

Signaling and Communication in Plants

Tariq Aftab *Editor*



Metals and Metalloids in Plant Signaling

 Springer

Signaling and Communication in Plants

Series Editor

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This book series will be devoted to diverse aspects of signaling and communication at all levels of plant organization, starting from single molecules and ending at ecological communities. The individual volumes will interlink molecular biology with plant physiology and the behavior of individual organisms, right up to the system analysis of whole plant communities and ecosystems.

Plants have developed a robust signaling apparatus with both chemical and physical communication pathways. The chemical communication is based either on vesicular trafficking pathways or accomplished directly through cell-cell channels known as plasmodesmata. Moreover, there are numerous signal molecules generated within cell walls and also diffusible signals, such as nitric oxide, reactive oxygen species and ethylene, penetrating cells from extracellular space. Physical communication on the other hand is based on electrical, hydraulic, and mechanical signals.

The integrative view of this book series will foster our understanding of plant communication throughout the individual plant and with other communicative systems such as fungi, nematodes, bacteria, viruses, insects, other plants, and predatory animals.

Tariq Aftab
Editor

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Preface

In the ever-evolving field of plant biology, one of the most captivating and intricate stories is the dialogue between plants and the elements—particularly metals and metalloids. This edited book, “**Metals and Metalloids in Plant Signaling**” seeks to unravel the captivating narrative of how these chemical entities, which are often hidden beneath the soil or coursing through the plant’s vascular system, profoundly impact the life and destiny of plants.

The plant kingdom, an exemplar of adaptive resilience, has developed an astonishing array of strategies to perceive, respond to, and utilize metals and metalloids. From the essentiality of metals like iron and copper in photosynthesis and respiration to the enigmatic role of metalloids like arsenic in stress responses, this book journeys through the multifaceted world of plant-element interactions.

Our exploration begins with a comprehensive overview of the transporters and receptors that plants employ to sense and acquire metals from their environment. We delve into the molecular mechanisms governing the exquisite interplay between plants and metals, from uptake and storage to detoxification and cellular transport. Throughout these chapters, we uncover the complexities of plant metal homeostasis and the pivotal role of metallochaperones, efflux transporters, and metalloenzymes. As we navigate further, we encounter the enigmatic world of metalloids, elements that blur the line between essentiality and toxicity.

This volume unravels the intricate signaling pathways that plants deploy to cope with metalloids such as arsenic, boron, and selenium. We explore how these elements, often viewed with trepidation, can be harnessed by plants to enhance their resilience in challenging environments. Additionally, we investigate the intersections of metal and metalloid signaling with other vital physiological processes. From the regulation of growth and development to the orchestration of stress responses and immune defenses, the influence of these elements on plant biology is profound and multifaceted.

While our primary focus is on the molecular and cellular aspects of plant-element interactions, we also extend our gaze to ecological implications. The chapters in this book illuminate how plant metal/metalloid interactions reverberate throughout

ecosystems, impacting nutrient cycling, and the phytoextraction of heavy metals from contaminated soils.

I owe immense gratitude to the dedicated scientists and experts who have contributed their knowledge and insights to this volume. Their collective expertise illuminates the complex web of interactions that governs the relationship between plants and metals/metalloids. May this book serve as a guiding light for researchers, educators, and students in the field of plant science, fostering a continued exploration of the hidden world beneath our feet—the world where plants and elements engage in an intricate and enduring dialogue.

Finally, I extend my appreciation to friends, research students, and the editor's family members for their invaluable moral support, blessings, and inspiration throughout the book's compilation process. Additionally, I would like to express my gratitude to the Springer Nature team for their unwavering cooperation and support at all stages of the book's production.

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About the Editor



Dr. Tariq Aftab received his Ph.D. in the Department of Botany at Aligarh Muslim University, India, and is currently an Assistant Professor there. He is the recipient of a prestigious Leibniz-DAAD fellowship from Germany, Raman Fellowship from the Government of India, and Young Scientist Awards from the State Government of Uttar Pradesh (India) and Government of India. After completing his doctorate, he has worked as Research Fellow at National Bureau of Plant Genetic Resources, New Delhi and as Post-doctorate Fellow at Jamia Hamdard, New Delhi, India. Dr. Aftab also worked as Visiting Scientist at Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany, and in the Department of Plant Biology, Michigan State University, USA. He is a member of various scientific associations from India and abroad.

He has edited 20 books with international publishers, including Elsevier Inc., Springer Nature and CRC Press (Taylor & Francis Group), co-authored several book chapters, and published over 80 research papers in peer-reviewed international journals. His research interests include physiological, proteomic, and molecular studies on medicinal and crop plants.

An Overview of Metal and Metalloid Toxicity and Signaling in Plants



Devendra Singh, Sunil Kumar Verma, Kaiser Iqbal Wani, and Tariq Aftab

Abstract Anthropogenic factors are mostly to blame for the rising incidences of metal and metalloid toxicity in the world. Given that it has an effect on the production of crops; metals and metalloids can go through the food chain and, lead to bio-magnification and subsequent environmental changes that affect human health. Throughout evolution, plants have created sophisticated defenses against these biotic and abiotic stressors. The accumulation of these heavy metals and metalloids disrupts essential functions in plant cells. By producing excess reactive oxygen species, indirectly or directly, heavy metals can affect plants in a number of ways. By enhancing defense responses, including sequestration within vacuoles, metal chelation, metal intake regulation via transporters, and anti-oxidative process amplification, plants combat such environmental metal overexposure. Plants respond to these stressors in this manner and the complex signaling networks interact within the cell to translate external inputs into an intracellular reaction. The 3 important signaling mechanisms involved—calcium, hormone, and mitogen-activated protein kinase (MAPK) signaling are addressed herein book chapter. A significant element in controlling heavy metal stress is played by regulators other than signaling components, including microRNAs and transcription factors. This book chapter highlights the critical part MAPKs play in synchronizing control of other signaling regulators and components in stress caused by metals. Additionally, we also discussed chelators and metal transporters which are controlled by mitogen-activated protein kinase signaling.

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1 Introduction

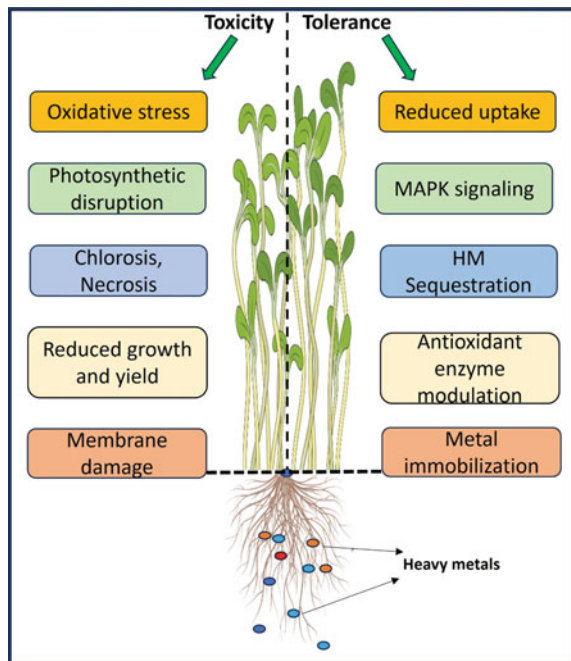
Only trace amounts of heavy metals are necessary to support life and their overuse damages cells. Heavy metals prevalent in the surroundings have an antagonistic consequence on the growth of many organisms. Both the plant and animal kingdoms have been known to be disturbed by these metals. They have a very well-documented negative influence on our agriculture (Tchounwou et al. 2012). A high heavy metal concentration causes harm on the cellular level through a variety of processes. The most systematic process is the generation of reactive oxygen species (ROS), which leads to oxidative stress. Other mechanisms involve the biomolecule inactivation via critical metal ions displacement or else through key functional group blocking (Stohs and Bagchi 1995). The examples of metals that can act by displacing functional groups or necessary metal ions are Hg, Pb, Cd, As, and Cr. Other metals, for example, Mn, Zn, Al, Ni, and Cd, along with Pb produce ROS by indirect pathways. In contrast, redox-active metals, for instance, Fe and Cu, directly produce ROS through redox reactions. The activation of ROS-producing enzymes like NADPH oxidases or the removal of necessary cations from the enzymes binding sites and activity inhibition are two illustrations of indirect ROS formation. Standard physiological levels of ROS enact critical functions (Chauhan et al. 2022), whereas their enhanced production worsens cell function (Mani et al. 2017). The chelating compounds in plants like phytochelatin (PCs), metallothionines (MTs), etc. demonstrate protection against these heavy metal ions via vacuole sequestration. Not all of the defense reactions exhibited by plants are caused by signaling cascades, but a significant portion of them are a result of their ability to receive signals from upstream receptors and pass them into the nucleus, where they regulate a number of genes involved in defense (Jalmi and Sinha 2015). Receptors like ERECTA (ER), ethylene resistance 1/2 (ETR1/2), FLS2, EF-Tu receptor (EFR), SIT1, protein kinases (RLKs), and others are identified to sense signals and are intensively investigated in plant stress and development (Gupta et al. 2009; Lackman et al. 2011). MAPK signaling, hormone signaling and calcium signaling are the main signaling networks that are active in metal stresses as well as other environmental stresses (Luan et al. 2002). Numerous calcium-sensing proteins, for instance, calcineurin B-like proteins (CBLs), CDPKs and CMLs, calmodulins (CaMs), are involved in calcium signaling. These proteins attach to Ca^{2+} and activate several signaling pathways downstream (Dodd et al. 2010; Steinhorst and Kudla 2013). There are various plant hormones that contribute to the metal stress response in the case of hormone signaling (Chen et al. 2014; Vitti et al. 2013). The most common and sophisticated signaling module among the others is the mitogen-activated protein kinase (MAPK) signaling, which is made up of the 3-tier phosphorylation modules MAPKs (Sanders et al. 2002), MAPKKs (Zhao et al. 2014), and MAPKKKs. Abiotic as well as biotic stress tolerance is largely recognized to be provided by MAPKs (Hamel et al. 2006; Patra et al. 2018).

The signaling molecule creation, in addition to stress-related proteins like chelators and metal transporters, is a marker of the molecular reaction of plants to metal stress. They reduce toxicity caused by heavy metal via sequestering and chelating

them within plant vacuoles, which act as transitory storage for both beneficial and harmful metabolites (Mendoza-Cózatl et al. 2011; Verbruggen et al. 2009). Grounded on this capability, plants are currently frequently utilized in the process of phytoremediation, which removes the environmental contamination of heavy metals (Salt et al. 1998).

Transporters located in parenchyma cells of partner cells of the phloem and xylem carry out the transportation of heavy metals necessary for their translocation. In the phloem and xylem, the transporters are primarily responsible for loading and unloading of metal ions. Metallothionines, PCs, nicotinamide, and glutathione are Cys-rich metal-binding peptides that are significant participants in metal transport (Singh and Sharma 2015). Findings showing the involvement of Cys-rich metal binding peptides and metal transporters in the absorption, transportation, and arsenic metal detoxification have been explained (Kumar et al. 2015). The capability of vacuoles to sequester metals (VSC), in addition to transporters and chelators, is crucial for metal distribution. In response to a changing environment, the VSC is adjusted by interactions between ion chelators and membrane-localized transporters (Peng and Gong 2014). The heavy metal toxicity towards plants will be governed through VSC regulation. Studying VSC's regulatory mechanisms and how they ultimately affect metal transport and sequestration is crucial. In order to control the movement of metals, it is also crucial to research how plants perceive and transmit metal signals. Figure 1 represents the HM effect on the plant.

Fig. 1 Heavy metal toxicity and tolerance strategies in plants



This chapter will primarily focus the action of heavy metal mechanism, various signaling elements besides additional regulators elicited by stress caused by heavy metal, the plant signaling effect on downstream defense reactions, coupled with the incomplete work achieved on metal transporters regulation by MAPKs which even so uncharted in plants.

2 Heavy Metal Effect on Plant Signaling

The difficulty of the plant to avoid ecological stresses like metal pollution has sparked the creation of numerous methods to successfully observe, distinguish, and subsequently acclimatize to such challenges (Singh et al. 2022a). Plants that are exposed to heavy metals respond through changing the biochemical and molecular cell systems (Maksymiec 2007). Undoubtedly, a noteworthy signal transduction network operated through several signal transduction units within a plant cell is what triggers this response (Singh and Sharma 2015). The plants final response is demonstrated by the synthesis of metal binding as well as metal transporter proteins that aid the plant in coping with disproportionate metal stress (Peng and Gong 2014). Initial metal toxicity signs in many crops are recognized to resemble erstwhile ecological stresses (Chen et al. 2001; Rucińska-Sobkowiak 2016; Yadav 2010). This response commonality demonstrates the connectivity of complex signaling networks.

3 MAPK Signaling Under Heavy Metal Stress

Most decisive and extremely conserved signaling molecules, MAPKs work during a variety of developmental processes and in response to extensive series of stressors (Sinha et al. 2011). Three tiers of components make up the MAPK cascade (Hamel et al. 2006). The phosphorylation events are mediated by MAPKs, MAPKKs, and MAPKKKs from the upstream receptor to the downstream target (Fig. 2). A significant number of cellular activities are controlled by MAPK signaling, which controls the transfer of signals associated with stress. Stress caused by heavy metal is one of the abiotic stimuli that has had a significant impact on MAPK signaling pathways. It is known that some metal ligands and the ROS molecules produced during metal stress can activate MAPKs (Jalmi and Sinha 2015; Jonak et al. 2004; Smeets et al. 2013).

Numerous publications demonstrate how heavy metals cause MAPKs to activate (Singh and Agarwal 2021; Ding et al. 2011; Yeh et al. 2007). However, very limited investigations have been carried out to demonstrate the reactions to additional metals, including Pb, Zn, and Fe (Rao et al. 2011). Similar to this, comprehensive research to unravel a full MAPK signaling cascade in response to particular metal stress is intangible (Jonak et al. 2004). The most well-known MAPKs in Arabidopsis are

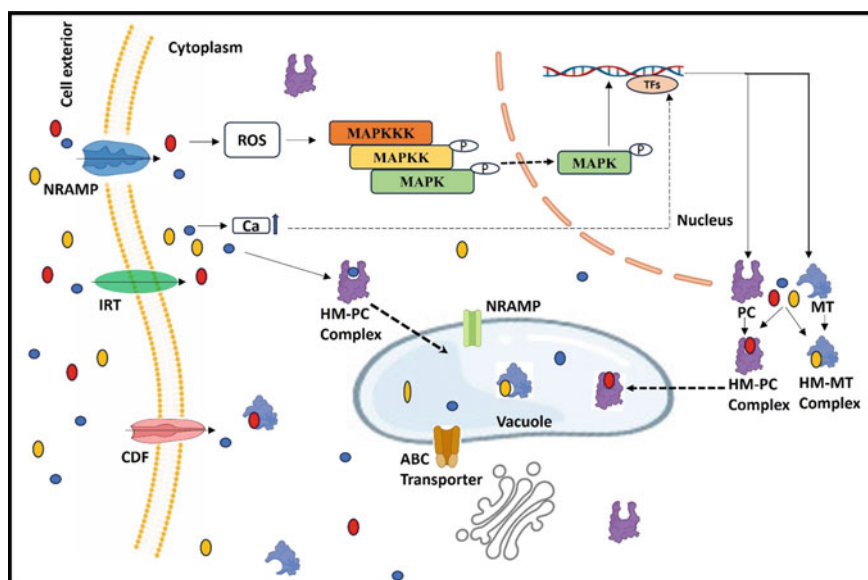


Fig. 2 Schematic representation of the uptake and signaling of heavy metals (represented by different colored circles) in plants. Inside root cells, the heavy metals trigger different signaling pathways like MAPK and Ca signaling for plant protection and metal sequestration into different organelles

MPK6 and MPK3, which are triggered by a variety of stimuli and identified to be stimulated by CuSO_4 and CdCl_2 (Liu et al. 2010; Takahashi et al. 2011).

Plants are already known to produce ROS when exposed to heavy metals, and its generally acknowledged that these ROS molecules play a significant role in activating MAPK signaling. Additionally, MAPK pathways control ROS production through positive feedback. Additionally, the OXII-MPK6 cascade initiated via reactive oxygen species controls ROS generation (Jalmi and Sinha 2015). These investigations offer hypothesis and connection between MAPK cascades and ROS molecules under various metal stress conditions (Pitzschke et al. 2009).

4 The Role of Calcium Signaling in Stress Caused by HM

Calcium ion functions as unanimous plants secondary messenger in their response and in regular function to environmental challenges (Sanders et al. 2002). Numerous stressors cause complicated interactions and signal transduction pathways, resulting in a change in the free Ca^{2+} cytosolic content (Steinhorst and Kudla 2013). Highly sensitive calcium sensor proteins detect this brief rise in cytosolic concentration and convert the chemical signal into a biological reaction (Luan et al. 2002). Numerous calcium-sensing proteins are present in plants (Rudd and Franklin-Tong 2001). These

proteins bind to Ca^{2+} and activate several downstream signaling cascades (Kumar et al. 2022a).

Numerous research has been conducted in numerous species of plant, comprising tomato, *Glycine max*, *Vitis vinifera*, and chickpea to determine the role of Ca^{2+} -binding like proteins plus Ca^{2+} sensor proteins in increased tolerance to diverse abiotic stimuli (Tripathi et al. 2009; Ahammed et al. 2013; Alani et al. 2012; Das et al. 2022). To reduce stress caused by heavy metals, research has shown that the exogenous injection of Ca^{2+} can modify the biochemical and physiological responses. Its been demonstrated that the exogenous Ca^{2+} addition increases the activity of antioxidant enzymes (Ahmad et al. 2015; Sharma et al. 2022). Regardless of abundant publications, our understanding of response mechanisms through which they are controlled is yet scanty and needs extra description.

An intriguing Arabidopsis seedlings study revealed that cross-talk between signaling pathways is necessary to counteract stress caused by heavy metals. Ca^{2+} reduces the Cd toxic effects by sustaining auxin homeostasis, which is how the subject plants were able to withstand the effects of Cd. Additionally, yeast cell research has suggested that the Ca^{2+} -ATPases of Golgi and vacuolar membranes play a role in dealing Cd toxicity. This is accomplished by working together with the Glutathione-conjugated transporter Ycf1p (Mielniczki-Pereira et al. 2011), whose activity is once again regulated by phosphorylation, introducing a line amongst several signaling pathways in response to ecological stimuli.

It is known that CDPK and MAPK (Takahashi et al. 2011) collaborate to transmit signals in retort to environmental changes so that organisms can adjust to their surroundings (Opdenakker et al. 2012; Wurzinger et al. 2011). In rice, it is discovered that a CDPK named CPK18 was an MPK5 upstream kinase, phosphorylating MPK5 on the threonines 14 and 32. Additionally, Ca/CaM and MKK3 jointly activate MPK8, which in response to mechanical stress, controls the NADPH oxidase expression adversely (Xie et al. 2014). According to the report, Ca^{2+} increases the CDPK-like kinase activity, which in turn triggers MAPK activation and Pb^{2+} -mediated cell death (Huang and Huang 2008). In addition, it has been revealed that calmodulins influence the MAPK signaling pathway, which outlines a potential scenario for how they might interact with metal stress. Therefore, it is very helpful in increasing our understanding of the significance of signaling cross-talk in addition to control of Ca^{2+} signaling in a plant with stress caused by heavy metal (Tebar et al. 2002).

5 Hormone Signaling During Heavy Metal Stress

The root architecture of plants cultivated in metal-polluted environments is very important and the remodeling of root structural design in plants could be employed as an escape method from stress caused by heavy metal (De Smet et al. 2015). As a result, numerous studies have documented how these phytohormones contribute to root system architecture being modified in heavy metal stress response. Auxin is a

vital growth hormone that affects both stress and developmental responses in the environment (Potters et al. 2007). The regulation of auxin homeostasis, which includes auxin stability, transport, and redistribution, directly influences how plants react to metal stressors. PIN2 and AUX1 mediate basipetal auxin transport via outer root cell layers (Rashotte et al. 2000). Auxin-related genes like ABCB family, Gretchen Hagen (GH3) genes, *YUCCA* (*YUC*), *TIR1*, *CYP79B2* and *CYP79B3*, *PAT1*, and *ABCB* family (Wang et al. 2015) exhibit variable and dynamic expression in plants metal stress response.

Auxin signaling and its transport are influenced by MAPK signaling (Tsai et al. 2012; Singh et al. 2022b). A fascinating study revealed a link between MAPKs and auxin/cytokinin, and OsMKK4/5-OsMPK3/6 was identified as an equally critical actor in the auxin/cytokinin interaction that controls the OsPIN1b/9 expression pattern. It's still unclear, nevertheless, how auxin response regulation via MAPK signaling plays a role in stress caused by metal (Singh and Sharma 2015). The link concerning MAPK signaling and auxin signaling in Cd stress was demonstrated in an interesting rice study. When exposed to Cd stress, MAPK was found to be negatively regulating the majority of important auxin signaling genes expression, including *YUCCA*, *PIN*, *ARF*, and *IAA*, as well as genes linked to the cell cycle. This sturdily advocates MAPK signaling plays a significant role in controlling auxin signaling under heavy metal stress (Zhao et al. 2014).

Cytokinins are N⁶-prenylated adenine derivatives that control how plants respond to abiotic as well as biotic stimuli along ability to grow and develop (Perilli et al. 2010). According to certain studies, Cytokinins can reduce the toxicity caused by heavy metals. Cytokinins restored inhibition of the chloroplast membranes and photosynthetic pigment, enhancing photosynthetic capability along with primary metabolite levels in plants under heavy metal stress. Soluble sugars, free amino acids, and proline that mitigated the growth- and photosynthesis-inhibiting effects of Cd can likewise be modulated by exogenous kinetin administration (Piotrowska-Niczyporuk et al. 2012).

A major element of plant growth is controlled by the gaseous hormone ethylene. ACC oxidase (ACCO) catalyzes the transformation of ACC to ethylene, which is produced during its biosynthesis by ACC synthase, which changes AdoMet into ACC. Numerous biotic and abiotic stimuli control the expression of the multigene families that code for ACC synthase and ACCO (Kende 1993). Ethylene's significance in controlling plant metal stress responses is supported by numerous reports. Metal and concentration both affect how metal stress affects ethylene synthesis in plants (Thao et al. 2015). Rice has the following five major ET synthesis genes: *OsACO6*, *OsACO5*, *OsACO2*, *OsACO1*, and *OsACS2*, coupled by the transcription factors *ERF1*, in addition, AP2 (Keunen et al. 2016; Chauhan et al. 2023). Under Al stress, root growth is inhibited, and Al treatment led to an increase in ethylene production (Montero-Palmero et al. 2014; Raj et al. 2019; Tian et al. 2014).

In addition to their impact on ethylene synthesis, heavy metals also have an impact on ethylene signaling. The illustration of several ethylene response factors, as well as ERF1, ERF2, and ERF5, increases after exposure to copper (Weber et al. 2006).

6 MicroRNA Regulation in Heavy Metal Stress

In addition to the role signaling pathways play in transferring stimuli related to heavy metals and controlling plant response, it has been discovered that additional regulators, like small RNAs, have a significant impact on how plants react to metal stress. Small RNAs, like microRNAs, are non-coding RNAs with twenty to twenty-four nucleotides that control the post-transcriptional stage of gene expression via preventing the degradation of mRNA or suppressing translation (Raghuram et al. 2014). Different miRNA families have been demonstrated to be capriciously controlled mutually geographically and temporally by means of deliberations wavering from species to species (He et al. 2016).

In recent times, transcriptome analysis throughout the entire genome and next-generation sequencing has been utilized in miRNA determination that respond to stress caused by heavy metal in a variety of plant species (Ding et al. 2011). Through various demonstrations, it has been observed that different conserved miRNAs are variably controlled under stressful and normal circumstances (Bukhari et al. 2015).

Different miRNAs are regulated differently by plants that are subjected to excessive Cd content. Cd exposure, for instance, alters the expression of a number of conserved miRNAs in rice (Ding et al. 2011). While 12 miRNAs were found to be down-regulated in response to Cd stress, the miR441 expression was noticeably up-regulated, miR192 was downregulated and was predicted to be target the ABC transporter. Under Cd Stress, rice seedling growth and seed germination were drastically reduced by overexpression of miR192 when linked to wild-type plants which imply; when miR192 levels are reduced, ABC transcripts start to accumulate and eventually, during Cd stress contributes to Cd requisitioning with the help of ABC transporter (Tang et al. 2014).

It has been discovered that most plant species experience downregulation of key miRNAs under cadmium stress, including miR159 and miR166 (Pandey et al. 2015). It has been demonstrated that numerous Cd-responsive miRNAs target the genes involved in the heavy metal detoxification (Srivastava et al. 2013). Deep sequencing in mustard, as well as rice, has recently been used in research to identify many As-sensitive miRNAs (Kumar and Verma 2022; Singh et al. 2022d, e, f). According to their findings, miR393, miR397, and miR408 were upregulated, while miR172's expression was noticeably downregulated. According to research, miR408 specifically targets proteins that contain copper (Srivastava et al. 2013). Additionally, it was noticed that under conditions of heavy metal stress, ROS cause downregulation in the laccase-targeting miR397 and the activation of lipid peroxidation. Through the buildup of laccase enzymes might result in positive regulation of lignin production (Jones-Rhoades and Bartel 2004).

A significant plant development limiting factor that interferes with cellular redox equilibrium is aluminum. Two significant genes *ATP sulfurylase* (*APS*) and *SULTR2:1* ensued, discovered targets for miR395 that are known to induce by the sulfur shortage, Cd stress coupled with Al stress. These 2 genes result in the creation

of PCs and GSH, the two main compounds involved in the chelation of metal (Matthewman et al. 2012).

The miRNA expression is influenced by other metals like mercury, lead, and chromium. In *M. truncatula*, mercury treatment caused differential miRNA regulation, with miR167 and miR172 upregulated, and miR169, miR164, miR172, miR398 and miR156 downregulated. miR156, miR398, and miR399 were downregulated in cotton seedlings treated under Pb. Heavy metals' differential regulation of these crucial miRNAs could have a substantial negative plant development effect by changing a variety of pathways (Smeets et al. 2013).

According to a study, Cd and Cu treatment caused OXI to regulate miR398b/c, illuminating the relationship amongst MAPK along with miRNA signaling. Upstream from MPK6, OXI is a part of the MAPK cascade which regulates the synthesis of ROS. Furthermore, it is discovered that a number of transcription factors that are recognized downstream targets of MAPKs are also targets of miRNA. These findings clarify the idea that during the stress response there is interplay between several plant components (Singh et al. 2022c; Zhao et al. 2005, 2014).

7 Modulation of Transcription Factors Under Stress from Heavy Metals

The major issue in the modern world is heavy metal poisoning (Ogawa et al. 2009). As previously mentioned, plants have developed diversity in mobilization and detoxifying systems to neutralize heavy metal stress (Shim et al. 2010; Yanhui et al. 2006). Complex signaling network activation is a significant contributor to the tolerance of stress caused by heavy metals (Farinati et al. 2010; Wang et al. 2010). According to numerous reports, exposure to heavy metals activates the MAPK signaling downstream targets cascade. Potential downstream MAPK targets include transcription factors like basic leucine zipper (Roelofs et al. 2008).

In plants, transcription factors controls the gene expression that regulates a variety of developmental processes and defensive mechanisms (Yanhui et al. 2006). Findings revealed that after being exposed to Cd, rice exhibits various time-dependent increases in the expression of the majority of the transcription factors from the families NAC, WRKY, DREB, and MYB, AP2 (Ogawa et al. 2009). A huge family of transcription factors with a variety of eukaryotic roles is the MYB family (Dubos et al. 2010). Earlier reports have demonstrated that Zn and Cd metal stressors in Arabidopsis strongly activated MYBs. It has been correspondingly discovered that Zn/Cd-hyperaccumulator *Thlaspi caerulescens* showed lower metal sensitivity than the MYB72 loss of function mutant in Arabidopsis. Lately, Li et al. (2016) discovered MPK4 is light-induced and controls the transcription factor MYB75/PAP1 to control the production of photoprotective anthocyanins. A clue that MYBs may operate as possible MAPK substrates under heavy metal stress comes from altered MYB gene expression and MAPK activity in response to Cd stress.

Another class of transcription factors, known as plant bZIP factors, protects against environmental challenges such as heavy metal stress. According to reports, exposure to Cd may stimulate the bZIP transcription factors expression (Opdenakker et al. 2012; Ramos et al. 2007). According to a report, even the direct relationship between MAPKs and bZIP transcription factors was not revealed in the setting of stress induced by heavy metal (Djamei et al. 2007). Furthermore, Cd also affects the expression of 2 members of the AP2/ERF family in Arabidopsis: ERF5 and ERF1 (Herbette et al. 2006).

Overall, stress induced by heavy metal activates a number of signaling mechanisms, including MAPK cascades. Despite the fact that findings on MAPK participation upstream of transcription factors in metal stress remain quite rare, the results above showed that they do interact with transcription factors as well as mediate plants' tolerance in handling stress induced by heavy metal.

8 Metal Transport and Sequestration Using MAPK Signaling

Plant roots react in a variety of ways when exposed to heavy metal. Metal is first bound with the roots cell wall and then metal influx occurs through the plasma membrane. By releasing metal ions into the apoplast and chelating amino acids, organic molecules, PCs, and MTs in the cytoplasm, the high level of metal influx is controlled (Fig. 2) (Mendoza-Cózatl et al. 2011). These metal–ligand complexes are carried to the tonoplast and deposited in the vacuoles for storage. This entire cycle of metal absorption, transit, chelation, and sequestration involves a number of molecules. These metal chelators and transporters are doing their jobs and defending plants from metal toxicity (Verbruggen et al. 2009).

The crucial signaling components that transmit numerous signals connected to stress, MAPKs, are identified that are triggered by stress induced by heavy metal, as was formerly stated (Fig. 2). MPK6 and MPK3 are well-known to be activated and expressed via an extensive variety of metals and are the ones with the best characteristics. These MAPKs have been significantly impacted by cadmium and copper in a variety of species. We can learn more about MPK3 and MPK6's role in maintaining metal homeostasis by looking at how they are up-regulated during retort to Cu and Cd-responsive chelators or downstream metal transporters. Studies on the final impact of their activation, however, remain intangible in plants. Although there have been substantial publications on the control of metal transporters by MAPKs in mammals, similar interactions can still occur in plants.

The main categories of metal transporters investigated include NRAMP, CDF, ABC, CPx- and P1B-ATPases, ZIP, and heavy metal transport ATPases (Singh and Agarwal 2021). The ability of ZIP members in the direction of transporting divalent cations was initially discovered in plants (Eide et al. 1996). Iron is primarily transported via the ZIP family member *IRT1* gene from Arabidopsis, which results

in high-affinity Fe absorption. *IRT1* is triggered inside 24 h of Fe-deficient circumstances in environments where iron is limited and is only found in the roots. Plants overexpressing *IRT1* assemble large amounts of Zn and Cd along with Fe (Connolly et al. 2002).

Further ZIP participants according to research, ZIP1 and ZIP2 are Mn and Zn transporters in roots that help Mn and Zn migrate into the xylem parenchyma (Singh et al. 2022d, e, f). Both genes' expression is primarily restricted to the root stele in accordance with their respective roles (Milner et al. 2013). This shows that metal transport in plants involves both hormone pathways and MAPK signaling. While there is only one report of MAPK being involved in controlling the metal transporter in plants, this idea has been well investigated in animals. Metal transporters are as responsible for activating MAPKs.

Family of additional metal transporters NRAMP is involved in many different types of organisms. A number of the NRAMP genes, which are found in two subfamilies in plants, are up-regulated in the presence of low levels of Fe, Mn, and Cd. However, there is still a lack of functional characterization of plant NRAMP transporters. A few research on animals points to MAPKs as the regulators of the NRAMP1 transporter (Moisan et al. 2006). Additionally, a different study suggested that NRAMP1 may influence the MAPK pathway (Zhang et al. 2000).

Studies have shown that MAPKs can also be activated by metal chelators, in addition to transporters activating MAPKs or MAPKs activating transporters. The crucial metal chelators are the cysteine-rich short peptides known as PCs and MTs, which have the ability to bind metal.

9 Conclusion

According to the chapter, heavy metals greatly influence plants by altering how they operate on many different levels. Under heavy metal stress many signaling pathways are activated, which are distinguished in taking part in a significant function in enhancing resistance to environmental challenges. MAPK signaling pathway is one of these crucial signaling pathways that have substantial responsibility toward controlling response against stress. When signaling pathways are active, other downstream components are active and functional, which changes how genes are expressed. In this study, it is undoubtedly stated how heavy metals affect MAPK activation, hormone, and calcium signaling, as well as more regulators, including miRNAs and transcription factors. MAPK signaling may have a substantial part in the heavy metals stress, according to several research conducted by several scientific groups. To understand the impact of stress caused by heavy metals, a comprehensive analysis of the MAPK cascade is necessary.

Additionally, this chapter gathers the findings demonstrating the interaction of calcium, auxin, and ethylene signaling with MAPK signaling in retort to stress caused by heavy metals. Nevertheless, there aren't many reports on the MAPKs' regulatory network. It can be very helpful to research the significance of this signaling heavy

metal stress cross-talk in plants. The interaction among MAPK signaling and another regulator, in triggering a reaction in contradiction of metal stress, is also summarized in this study. However, the limited information available on the regulatory network of transcription factors and MAPKs points to the need for more thorough research. Additionally, research on how metals and metal transporters activate MAPKs is followed by MAPKs controlling those activations. However, incomplete research makes this region in plants a mystery. Investigating the controls over these metal transporters will help a lot in figuring out how plants tolerate metal stress.

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Metalloids Accumulation and Translocation in Plants



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Abstract Metals and Metalloids are posing a great threat to the ecosystem. Various elements including Boron, Silicon, Arsenic, Cadmium, Germanium, Aluminum, Antimony, Tellurium, Palladium, and others are considered metalloids which possess both the properties of metals and non-metals. Studies reveal that plant cells use transporters from the aquaporin family to facilitate the entry of metalloids. Excess intake of metalloids poses stress to plant cell. Upon entering the plant, metalloids are distributed to various tissues and organs, which can result in different physiological effects. The signaling of auxin is crucial in regulating plant responses to changes in the environment and in establishing defense mechanisms against the harmful effects of exposure to toxic metals and metalloids. The presence of metalloids is one of the environmental stresses that can trigger the production of reactive oxygen species (ROS) in plants, although plants have different signaling pathways to reduce ROS accumulation. Number of gene families including *NRAMP*, *WRKY*, *ERF*, *MYB*, *NIP*, *IRT*, *HMA*s, *STAR1*, *HAC*, *PHT*, *LCT*, *Lsi*, *ZIP* and *PIP* are involved in the regulation of uptake and transportation and toxic metalloids. Research on these gene families can further allow us to improve the plant defense system so that plants will be able to withstand this serious abiotic stress.

1 Introduction

The escalating levels of pollutants represent the most significant environmental challenge of current era, contributing significantly to climate change and having severe implications for the ecosystem. Among these pollutants are metals and metalloids, which pose a particular threat to various life forms due to their toxicity. These trace

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elements can originate from either lithogenic or anthropogenic sources in the soil (Antoniadis et al. 2017). The group of elements known as “metalloids,” consists of six elements: boron (B), silicon (Si), arsenic (As), germanium (Ge), antimony (Sb), and tellurium (Te). In periodic table these elements are located on the dividing line between metals and non-metals and display characteristics that are intermediate between these two groups of elements. The accomplishment of phytoremediation tools and the providence of these elements in the environment are dependent on their availability and mobility. The effects of trace metal/metalloid-induced toxicity may not always be immediately apparent, as soil complexity, plant adaptation, and the period of their existence in the topsoil can all have an impact (Talukdar et al. 2015).

Researchers have recently focused on understanding how plants can incorporate, distribute, respond to, and adapt to elements such as arsenic (As), boron (B), and silicon (Si) at the molecular level. It has been discovered that metalloids, which include these elements, use transporters from the aquaporin family to enter plant cells. These transporters allow metalloids to enter plant cells in a neutral protonated form due to their similar shape to glycerol, which is a common substrate for aquaporins (Sharma et al. 2021; Mukhopadhyay et al. 2014). Despite of recent researches, the mechanisms involved in signaling, molecular response, and physiological adaptation to elements like As, B, and Si are still being explored. However, there is a dearth of information available regarding the phytotoxicity of elements such as Ge, Sb, and Te, this could be because Ge, Sb, and Te are not as environmentally relevant as other metalloids, which could explain the limited information available regarding their phytotoxicity. The focus of metalloid-dependent signaling in plants has been on As, B, and Si. The study of interactions between plants and metals as well as the advancement of phytoremediation technologies depend on this integration. In spite of the tremendous advancements achieved in this area recently, little has been known about on how plants perceive the toxicity stress caused by metalloids like boron and arsenic. While there have been advancements in understanding certain other abiotic stresses, the precise sensing mechanisms and true metalloid sensor(s) for boron and arsenic remain unclear (Rajabpoor et al. 2019; Lamers et al. 2020). The downstream signaling elements or effectors in plants often show a significant overlap in their response to various abiotic stresses, making them appear nonspecific. However, these effectors are responsible for coordinating plant responses and adaptations to specific stressors with remarkable accuracy (Pommerrenig et al. 2015).

2 Plant Reaction in Response to Metalloid Stress

Metalloids represent a group of elements that possess both metallic and non-metallic properties. A significant threat to crop growth is associated with As and Sb. In list of hazardous materials made by Agency for Toxic Substances and Disease Registry, Arsenic is one among the top most hazardous substances (Genthe et al. 2018). A phosphate analog named arsenate (AsV), penetrates plants through phosphate transport systems. Problems regarding its effects on human health have been raised as a

result of the buildup of arsenic in the tissues of significant crops and its subsequent transfer to cereals (Panauallah et al. 2009). While plants generally exhibit tolerance towards antimony (Sb), higher concentrations of this metalloid can hinder growth, photosynthesis, and nutrient uptake, and decrease cellular metabolite synthesis. On the other hand, selenium (Se), unlike boron (B) that is essential for growth and development of plants, is not a required element but is known to boost antioxidant activity and productivity. Selenium accumulation results in stunted growth, shorter roots, and reduced photosynthesis efficiency due to elevated levels of boron, whereas elevated levels of boron result in chlorosis of leaves and weakened shoots (Espinosa-Vellarino et al. 2020). Silicon is known to enhance plant growth and productivity, but excessive amounts can also induce abiotic stress (Sharma et al. 2019). An important source of phytotoxicity is metalloid stress, one of the lesser known abiotic stresses (Adrees et al. 2015). There are also substances including nitric oxide, hydrogen sulfide, and melatonin, that regulate other physiological processes such as auxin, ethylene, gibberellin, cytokinin, and abscisic acid (Thao et al. 2015; Kohli et al. 2019).

Auxin signaling is essential for controlling how plants respond to environmental changes and how they establish defenses against toxic metals and metalloid exposure. In fact, introducing auxin-producing microorganisms into the rhizosphere of plants under metalloid stress can improve plant output and adaptability (Vacheron et al. 2013). Auxins play an important role to reduce the concentration of ROS produces in different cellular compartments, including mitochondria, plastids, peroxisomes, and cytoplasm under the metalloids stress (Krishnamurthy and Rathinasabapathi 2013). When plants are exposed to toxic levels of metalloids, they have a feedback mechanism to maintain auxin homeostasis. Degradation and/or transport of auxin results in an increase in adaptability under adverse conditions, which improves adaptability. When plants are exposed to toxic levels of metalloids, several auxin-responsive genes may also change their transcript levels (Molnár et al. 2018).

3 Metalloids Homeostasis and Signaling During Plant Uptake

Metalloids are essential for plant growth but can be toxic to plants when present in excess. Plant uptake of metalloids involves a complex process of homeostasis and signaling mechanisms that regulate their uptake, transport and distribution within the plant (Ducic and Polle 2005). Homeostasis mechanisms regulate the uptake of metalloids in plant roots by maintaining the balance between uptake and efflux (Liu et al. 2019). Metalloids can enter plant cells through channels and transporters but are also expelled from the root cells by efflux pumps. The transporters and pumps responsible for metalloid uptake and efflux are regulated by several genes, such as the *ACR3* gene in *Arabidopsis thaliana*, which encodes a transport protein that mediates the uptake and efflux of As. Signaling mechanisms play a crucial role in metalloid uptake and distribution in plants. Signaling events caused by metalloid stress regulate