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5

Role of Transporters during Heavy Metals Toxicity in Plants

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Abbreviations

Al,	Aluminum
Cd,	Cadmium
CDF,	Cation diffusion facilitator
CEC,	Cation exchange capacity
Cr,	Chromium
GDH,	Glutamate dehydrogenase
GOGAT,	Glutamate synthase
GS,	Glutamine synthetase
Hg,	Mercury
HMs,	Heavy metals
MAPK,	Mitogen-activated protein kinase
MTs,	Metallothioneins
Ni,	Nickel
NR,	Nitrate reductase
NRAMP,	Natural resistance-associated macrophage protein
Pb,	Lead
ROS,	Reactive oxygen species

5.1 Introduction

Heavy metals (HMs) are metallic elements having comparatively higher densities and atomic weights. The major sources of HMs contamination in the agroecosystem are corrosion of metals, soil erosion and subsequent leaching and suspended sediments, industrial wastes and extensive use of HM-contaminated chemical fertilizers (Turkyilmaz et al. 2019). The most well-known HM-pollutants are Zn^{2+} , Fe^{2+} , Cu^{2+} , Mn^{2+} and Co that are toxic to plants whereas some other metals like Cd^{2+} , Hg^{2+} and Pb^{2+} are not yet known as highly toxic to plants. Even at lower concentrations, HMs tend to alter plant growth owing to their effect on physiological and metabolic processes and enzymatic activities in plants (Singh and Kalamdhad 2011; Sytar et al. 2013). Most importantly, higher concentrations of HMs in cells trigger the production of excessive reactive oxygen species (ROS) that cause gradual cell death, leading to a substantial reduction in growth and yield of crops (Nasim and Dhir 2010; Hasanuzzaman et al. 2020; Saleem et al. 2020). The availability of mineral nutrients in the soil hinders many fundamental cellular processes and down-regulates the overall plant growth performances (Nihorimbere et al. 2011). The presence of excessive amounts of HMs in the rhizosphere can reduce the uptake and translocation of essential nutrients by the plants (Seshadri et al. 2015). Moreover,

exposure to certain HMs can alter uptake and assimilation of nitrogen (Chandrakar et al. 2018) and can create an artificial deficiency of any particular nutrient (Schjoerring et al. 2019). Usually, nutrient deficiency symptoms in plants include stunted growth, senescence and yellowing of leaves, plant tissue death, etc., caused by the reduction of chlorophylls and other pigments needed for photosynthesis (Singh and Kalamdhad 2011). Reduced crop yield and quality are the common consequences of nutrient deficiency. It has been inferred that HMs toxicity has emerged as a serious threat to the environment and food security globally.

Many transporter proteins are embedded in the cellular and vacuolar membranes as well as in the membranes of different subcellular organelles that are mainly involved in HMs transportation from one organelle to the other and further eliminate it out from the plants (Hedrich et al. 2015). In each cellular compartment, there exists a set of peculiar transporters that perform versatile functions related to transportation and homeostasis of HMs (Forbes and Gros 2001). Among those, HM ATPases, natural resistance-associated macrophage protein (NRAMP) family, cation diffusion facilitator (CDF) family, Zn transporters (ZIP) family and the cation antiporter stook are significant attention in recent years (Nevo and Nelson 2006; Goswami et al. 2012; Cotrim et al. 2019). It is important to understand the interactive functions of HM transporters for the breeding of HM-tolerant crops. This study aims to critically synthesize and analyze the crucial features of HMs transporters in plants about their structures, functions and regulatory roles in diversified organisms. It is important to describe the transporter's role in HMs uptake, transportation, accumulation and reduction by plant root.

5.2 Heavy Metal-Induced Phytotoxicity

Certain trace metals (Cu^{2+} , Mn^{2+} , Fe^{2+} and Zn^{2+}) at an optimal cellular concentration play important roles as co-factors of many enzymes while at excessive levels cause toxicity (Sudre 2009). Toxic metals like Cd^{2+} , Co^{2+} and Ni^{2+} lead to the suppression of plant growth by disrupting transport activities and cellular homeostasis. The NRAMP protein family members are crucial owing to their function of transporting various ions (such as Mn^{2+} , Zn^{2+} , Cu^{2+} , Fe^{2+} , Cd^{2+} , Ni^{2+} and Co^{2+}) while acting as metal ion transporters (Nevo and Nelson 2004, 2006).

Excessive Cu^{2+} may exert detrimental effects on crop growth and production (Ravet and Pilon 2013, Tahjib-UI-Arif et al. 2020). Therefore, plants need to control Cu^{2+} homeostasis strictly to maintain an equilibrium condition at the tissue

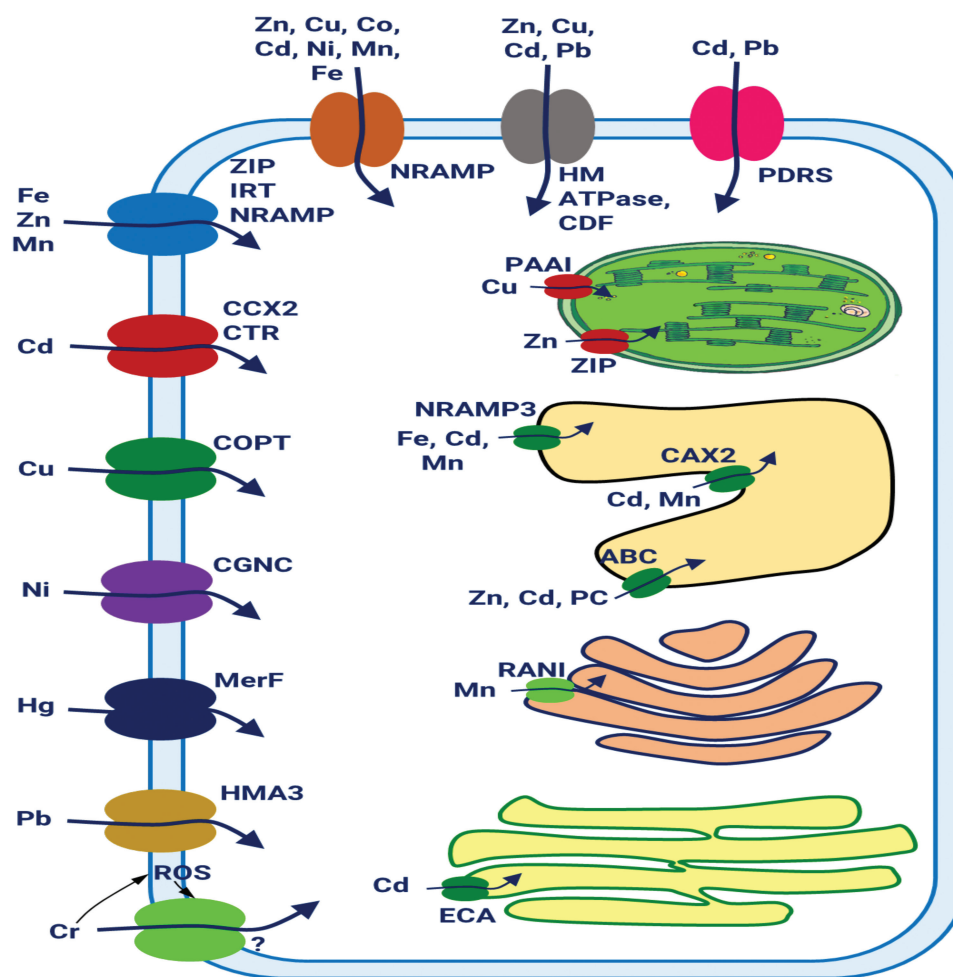


FIGURE 5.1 Cellular mechanisms involved in transport and uptake of HMs with metal transporters (Modified from Soliman et al. 2019; Williams et al. 2000; Guerinot 2000; Jain et al. 2018). **Abbreviations:** ABC – ATPases; Cd – cadmium; CDF – cation diffusion facilitator; Co – cobalt; Cr – chromium; Cu – copper; Fe – iron; Mn – manganese; Ni – nickel; Hg on to the HMs – heavy metals; Pb – lead; Zn – zinc ROS – reactive oxygen species; NRAMP – natural resistance-associated macrophage protein; PDRS – pleiotropic drug resistance transporters; ZIP – ZRT-IRT-related protein.

level (Figure 5.1). Contrarily, high-affinity nitrate transporters belonging to the NRT2 family up-regulate under low to medium Cu^{2+} levels, but this up-regulation remains ineffective in restoring N absorption by roots to original pre-toxicity levels (Puig 2014). Under Cu^{2+} toxicity, plants display diversified responses caused by genes modulating which tend to regulate nitrate uptake using low-affinity nitrate transporters as well as proton pumps.

A higher concentration of Al^{3+} is toxic for many crop plants (Krstic et al. 2012). It has been regarded as a non-essential element for plant growth; rather its excessive concentration leads to toxic effects on plants (Gupta et al. 2013; Krstic et al. 2012). Al^{3+} toxicity is dominant in acid soils, so excess Al^{3+} inhibits the uptake of nutrients from acidic soils. The cessation in root elongation has been reported as the primary symptom of Al^{3+} phytotoxicity, which may happen within 1 h after the exposure to Al^{3+} stress (Gupta et al. 2013; Krstic et al. 2012). Al^{3+} significantly affects the cell wall, plasma membrane, cytoskeleton and signal transduction pathways and triggers oxidative stress which hampers cytosolic calcium homeostasis, magnesium uptake, and auxin polar transport consequently leads to

inhibition of cell elongation and cell division (Lal 2010). Al^{3+} also inhibits NO_3^- transport across the membrane (Zhao and Shen 2018). Thus, the inhibition of NO_3^- uptake may happen due to the binding of NO_3^- transporters by the intracellular Al^{3+} (Kronzucker et al. 1999). However, the activity of nitrate reductase (NR) is inhibited by Al^{3+} exposure owing to a sharp decline in the accumulation of internal NO_3^- content (Wang et al. 2013). The NR activity is stimulated by Al^{3+} in lower concentration caused by enhanced uptake of NO_3^- (Jiang et al. 2018). The effects of Al^{3+} on the activities of close-in action enzymes in plant Jiang, metabolisms such as glutamine synthetase (GS), glutamate synthase (GOGAT) and glutamate dehydrogenase (GDH), and potential aims for improving N use efficiency in the plant are still uncertain (Zhang et al. 2018). Plants detoxify Al^{3+} in two ways viz., by excluding Al^{3+} from the root tips (exclusion mechanism), and by sequestering excessive Al^{3+} that enters the plant system (internal tolerance mechanism) (Lal, 2010).

Nickel (Ni^{2+}) in the plant is usually absorbed in ionic form, but being the non-essential element is not needed for plant growth and development. Ni^{2+} has effects on root and soil

because its mobility within the plant is usually higher than the other HMs (Gill 2014). Exposure to higher Ni^{2+} concentrations significantly inhibited plant growth (Maheshwari and Dubey 2007).

Lead (Pb) is found in the inorganic form in the environment. Among known soil pollutants, Pb is regarded as one of the most toxic metal pollutants (Dutta et al. 2018), which gets released as a byproduct of numerous industrial processes and exists in all environmental compartments (soil, water and living organisms). Plants get exposed to Pb through its transportation from soil solution as well as in the form of aerosols from the air. The low mobility of Pb in the soil supports its accumulation mostly in the topsoil (Ahmadipour et al. 2014). The Pb uptake by plants is coordinated by cation exchange capacity (CEC) and pH of growth media along with the size of Pb particles and other agro-botanical characteristics. Excessive Pb causes several toxicity syndromes in plants such as chlorosis, stunted growth and blackening of the root system (Sharma and Dubey 2005). The Pb toxicity leads to the inhibition of photosynthesis, unbalancing of minerals and water uptake, alteration of hormones synthesis and membrane structure, and their permeability levels (Sharma et al. 2016). The biological function of Pb is not yet known but it can cause morphological, physiological and biochemical dysfunctions in plants (Fahr et al. 2013).

The plants use diversified morphological, physiological and biochemical adaptations in response to Pb toxicity, which assists in its detoxification and imparts tolerance against Pb stress (Jiang et al. 2020). Under Pb stress, plants have developed numerous tolerance mechanisms especially related to changes in root systems for lower Pb absorption (Pourrut et al. 2011). Gill et al. (2014) postulated that plant roots rapidly respond in the response of Pb either (i) by callose synthesis, which creates a barrier against Pb entrance (ii) by Pb uptake in higher concentration and subsequent sequestration in the vacuole along with modifications in root growth (iii) by Pb translocation to the leaves.

5.3 The Role of the Transporter in the Regulation of Heavy/Toxic Ions in Cellular Environments

Plants tend to maintain optimal nutrients content under adverse soil conditions by altering root architecture, activation of transport systems in roots, and developing associations with soil microbes. Plants are required to initiate nutrients uptake from the solution of soil and transporting the acquired nutrients through the xylem system to leaves. Besides free diffusion, mechanisms of nutrients transport have been classified into three groups including facilitated diffusion, group translocation and active transport (Yadav 2010; Viehweger 2014). There are several nutrients transporters to uptake the elements from the soil by roots (Wang et al. 2006), such as high-affinity transporter nitrate transporter (NRTs) (Fan et al. 2017; Naz et al. 2019), nitrate transporter *DsNRT3.1* (also known as the nitrate assimilation-related protein), ammonium transporters (AMTs) to uptake and transport ammonium root to shoot (Lima et al. 2010), Mn transporter *NRAMP* (Lanquar et al.

2010), yellow stripe-like (*YSL*), ZIP (zinc-regulated transporter/iron-regulated transporter [*ZRT/IRT1*]-related protein), cation exchanger (CAX) (Socha and Gueriot 2014), calcium cation exchangers (CCX), *CDF/MTP*, P-type ATPase, vacuolar Fe transporter (VIT), etc. Among Zn transporters present in roots, ZIP1, ZIP2, ZIP9 and IRT3 are the most active and prominent (Moreira et al. 2018), while ZIP4 plays a vital role in transporting Zn across the membranes of the chloroplast (Bin et al. 2018). These proteins transporter varies in their binding potential and specificities to Zn transportation. Potassium channels and secondary potassium transporters can mediate potassium transporter membrane transport of K^+ . Moreover, three potassium transporters have been identified including K^+ -permeases (KT/HAK/KUP), the K^+ -Trk/HKT, and cation proton antiporters (CPAs). For the transportation of sulfate, S-metabolite transporters have been recognized as the most crucial S-transporters (Takahashi 2019). Furthermore, numerous transporters are reported to participate in the transport of inorganic phosphate (Pi). For instance, a protein transporter called Pht1 mediates Pi acquisition from the soil solution and likely to be involved in Pi transport to plant tissues (Li et al. 2019). Different factors such as topology, type of functions, expression sites of the genes, etc., assist to determine the role of these metal transporter families. Fe, Zn, Mn uptake by ZIP, IRT and NRAMP transporter while the CCX2 for cadmium, As COTP1, is in charge for Cu^{2+} uptake, Zinc transporters ZRT1 and ZRT2 expression sequence correspondence to IRT1 and could resourcefully transport zinc. CGNP is responsible for nickel uptake and transfer from the soil. MerF is in charge of Hg in bacteria while in the higher plant not know thus hypothetically possibility MerF may be responsible also in the plant. HMA3 transporter for Pb, while in Arabidopsis have been discord HMA4 (be appropriate to the Zn/Cd//Pb/Co group). For Cr, many mechanisms are working under stress like ROS defense mechanism, antioxidant enzymes (SOD: superoxide dismutase, CAT: catalase, APX: ascorbate peroxidase, GPX: glutathione peroxidase, GSH: glutathione reduce, and GSSG: glutathione oxidase). However, PCs and MTs are chelating properties that chelate the toxic ions by breaking down complex compounds (Jain et al. 2018).

For example, 18 YSL genes have been found to responsible for the transport of Fe in rice. It is interesting to note that this transporter gets up-regulated Fe-limited conditions deficiency and resided at the plasma membrane of the root epidermis. The vacuolar Fe transporter 1members (VIT1) of the *NRAMPs* gene family resolve the uptake of different divalent cations. In *Arabidopsis*, *AtNramp1*, *AtNramp3* and *AtNramp4* can complement the Fe uptake mutant of yeast, revealing that these proteins can mediate Fe transport in the (Table 5.1) different nutrients transporter on Arabidopsis, AMT1;1, AMT1;3 ammonium uptake capacity under lack viability of nitrogen, AtNRT2.1 promotes an effect on root growth, AtNramp2 Mn-influx transporter and to remobilization of Mn from old to young leaves. AtMRS2-11 magnesium transport into chloroplasts/plastids. AtSultr, S-nutrition is up-regulated by inadequate S-nutrition. KUP7 K^+ uptake in Arabidopsis roots and also can participate in K^+ transport into xylem sap, TRH1 is essential for root hair/lateral root elongation. BOR1 is required for endocytosis. BOR2 root elongation under low B supply. We

TABLE 5.1

Different Nutrients Transporters in Crop Plants and Their Role in Uptake Transportation and Assimilations

Transporters	Metals/Nutrients	Plant Species	Functions	References
Different nutrient transporter in various crops				
OsNRT2.1	NO ₃ ⁻	Rice	Overexpressing OsNRT2.1 stimulates root growth upon NO ₃ ⁻ treatment under active polar auxin transport.	Naz et al. (2019); Fan et al. (2017)
OsNRT2.1, OsNRT2.2 & OsNRT2.3a	NO ₃ ⁻	Rice	Uptake under the low and high concentration ranges.	Yan et al. (2011)
OsNRT2.3b	NO ₃ ⁻	Rice	Nitrate transporter OsNRT2.3b can improve NUE activity under plant adaption to varied N supply forms.	Fan et al. (2016)
OsNRT2.4	NO ₃ ⁻	Rice	OsNRT2.4 responded to changes in auxin supply, unlike all the other NRT2 genes.	Feng et al. (2011)
AMT1;1 and AMT1;3	NH ₄ ⁺	Arabidopsis	AMT1; 1 and AMT1; 3 boost uptake of ammonium under nitrogen-limited conditions.	Loqué et al. (2006)
AtAMT1;4	NH ₄ ⁺	Arabidopsis	AtAMT1; 4 mediates uptake of ammonium across pollen's plasma membrane and thus contributes to nitrogen accumulation.	Yuan et al. (2009)
AMT1;3	NH ₄ ⁺	Arabidopsis	Ammonium multiplies nitrate effect for boosting root development by stimulating lateral root branching.	Lima et al. (2010)
PttAMT1.2	NH ₄ ⁺	Populustrichocarpa	Ammonium could be a major N source delivered from the fungus toward the plant in symbiosis.	Selle et al. (2005)
NRAMP1	Mn	Arabidopsis	NRAMP1 is a physiological manganese transporter in Arabidopsis.	Cailliatte et al. (2010)
AtNramp2	Mn	Arabidopsis	The vascular bundle-localized Mn-influx transporter OsNRAMP3 participated in Mn distribution and contributes to Mn remobilization from old to young leaves.	Yang et al. (2013)
OsNramp3	Mn	Rice	OsNramp3 localized at the nodes reacts to various Mn concentrations by differing responses to changes in Mn levels.	Shao et al. (2017)
AtNRAMP3 and AtNRAMP4	Mn	Arabidopsis	It plays a vital role in Mn translocation from the vacuole to chloroplasts of mesophyll cells.	Lanquar et al. (2010)
HvIRT1	Mn	Barley (<i>Hordeum vulgare</i>)	HvIRT1 is responsible for Mn ²⁺ uptake in roots of barley and contributes to genotypic differences in Mn ²⁺ uptake kinetics.	Pedas et al. (2008)
Nramp5	Mn and Cd	Rice	It is a main Mn and Cd transporter from soil solution to root cells.	Sasaki et al. (2012)
NRAMP 2	Mg	Arabidopsis	NRAMP2 performs Mn remobilization in Golgi apparatus for boosting root growth.	Gao et al. (2017)
AtHMA3	Cd/Pb	Arabidopsis	AtHMA3, a plant P1B-ATPase is Cd/Pb transporter in yeast.	Gravotet al. (2004)
OsCCX2	Cd	Rice	It is a vital transporter of Cd which leads to accumulation in grain through Ca translocation pathway.	Zhou et al. (2019)
OsLCT1	Cd	Rice	Transporter gene for phloem Cd transport in plants.	Uraguchi et al. (2011)
SaNramp6	Cd	Arabidopsis/cloned <i>Sedum alfredii</i>	SaNramp6 may play a significant role in improving Cd accumulation, transgenic plants for phytoremediation.	Chen et al. (2017)
(YSL) transporter	Fe		Facilitates mechanisms for long-distance Fe transport.	Bashir et al. (2013)
TaVIT2	Fe	Wheat	Triggers transportation of vacuolar Fe in the endosperm.	Connorton et al. (2017)
IRT2	Fe	Arabidopsis	IRT2 transporter under iron-limited conditions is responsible for iron and zinc uptake from the soil.	Vert et al. (2001)
IRT1	Fe	The plant-soil interface	Radial transportation of iron via vascular tissues involving efflux transporters.	Barberon et al. (2014)
IRT1	Fe	Arabidopsis	It is also called peanut Fe transporter especially under Fe-limited conditions.	Ding et al. (2010)
OsNRAMP1	Fe	Rice	The iron transporter OsNRAMP1 in Cd uptake and transport in rice.	Takahashi et al. (2011)
Fe transporter 1 (VIT1)	Fe	Crops	Crystal structure of plant vacuolar iron transporter VIT.	Kato et al. (2019)
OsFRDL1	Fe	Rice	Essential for efficient translocation of iron in rice.	Yokosho et al. (2009)

(continued)

TABLE 5.1 (continued)

Different Nutrients Transporters in Crop Plants and Their Role in Uptake Transportation and Assimilations

Transporters	Metals/Nutrients	Plant Species	Functions	References
Different nutrient transporter in various crops				
IRT1	Fe	Arabidopsis	IRT1 expression under iron deficiency in Arabidopsis roots.	Eide et al. (1996)
TgVit1,	Fe	Arabidopsis	TgVit1 is responsible for the blue coloration as a vacuolar Fe transporter in tulip petals.	Momonoi et al. (2009)
AhNRAMP1	Fe	Peanut	The AhNRAMP1 is possibly involved in iron acquisition in peanut plants.	Xiong et al., (2012)
LeIRT1	Fe	Tomato	LeIRT1 expression, localization and regulation which is iron transporter in tomato roots.	Schikora et al. (2006)
OsZIP4	Zn	Rice	It is a Zn transporter which translocates Zn within rice plants.	Ishimaru et al. (2005)
OsZIP5	Zn	Rice	It facilitates Zn distribution within the rice.	Lee et al. (2010)
OsZIP1, OsZIP3 and OsZIP4	Zn	Rice	OsZIP1, OsZIP3 and OsZIP4 in the roots and that of OsZIP4 in the shoots of both genotypes, indicating that all these genes may participate in rice zinc nutrition.	Chen et al. (2008)
OsZIP3	Zn	Rice	Zn distribution in the developing rice tissues.	Sasaki et al. (2015)
OsZIP1, OsZIP3, OsZIP4, OsZIP5, OsZIP8,	Zn	Rice	The genes which participate in the different growth stages of rice.	Bashir et al. (2012)
OsZIP7	Zn	Rice	OsZIP7 is a good candidate for developing Zn bio-fortified rice.	Ricachenevsky et al. (2018)
OsZIP1	Zn	Rice	OsZIP1 function in epigenetic modification under Cd stress.	Liu et al. (2019)
OsMGT1	Mg	Rice	OsMGT1 supports Mg uptake through roots. The up-regulation of OsMGT1 confers Al tolerance in rice via enhancing Mg concentration in the cell.	Chen et al. (2012)
AtMRS2-11	Mg	Arabidopsis	The AtMRS2-11 gene playing a role in magnesium transport into chloroplasts/plastids.	Drummond et al. (2006)
OsMGT1	Mg	Rice	OsMGT1 is regulating transport activity of OsHKT1 under salt stress; a main transporter for the removal of Na ⁺ from the xylem sap at the root mature zone.	Chen et al. (2017)
OsMGT1	Mg	Rice	OsMGT1 plays an important role in rice Mg import and is required for the resistance to Mg deficiency.	Zhang et al. (2019)
PtrMGT5	Mg	<i>Poncirus trifoliata</i>	PtrMGT5 supports Mg homeostasis in citrus plants by getting involved in the absorption and transport of Mg.	Liu et al. (2019)
CorA/MRS2/MGT-type;ZmMGT10	Mg	Arabidopsis.	Mg transporter of maize which can enhance the tolerance to Mg deficient conditions by improving Mg ²⁺ uptake in the transgenic plants of Arabidopsis.	Li et al. (2017)
ZmMGT12	Mg	Maize	ZmMGT12 possessed Mg ²⁺ transportability and characterized by a high protein sequence identity with Arabidopsis AtMGT6 and rice OsMRS2-6.	Li et al. (2018)
AtMGT1 and AtMGT10	Mg	Arabidopsis	AtMGT1 and AtMGT10 are Mg ²⁺ transporters which can complement bacterial or yeast mutant lacking Mg ²⁺ transport capacity.	Chen et al. (2009)
OsPht1; 4	P	Rice	OsPht1;4 is phosphate transporter which involved in rice phosphate homeostasis.	Ye et al. (2015)
OsPT1	P	Rice	It accumulates in plant shoot in double concentration compared to wild-type plants.	Seo et al. (2008)
OsPT8	P	Rice	It triggers Pi homeostasis in rice and promotes plant growth.	Jia et al. (2011)
OsPT1	P	Rice	OsPT1 is involved in the OsPHO2-regulated Pi pathway.	Sun et al. (2012)
OsPT4	P	Rice	It facilitates As (V) uptake and transportation along with producing low As-accumulating rice.	Ye et al. (2015)

OsNRT2.3b	P	Rice	OsNRT2.3b may upregulate expression levels of OsPT2, OsPT8 and OsPHR2 in roots and of OsPT1 and OsPHR2 in shoots of rice. OsNRT2.3b overexpression can improve P uptake and accumulation in rice.	Feng et al. (2017)
TaPT2 Pi-	P	Pi-deprived Wheat	It regulates P level in specified tissues in both monocots and dicots.	Tittarelli et al. (2007)
OsNLA1	P	Rice	Roles of OsNLA1 in maintaining Pi homeostasis in rice.	Yang et al. (2017)
OsSultr1;1	S	Rice	OsSultr1;1 is a rice high-affinity sulfate transporter that participates in maintaining sulfur demand under arsenic (As) stress.	Kumar and Khare (2019)
OsLsi1 and OsLsi2	S	Rice	OsLsi1 and OsLsi2 are potent transporters of As in rice. Greater S supply immobilized the As in roots and lowers its translocation to shoot.	Dixit et al. (2016)
AtSultr2;2	S	Arabidopsis	Roots play a significant role to transport sulfate via the phloem.	Davidian and Kopriva (2010)
AtSultr2;1	S	Arabidopsis	It is synthesized in roots during sulfate deficiency which increases mRNA level.	Buchner et al. (2004)
AtSultr1;3	S	Arabidopsis	It restricts sulfate movement to other tissues from cotyledons.	Hawkesford (2003)
AtSultr	S	Arabidopsis	It is a set of four transporters synthesized under inadequate S-nutrition which assists S uptake and translocation.	Tombuloglu et al. (2017)
AtHAK5, AKT1	K ⁺	Arabidopsis	AtHAK5 is supporting a high-affinity K ⁺ uptake system in Arabidopsis roots.	Gierth et al. (2005); Pyo et al. (2010)
TRH1 and AKT1	K ⁺	<i>Arabidopsis thaliana</i>	These are functional in the root hair and transport potassium in varying concentrations.	Desbrosses et al. (2003)
OsHAK5	K ⁺	Rice	It boosts K acquisition by roots and facilitates its transport to shoots from roots under K-deficient conditions.	Yang et al. (2014)
KUP7	K ⁺	<i>Arabidopsis thaliana</i>	It is involved in K ⁺ uptake with a possible role in K ⁺ transportation into xylem sap.	Han et al. (2016)
TRH1	K ⁺	<i>Arabidopsis thaliana</i>	It mediates K ⁺ uptake and translocation along with promotes root hair elongation.	Rigas et al. (2001)
BOR1	B	<i>Arabidopsis thaliana</i>	It has a non-essential role in endocytosis but plays a crucial function in multi-vesicular bodies for subsequent degradation in vacuoles.	Takano et al. (2005)
BOR1	B	<i>Arabidopsis thaliana</i>	Its functions are regulated by B availability as it tends to hamper excessive accumulation of B in shoots.	Kasai et al. (2011)
BOR1	B	Rice	It promotes efficient uptake of B and subsequent loading to the xylem.	Nakagawa et al. (2007)
AtBOR1	B	<i>Arabidopsis thaliana</i>	AtBOR1 encodes an efflux boron transporter. It is shown different expression throughout the reproductive development of <i>Vitis vinifera</i> L.	Pérez-Castro et al. (2012)
BnaC4.BOR1;1c	B	<i>Brassica napus</i>	BnaC4.BOR1;1c is an AtBOR1-homologous B transporter gene expressing in both shoot nodes and roots.	Zhang et al. (2017)
OsBOR4	B	Rice	OsBOR4 is a boron efflux transporter responsible for normal pollen germination and/or tube elongation.	Tanaka et al. (2013)
BOR2	B	<i>Arabidopsis thaliana</i>	BOR2, a B transporter that supports root elongation and cross-linking of RG-II under low B supply.	Takada et al. (2014)
Lsi1 and Lsi2	Si	Rice	Lsi1 is required for the transport of Si through the cells of the exodermis and endodermis.	Ma and Yamaji (2008)
Lsi1, Lsi2 and Lsi6	Si	Rice	It mediates the uptake of Si from the soil solution.	
HvLsi1	Si	Barley	It serves as a Si influx transporter which performs radial transport through the layers of epidermal and cortical membranes in basal roots.	Chiba et al. (2008)
TaLsi1	Si	Wheat	TaLsi1 is indeed a functional Si transporter as its expression in Arabidopsis leads to increased Si uptake.	Montpetit et al. (2012)

discuss some transporter for each metal that transports and uptake the nutrient in the medium and soil and how is important for plant and crop growth.

This transporter is responsible for transporting nutrients, helping in plant growth and development. There are some transporters responsible for dual nutrient transport and are directly correlated to each other. For example, Nramp5 is responsible to transport Mn and Cd in rice crop, AtHMA3 in Arabidopsis crop, and Cd/Pb SaNramp6 may play a significant role in improving Cd accumulation in transgenic plants for phytoremediation.

5.4 Frequent Mechanism Working as Network inside the Cell

Numerous mechanisms are involved in the HMs transfer across cell membranes in plant roots (Table 5.2). Some of the proteins are highly selective and tend to interfere with the movement of essential metals from the extracellular environment. For instance, DCT1 (divalent cation transporter1; also known as NRAMP2 or DMT1) serves as vital transporter of Fe²⁺ and other divalent metals, however, it has also been known to mediate uptake of toxic metals (Cd²⁺, Pb²⁺, etc.) (Ballatori 2002). The underlying mechanism is the potential of HMs to interact with the binding sites reserved for essential metals through which these gain access to various cellular compartments leading to disorganizing of normal biochemical and physiological functions. Another major mechanism by which metals traverse cell membranes and produce cell injury is by forming complexes whose overall structures mimic those of endogenous molecules (Ballatori 2002).

It is known that chromate and molybdate can mimic sulfate to support normal cellular functions (Bridges and Zalups 2005). The arsenate and vanadate for transport and metabolism can compete with phosphate in biological systems (Finnegan and Chen 2012). From the first step at root exudation, and some microorganisms are surrounding the rhizosphere which can tolerate the movement of metal ions from the soil. The

various networks are involved many transporters to uptake and accumulate HMs. Under HMs, stress conditions increasing the synthesis of different phytohormones, shown a greater level of oxidative ROS and some ions such as Ca²⁺ ions, K⁺ ions, Ca–Calmodulin system. The mitogen-activated protein kinase (MAPK) system is also up-regulating the genes related to metal toxicity. Emamverdian et al. (2015) reported that the high level of Ca²⁺ is identified in the plants under HMs stress effects and able to assist in the metabolism process in changed stress environments. There are some chemicals in the plant chloroplast that cannot able to dissolve in the cell, and that time plants produce chelation and metallothioneins (MTs) that able to bind those chemicals with metals and isolate them to stable forms. These plant toxic metal-chelating proteins such as MTs which contain two classes 1 MTs and 2 MTs (Robinson et al. 1993).

Later, the protein functions as a defensive element against free radicals' toxicity for plants while essential nutrients help to down-regulate the toxic metals by MTs genes. The heavy and toxic metals affect the uptake of essential nutrients by roots, while the toxic effects of HMs are reduced by essential nutrients. After the transporters, the plant cytoplasm transported these metals to other cell parts to eliminate them from cells. The transporters like PAA1 and ZIP in the plastid, NRAMP 3, ABC and CAX2 in vacuoles, RAN1 in the Golgi apparatuses organelle and ECA transporter proteins in the endoplasmic reticulum are involved to translocate the heavy metal ion (HMI) in plants (Jain et al. 2018).

5.5 Conclusions

This chapter provides comprehensive knowledge about the starring role of metal transporters on plant growth and development under HMs stress. It was highlighted that how metals transporters' mechanisms are involved in response to HMs stress in plants and their particular role in metallic toxicity in crops or soils. The different nutrients transporter in crops and plants that are responsible for uptake transport and

TABLE 5.2
Mechanisms Involvement in Response to HM Toxicity in Plants

Mechanism	Expects	Functions	Organelle	References
CDF	Metals chelate		Cytoplasm	Chen et al. (2009)
CA-CalmodulinMPK signaling	Increased proteins synthesis under metal toxicity	Signal transduction response for HMs.	Vacuole	Maksymiec (2007)
Plasma membrane (PM) ATPase	Signal transduction in response to metals	Metal ions entrance into roots from the soil solution.	Plasma membrane	Janicka-Russak et al. (2008)
Metal ion uptake from the soil	Signal transduction in response to metals	Surrounding root.	Outside root cell	Callahan et al. (2006)
Chelating compound like PCs MTs	HMs chelation in the cytosol	Metals transportation to shoots from the root.	Cytosol	Jain et al. (2018)
SOD, CAT	Oxidative stress mechanism	Metal ions distribution to organelles cells.	Plasma membrane	Sharma et al. (2016)
Receptors	The presence of roots and some microorganisms near the root layer	Receptors allow metal ions to move from the soil.	Outside root cell	Skórzyńska-Polit (1998); Maksymiec (2007)

assimilations were described together with their functions. In addition to the microbial effects, interactions between essential metals and HMs may impart effects on plant N-fixation potential. In conclusion, the HMs not only can affect plants and soil microorganisms but also the functions of different metal transporters which are essential in molecular studies for understanding all interactions between essential nutrients, HMs and transporter in the system plant crop and soil microorganisms.

5.6 Future Perspectives and Strategies

- a. There is a dire need to identify and develop mechanisms to regulate the transporter genes involved in the uptake of heavy and toxic metals from the soil, to reduce metal toxicity for plants.
- b. There is a need to identify the nutrient transporters link to each other such as up-regulation and down-regulation genes during toxic effects of HMs.
- c. There exists the need to conduct further molecular and mechanism enzymatic studies in vegetables for being the most sensitive to HMs stress.
- d. Studies must be executed to introduce CRISPER-case9 technology to reduce all kinds of toxic effects of HMs on plants and crops under soil contamination and environmental pollution.
- e. Development of the microbial organism also holds potential as these maintain close interaction with plant roots and thus have the potential to assimilate HMs without causing additional toxic effects for plants.

5.7 Conflict of Interest

Authors declare no conflict of interest.

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