Chapter 10
Heavy Metal Uptake and Transport in Plants

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10.1 Introduction

Plants have developed different biochemical systems to overcome the heavy metal-induced stresses. An increase in the metal ion concentration in soil, metallothioneins, stress proteins, etc. results into reactive oxygen species (ROS) production that ultimately leads to programmed cell death. To deal with such problems, plants have developed certain defense mechanisms or adaptation strategies including restriction of metal ion uptake, metal export from the plant, chelation and compartmentalization, etc. These processes involve metal transporters, i.e., copper transporter family, ZIP (ZRT-IRT-like protein) family, NRAMP (natural resistance-associated macrophage protein) family of transporters, MATE (multidrug and toxic compound extrusion) protein transporters, HMA (heavy metal ATPase) transporters, oligopeptide transporters, ABC (ATP-binding cassette) family of transporters, and cation-diffusion facilitator family of transporters. These transporters act through a series of signaling events like phosphorylation cascades, hormones, mitogen-activated protein kinases, and calcium-calmodulin systems, ultimately leading to the balance of nutrients in the plant necessary for its survival.

Trace quantities of some heavy metals are essential for plant metabolism; however, at higher concentration they are potentially toxic to plants and soil ecosystem (Nagajyoti et al. 2010). Applying inorganic fertilizers leads to the buildup of metals in soils (Li et al. 2010b). Soil and sediments obtained from

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domestic water sources are found to possess radioactive elements along with heavy metals (Muhammad et al. 2012). In addition to other heavy metals, polonium-210 is found in the vicinity of phosphate fertilizer industry as a major contaminant source (Aoun et al. 2010). Mining, smelting, and coal-fired power plants also contribute to the accretion of heavy metals in soils and plants (Okedeyi et al. 2013). High altitude points with comparatively less anthropogenic activities are usually less infested with these metals (Cheng et al. 2013). Plains are largely affected due to extensive human activities.

Over a period of time, the accumulation of heavy metals in soil affects the quality of agricultural soil, which leads to transmission of toxic metals to the human diet as a consequence of increased crop uptake (Reis et al. 2012). Bioaccumulation of these metals in the edible parts of plants increases the crop risk to human health as observed in *Brassica chinensis* and other vegetables (Li et al. 2012). High salt contents in the soils result into reduction of alkalinity, inhibition of seed germination, and unavailability of Mn that results into the depletion of vegetation. Heavy metal accumulation in soils leads to reduction in the faunal diversity. As described in a study ore-concentrating factory caused 1.5–6.3-fold decrease of microorganisms and 3–4-fold decrease of streptomycetes, hence decreasing their number and diversity as well (Hryshko and Syshchykova 2010). Guo et al. (2011) studied that the metabolic activities of various microbial communities inhabiting polluted soils are also affected. The utilization of carbon sources by soil microbes was activated in slightly polluted soils where as in heavily polluted soils the carbon source utilization was inhibited (Guo et al. 2011). It can affect plants with the decreased chlorophyll and increased peroxidase activity resulting in the damage to plants (Li et al. 2010a). In the soil, metabolic characteristics of different microbial organisms vary with the pollution intensity. With the increase in pollution, the decrease in carbon source utilization and the decrease in the activity of enzymes like urease, alkaline phosphatase, catalase, sucrase, protease, and cellulose takes place that results into damaging effects (Guo et al. 2012). Risks from the intake of polluted vegetables are of great concern as the presence of metals is observed in the edible parts of selected *Brassica* species (Khan et al. 2010). The distribution of these metals in surface top soil like zinc, lead, and copper can directly affect the health of workers besides other ecological concerns (Fujimori and Takigami 2014). When this polluted soil was decontaminated using clean water, the stored acidity was reduced after a long period of time showing the difficulty in reducing the contamination (Chen et al. 2010). Heavy metals can pose a serious risk to food chains and freshwater. Composts are well suited for revegetation of contaminated soil, but care should be taken in order to avoid any complication (Farrell et al. 2010).

10.2 Restriction of Metal Ion Uptake from Soil

Metal availability and transport in the rhizosphere are influenced by microorganisms and root exudates. Root exudates are described as the substances which are released into the medium, present in the vicinity of healthy and intact plant roots (Bais et al. 2006). Literature survey reveals a variety of compounds released by intact roots, which include enzymes, peptides, amino acids, sugars, vitamins, nucleotides, organic acids, fungal stimulators, attractants, inhibitors, and other miscellaneous compounds (Bais et al. 2006; Dakora and Phillips 2002).

In higher plants, well-organized systems for obtaining inorganic nutrients as well as metal ions from the soil are present. Such systems are based on a few transport mechanisms. It is known that heavy metals are cotransported in the roots through the plasma membrane (Krämer et al. 2007). Metals enter into the cells through cation transporters with a wide range of substrate specificity. Since toxic heavy metals such as Pb and Cd with no known biological functions are also transported by same mechanisms, specific transporters do not exist (Silver et al. 2002).

10.3 Metal Ion Binding to Extracellular Exudates

The major function of root exudates is to prevent metal uptake inside the cells and also their chelation. For example, histidine and citrate are present in root exudate which chelate Ni and reduce its uptake from the soil (Hooper et al. 2010). The release of citrate in root exudates of maize and that of malate in sorghum (*Sorghum bicolor*) helps to prevent Cd from entering the plant (Pinto et al. 2008). Moreover, release of certain oxidants and oxygen in the rhizosphere results in iron plaque formation on the root surface which has been suggested as a mechanism to prevent heavy metal toxicity. This plaque prevents Cd from entering into the roots by adsorbing and sequestering Cd onto root surface in rice plant (Liu et al. 2008). Although excluding excess heavy metals from plant is helpful in preventing heavy metal stress, some tolerant and hyperaccumulator plants have a higher uptake level as compared to sensitive plants, so other mechanisms also exist (Rascio and Navari-Izzo 2011).

10.4 Metal Ion Binding to the Cell Wall

The exclusion of metal ions from the cell is an important heavy metal tolerance strategy in plants. The metal content of root cells is also controlled by binding of metal ions such as Zn and Cu in the apoplast. Large portions of heavy metals are accumulated in plasma membrane-cell wall interface (Hossain et al. 2012). The

CEC (cation exchange capacity) of a plant is essentially controlled by the available exchange sites on the cell walls. Cation binding sites for metal exchange are present on the root cell walls. These influence greatly the availability of ions for uptake (Morley 2010). The cell wall plays a key role in the immobilization as well as uptake of toxic heavy metal ions into the cytosol by providing histidyl groups, pectic sites, and extracellular carbohydrates such as mucilage and callose. Composition of cell wall is the characteristic of a specific plant genotype (DalCorso et al. 2013). Thus, different plant genotypes possessing chemically distinct root cell walls have dissimilar sensitivities to a specific metal toxicity. The cell wall has limited number of binding sites and it is in direct contact with metal ions; this suggests that it has minor impact on metal tolerance (YANG et al. 2005; Clemens 2006). The function of the cell wall in metal tolerance is, however, still unclear.

10.5 Heavy Metal Transport Through the Plasma Membrane in the Root

Various families of plasma membrane transporters have evolved in plant cell membranes which are significantly involved in the uptake and homeostasis of metal ions (Wang et al. 2011). Metal transporters on plasma membrane and tonoplast maintain physiological concentrations of heavy metals in a cell, but they may also contribute to heavy metal stress responses. Such transporters belong to the heavy metal P_{1B}-ATPase, the NRAMP, the CDF, and the ZIP families (Lee et al. 2010a; Maestri et al. 2010). The biological function, cellular location, and metal specificity of most of these transporters are still unknown. These metal ion transporters were discovered by complementation in mutant *Saccharomyces cerevisiae* organisms which were defective in metal uptake (Manara 2012).

10.6 ZIP Family

This is one of the principal metal transporter families involved in metal uptake. The first identified proteins of this family are ZRT and IRT-like protein, and this is where the name ZIP comes from. The first ZIP transporter discovered by expression cloning in yeast double-mutant strain (*fet3fet4*, which have impaired iron transport) was the *A. thaliana*, IRT1. Certain ZIP proteins are expressed in *A. thaliana* shoots and roots in response to Zn or Fe loading, as a part of stress response (Nishida et al. 2008). Up to now over 25 ZIP family transporters have been identified. On the basis of amino acid similarities, the respective genes fall into two subfamilies (Grotz et al. 1998; Claus and Chavarría-Krauser 2012).

The ZIP families of transporters are involved in the translocation of divalent cations across cellular membranes, and they are found in many plants, bacteria, fungi, and animal species. IRT1 functions in Fe, Zn, Cd, and Mn transport, so, in plants with Fe deficiency once IRT1 is expressed, it can also transport other divalent metals. It was observed that Cd competes with Fe for uptake in IRT1-expressing yeast. So in order to overcome Cd toxicity, one must increase the Fe concentration in soil. In *A. thaliana*, Ni excess induces the expression of IRT1, which is involved in accumulation and uptake of Ni (Thomine et al. 2000).

The Zn transporters of yeast, ZRT1 and ZRT2, are two other members of ZIP family. They were discovered on the basis of their similarity with IRT1 which is 54–65 %. Studies have demonstrated that normally yeast has two systems of Zn uptake (Claus and Chavarría-Krauser 2012). One system has high affinity and is activated only in Zn deficit cells, and the other has low affinity and is induced in cells with enough zinc. The transporter protein of the former is encoded by the ZRT1 gene, whereas ZRT2 gene encodes transporter of the latter (Guerinot 2000; Manara 2012).

Similar method was used in the identification of IRT1 and ZIP1, ZIP2, and ZIP3 genes of the *A. thaliana*. It has been found that these three proteins are not involved in Fe transport, but they have significant role in Zn transport and are the first zinc transporter genes to be cloned (Lin and Aarts 2012). Another *A. thaliana* ZIP identified via analysis of the genomic sequence is ZIP4, which is induced in shoots and roots by Zn deficiency (Küpper and Kochian 2010). In another study on rice, the OsZIP8 gene which encodes a plasma membrane Zn transporter was characterized, and it was found that it is upregulated in roots and shoots under Zn deficiency (Lee et al. 2010b).

In the study on maize (*Zea mays)*, nine ZIP-encoding genes were recognized. Transgenic studies showed that all ZmZIP (*Zea mays* ZIP) proteins are present on plasma membrane and ER (endoplasmic reticulum); a variable region between TM-3 and TM-4 and a conserved transmembrane domain are present. During different developmental stages of embryo and endosperm, the expression patterns of all genes were studied and variations were observed. It was found that the buildup of ZmZIP6 and ZmIRT1 was greater in the late developmental stages of embryo, whereas ZmZIP4 was upregulated in early stages. Moreover the expression of ZmZIP5 was found correlated with the middle stage of the development of endosperm and embryo (Li et al. 2013). In Fabaceae family the Zn homeostasis was studied in legume *Medicago truncatula* model; Zn transporters from ZIP family were characterized. Three of the six ZIP studies were found to be involved in Zn transport which are MtZIP1, MtZIP6, and MtZIP5 (Stephens et al. 2011).

10.7 NRAMP Family

NRAMP family has been demonstrated to transport a variety of heavy metal ions like Mn, Cu, Fe, Zn, Cd, Ni, and Co in eukaryotes, including plants, fungi, animals, and the bacteria also. NRAMP is an acronym of natural resistance-associated macrophage protein (Sasaki et al. 2012). The *A. thaliana* NRAMPs 1, 3, and

4 are found to be the cause of Fe, Mn, and Cd transport. When studied in yeast, NRAMP 6 transported Cd only and the function of NRAMP 2 is still unknown although it showed no transport activity for Fe. In rice (*Oryza sativa*), there are six and in *A. thaliana* genome, there are seven members (Sasaki et al. 2012). NRAMP 1 expressed in the cell membrane of root cells has high affinity for Mn. NRAMP 3 and 4 are located in tonoplast and function in Fe transport from vacuole (Cailliatte et al. 2010). Recently it has been reported that NRAMP 3 and 4 are also involved in intracellular transport of Mn like Fe. In rice, only 2/7 NRAMP genes have been sequenced and characterized. In yeast NRAMP 1 transported Cd and Fe but not Mn. NRAMP 1 is predicted to have a role in the uptake and transport of Cd within plants, but exact function of OsNRAMP1 (rice NRAMP 1) is unknown (Cailliatte et al. 2010; Sasaki et al. 2012). NRAMP 4 gene was isolated from *Thlaspi japonicum*, which is a Ni hyperaccumulator species. It showed its capability for Ni transport but in yeast it didn't transport Mn, Cd, or Zn (Lin and Aarts 2012).

10.8 Copper Transporter Family

The copper transporter (COPT/Ctr) is found in plants, eukaryotes, animals, and fungi. The *A. thaliana* copper transporter was identified by functional expression mutation of the yeast mutant strain ctr l-3, which is copper uptake defective (Sancenón et al. 2004; Klaumann et al. 2011). All proteins of this family contain three TM (transmembrane) regions, TM1, TM2, and TM3. There is a short connecting sequence between TM2 and TM3 which is reported to have an essential function, and it binds the two regions tightly at the extracellular side of the membrane (Yuan et al. 2011). COPTR/Ctr proteins can form homodimer or heterocomplex with themselves or other proteins which are also associated with copper transport. Such heterocomplex is predicted to provide a channel for Cu passage through lipid bilayer. The presence of COPTR on lysosomal membrane shows that they are involved in both intracellular and extracellular transports of Cu ions. Their expression is upregulated in conditions of Cu deficiency and is downregulated when copper is in excess (Yuan et al. 2014).

In rice, COPTR family comprises of seven members, COPTR1–7. The rice COPTR family has all conserved features. COPTR 1 and COPTR 5 make homodimers and heterodimers also. In *A. thaliana* COPTR 5 is found important for Cu transport, mainly efflux from the vacuole at cellular level, and in the plant as a whole it is involved in the interorgan transportation of Cu ions from the root to important organs like reproductive organs (Klaumann et al. 2011). In some cases the COPTRs have also been found to be involved in the uptake of other substances also. Nonetheless, in a study it is demonstrated via mutant yeast strains that rice COPTRs cannot transport Zn and Fe alone. The yeast mutants (zrt1zrt2ZHY3) are missing in the zrt1 and zrt2 proteins required for Zn uptake. When the mutant cells are transformed with any one of the rice COPTRs, they are unable to grow in selective medium without Zn supplement (Yuan et al. 2011).

10.9 Plant Responses to Heavy Metals at Root-Shoot Level

Several types of proteins contribute in the transport of metals from the root to shoot. Soon after the metals are taken by the roots, metal ions move toward the xylem to be transported to the shoots in the form of complexes with various chelators (Migeon et al. 2010). Organic acids, e.g., citrates and malates, and various amino acid derivatives, e.g., histidine and nicotianamine (NA), are chelators of Fe, Ni, and Cu chelators in the xylem (Manara 2012). As the phloem translocates from source to sink, metal ions move along. Hence, phloem sap contains metals obtained from source tissues, like Fe, Cu, Mn, and Zn. In phloem only NA is present as chelator (Curie et al. 2009; Hossain et al. 2012).

10.10 Heavy Metal Transporting P-Type ATPase (HMAs) Transporter Family

The HMAs are involved in the transport of metal ions between cellular compartments, cytoplasm and xylem. They are basically involved in the efflux of heavy metal ions from the cytoplasm by transport across the plasma membrane or into organelles in *A. thaliana* and some hyperaccumulator species (Rascio and Navari-Izzo 2011). In a study it was found that in rice (*Oryza sativa*), the HMA2, i.e., OsHMA2, preferentially delivers Zn to developing tissues. It was found that OsHMA2 is expressed mainly in the mature zone of the roots and nodes. Its expression remains unaltered by Zn deficiency or excess (Yamaji et al. 2013). An efficient and well-organized transportation of metals from the root to shoot is a hallmark of hyperaccumulator plants. HMA4 is predicted to be located in the root and plays an important role in loading metals into the xylem, not only in hyperaccumulator plant *T. caerulescens* but also in *A. thaliana*. HMA3 is present on tonoplast and is Cd specific. It's responsible for confiscation of Cd in leaf vacuoles (Xu et al. 2010). In a study using transgenic strategies, in hyperaccumulating rice species (*Oryza sativa*), OsHMA3 gene was identified that controls root to shoot Cd transport. It basically encodes a P_{1B}-ATPase transporter and found to be localized to tonoplast (Miyadate et al. 2011). Overexpression of HMA4 and HMA3 generates tolerance in *A. thaliana* against Zn and Cd. HMA5 of *A. thaliana* is also expressed in roots and other organs but in response to Cu (Xu et al. 2010).

10.11 Multidrug and Toxic Compound Extrusion (MATE) Protein Family of Efflux Proteins

The MATE proteins have been identified in many eukaryotes and prokaryotes including plants. These are basically the efflux proteins involved in extrusion of toxic compounds from cell (Buer et al. 2010). In recent studies it has been demonstrated that a cluster of genes in plants encodes the citrate transporter, which plays a role in detoxification of aluminum and translocation of Fe from roots to shoots (Yokosho et al. 2010). They participate in the loading of Fe and citrate into the vascular tissue in the roots. In order to transport Fe from the root to shoots, ferric citrate complexes must form (Durrett et al. 2007). In another study with rye plant, the two mate genes, ScFRDL1 and ScFRDL2, of rye were characterized. The former is involved in translocation of Fe and the latter is activated by Al (Maron et al. 2010). It is found that both of them are localized to root tip endodermal cells and play a role in efflux of citrate into the xylem (Magalhaes 2010; Durrett et al. 2007).

10.12 Oligopeptide Transporter Family

The oligopeptide transporters (OPT) are a superfamily of oligopeptides found in animals, plants, and fungi. They are predicted to have 13–16 transmembrane domains (Xiang et al. 2013). These transporters are capable of transporting wide range of substrates. The YSL, i.e., yellow stripe 1 protein is specific for plants, takes its name from maize yellow stripe 1 protein (YS1). The maize YS1 transporter is involved in translocation of Fe, Ni, Cu, Zn, and, to some extent, Cd and Mn. These ions are chelated prior to translocation either by NA or phytosiderophores (Lubkowitz 2011). In a study nine OPTs belonging to peptide transporter group of genes in rice (*Oryza sativa*) were identified based on some similarity with maize YS1 gene. They were named OsOPT1 to OsOPT9 and are expressed in roots, stems, hulls, leaves, embryo, and pedicles, but not in every tissue. It was demonstrated that OsOPT1, OsOPT3, OsOPT4, OsOPT5, and OsOPT7 are capable of transporting ferrous or ferric iron chelated to NA (Vasconcelos et al. 2008). Similarly eight YSL transporters were identified in *A. thaliana*, AtYSL1 to AtYSL8. These are also widely expressed and involved in translocation of chelated iron. AtYSL1 is expressed in leaf xylem parenchyma and pollen as well. AtYSL2 is expressed in shoot and root tissues (Cao et al. 2011; Stacey et al. 2006).

10.13 Complex Formation and Compartmentalization of Heavy Metals in Cytosol

If the heavy metal ion is not to be utilized in any metabolic activity inside the cell immediately, it may rise to toxic concentration. Plants have developed mechanisms to prevent toxicity caused by them. If the concentration of that metal increases a specific threshold, mechanism to sequester this condition activates (DalCorso et al. 2008). One such strategy is to transport heavy metals out of the cell into the apoplast as described above or to store them in vacuole, in clearing the cytosol from metal. Another strategy used by most of the plants is phyto-chelation by various compounds (DalCorso et al. 2008, 2010).

10.14 Metal Sequestration in the Vacuole

Cytosol and other cellular compartments are to be cleared of the toxic metals because sensitive metabolic activities take place there (DalCorso et al. 2010). Therefore central vacuole is the most appropriate region for this. The main storage compartment for metal ions in plant cell is vacuole (Marschner and Marschner 2011). Several families of intracellular transporters found on tonoplast have been identified in plants involved in this compartmentalization.

10.15 ABC Family of Transporters

ABC transporters, i.e., ATP-binding cassette transporters, are capable of transporting xenobiotics and chelated metals into the vacuole. The subfamily MRP is now redefined as the class C of ABC proteins, i.e., ABCC transporters, and they are found in all eukaryotes. In *A. thaliana* 15 ABCC genes have been described, and these proteins are localized on tonoplasts, even though some may also be found on plasmalemma (Wanke and Kolukisaoglu 2010). Of these, ABCC11 and ABCC2 are best studied. These two proteins (ABCC11 and ABCC2) act together in PC transport response to heavy metal ions. ABCC1 and ABCC2 have been demonstrated to transport PC-Cd into the vacuole, thereby having a role in Cd sequestration, whereas the role of ABCC3 remains unclear in Cd transport (Noctor et al. 2013).

10.16 Cation-Diffusion Facilitator Family of Transporters

Proteins of the CDF family proteins play a role in homeostasis of Cd, Zn, Fe, and Co in plants, animals, and some other microbes. The CDF family proteins comprise of six transmembrane domains, a conserved sequence between transmembrane domains 1 and 2, histidine-rich cytosolic regions at both termini; this histidine-rich region acts as a sensor of metal concentration (Kawachi et al. 2008). In most bacterial cells, CDF proteins are found to cause metal tolerance by exporting the cations out of the cell or inside in the case of Zn for storage and detoxification (Haney et al. 2005).

10.17 HMA and NRAMP Family of Transporters

As mentioned above P_{1B}-ATPases (HMAs) are the cause of efflux of metal ions from the cytosol. The *A. thaliana* HMA has a major role in detoxification of various metals including Pb, Zn, Co, and Cd through storage in the vacuole. The NRAMP transporters such as *A. thaliana* NRAMP3 and NRAMP4 are found in the tonoplast and their function is still unknown. But the overexpression of NRAMP3 increases Cd sensitivity (Sasaki et al. 2012; Rascio and Navari-Izzo 2011).

10.18 Conclusion

Presence of toxic heavy metals in the environment leads to numerous health hazards. Environmental pollution is an outcome of promptly growing population and increasing anthropogenic activities. This is an alarming and serious matter as soil contamination leads to plant toxicity ultimately resulting in food chain contamination. The main pollutants present in the soil are Zn, Cu, Ni, Cd, Al, As, Fe, Co, Se, and Cr. These metals when exceed threshold concentrations become hazardous. Plants adopt different molecular and cellular adaptations in order to combat heavy metal toxicity through various tolerance responses. By this, plants ultimately respond and reduce the health risks associated with heavy metals. Plants also shield themselves from heavy metal toxicity by activating different antioxidant systems which may be enzymatic or nonenzymatic. Different plants elicit symptoms against particular heavy metal toxicity through different mechanisms. Similarly the response and tolerance mechanisms also vary. Therefore, it is difficult to state a common tolerance mechanism against different heavy metals. Significant progresses have been achieved in understanding heavy metal responses, tolerance, and toxicity mechanisms. Many important components that ensure heavy metal tolerance have been identified but still many key questions are unanswered. GSH is the most significant nonenzymatic antioxidant molecule utilized by plants against heavy metal stress. The reviewed literature confirms the crucial role of glutathione (GSH) defense and tolerance against various heavy metals. Soil remediation strategies on the other hand can be used to protect plants against heavy metal toxicity. It is known as a challenging process by researchers but has numerous advantages. Phytoremediation, phytoextraction, rhizofiltration, and phytostabilization are the currently known types of soil remediation.

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