




# Phytohormone Priming: Regulator for Heavy Metal Stress in Plants

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## Abstract

Phytohormones act as chemical messengers and, under a complex regulation, allow plants to sustain biotic and abiotic stresses. Thus, phytohormones are known for their regulatory role in plant growth and development. Heavy metals (HMs) play an important role in metabolism and have roles in plant growth and development as micronutrients. However, at a level above threshold, these HMs act as contaminants and pose a worldwide environmental threat. Thus, finding eco-friendly and economical deliverables to tackle this problem is a priority. In addition to physicochemical methods, exogenous application of phytohormones, i.e., auxins, cytokinins, and gibberellins, can positively influence the regulation of the ascorbate–glutathione cycle, transpiration rate, cell division, and the activities of nitrogen metabolism and assimilation, which improve plant growth activity. Brassinosteroids, ethylene and salicylic acid have been reported to enhance the level of the anti-oxidant system, decrease levels of ROS, lipid peroxidation and improve photosynthesis in plants, when applied exogenously under a HM effect. There is a crosstalk between phytohormones which is activated upon exogenous application. Research suggests that plants are primed by phytohormones for stress tolerance. Chemical priming has provided good results in plant physiology and stress adaptation, and phytohormone priming is underway. We have reviewed promising phytohormones, which can potentially confer enhanced tolerance when used exogenously. Exogenous application of phytohormones may increase plant performance under HM stress and can be used for agro-ecological benefits under environmental conditions with high HMs level.

**Keywords** Strigolactones · Priming · Phytohormones · Toxicity · HMs · Phytoremediation · Phytoextraction

## Introduction

In terms of the degree of danger to the human population across the globe, heavy metals (HMs) are thought to be in second place among pollutants. In the last few decades, HMs have pulled ahead of pesticides and well-known pollutants such as carbon dioxide and sulfur dioxide (Chen et al. 2007). It is predicted that HMs may become the most dangerous contaminant, possibly surpassing solid and nuclear waste (Lajayer et al. 2017). It has been reported that 70% of all HMs and their compounds routed in the human body came from food (Jaishankar et al. 2014). HMs are released into the atmosphere, soil, and water from a variety of sources and from anthropogenic activities (Tchounwou et al. 2012). Later, they are introduced into the food chain, and thus metal toxicity raises the risk and poses concerns for humans and animals. As this review is devoted to the role of phytohormones under HMs contamination in plants, it should be noted that some trace metals are necessary for plant growth and metabolism, but within reasonable limits. HMs in high

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doses are considered to be harmful for plants (Kumar et al. 2016). Apart from the direct impact of bioactive metals on plants, cell toxicity also occurs by excess production of reactive oxygen species (ROS), which inhibit anti-oxidants and causes oxidative stress (Nanda and Agrawal 2016; Rui et al. 2016). Plants are well adapted, but the resistance depends on the capacity to prevent oxidative stress and tight regulation of anti-oxidant systems, under HMs stress (Syta et al. 2013; Choudhury et al. 2017; Lajayer et al. 2017). In plants, the permeability of the cell membrane, the synthesis of many biochemical compounds, growth and reproduction are negatively affected by HMs (Munzuroglu and Geckil 2002), thus affecting food quality and yield. This results in lowering of the plant's maximum genetic potential in terms of growth, development and other related activities (Bücker-Neto et al. 2017).

In recent years, much attention has been given to developing strategies to alleviate HM toxicity in crops and agricultural systems, to fulfil the global food demand. Physicochemical techniques employed for the clean-up of contaminated sites include excavation, stabilization or in situ fixation (i.e., by adding chemicals to change the metal structure so that it does not get absorbed by plants), and washing of soil (physicochemical extraction) (Bradl and Xenidis 2005). However, these physicochemical processes are not cost-effective or efficient (Schnoor 1997). Therefore, the search for eco-friendly, cost-effective and reproducible solutions for the remediation of HM contaminated soils must be a priority.

Environmental and biological scientists work in synergy to develop alternatives and potential strategies to combat adverse effects of HM pollution. Agricultural soils contaminated with HMs pose serious environmental issues. The application of exogenous phytohormones to modulate the biochemical and molecular mechanisms so that plants become equipped to restore land contaminated by pollutants is a promising technique. Thus, the purpose of this review is to summarize the current understanding of the regulation of HM stress through phytohormone priming and its future promise.

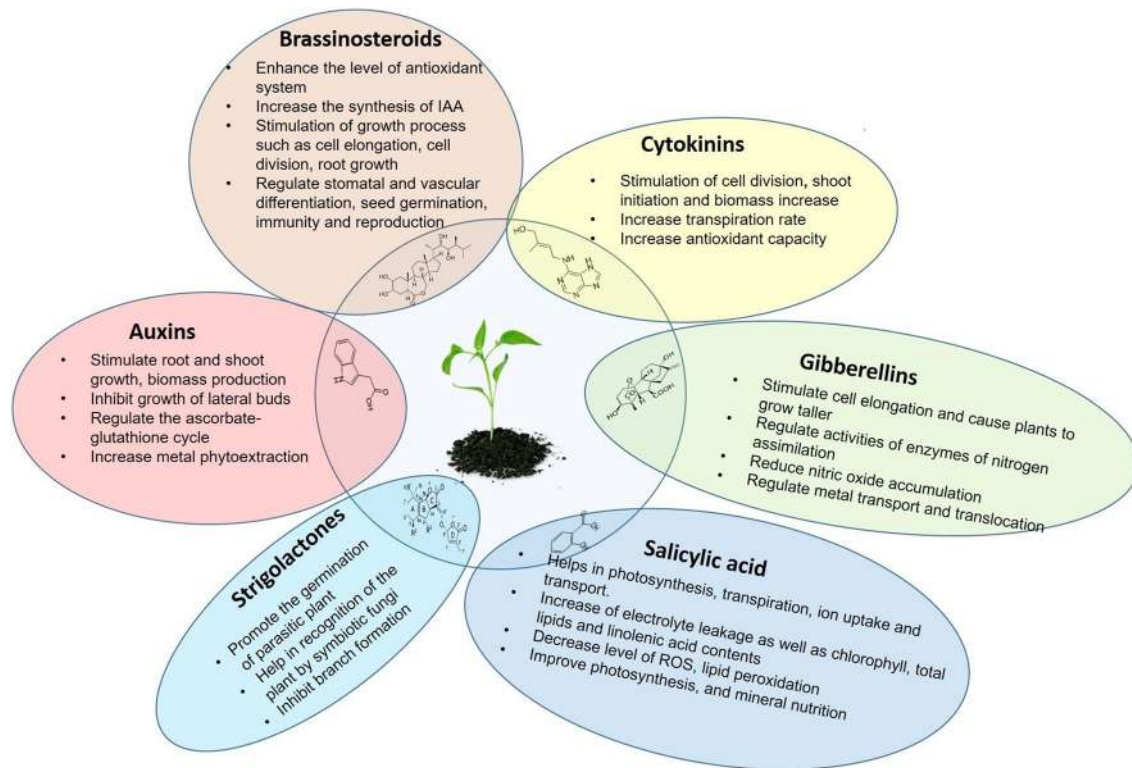
## Phytohormones and Their Significance for Plants

Phytohormones are small signaling compounds, which act to some degree on virtually every aspect of plant growth and development. The mechanism of the action for different hormones for different processes can be very different. Thus, it has been observed that a single hormone can regulate a diverse array of cellular and developmental processes, whereas, at the same time, multiple hormones may be involved in the regulation of a single process (Gray

2004). Phytohormones such as indole-3-acetic acid or auxin (IAA), cytokinin (CK), ethylene (ET), abscisic acid (ABA), gibberellin (GA), brassinosteroid (BR), salicylic acid (SA), jasmonic acid (JA) and the recently identified strigolactone (SL) are phytohormones that are crucial for the growth and development of plants and also in signaling and crosstalk (Fig. 1). Phytohormones support and manage plants against biotic and abiotic stresses (Bücker-Neto et al. 2017; Nishiyama et al. 2011; Colebrook et al. 2014; Xu et al. 2016). Phytohormones as regulators of HM absorption have been used in agronomical crop management practices to alleviate metal toxicity (Piotrowska-Niczyporuk et al. 2012). It has been found that exogenous application of phytohormones is safe to use and gives promising results for plants under HM toxicity (Zhu et al. 2012, 2013; Agami and Mohamed 2013; Masood et al. 2016). Phytohormones such as CKs, IAAs, BRs, GAs and SA, and so on, have significant roles in signaling, and in biochemical and defence pathways, but the mechanism of providing relief from HM stress is nowadays a topic of global interest (Bücker-Neto et al. 2017). Therefore, phytohormone priming is carried out with the aim of enhancing future research for the management of crop stress.

## Behavior of Phytohormones During HM Stress Response

Phytohormones are the most important endogenous molecules for modifying physiological and molecular reactions, and are critically required by the plant for its survival under HM stress (Fahad et al. 2015). Phytohormones in very low concentrations regulate cell membrane permeability, enzyme activity and secondary metabolites, growth, and reproduction (Wani et al. 2016). HM toxicity in plants is manifested as the retardation of plant growth and development, which results because of its accumulation in the aboveground and underground organs of a plant. As a rule, a heavy dose of HMs leads to a decrease in the root and shoot biomass in many plant species, which is normally regulated by phytohormones. Several HMs in high concentrations have been shown to cause a delay in seed germination. Cadmium (Cd), copper (Cu), lead (Pb), and nickel (Ni) are considered highly toxic for the plant germination process, and seeds may vary in their stress response to different HMs (Wang et al. 2011; Sethy and Ghosh 2013). Ni modulated the enzymatic activity of amylase, ribonuclease and protease enzymes, thus reducing seed germination and growth activity (Ahmad and Ashraf 2011). The oxidizing ability of roots, the activity of peroxidases and polyphenol oxidases, the activity of enzymes of carbohydrate metabolism— $\alpha$ -amylases,  $\beta$ -amylases, acid phosphatases and acid invertases—were severely inhibited under Pb exposure (Singh et al. 2011). Protein oxidative damage was due to oxidative stress under



**Fig. 1** Important roles of six important phytohormones in plants

Cu stress and catalase activity was also observed to be decreased (Pena et al. 2011). Cd toxicity stimulates the expression of the glutathione peroxidase enzyme and glutathione reductase activity (Smiri et al. 2011). The reaction of plants to HM stress depends on the concentration and kind of HMs and on complex interactions with other stresses. The effect of phytohormones on HM stress has been evaluated on model plants or plants having the potential for phytoextraction (Bulak et al. 2014).

## Phytohormones and HM Toxicity

ABA is designated as an essential phytohormone having a role in abiotic stresses. In response to environmental stresses, a rapid increase in endogenous ABA levels has been observed, which activates the specific signaling pathways and modulates gene expression levels in the plant (Brien and Benkova 2013). Exposure to HMs such as cadmium (Cd), mercury (Hg), copper (Cu), arsenic (As) and so on induces expression of ABA biosynthetic genes and in turn increases the endogenous levels of ABA (Hollenbach et al. 1997; Bucker-Neto et al. 2017). ABA transcriptionally regulates up to 10% of protein-encoding genes (Nemhauser et al. 2006; Wani et al. 2016). The mechanism behind the role of induced ABA in response to HMs needs to be explored.

Promising results have been observed by the utilization of ABA-deficient and ABA-insensitive mutants towards Cd sensitivity and have shown that Cd-induced growth inhibition is not a result of ABA signaling, but instead the increased ABA level upon HM stress might be regulating stomata closure to regulate water balance in plants (Sharma and Kumar 2002). How exogenous application of ABA can regulate the HM response is still an area to be explored. ABA might act as a trade-off between plant responses to the stress induced by HMs, thereby triggering a balance between survival and growth.

IAA is one of the most multi-functional phytohormones and is responsible not only for the development of plants under normal conditions but also for plant growth under stress conditions (Kazan 2013). IAA plays a basic role in the adaptation of plants under salt stress, and is noted to increase under salt or HMs stresses. The elevated IAA level has been connected with growth reduction, which can be a result of changed hormonal balance under stress conditions (Fahad et al. 2015). The hormone interaction and miRNAs expression in the regulation of HM (As) response has been suggested under exogenous supply of IAA. It was shown to improve growth of plants under HM (As) stress (Srivastava et al. 2013). IAA, ROS, and ET crosstalk and cooperate during the signaling pathway with alteration in the root system of plants (Camacho-Cristóbal et al. 2015). It has been

reported that PINFORMED1 (PIN1) protein participates in IAA distribution under conditions of HM stress. For example, under boron (B) starvation, IAA distribution is altered, which leads to lower regulation of the PIN1 protein and limitation of root elongation (Li et al. 2015).

The anti-oxidative system of plants involves glutathione reductase (GR), glutathione sulfotransferase (GST), superoxide (SOD), ascorbate peroxidase (APX), catalase (CAT) and peroxidase (POD) enzymes. These enzymes take part in stress response and can be regulated by BRs under different environmental stresses (Cao et al. 2005). Seventy BRs have been identified among plant steroids, which are able to coordinate phytomorphogenesis, germination of seeds, cell division and elongation, flowering, vascular differentiation, formation of stomata, male fertility, and plant senescence (Mandava 1988; Vardhini 2014). Endogenous BRs are present in roots, leaves, shoots, vascular cambium, flower buds, fruits, pollen, seeds (Bajguz and Hayat 2009) and can be responsible for the support of plant growth under HM stress. 24-Epibrassinolide (EBL) is an important plant growth hormone that has the potential to reduce HMs (Shahzad et al. 2018).

The GAs are a broad class of tetracyclic diterpenoid carboxylic acid compounds, but just one form of GAs, GA<sub>1</sub>, is able to function as a growth hormone in higher plants (Sponsel and Hedden 2004). The GAs positively affect seed germination, stem elongation, leaf expansion, flower and trichome initiation and the development of fruits (Yamaguchi 2008). GAs support the development of plant adaptation and resistance to various abiotic stresses and have protective effects on the toxicity of HMs (Maggio et al. 2010). GAs may act occasionally in the paracrine signaling pathway, but there is still a mystery regarding the exact mechanism of GAs movement/transport in plants (Gupta and Chakrabarty 2013). He et al. (2012) reported the role of GAs in increasing stress tolerance in wheat by enhancing the expression of the TaMYB73 gene. DELLA proteins, which are well-known repressors of GA responses, have recently been shown to be involved in stress avoidance (Wild and Achard 2013). A low concentration of HM (Zn) is able to increase the content of GA<sub>3</sub>, whereas higher concentrations decrease the GA<sub>3</sub> level (Atici et al. 2005).

Other growth plant hormones, CKs, play a regulatory role in modulating plant development and their endogenous concentration under stress conditions can be altered, which indicates the involvement of CKs in stress tolerance (Brien and Benkova 2013). HM stress decreases CK production and transport from roots. CKs during HM stress participate intensively in interactions with other hormones (Ha et al. 2012). CKs are often antagonists of ABA (Pospíšilová 2003a) and changes in the levels of both plant hormones under HM stress can be dependent on each other as a result of their crosstalk.

A naturally occurring phenolic compound, SA, is linked to the defence response of plants under HM stress. SA participates in the coordination of plant growth and development, ripening, and responses to abiotic stresses (Rivas-San and Plasencia 2011). SA together with ABA is implicated in the regulation of drought response (Miura and Tada 2014). Plant resistance to salinity, heat, and cell death under various hypersensitive stresses can also be regulated by the presence of SA (Fahad and Bano 2012; Khanna et al. 2016). Cd exposure increases free SA content of barley (*Hordeum vulgare*) roots and it has been observed that SA can alleviate Cd toxicity by influencing mechanisms of Cd detoxification, other than the activation of the anti-oxidant defence system (Metwally et al. 2003).

SA often acts in combination with other phytohormones such as JA and ET (Jia et al. 2013). The biosynthesis of hormones and their transport and accumulation generate a cascade of signaling pathways, which are part of the plant stress response (Matilla-Vazquez and Matilla 2014). The activity of ET biosynthetic enzymes increases and, under HM exposure, MAPKs phosphorylate ACS2 and ACS6 (Skottke et al. 2011; Bucker-Neto et al. 2017).

It has been observed that ET, ethane, ethanol, and acetaldehyde production has been increased under HM stress (Gora and Clijsters 1989). Photosynthetic processes regulated by ET depend on the plant's sensitivity to ET (Iqbal et al. 2012). It was reported that increasing 1-aminocyclopropane carboxylic acid (ACC) synthase (ACS) activity stimulates ET synthesis under the effects of HMs such as Cd and Cu (Pell et al. 1997). At comparably low concentrations of HMs, ET production was enhanced, but under the application of higher concentrations of HMs, this effect progressively disappeared (Gora and Clijsters 1989).

S-Adenosylmethionine synthetase participates in the ET synthesis stage from methionine to S-adenosylmethionine. S-Adenosylmethionine is a capable substrate for synthesis of 1-aminocyclopropane-1-carboxylic acid by 1-aminocyclopropane-1-carboxylic acid synthase. Induction of expression ACS genes in potatoes has been observed under a Cu effect. ACS transcript accumulation under Cu exposure has been found for different varieties of tobacco (Schlagnhauser et al. 1997). Under chromium (Cr) signaling, the expression of four ET biosynthesis-related genes (ACO4, ACO5, ACS1 and ACS2) confirms the ET participation in rice seedlings (Trinh et al. 2014).



## Exogenous Application of Hormones in the Adaptation of Plants Under HMs Stress

The study in the area of exogenous application of phytohormones in plant responses under HMs stress effects is in a naïve form, which is due to its high potential in plant tolerance mechanisms, being eco-friendly and cost effective. Recent studies have shown how plant hormones can regulate and integrate growth responses to various environmental cues to sustain plant development and growth (Bücker-Neto et al. 2017). The exogenous application of phytohormones has been observed to alleviate the toxic impact of HMs (Table 1). The plant responses to CKs have been evaluated mostly by exogenous application, and external stress also enhances their endogenous levels via uptake and enhanced biosynthesis of proteins and some secondary metabolites (Pospíšilová 2003b).

Under HMs, exogenous phytohormones stimulated the increase of soluble phenolics and free proline contents in wheat seedlings (Ergün and Öncel 2012). The ABA and GA<sub>3</sub> hormones in interaction with Pb and Zn may cause an increase in total phenolic content, but hormones in interaction with Cd prevent an increase in phenolic compounds (Fuhrer 1982; Ahmad et al. 2015). The effect of HMs alone or in combination with phytohormones have completely different influences on plants, depending on the type of plant, its development stage, HM concentration and the duration of treatment. Therefore, prolonged Pb treatment together with GA<sub>3</sub> influenced the soluble protein content in a positive manner (Nuray and Işıl 2012).

IAA at low and high concentrations was observed to influence Cd toxicity differently, which was dependent on the regulation of the ascorbate–glutathione cycle and other anti-oxidant activities (Bashri and Prasad 2015). IAA increased Cd, Pb and Zn phytoextraction and stimulated root and shoot growth (Fässler et al. 2010; Hadi et al. 2010). Exogenous application of IAA, GA<sub>3</sub>, and citric acid increased plant biomass (Aderholt et al. 2017). Application of GAs regulated enzymatic activities in nitrogen assimilation with further reduction of nitric oxide accumulation (Gangwar et al. 2011; Zhu et al. 2012). GAs inhibited iron (Fe) translocation by suppressing OsYSL2 gene expression in addition to regulation of Fe transport and translocation (Wang et al. 2017).

An increase in the biomass production via stimulation of cell division, anti-oxidant capacity and shoot initiation has been observed after exogenous application of CKs (Tassi et al. 2008). CK application was able to increase the transpiration rate which can affect the photosynthesis process and stimulate an increase in plant biomass (Cas-sina et al. 2011; Piotrowska-Niczyporuk et al. 2012).

*Arabidopsis* as a plant model has been investigated for interactions between BRs and stress signaling to understand the correlation between plant growth and signaling pathways under stress. It was established that exogenous application of BRs represses microbe-associated molecular patterns with further activation of the general stress response, but enhances the wound-triggered general stress response (Bjornson et al. 2016). Under exogenous BRs, there is enhancement in the anti-oxidant machinery (catalase, peroxidase, superoxide dismutase and glutathione reductase enzymes) together with a decrease in ROS, malonaldehyde (MDA) and carbonyl levels (Rady 2011; Ramakrishna and Rao 2012). BRs also stimulate the synthesis of IAA which helped in the stimulation of growth processes (Choudhary et al. 2011).

Salicylic acid was also observed to decrease the level of ROS, and lipid peroxidation, whereas it increased the electrolyte leakage, chlorophyll content, total lipids, and linolenic acid contents (Shi and Zhu 2008; Belkhadi et al. 2010; Kazemi et al. 2010). This helps in the increase in improved photosynthesis, and mineral nutrition (Xu et al. 2015a, b). Capability of plants to HM stress on the physiological responses level is significant in cases of plant productivity (Bücker-Neto et al. 2017). Literature analysis had shown that IAAs, CKs, and GAs positively affect the level of metal accumulation and improve plant growth and tolerance to the stress (Bulak et al. 2014). Exogenously applied MeJA to Cd-stressed *O. sativa* showed modulation in the activity of CAT, SOD and GR along with glutathione pools (Per et al. 2018; Singh and Shah 2014). In *Kandelia obovate*, exogenous application of MeJA also maintained endogenous levels of JA and controlled stomatal aperture, reduced the transpiration rate and inhibited Cd uptake and reduced photosynthetic damage (Chen et al. 2014; Per et al. 2018). Additionally, the expression was enhanced in Cd-treated plants, whereas exogenously applied MeJA significantly restored the expression of the type-2 metallothionein gene (KoMT2) in leaves (Chen et al. 2014).

The concentrations of exogenous phytohormones turn out to be significant in plant growth regulation and reactions to environmental condition changes (Song et al. 2014; Piotrowska-Niczyporuk and Bajguz 2014). A significant difference in the plant growth effects of natural and synthetic auxins was not observed, but dose-dependent changes have been observed (Piotrowska-Niczyporuk and Bajguz 2014).

Plant growth and development is dependent upon photosynthetic activity (Xu et al. 2015a, b), and the correlation between phytohormones and photosynthetic processes under HM stress conditions has been studied (Gururani et al. 2015). Under HM stress, the capacity of energy trapping by PSII reaction centers is increased by IAAs (Ouzounidou and Ilias 2005). BRs supported increased chlorophyll accumulation together with higher  $P_N$  and stomatal conductivity

**Table 1** Cataloguing of phytohormones, their effect on adaptive response of different plants under different HMs

Plants	Part of plant	HM	Adaptive reaction of plants	References
<b>Brassinosteroids</b>				
Mustard ( <i>Brassica juncea</i> )	7-day-old seedlings	Cu	Improvement in shoot emergence, blocked Cu metal uptake and accumulation in plants	Sharma and Bhardwaj (2007)
Radish ( <i>Raphanus raphanistrum</i> subsp. <i>sativus</i> )	Whole plant at harvest stage	Cu	Decreasing Cu toxicity	Choudhary et al. (2010)
Mustard ( <i>Brassica juncea</i> )	Leaves of 40 DAS plants	Ni	Activation of the root and shoot growth Decreasing Ni toxicity Stimulation of plant growth	Alam et al. (2007)
			Activation of net photosynthetic rate Increase in chlorophyll content, nitrate reductase and carbonic anhydrase activities	
			Increase activity of catalase, peroxidase, superoxide dismutase and glutathione reductase	
Rapeseed ( <i>Brassica napus</i> )	Cotyledons of 14-day-old seedlings	Cd	Decreasing Cd toxicity Damage of photochemical reaction centers Support of efficient photosynthetic electron transport	Janezko et al. (2005)
Radish ( <i>Raphanus raphanistrum</i> subsp. <i>sativus</i> )	Leaves	Cd	Stimulation of photosynthetic activity	Anuradha and Rao (2009)
Bean ( <i>Phaseolus vulgaris</i> L.)	Leaves, roots of plants 30 DAS	Cd	Increase activity of catalase, peroxidase, superoxide dismutase and glutathione reductase	Rady (2011)
Chickpea ( <i>Cicer arietinum</i> )	Leaves of plants during 60 DAS	Cd	Enhanced the level of anti-oxidant system, protects the photosynthetic machinery and the plant growth	Hasan et al. (2008)
Radish ( <i>Raphanus raphanistrum</i> subsp. <i>sativus</i> )	7-day-old seedlings	Zn	Alleviation of oxidative stress via induced lowering of ROS levels, MDA and carbonyl levels	Ramakrishna and Rao (2012)
<i>Chlorella vulgaris</i>	Algal cells	Zn	Blocking the HMs accumulation in the cells	Bajguz (2000)
Mungbean ( <i>Vigna radiata</i> L. Wilczek)	Leaves and roots of 14-day-old seedlings	Al	Increase activity of catalase, peroxidase, superoxide dismutase and glutathione reductase	Ali et al. (2008a, b)
Radish ( <i>Raphanus raphanistrum</i> subsp. <i>sativus</i> )	7-day-old seedlings	Cr	Enhancing the IAA synthesis Support of plant growth	Choudhary et al. (2011)
<i>Pisum sativum</i> L.	Leaves, stems, roots of 40-day-old plants	Cd	Modulation of negative Cd effect via stabilization of photosynthetic efficiency, photochemical quenching, leaf relative water content and gas exchange parameters Maintained anti-oxidant levels Activation of glyoxalase I (GlyI) accumulation	Jan et al. (2018)

Table 1 (continued)

Plants	Part of plant	HM	Adaptive reaction of plants	References
Mustard ( <i>Brassica juncea</i> L.)	Leaves of 10-day-old seedlings	Pb	Co-application of 24-epibrassinolide and salicylic acid improving growth, contents of pigment of metal-stressed plants	Kohli et al. (2018a)
Mustard ( <i>Brassica juncea</i> L.)	Leaves, shoot and root of 30, 60, and 90 days after sowing	Pb	Glutathione, ascorbic acid, and tocopherol contents were significantly enhanced	Kohli et al. (2017)
Mustard ( <i>Brassica juncea</i> L.)	Roots and shoots of 7-day-old seedlings	Cu	Co-application of 24-epibrassinolide and salicylic acid improving growth, contents of pigment of metal-stressed plants Enhanced levels of phenolic compounds Exogenous application of castasterone improved anti-oxidative defense system by modulating the ascorbate–glutathione cycle and amino acid metabolism	Yadav et al. (2018)
Mustard ( <i>Brassica juncea</i> L.)	Leaves of plants 30 days after sowing	Cd	Increasing the contents of secondary plant pigments (flavonoids and anthocyanins) and proline Enhanced phytoene synthase and chalcone synthase genes activity Restores photosynthetic pigments	Kaur et al. (2017)
Cytokinins				
Sunflower ( <i>Helianthus annuus</i> L.)	Leaves, stems, roots of 49-day-old plants	Pb, Zn	Positively assist the phytoextraction increasing the biomass production via stimulation of cell division and shoot initiation Increasing of plant transpiration	Tassi et al. (2008)
<i>Abyssum murale</i> Waldst. & Kit	Leaves, whole plants	Ni	Increasing of plant biomass and transpiration rate	Cassina et al. (2011)
Chlorella Chlorella ( <i>Chlorella vulgaris</i> L.) Chlorella ( <i>Chlorella vulgaris</i> L.)	Algal cells	Cd Cu, Pb	Inhibition of HM absorption Increase of primary metabolite level Activation of algal growth Increasing of anti-oxidant capacity in cells	Piotrowska-Nieczyporuk et al. (2012)
Auxins				
Sunflower ( <i>Helianthus annuus</i> L.)	Roots, shoots	Pb, Zn	Increase metal phytoextraction Increase root and shoot growth	Fässler et al. (2010)
Maize ( <i>Zea mays</i> L.)	Leaves, stems and roots of 60-day-old plants	Pb	Increase metal uptake and translocation Increase plant growth	Hadi et al. (2010)
Switchgrass ( <i>Panicum virgatum</i> L.) Wheat ( <i>Triticum</i> sp.)	Roots, shoots Leaves of plants after 56 days of sowing	Pb Cd	Increase plant biomass Progress anatomical structure of leaf Increase plant growth Promoting of the anti-oxidant system	Aderholt et al. (2017) Agami and Mohamed (2013)

Table 1 (continued)

Plants	Part of plant	HM	Adaptive reaction of plants	References
Fenugreek ( <i>Trigonella foenum-graecum</i> L.)	Leaves, shoots, roots of plants after 30 days of sowing	Cd	Regulation of the ascorbate–glutathione cycle	Bashri and Prasad (2015)
Arabidopsis ( <i>Arabidopsis thaliana</i> L.)	Roots of seedlings	Cd	Regulation of anti-oxidants activity Stimulation of hemicellulose 1 synthesis Increasing metal fixation capacity of root cell walls	Zhu et al. (2013)
Gibberellins				
Pea ( <i>Pisum sativum</i> L.)	Roots and shoots of seedlings after 11 days of sowing	Cr	Increase activity of anti-oxidative enzymes Increase activities of enzymes of nitrogen assimilation	Gangwar et al. (2011)
Arabidopsis ( <i>Arabidopsis thaliana</i> L.)	Roots of seedlings	Cd	Reduction of nitric oxide accumulation and metal content Stimulate expression of Cd <sup>2+</sup> uptake related gene-IRT1	Zhu et al. (2012)
<i>Parthenium hysterophorus</i>	Roots, stems and leaves of 60-day-old plants	Cd	Increase plant growth and biomass	Hadi et al. (2014)
Rice ( <i>Oryza sativa</i> L.)	Roots and leaves of seedlings	Fe	Regulation of metal transport and translocation	Wang et al. (2017)
Salicylic acid				
Cucumber ( <i>Cucumis sativus</i> L.)	Leaves, stems and roots of 33-day-old plants	Mn	Decrease level of ROS and lipid peroxidation Increase anti-oxidants—ascorbate and glutathione Inhibit metal transport	Shi and Zhu (2008)
<i>Linum usitatissimum</i> L.	Roots, stems, leaves of seedlings	Cd	Increase of electrolyte leakage Raise chlorophyll, MDA and total lipids content	Belkhadri et al. (2010)
Rapeseed ( <i>Brassica napus</i> L.)	Roots, shoots and leaves of 31-day-old plants	Ni	Increase the linolenic acid content Increase activities of the anti-oxidant enzymes	Kazemi et al. (2010)
Peanut ( <i>Arachis hypogaea</i> )	Roots, shoots and leaves of 35-day-old plants	Cd	Decrease level of lipid peroxidation, H <sub>2</sub> O <sub>2</sub> and proline accumulation Alleviation of metal toxicity Improved growth, chlorophyll content, photosynthesis, and mineral nutrition Stimulate activities of anti-oxidant enzymes Increase content of non-enzymatic anti-oxidants	Xu et al. (2015a, b)
Malting Barley ( <i>Hordeum uhulgare</i> L.)	Leaves of three-leave stage seedlings	Zn, Cu, Mn, Cd, Hg, Pb	Inhibitive effects on the activities of CAT and SOD at higher concentrations Small changes on the activities of CAT and SOD at lower concentrations	Song et al. (2014)



Table 1 (continued)

Plants	Part of plant	HM	Adaptive reaction of plants	References
Mustard ( <i>Brassica juncea</i> L.)	Leaves, shoots and roots of 10-day-old seedlings	Pb	Combined effect of 24-epibrassinolide and salicylic acid resulted in enhancement of HM tolerance index and relative water content. A significant decline in dry weight, metal uptake, thiol, and polyphenol contents was observed	Kohli et al. (2018b)
Mustard ( <i>Brassica juncea</i> L.)	Roots, shoots and leaves of 30-day-old plants	Pb	Up-regulated gene expression of SOD, POD, CAT, GR, GST 1 genes was in response to 24-epibrassinolide + salicylic acid combined treatments Enhancement of osmolytes content Alteration of anti-oxidative defense system	Kohli et al. (2018c)
Ethylene				
Mustard ( <i>Brassica juncea</i> L.)	Leaves of plants after 30 days of sowing	Ni, Zn	Support efficient PS II activity, photosynthetic nitrogen use efficiency and higher RUBISCO activity and	Khan and Khan (2014)
Mustard ( <i>Brassica juncea</i> L.)	Leaves and roots of plants after 30 days of sowing	Cd	Decreasing H <sub>2</sub> O <sub>2</sub> and superoxide accumulation via decreasing ET and glucose sensitivity Greater cysteine and methionine content Increasing of reduced glutathione content	Khan et al. (2016)
Pigeon pea ( <i>Cajanus cajan</i> )	Seeds	Cd	Improving germination	Sneideris et al. (2015)

*Cu* copper, *Ni* nickel, *Cd* cadmium, *Zn* zinc, *Al* aluminum, *Cr* chromium, *Pb* lead, *Fe* iron, *Mn* manganese, *Hg* mercury

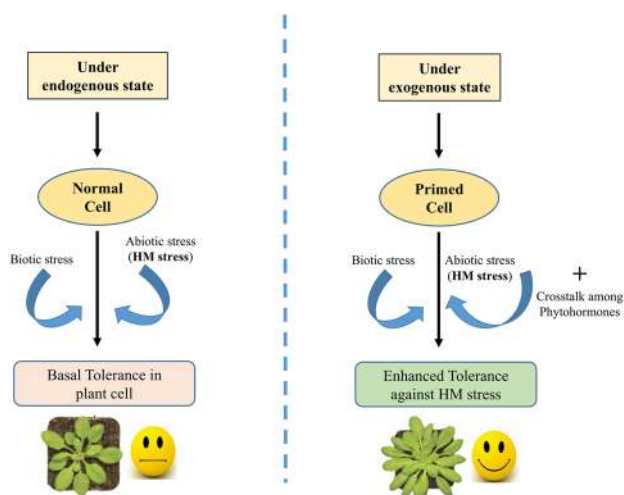
is improved (Hayat et al. 2007; Ali et al. 2008a, b). Under exogenous BR application on plants growing under HMs conditions, the PSII reaction centers have elevated electron transport, energy absorption with further trapping and effective oxygen-evolution (Janeczko et al. 2005).

Exogenous ET has an important role during senescence and promotes ripening in horticultural crops (Agarwal et al. 2012). The potential of combined application of exogenous ET and sulfur could synergistically upgrade photosynthetic performance under Cd effects (Khan et al. 2016). The authors claimed that the impact was observed due to an increase in the concentration of sulfur-containing amino acids and thiol production.

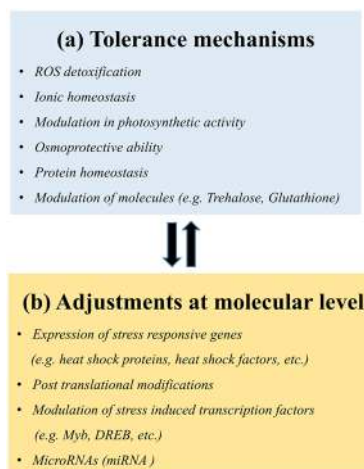
The most recently discovered phytohormone class called as strigolactones (SLs), are carotenoid-derived phytohormones. SLs are found in many different plants including higher plants like rice, *Arabidopsis*, and so on (Xie et al. 2010). Plant development and their interactions with the environment are related to SLs (Gomez-Roldan et al. 2008; Leyser 2009). A synthetic SL analog, GR24, was discovered recently and widely used for the regulation of plant growth and development (Marzec 2016). However, a few reports related to the role of SL in HM stress and phytoextraction upon exogenous use exist including the effects on plant growth under Cd stress. There are many ameliorative ways for Cd toxicity but mechanisms of Cd toxicity removal in plants, by the exogenous application of phytohormone, are important. Upon the exogenous use of GR24 (a synthetic SL phytohormone), Cd phytotoxicity and uptake in switchgrass, a warm-season C4 perennial grass, a reduction of Cd concentration was exhibited. However, Fe and Zn levels increased due to additional GR24 which was related to the competition between Cd and other elements (Tai et al. 2017). GR24 acted as a positive regulator of chlorophyll synthesis and exogenous GR24 alleviated this decrease in chlorophyll content. By contrast, Woo et al. (2004) reported that leaf senescence symptoms were delayed in (*max2/ore9*) mutants with SL deficiency. An SL-deficient mutant, *dad1*, was observed in petunias showing the role of a SL negative effect on chlorophyll synthesis (Snowden et al. 2005). The upcoming data related to SLs suggest crosstalk with other hormones and particularly during HM stress there also exists crosstalk between phytohormones.

## Conclusion and Future Perspective

Exogenous application of BRs, CKs, IAAs, GAs, SA and SLs can increase the level of anti-oxidants, decrease the level of ROS together with lipid peroxidation, and stimulate plant growth (Fig. 2). Thus, plants may survive better with phytohormone priming in HM-contaminated areas (Fig. 3). This review provides insight on the role of



**Fig. 2** Probable mechanism of phytohormone priming regulation under HM toxicity



**Fig. 3** Phytohormone priming as a means for acquired HM stress tolerance. Pretreatment using exogenous phytohormones prime plant cells toward enhanced tolerance to HM stress

exogenous phytohormone application for enhancing and developing defence strategies of plants. The data presented in this mini review can be used for developing agro-ecological technology based on the exogenous application of phytohormones to improve tolerance under HM contamination which may contribute to the agricultural or ecological sectors, and explore ways for further improvisation. However, suitable bio-formulations may be laboratory-tested after further research to be used for reclamation of contaminated soils. This low input technique is sustainable and will help in reclamation of HM contaminated soils, thus increasing the quality and crop yield in such areas.

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## Compliance with Ethical Standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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