthase; GSH: glutathione; GSSG: oxidized glutathione; GR: glutathione reductase; GPX: glutathione peroxidase; F_v/F_m: maximal quantum yield of PSII photochemistry, or efficiency of PSII; NAA: alpha-naphthaleneacetic acid; ABA: abscisic acid; CTK: cytokinin; GA_3: Gibberellin A3.

hormones (auxin, gibberellic acid, cytokinin, and brassinosteroids) and stress-response hormones (abscisic acid, ethylene, salicylic acid, and jasmonic acid), which have different functions in alleviating abiotic stress in plants (Table 1).

2.1. Phytohormone contents in plants

The contents of plant hormones are shown in Figure 2. Different plants contain different amounts of hormones, which are often based on fresh weight. The contents of auxin, cytokinin, abscisic acid, salicylic acid, and jasmonic acid are relatively high in plants at $1 - 1000\,\mu g\ kg^{-1}$ (Bajguz & Tretyn, 2003; Deng et al., 2017). The contents of gibberellic acid are lower in plants at $0.1 - 100\,\mu g\ kg^{-1}$ (Deng et al., 2017). The contents of brassinosteroids are the lowest in plants at $0.01 - 0.1\,\mu g\ kg^{-1}$ (Bajguz & Tretyn, 2003). For gaseous hormone ethylene, its contents are at $0.01 - 10\,\mu L\ kg^{-1}$.
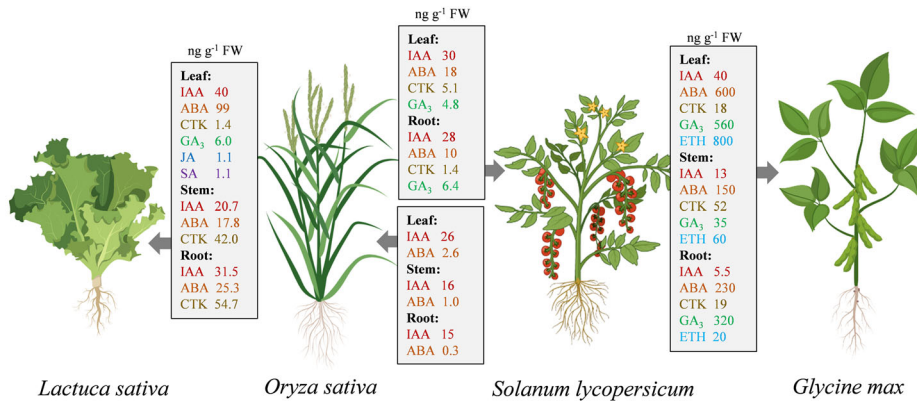
Figure 2. The maximum concentrations of different hormones in different plants (Ahmad & Li, 2021; Arkhipova et al., 2005; Formentin et al., 2018; Li et al., 2018; X. Y. Liu et al., 2018; Navarro-Leon et al., 2016). Abbreviations: IAA: indole-3-acetic acid; CTK: cytokinin; GA: gibberellic acid; BRs: brassinosteroids; ABA: abscisic acid; JA: jasmonic acid; SA: salicylic acid; ETH: ethylene.

The contents of phytohormones vary with plant species and tissues (Figure 2; Ahmad & Li, 2021; Navarro-Leon et al., 2016). For example, gibberellic, jasmonic, and salicylic acids mainly exist in the leaves of lettuce, with little in the stems or roots. The contents of natural auxin IAA (indole-3-acetic acid) in the roots decrease in the order of lettuce > tomato > rice > soybean (Figure 2).

Generally, metal(loid)-induced abiotic stress increases the stress-response hormones level while decreasing the growth-promoting hormones level, leading to lower plant biomass (Guo et al., 2019; Srivastava et al., 2013). For example, stress-induced H_2O_2 production decreases its auxin levels and increases abscisic acid accumulation to coordinate plant growth (Liu et al., 2022).

2.2. Impacts on photosynthesis in plants

Photosynthesis is critical for plant growth and development, which is regulated by phytohormones. For example, brassinosteroids enhance chlorophyll content by increasing chlorophyll biosynthesis enzymes (Siddiqui et al., 2018). However, photosystem-II in the photosynthesis system splits water to oxygen, generating reactive oxygen species (ROS) as a byproduct, which destabilizes photosystem-II repair protein-D1 and leads to photoinhibition in plants. Fortunately, brassinosteroids promote protein-D1 stabilization, thus enhancing photosystem-II efficiency in plants (Siddiqui et al., 2018). Moreover, brassinosteroids also increase the stomatal aperture to allow more CO_2 uptake into the photosynthesis system (Serna et al., 2012). Further, brassinosteroids induce formation of ribulose bisphosphate carboxylase/oxygenase in the Calvin cycle, the most common CO_2 fixation pathway in plants, thereby increasing sugar synthesis (X. J. Li et al., 2016). Thus, brassinosteroid-mediated increase in photosynthetic efficiency enhances plant growth and development.

Other phytohormones also play a role in plant photosynthesis. For example, abscisic acid is a well-known regulator of stomatal closure, which decreases photosynthesis by limiting CO_2 diffusion (Pinheiro & Chaves, 2011), while cytokinins, auxin, and ethylene induce stomatal opening (Zlobin et al., 2020). In addition, gibberellin plays a positive role in enhancing photosynthesis activity and promotes chloroplast biogenesis (X. J. Li et al., 2016).

However, the effects of methyl jasmonate on photosynthesis are dose-dependent. Methyl jasmonate is a plant signal-regulating morphogenesis, which responds to abiotic stress. For example, application of 1.1–2.2 mM methyl jasmonate enhances photosynthesis in trifoliate orange. In contrast, application of 4.4 mM methyl jasmonate to trifoliate orange decreases its photosynthesis (Kurowska et al., 2020). This is because higher jasmonate inhibits stomatal development in plants

(Han et al., 2018), thereby reducing plant photosynthesis. However, our knowledge on the mechanisms of hormone-mediated regulation of photosynthesis is still fragmentary.

2.3. Impacts on nutrient uptake in plants

Phytohormones promote plant growth by coping with nutrient deficiency. Plant responds to nutrient deficiency by growing more roots. For example, Mg-deficiency elevates the auxin levels in *Arabidopsis thaliana* roots (M. Liu et al., 2018), which helps to regulate root hair development (M. Liu et al., 2018). Further, K-deficiency increases the ethylene levels in *A. thaliana*, which stimulates root hair growth (Hogh-Jensen & Pedersen, 2003; Shin & Schachtman, 2004). Similarly, under B deficiency, *A. thaliana* increases brassinosteroids to promote its root growth (Zhang et al., 2021).

Phytohormones also play a role in nutrient homeostasis in plants. For example, both auxin and abscisic acid play a role in Mg and Fe homeostasis, which are important for photosynthesis (David-Assael et al., 2006; Shahid et al., 2020). In addition, salicylic acid increases Mg uptake in watermelon plants and brassinosteroid increases Mg and Zn uptake in rice plant (Guedes et al., 2021; Moustafa-Farag et al., 2020). Further, Zn is an important component of many enzymes, thereby participating in chloroplast synthesis in plants. The effects of jasmonic acid on nutrient uptake in plants are plant-dependent. For example, 1 mM methyl jasmonate increases the Fe and Zn content in soybean and sunflower while decreasing that in tomato plants (Li et al., 2017).

3. Effects of metal(loid)s on plant growth and hormone contents

3.1. Toxic effects of metal(loid)s on plants

Toxic metal(loid)s, including As, Cd, Cr, Hg, and Pb, enter plants mostly via root uptake (Ali et al., 2021; Peralta-Videa et al., 2009). The accumulated metals dominantly localize in the roots, with only a small proportion being translocated to the shoots. For As, both AsV and AsIII can be taken up by plant roots, with AsIII being more toxic and mobile than AsV (Peralta-Videa et al., 2009; Tang & Zhao, 2021). Once taken up, AsV is rapidly reduced to AsIII in the roots, which is often extruded outside the roots (Deng et al., 2020). Similar to As, CrVI can also be reduced to CrIII in the roots (de Oliveira et al., 2015), with CrVI being more toxic than CrIII. Compared to CrVI, CrIII is less soluble, which is mostly concentrated in the roots (de Oliveira et al., 2018). Among cationic metals, Cd is of most concern as it can be readily taken up by plants, which accumulate more than other metals in their tissues (Rasafi et al., 2022).

Hormesis is a tendency for low levels of stress to stimulate rather than reduce plant responses like growth. So plant growth stimulation has been observed after exposing plants to tolerable concentrations of metal(loid)s (Carvalho et al., 2020; Poschenrieder et al., 2013). However, at higher concentrations, metal(loid)s are toxic to plants, which include: (1) reducing plant growth by damaging cell membrane (Nagajyoti et al., 2010); (2) increasing oxidative stress by forming ROS (Shahid et al., 2020); and (3) disrupting nutrient uptake and inhibiting metabolic processes (Kupper & Kochian, 2010). Under metal(loid)-stress, cells often undergo lipid oxidation, leading to membrane damage and impaired DNA repair (Valko et al., 2005). For example, AsV competes with phosphate uptake, which uncouples the oxidative phosphorylation and inhibits cell energy supply (Tang & Zhao, 2021). Besides, Hg can replace Mg from chlorophyll and Zn from photosystem II, causing toxicity to plants (Patra et al., 2004).

3.2. Effects of metal(loid)s on phytohormones

Synthesis of phytohormones in plants is impacted under metal(loid)-stress, which plays a crucial role in plant's stress adaptation. The role of hormones in response to metal(loid)s is well-known (Ronzan et al., 2018; Shahid et al., 2020).

3.2.1. Effects on auxin, gibberellin, cytokinin, and brassinosteroids in plants

All four phytohormones play an important role in regulating plant growth and development under abiotic stress (Table 1). In plants, metal(loid)s can alter auxin levels, with its transportation to the roots being inhibited, thereby reducing plant growth. Among known auxins, IAA is the most predominant and well-known. For example, IAA level decreases in mustard roots under $300\,\mu M$ AsV stress, and in rice roots under $5\,\mu M$ Cd stress (Srivastava et al., 2013; H.-Q. Wang et al., 2021).

There are numerous members of auxin efflux gene in *PIN* family in plants (Lu et al., 2015), which likely play an important role in its transport from the shoots to roots. By inhibiting *OsPIN5* synthesis in rice and *AtPIN1* synthesis in *A. thaliana*, Cd and As lower the auxin accumulation in the roots to reduce root growth (Fattorini et al., 2017; Ronzan et al., 2018). Further, metal(loid)s suppress auxin biosynthesis in the roots. For example, Cd suppresses the expression of auxin biosynthesis gene *OsYUCCA7* in rice roots (H.-Q. Wang et al., 2021). Thus, auxin biosynthesis and transportation in the roots is inhibited by metal(loid)-stress, including Cd and As (Betti et al., 2021; Ronzan et al., 2018). Further, the data suggest that lower auxin accumulation in meristematic tissue reduces root growth.

Besides auxin, metal(loid)-stress decreases gibberellic acid (GA) production in plants. For example, $100-400\,\mu M$ AsV reduces the GA_3 content to $0.7-2.1\,\mu g\,g^{-1}$ in Faba bean, while $27\,\mu M$ Cd decreases the GA_3 content to $3.49\,\mu g\,kg^{-1}$ in wheat (J. J. Guo et al., 2019; Mohamed et al., 2016). Based on the transcriptome analysis of rice, $25\,\mu M$ AsV inhibits the expression of its gibberellin genes (Huang et al., 2012).

Further, metal(loid)-stress decreases the cytokinin production in plants. For example, $27\,\mu M$ Cd decreases the cytokinin content to $6.35\,\mu g\,kg^{-1}$ in wheat and $30\,\mu M$ AsV decreases the cytokinin content in *A. thaliana* (J. J. Guo et al., 2019; Mohan et al., 2016). Transcriptome analysis of rice reveals strong expression of its cytokinin deactivation genes under $25\,\mu M$ AsV stress (Huang et al., 2012). Further, AsV down-regulates other genes, including cytokinin synthesis genes and response regulator genes in plants (Mohan et al., 2016). The decrease in cytokinin may be due to metal(loid)-induced oxidative stress, resulting in oxidative degradation of cytokinin (Hashem, 2014). In short, both As and Cd reduce the content of phytohormones including auxin, gibberellins, and cytokinin in plants, thereby reducing their growth.

Unlike cytokinin, metal(loid)-stress increases the brassinosteroid production in plants. For example, AsV promotes the brassinosteroid synthesis in mustard plants, while the brassinosteroid signaling pathway is activated in *A. thaliana* under $50\,\mu M$ Cd exposure (Kanwar & Bhardwaj, 2015; Villiers et al., 2012). Metal(loid)-induced synthesis of brassinosteroids is probably a anti-stress defense strategy adopted by plants (Kanwar & Bhardwaj, 2015). Since brassinosteroids regulate cell division and elongation, they probably play a vital role in plant growth under metal(loid)-stress (Peleg & Blumwald, 2011).

Plants can regulate growth-promoting hormone levels to cope with metal(loid)-stress. Metal(loid)s often promote brassinosteroids synthesis while inhibit auxin, gibberellins, and cytokinin synthesis (Nazir et al., 2021). At low concentrations, these growth-promoting hormones are insufficient to alleviate metal(loid)-induced growth inhibition. As such, exogenous hormone supply can help to mitigate metal(loid)-induced stress in plants (Ruzicka et al., 2009).

3.2.2. Effects on abscisic acid, ethylene, salicylic acid, and jasmonic acid in plants

These four hormones play an important role in reducing plant toxicity under metal(loid)-induced abiotic stress (Table 1). It is known that metal(loid) induces the production of abscisic acid in plants, which reduces stomatal conductance, thereby affecting photosynthesis and plant growth (Mohamed et al., 2016). In plants, increased abscisic acid contents equate to increased resistance levels (Christmann et al., 2006). However, under low metal(loid) stress, increased abscisic acid content causes hormesis, contributing to plant growth (Shahid et al., 2020). While 25 μM AsIII increases the abscisic acid levels to 0.19 mg kg^{-1} in rice, 100 μM Cd increases the abscisic acid levels to 1.72 mg kg^{-1} in potato plants (Yadav et al., 2021; Stroiński et al., 2010). In rice, the expression levels of abscisic acid biosynthesis genes are upregulated by both Cd and As (Huang et al., 2012; Tan et al., 2017).

Besides abscisic acid, metal(loid) induces the production of other hormones, including ethylene, salicylic acid, and jasmonic acid in plants. A higher level of ethylene reduces plant growth via altering its central metabolism and cell wall composition (Nascimento et al., 2021). Unlike ethylene, higher levels of salicylic acid and jasmonic acid increase plant growth by enhancing its chlorophyll synthesis and photosynthesis (Farooq et al., 2016; Moussa & El-Gamal, 2010). For example, 50 μM Cd increases the contents of ethylene, salicylic acid and jasmonic acid in pea plants, which is also observed under As stress (Drzewiecka et al., 2018; Rodriguez-Serrano et al., 2006; Yadav et al., 2021). Under metal(loid)-stress, ethylene activity increases with the metal(loid) levels in plants (Emamverdian et al., 2020). Transcriptome analysis of rice reveals strong expression of biosynthesis genes of ethylene and jasmonic acid under 25 μM AsV stress (Huang et al., 2012). The enhanced salicylic acid and jasmonic acid are beneficial, while ethylene is toxic to plant growth. This is supported by the fact that the addition of aminovinylglycine, an inhibitor of ethylene synthesis, inhibits ethylene synthesis, thereby improving plant growth in Cd-exposed plants (Zhou et al., 2018).

4. Role of phytohormones in mitigating metal(loid)-induced abiotic stress in plants

Taking a comprehensive view of phytohormone's functions under metal(loid)-stress, this review focuses on the mechanisms of phytohormones in mitigating metal(loid)-induced stress in plants (Figure 1). Different phytohormones function differently in alleviating metal(loid)-stress, including increasing plant growth, antioxidant defense system, nutrient uptake and cell wall synthesis, and decreasing metal(loid) accumulation (Table 1; Figure 3). Since phytohormones help to alleviate metal(loid)-stress, they can be applied to alleviate plant toxicity. Here we mainly focus on the associated mechanisms of phytohormones in regulating plant growth, antioxidant defense, nutrient and metal(loid) uptake, and cell wall synthesis in plants.

4.1. Auxin mediates root growth under metal(loid)-stress

Root growth inhibition is common for plants under metal(loid)-stress (Tu et al., 2021), which is associated with reduced auxin accumulation in plant meristematic tissue. Since plants take up water and nutrients from soil through the roots, root plasticity is an important adaptive trait (Ogura et al., 2019). Plants adapt to abiotic stress by changing root growth, in which auxin plays a central role in controlling root growth (Tu et al., 2021; Table 1). Root cells near the tips divide frequently under proper auxin levels, thereby promoting root elongation and differentiation in *A. thaliana*, but higher auxin levels make cells quiescent (Petersson et al., 2009). For example, application of low auxin levels at 200 nM stimulates mitotic activity, resulting in a larger meristematic zone in plants (Ruzicka et al., 2009).

Under metal(loid)-stress, reduction in auxin decreases the formation of lateral roots in plants (Ronzan et al., 2019), so application of auxin increases their root growth (He et al., 2022). This is
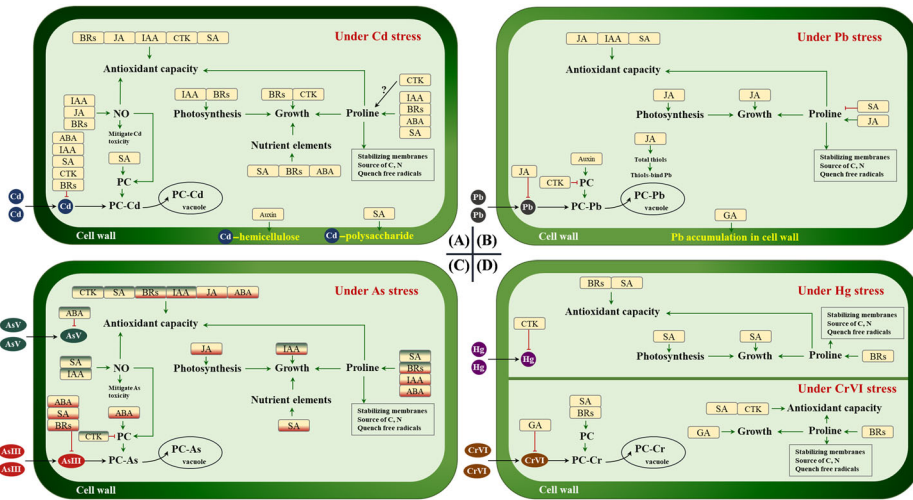
Figure 3. Strategies of different phytohormones in alleviating metal(loid) toxicity in plants. Effects of phytohormones on plants under Cd stress (A), Pb stress (B), As stress, with hormones of green color for AsV stress and red color for AsIII stress (C), and Hg and CrVI stress (D). Green arrows indicate positive regulation, and *T* bars denote negative regulation. Abbreviations: IAA: indole-3-acetic acid; CTK: cytokinin; GA: gibberellin; BRs: brassinosteroids; ABA: abscisic acid; JA: jasmonic acid; SA: salicylic acid; PC: phytochelatin.

because auxin is a key phytohormone in controlling lateral root formation (Betti et al., 2021). Under metal(loid)-stress, auxin biosynthesis gene expression in the leaves and transportation gene expression in lateral roots are lower (Fattorini et al., 2017), leading to lower auxin levels in the lateral roots. For example, Cd reduces the auxin levels in the roots by repressing the expression of auxin efflux genes *PIN1*, *PIN3*, and *PIN7* in *A. thaliana*, thereby inhibiting root meristem growth (Yuan & Huang, 2016). Similar findings reveal alteration in the expression of *BjPIN5* and *BjPIN3* in leaves and roots of *Brassica Juncea* under As stress (Praveen et al., 2019).

Furthermore, auxin regulates lateral root formation by working with jasmonate. For example, the application of jasmonate increases the lateral roots, suggesting that jasmonate may counteract As/Cd effects, specifically on lateral roots (Ronzan et al., 2019). The interactions between jasmonate and auxin signaling pathways activate root steam cells to promote plant root growth (Betti et al., 2021). The MYB gene family consists of a vast and diverse class of proteins, which involve from cell cycle and morphogenesis to stress signaling regulations. Auxin-salicylic acid crosstalk under metal(loid)-stress is regulated by the signaling network of the *OsMYB-R1* transcription factor. Tolerance to Cr stress in rice plants is observed in *OsMYB-R1*-overexpressing lines, which manifests by a significant increase in lateral root and higher auxin accumulation (Tiwari et al., 2020). However, the auxin signaling routes mostly appear to function as a downstream component to those phytohormones in plants (Mathur et al., 2022).

Besides salicylic acid, other phytohormones play a role in controlling the auxin levels under metal(loid)-stress. Among phytohormones, brassinosteroids, cytokinin, gibberellic acid, and salicylic acid can increase the auxin level in plants under metal(loid)-stress. In this case, a decrease in cytokinin levels lowers the auxin levels in plants (Mohan et al., 2016; Ronzan et al., 2018). This is because cytokinin induces the expression of auxin biosynthesis genes to enhance its production, thereby catalyzing the conversion of indole pyruvic acid to auxin in plants (Di et al., 2016; Zhou et al., 2011).

In addition, the interactions of auxin and cytokinin/salicylic acid regulate the root development in plants (Tiwari et al., 2020). For example, in the roots, auxin induces meristematic cell division, whereas cytokinin promotes cells to switch from the meristematic to differentiated state by inhibiting auxin signal (Su et al., 2011). In addition, application of brassinosteroids on radish seedlings increases its auxin contents under CrVI stress, while application of salicylic acid on

wheat increases its auxin contents under Cd stress (Choudhary et al., 2012; Shakirova et al., 2016; Table 1). Transport of polar auxin by multiple hormonal pathways has been reviewed by Semeradova et al. (2020). However, the interrelations among auxin and other phytohormones under metal(loid)-stress remain unanswered, which needs further investigations.

4.2. Brassinosteroid enhances antioxidant system under metal(loid)-stress

Under metal(loid)-stress, apart from direct toxicity, excess production of reactive oxygen species (ROS) causes oxidative stress in plants (Sytar et al., 2019). In this case, their antioxidant system is important for plants to cope with oxidative stress by decreasing ROS accumulation and lipid peroxidation (Table 1), which has also been demonstrated by proteomic analysis (Ovečka & Takáč, 2014). In plants, there are several important enzymatic antioxidants, including superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and glutathione peroxidase (GPX) (Sharma et al., 2016). Among these antioxidants, SOD catalyzes the dismutation of free radicals O_2^- into H_2O_2, with CAT and APX converting H_2O_2 into H_2O. While GR mediates conversion of oxidized glutathione (GSSG) to reduced glutathione (GSH), GPX mediates conversion of H_2O_2 to H_2O using GSH as a reductant. Besides enzymatic antioxidants, non-enzymatic antioxidants include GSH and ascorbate. While GSH regulates redox potential for amino acids and proteins by scavenging oxidative damage, water-soluble ascorbate acts as a substrate for ascorbate peroxidase, donating electrons to ROS.

Under metal(loid)-stress, brassinosteroid-induced higher activities of antioxidant enzymes help to cope with oxidative stress in plants (Table 1; Guedes et al., 2021). The capacity of brassinosteroid to boost the antioxidant defense system of plants has been used to tolerate multiple abiotic stress, including metal(loid)s (Table 1; Jan et al., 2018; Sharma et al., 2016). For example, under $100\,\mu M$ CrVI, $0.01\,\mu M$ brassinosteroid enhances rice tolerance by increasing its SOD, POD, CAT, and APX activities (Table 1; Basit et al., 2022). Further, application of $5\,\mu M$ brassinosteroid decreases its lipid peroxidation by increasing the SOD, CAT, and GR activity under $1\,mM$ Cd stress in bean plants (Table 1; Rady, 2011).

Brassinosteroid-mediated higher activities of antioxidant enzymes are mainly due to activation of their gene expression (Sharma et al., 2016). For example, $0.01-1\,\mu M$ brassinosteroid increases the gene expression of SOD, CAT, APX, and GR in rice under $0.5\,mM$ Cr stress (Table 1; Sharma et al., 2016). Since the external application of brassinosteroid induces transient apoplastic H_2O_2 formation, which upregulates stress-proteins and defensive enzymes to counter metal(loid)-stress in plants (Kour et al., 2021). For example, under $0.15-1.5\,mM$ Cu stress in tomato, application of $0.01\,\mu M$ brassinosteroid and/or $0.1\,mM$ H_2O_2 increases its ROS-scavenging enzyme activities, including SOD, POD, and CAT (Nazir et al., 2021). In addition, nitrate reductase reverses the positive effects of brassinosteroid by its reducing nitrous oxide content, suggesting nitrate reductase is a potential contributor of brassinosteroid-induced generation of nitrous oxide. This has been shown in the tolerance of pepper plants to Cd stress by accelerating its antioxidant enzymes (Kaya et al., 2020).

4.3. Salicylic acid promotes cell wall synthesis and nutrient uptake in plants

The cell wall is the first barrier for metals to enter plants, which plays a key role in metal detoxification in plants (Figure 1; Parrotta et al., 2015). Cell wall composition affects metal uptake by plants. For example, the binding of pectin, a component of cell wall, to metals can reduce their entrance to plants due to their negative charges (B. Guo et al., 2019; Hossain et al., 2006). To bind metals, pectin methylesterase needs to catalyze pectin demethylation, making free carboxyl groups to bind metals such as Pb in plants (Krzesłowska et al., 2016; Sheshukova et al., 2017).

Similarly, Hg and Pb can bind to low-methyl-esterificated pectin in the cell wall (Figure 1; Carrasco-Gil et al., 2011; Krzesłowska et al., 2016).

In addition, it is important to decrease metals from crossing the cell walls into the cytoplasm. As a kind of glucan, callose accumulation in cell wall prevents metals from penetrating into the cells, thus reducing the metal content in plants (O'Lexy et al., 2018). Further, plants can thicken cell walls through the accumulation of cellulose, hemicelluloses, and lignin to bind metals via complexing (Kovac et al., 2018). Phytohormones can influence the composition of cell wall, thus changing metal deposition on cell wall. Recently, the beneficial roles of salicylic acid in enhancing Cd tolerance have been reported in plants. For example, 100 μM salicylic acid enhances the synthesis of cell wall in tomato roots, thereby decreasing its Cd accumulation in the plant (Table 1; Jia et al., 2021). Similarly, Xu et al. (2015) found that 100 μM salicylic acid increased its Cd accumulation in peanut cell walls under 200 μM Cd stress (Table 1).

The hemicellulose and pectin in the cell wall are major components for Cd deposition due to their negative charges (Zhu et al., 2012). Using energy-dispersive X-ray microanalysis, Cd binding to plant cell walls is directly visualized (Wojcik et al., 2005). Salicylic acid application alters the lignin and hemicellulose composition of cell wall in *Brachypodium distachyon* by increasing its ferulic and p-coumaric acid content (Napoleão et al., 2017), because both ferulic and p-coumaric acid can cross-link with hemicellulose and lignin, reinforcing cell walls against digestibility (Buanafina, 2009; Jung et al., 2012). In addition, ferulic and p-coumaric acids also play a crucial role in mitigating As-induced oxidative stress in plants (Zulfiqar & Ashraf, 2022).

Besides cell walls, glutathione is important in protecting plants against Cd-induced oxidative stress, which is a component of phytochelatin involved in Cd chelation (Figure 1; Szalai et al., 2009). Salicylic acid (SA) is linked to glutathione biosynthesis. For example, the glutathione content is lower in Cd-stressed leaves in SA-mutant than in wild-type in *A. thaliana* (Guo et al., 2016). Furthermore, SA application increases its glutathione content in peppermint under Cd stress (Table 1; Ahmad et al., 2018). The SA-induced glutathione increase under Cd stress can be explained by (1) increased transcription in serine acetyltransferase, the precursor gene to catalyze cysteine formation (Freeman et al., 2005), (2) enhanced S uptake, a key element for GSH synthesis (Guo et al., 2016), and (3) increased activities of glutathione synthetase and glutathione reductase to maintain GSH in the reduced state (Guo et al., 2016). To further alleviate Cd stress, plants can sequester PC-Cd complexes into the vacuoles through ATP-binding cassette (ABC) transporters (Bovet et al., 2005). An ABC transporter from soybean is identified under salicylic acid induction (Eichhorn et al., 2006). However, whether ABC transporters are involved in SA-induced Cd tolerance needs further study.

Nutrients are necessary for plant growth, but their contents in plants are influenced by metals (X. H. Li et al., 2016). For example, Cd disrupts the C, N, and S metabolism in plants, which causes nutrient deficiency, including Zn, Ca, Mg, Mn, P, K, and Fe (Kupper & Kochian, 2010). Fortunately, SA can help to increase the nutrient content in plants under metal(loid)-stress (Table 1). For example, 100 μM SA increases the Fe, Ca, and Mg content in soybean under 53 μM Cd (Table 1; Drazic & Mihailovic, 2005), and 10 μM SA enhances the efficiency of nitrogen fixation and assimilation in chickpea plants under 223–893 μM Cd stress (Table 1; Hayat et al., 2014). This is because salicylic acid can alter the plasma membrane properties to increase the activity of H^+-ATPase, thereby facilitating plant nutrient assimilation under Cd stress (Gordon et al., 2004; B. Guo et al., 2019).

4.4. Abscisic acid decreases metal accumulation in plants

Several phytohormones, including auxin, brassinosteroids, gibberellin, jasmonic acid, abscisic acid (ABA), and cytokinin, can decrease plant metal uptake to alleviate its toxicity (Table 1; Figure 3). Among them, ABA is the most effective (Saha et al., 2021; Vishwakarma et al., 2017). Abscisic

acid is effective in decreasing the Cd accumulation in plants (Fan et al., 2014; Shen et al., 2017). For example, ABA decreases the Cd accumulation in rice shoots by regulating its stomatal closure to lower its transpiration rate (Figure 1; Hauser et al., 2017; Uraguchi et al., 2009). Further, application of ABA reduces its transpiration rate and Cd content in rice (Table 1; Hsu & Kao, 2003). However, application of ABA biosynthesis inhibitor, fluridone, reduces ABA accumulation, thereby increasing the transpiration rate and Cd content in rice (Hsu & Kao, 2003). Abscisic acid decreases its Cd translocation to the shoots by regulating its transpiration rate in rice (Hsu & Kao, 2005).

At the molecular level, Fan et al. (2014) reported that decreased Cd accumulation in ABA treatment correlates with the down-regulation of ABA-inhibited expression of iron-regulated transporter 1 (*IRT1*) in the roots of *A. thaliana* (Table 1), which is critical for Cd uptake in plants (Kobayashi & Nishizawa, 2012; Vert et al., 2002). However, Cd uptake in an *IRT1*-mutant fails to respond to ABA application, suggesting the important role of ABA in controlling Cd uptake in *A. thaliana* (Fan et al., 2014). Besides, the basic region/leucine zipper transcription factor abscisic acid-insensitive5 (*ABI5*) is involved in Cd accumulation. This is because its overexpression reduces whereas *ABI5* mutant increases the Cd accumulation in *A. thaliana* (Zhang et al., 2019).

5. Limitations and future research

An increased understanding of the functions of phytohormones in promoting plant growth and alleviating its metal(loid) stress is a key to increase crop yield and enhance food safety. In this review, we summarized the interactions of phytohormones and metal(loid)s in plants. Most studies focus on basic parameters, such as plant growth and antioxidant enzymes. Further studies should focus on the molecular mechanisms involved in phytohormone-mediated metal(loid) uptake, and the complex metal(loid) signaling network in plants also needs further study. Further, it is important to study the functions of multiple-hormones simultaneously in reducing metal(loid)-stress in plants. Our knowledge on the mechanisms of hormone-mediated regulation of photosynthesis and plant growth is still fragmentary, which needs more in-depth research. Efforts are also needed to investigate the effects of phytohormones-induced plant hormesis under metal(loid)-stress. The effective contents of phytohormones for different plants need to be determined, which helps to develop cost-effective and environment-friendly crop management system.

The relationship between phytohormones/signaling molecules and abiotic stress has been widely reported, while those under metal(loid)-stress are still scarce and need more research. It is important to investigate the interactions among phytohormones, signaling-molecules and metal(loid)s, and their functions in metal(loid)-stressed plants. This may help to decrease the metal(loid) content in plants and improve plant growth. However, phytohormones and signaling-molecule system are complicated, so attention should be paid to phytohormone analysis together with other physiological and biochemical parameters. The advanced genome editing tools have been widely used during the last decade, which may help to better understand phytohormone-regulated metabolisms in plants under metal(loid)-stress.

Disclosure statement

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