Molecular Mechanisms of Heavy Metal Tolerance in Plants

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1 Introduction

The physiology and molecular response of plants are interesting as plants as sessile creatures are exposed to constant environmental harsh conditions which can affect their growth and productivity negatively. Among adverse effects heavy metals' (HMs) impact is a crucial one which can affect plant physiology and metabolic pathways (Asgari Lajayer et al. 2019a). Heavy metal term is used for metals with a determined specific gravity (>5); however biologists use this term for various metal(loids) that are toxic for organisms. Arsenic (As), cadmium (Cd), calcium (Ca), cobalt (Co), iron (Fe), manganese (Mg), nickel (Ni), and zinc (Zn) are some

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M. Faisal et al. (eds.), *Cellular and Molecular Phytotoxicity of Heavy Metals*, Nanotechnology in the Life Sciences,
https://doi.org/10.1007/978-3-030-45975-8_8

of the important HMs (Asgari Lajayer et al. 2017a). Some of metals such as Ca, K, Na, Mg, Fe, and Zn are known as essential elements as they are involved in the proper function of different proteins in organisms. So they are vital for growth, development, and healthy life of all organisms on the planet. However, their concentration is vital and above a normal range they can be toxic (Asgari Lajayer et al. 2017b). HMs naturally exist in soil and water; however their contamination becomes one of environment experts' concerns recently. The challenge of HMs becomes worse and worse because of human's destructive industries (Asgari Lajayer et al. 2018). This leads experts to be concerned of the potential of various organisms, such as plants, to ameliorate HMs' negative effects on the environment. The entry of HMs into the human food chain is so dangerous which can show its detrimental effects in the future (Asgari Lajayer et al. 2019b). So, unraveling the complexity of HM phytoremediation can help experts to develop some efficient eco-friendly agents to decrease the negative impacts of HMs on the environment (Asgari Lajayer et al. 2017a, 2019a).

HMs have various range of negative effects (from weak to moderate to strong) on plants based on their oxidation states. The molecular and cellular levels of HM toxicity include protein and enzyme denaturation, functional group blocking, essential metal substitution, and membrane disruption (Rascio and Navari-Izzo 2011). All these modifications can result in photosynthesis inhibition and respiration (Fig. 1) (Ali et al. 2013). Methylglyoxal (MG) is the other toxic compound which has been identified recently to increase under various stresses (Ali et al. 2013; Sytar et al.

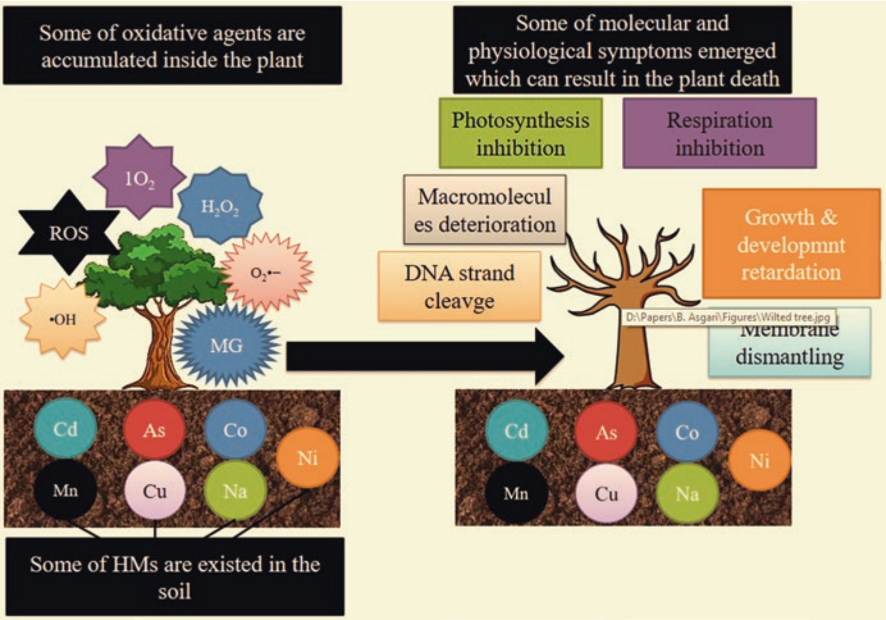

Fig. 1 The negative effects of heavy metals on plants

2013). The production of MG can interfere with plants' different mechanisms such as antioxidant defense system and photosynthesis that may eventually result in intensifying the generation of ROS (Dalvi and Bhalerao 2013; Viehweger 2014). Oxidative stress can deteriorate macromolecules (such as proteins), dismantle the membranes, cleave DNA strand, and finally demise the plant (Fig. 1) (Flora et al. 2008; John et al. 2012).

Changing physiological and biochemical processes, such as global gene expression, plants can develop their tolerance to stresses (Manara 2012). Plants use different strategies—avoidance and tolerance—to deal with the metal(loid)s. When the plant is able to restrict the absorption of metal(loid)s, it uses avoidance strategy. The plant does this by biosorption to cell walls, extracellular precipitation, reduced uptake, and increased efflux. However, when the plant is able to survive under high concentration of metal(loid)s, it uses tolerance strategy. The plant does this by chelating through amino acids, GSH, metallothioneins (MTs), and organic acids, or through compartmenting with vacuoles, and antioxidative defense mechanism upregulation (Hatata and Abdel-Aal 2008; Ali et al. 2013; Bielen et al. 2013). In this review chapter we prepare a comprehensive up-to-date knowledge about the way of plants' response to HM stresses. However, our major focus is on the MG and ROS metabolism and their relation to GSH. We also inspect the gene function and its relation to the MG and ROS detoxification mechanisms which are induced under HM stress.

2 Toxic HMs and Their Action in Plants

The manifestations of HM accumulation in plant cells are deferent. Redox active—directly involved in redox reactions—and redox inactive—not involved in redox reactions directly—are two groups of HMs. The exposure of plant to the redox-active HMs (Co, Cr, Cu, Fe) directly results in the generation of $O_2^{\bullet-}$, $^{\bullet}OH$, and H_2O_2 through Haber-Weiss and Fenton reactions (Asgari Lajayer et al. 2017a). However if plants are exposed to the redox-inactive HMs some indirect mechanisms, such as electron transport chain disruption, lipid peroxidation induction, and antioxidant defense mechanism malfunction, cause oxidative stress. HMs can strongly bind to O, N, and S atoms and play their destructive roles (Sharma and Dietz 2009). Due to this strong affinity of HMs they can easily inactivate enzymes. For instance, Cd binds sulfhydryl groups and inhibits the activity of enzymes and function of structural proteins (Nagajyoti et al. 2010). Enzymes often need HM ions to do their duties in bioprocesses. They are known as cofactors. Cu^{2+}, Mg^{2+}, Fe^{2+}, and Ca^{2+} are some of the important cofactors in the cell. These cofactors have precise action in their related enzymes and their displacement leads to loss or inhibition of enzyme activity. For instance, substitution of Mg^{2+} in RuBisCO with each of Zn^{2+}, Ni^{2+}, and Co^{2+} leads to inactivity of the enzyme (Kumar and Maiti 2013). Calmodulin-dependent phosphodiesterase activity is inhibited through displacement of Ca^{2+} by Cd^{2+} in calmodulin in radish (Nematshahi et al. 2012). HMs also damage the membrane. They cause protein thiol oxidation or cross-linking in membrane, inhibit the function of H^+-ATPase, and alter the fluidity of the membrane (Asgari Lajayer et al. 2019a). Plants accumulate MG in response to HM stress which eventually results in oxidative stress due to GSH content reduction (Fozia et al. 2008).

The toxicity of HM is contributed to three major reasons: (a) The production of MG and ROS is stimulated by alteration in the defense mechanism against antioxidant agents. They can also be produced through auto-oxidation or Fenton reaction. (b) Essential metal ion substitution with other (heavy) metals. (c) Binding of HMs to functional groups (such as carboxyl, histidyl, and thioyl) because of their high affinity to these groups (Tangahu et al. 2011).

3 Plant Responses to HM Stress

Plants trigger various metabolic and physiological modifications under HM exposure (Ghorbanpour et al. 2016). However, the responses are different between various HMs, because different HMs have different places to act in plants. The reduction in plant growth is the most prominent visual symptom (Nath et al. 2008; Nagajyoti et al. 2010). Chlorosis and necrosis, decreased seed germination rate, and decrease in the photosynthesis efficiency are related to molecular and biochemical alterations which are brought about by HM stress (Živković et al. 2012). Also, water uptake, evapotranspiration, and nutrient metabolism may be influenced under HM stress (Vezza et al. 2018). HMs can interfere with the uptake of elements, such as Ca, K, P, and Mg (Asgari Lajayer et al. 2017b). Plants' exposure to HMs usually affects the structure and function of thylakoids, so it can affect the photosynthesis complex directly. HMs cause the damage of thylakoid membrane through the release of some components from it (Muszyńska et al. 2018). Moreover, Mg can be replaced by some HMs. Chlorophyll synthesis may be reduced due to the destructive effect of HMs on the enzymes involved in the synthetic pathways of it (Asgari Lajayer et al. 2019c). HMs may also inhibit the function of enzymes related to CO_2 fixation. Therefore, HMs may interfere with both photosynthesis and carbon assimilation processes and eventually cause plant death (Ghorbanpour et al. 2016). For instance, photosynthesis rate of *Zea mays* L. is decreased under Pb stress (Ahmad et al. 2011). Also, the respiration inhibition of *Oryza sativa* L. was reported under the exposure of cadmium (Llamas et al. 2000).

HM toxicity causes the accumulation of extra ROS in plant cell. Some HM metals can directly generate ROS, such as Cu. However, others do this indirectly. For instance, Cd inactivates enzymes through LOX expression induction which eventually results in fatty acid oxidation. This triggers the production of ROS inside plant cells (Skórzyńska-Polit et al. 2006). Although ROS causes cell disturbances, plants' antioxidative defense mechanism helps them to overcome stresses such as the ones from HMs (Asgari Lajayer et al. 2017a).

4 The Molecular Basis of HM Tolerance

The response of plant to various stresses, such as HM stress, is the result of physiological and molecular interrelationship network. Therefore, study of this network, each mechanism individually and their genetic basis, is important to introduce some new tolerant species (DalCorso et al. 2010). Different plants use different mechanisms to cope with HM stress. Adaptive and constitutive mechanisms are two main mechanisms to cope with excess amount of HMs in the environment (Meharg 1994). Experts use all physiological, biochemical, and molecular approaches to unravel the mechanism of accumulation, adaption, and tolerance of HMs in plants. Synthesis of various amino acids, signaling molecules, and proteins occurs in the molecular level in plants under stressful conditions. For instance, recent studies proved the accumulation of heat-shock proteins (HSPs) under HM exposure (Zhao et al. 2011). The higher proline accumulation was reported in *Solanum nigrum* L. (a Cd hyperaccumulator) compared with *Solanum melongena* L. (a nonaccumulator) (Sun et al. 2007). This can prove the role of proline in detoxification processes of HMs. Some chelating compounds such as nicotianamine, phytosiderophores, and organic acids are released by plant roots and can influence the uptake of HMs (Dalcorso et al. 2010). Mitogen-activated protein kinases (MAPK) are triggered under HM stress. They have various forms with different kinetics which are induced under different stress pressures. For instance, *Medicago sativa* L. showed the activation of four different MAPKs (MMK2, MMK3, SAMK, and SIMK) under Cu and Cd stress. Cu stress induced the production of MAPKs more rapidly than the Cd stress (Jonak et al. 2004). Plasma membrane exclusion, immobilization, HM uptake and transport restriction, HM chelation, stress protein upregulation, and production of polyamines and signaling molecules such as nitric oxide and salicylic acid have also been reported (Zhu et al. 2011).

4.1 HM Uptake and Transport Restriction

To take up HM ions from the soil plants intercept HMs by their roots, take them up by their roots, and translocate them to the shoots. The uptake of the HMs through apoplast or symplast depends on the type of HMs. Most of the HMs are taken up to the plant through energy-consuming processes (Shahid et al. 2017). Avoidance strategy is a method to cope with HMs employed by plants. Plants avoid to take up excess amount of HMs based on this strategy. Complexing and precipitation are two avoiding strategies. Precipitation occurs through increasing the pH of root environment or excreting some anions (such as phosphate). For instance, the excretion of phosphate was shown in the aluminum-tolerant maize cultivars. The tolerant cultivars (South American 3) did not show toxicity symptoms; however, sensitive cultivars (South American 5 and Tuxpeño) showed (Pellet et al. 1995). It was also shown that oxalate secretion from the root apex of tomato helps the plant to exclude Cd from the root environment (Zhu et al. 2011). These findings suggest that HM-binding agent's excretion into the root environment plays an important role in HM-avoidance mechanism of plants.

4.2 The Hyperaccumulation Mechanisms of HMs

Plants which tolerate HMs often use three strategies to cope with them. These plants may restrict the translocation of HMs from root to shoot, or retain the root cell uptake, or chelate them and eventually store them into the vacuoles. There are rare plant species which are able to transport HMs from the root to the shoot efficiently. This translocation occurs through xylems which is driven by transpiration force probably (Salt et al. 1995). These plants are able to accumulate HMs even in low concentration from the environment. The concentration of HMs in the cell membrane of hyperaccumulators is unusually high. This can occur because of the high expression of HM transporters in the cell membrane. These transporters were identified in *Thlaspi caerulescens*, a Cd and Zn hyperaccumulator (Lombi et al. 2001). *T. caerulescens* has highly efficient chelating and intracellular compartmentalization mechanisms (Pilon-Smits and Pilon 2002). It has low concentration of HMs in root vacuoles, high translocation rate of HMs from the roots to the shoots, and high uptake of HMs to the leaves.

4.3 Chemical Modification

HMs can be assimilated into the organic molecules through metal-modifying enzymes. Changing the oxidation state of HMs is the other detoxifying mechanism that occurs through metal-modifying enzymes. Dimethyl selenide is the organic and less toxic form of selenite. This modification occurs through methyltransferase. Cr (VI), the toxic form of Cr, may be modified by chromate reductase and Cr (III), the nontoxic form of Cr, can be produced. For instance, water hyacinth (*Eichhornia crassipes*) is capable of detoxifying Cr (IV) through root uptake. Indeed this plant can accumulate the nontoxic form of Cr in its root and transport some part of this Cr to leaf tissues. Dicots can reduce Fe through reductase enzymes in their root cell membrane before uptake (Pilon-Smits and Pilon 2002). Totally, HM reduction is a useful phytoremediation mechanism to detoxify HMs.

4.4 Transcription Factor (TF) Modulation

Metal response-binding transcription factor 1 has a major role in response to and tolerance of HMs, as it triggers the activation of genes responsible for the detoxification, transport, and uptake of HMs in plants. Various TFs involved in HM stress response are identified in different plants. For instance, basic leucine zipper (bZIP), myeloblastosis protein (MYB), WRKY, and ethylene-responsive factor (ERF), from different TF families, control the expression of some genes responsible for the Cd stress tolerance (Bielen et al. 2013).

4.5 Proline Synthesis Under HM Stress

The proline accumulation under HM stress has been reported frequently (Tangahu et al. 2011; Guo et al. 2012). The increased level of proline in plant can produce an enhanced protection against Cd (Islam et al. 2009). HM-tolerant plants have elevated proline content in comparison with the nontolerant plants in the absence of HMs (Tangahu et al. 2011). Proline does not have a role in sequestering HMs. But its role is in the reducing of HM-induced damaging of free radicals. It was shown that the HM tolerance of the *Vigna radiata* L. increased by applying exogenous proline, because it enhances the amount of GSH and GSH-metabolizing enzymes (Flora et al. 2008). However, further research towards integration of the growth-inhibiting and -protecting properties of Pro is needed. Huang et al. (2010) studied the physiological and biochemical responses in leaves of two mangrove plant seedlings (*Kandelia candel* and *Bruguiera gymnorrhiza*) exposed to multiple HMs (Cd^{2+}, Pb^{2+}, and Hg^{2+}) and concluded that Pro, GSH, and PCs-SH in *K. candel* may play a more important role in ameliorating the effect of HM toxicity than in *B. gymnorrhiza*.

5 Transgenic Plants and HM Tolerance

Molecular biology is a strong field to study and improve the mechanism of HM tolerance in plants, as it can reveal key steps in this mechanism through molecular approaches such as genetic engineering (Pilon-Smits and Pilon 2002). Many genes are identified through classic genetics involved in uptake, sequestration, tolerance, chemical modification, and translocation. Moreover, regulatory genes are identified involved in regulating the related gene(s). Transferring and overexpressing of genes responsible for uptake, sequestering, translocation, and tolerance can be a successful approach to create some efficient plants capable of remediating HMs (Clemens et al. 2002). So the efficiency of HM phytoremediation depends directly on the processes such as metal uptake and translocation. Transferring the genes involved in any of these processes can enhance the efficiency of HM phytoremediation. Any combination of these genes can be overexpressed in transgenic plants. The overexpression of metal ligands and transporters, enzymes involved in the alteration of redox state of HM genes, can improve HM phytoremediation efficiency. Genetic engineering is capable of creating transgenic plants with different strategies to remediate HMs (Table 1). HMs can be accumulated in harvestable organs (phytoextraction) or absorbed to the root more than normal range (phytostabilization, rhizofiltration) by these plants. For instance, cysteine is the precursor molecule for the

Table 1 Transgenic plants with enhanced ability to bioremediate heavy metals

Plant	Transferred gene	Gene function	Heavy metal phytoremediated	References
Arabidopsis thaliana	Zinc finger transcription factor *AtZAT6*	Gene regulation	Cd	Chen et al. (2016)
Arabidopsis thaliana	*MAN3*	Encoding apoplastic endo-β-mannase	Cd	Chen et al. (2015)
Indian mustard (*Brassica juncea*)	*GS* and *γ-ECS*	Overproducing the enzymes gamma-glutamylcysteine synthetase (ECS) or glutathione synthetase (GS)	Cd and Zn	Bennett et al. (2003)
Indian mustard (*Brassica juncea*)	*γ-ECS*, *APS* or *GS*	Overexpression of adenosine triphosphate sulfurylase (APS), γ-glutamylcysteine synthetase (ECS), and glutathione synthetase (GS)	Se	Bañuelos et al. (2005), (2007)
Sterile line of poplar *Populus alba* X *P. tremula* var. glandulosa	*ScYCF1*	Encodes a transporter that sequesters toxic metal(loid)s into the vacuoles of budding yeast	Cd, Zn, Pb	Shim et al. (2013)
Arabidopsis thaliana	*ACBP1*	Overexpression of Arabidopsis acyl-CoA-binding protein binds Pb	Pb	Xiao et al. (2008)
Solanum lycopersicum	*Enterobacter cloacae ACC deaminase under* the control of CaMV 35S, *A. rhizogenes* RolD or tobacco pathogenesis-related PRB-1b promoters	Regulates stress-induced ethylene production	Several HMs	Grichko et al. (2000)
Brassica napus	*Enterobacter cloacae ACC deaminase*	Regulates stress-induced ethylene production	As (V)	Nie et al. (2002)
Petunia hybrida Vilm	*iaaM* and *ACC deaminase* genes	Plant senescence-inhibiting and growth-promoting regulation	Cu and Co	Zhang et al. (2008)
Indian mustard (Brassica juncea)	*AtAPS1*	Promotes selenate reduction as well as Se tolerance and accumulation	Se	Pilon-Smits et al. (1999)

synthesis of GSH, the predominant nonprotein thiol, which plays an important role in plant stress responses. GSH has been implicated in plant responses to toxic levels of HMs, as it is the precursor for the synthesis of PCs, the thiolate peptides involved in the detoxification of Cd and other HMs. Stimulation of the synthesis of building blocks for GSH may have been found to increase Cd tolerance in transgenic plants. *Arabidopsis thaliana* overexpressing cytosolic O-acetylserine(thiol)lyase gene (*OASTL*) showed Cd tolerance by increasing both cysteine and GSH availability (Domínguez-Solís et al. 2004).

6 Conclusion

The negative effect of HMs on organisms especially human being is one of the serious environmental concerns globally. HM bioremediation is a cost-effective and environmental friendly approach to decrease the entrance of HMs into the food chain. Phytoremediation is an effective bioremediation method. Therefore, molecular and cellular adaptation of plant cells in response to HM stress appears to be necessary to improve plant HM tolerance and detoxification. Identifying key pathways and components (enzymatic and nonenzymatic) of plants involved in the HM phytoremediation has paved the way of constructing efficient systems to bioremediate HMs from the soil, water, and air. Different HMs need different mechanisms to be bioremediated or tolerated. Moreover plants show completely different behaviors under excess amount of HMs in comparison with normal conditions. Many of these mechanisms have not been unraveled thoroughly and there is a need for extensive studies in this area. In addition, hypothesizing a common tolerance and bioremediation ability for all HMs is difficult. This requires experienced experts and more education in this field. The increasing identification and study of the remarkable natural variation in the capacity of plants to accumulate and tolerate HMs is continuing and will continue to provide a wealth of information. Therefore, concerted efforts by various research domains will further increase our understanding of the fundamental mechanisms involved in hyperaccumulation processes that naturally occur in metal-hyperaccumulating plants. This should allow us to develop plants that are more ideally suited for phytoremediation of HM-contaminated soils.

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