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REVIEW

Soil cadmium enrichment: Allocation and plant physiological manifestations

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Abstract Cadmium (Cd) in soil is enriched through several leaky management agricultural practices and natural resources. Cd enriched soil is inevitable cause of nutritional stress besides Cd induced toxicity symptoms and physiological malfunctions. Redox signals shift toward oxidative stress which accelerates cellular damage and elicits defense mechanism at the cost of growth. Plants get enriched with this toxic, abundant and undesirable element through 'mineral uptake system' non-specifically. Different components and pathways have been marked cooperating in cellular sequestration and systemic localization of Cd, escaped from avoidance and efflux. Cd induced metabolic alteration led to electron leakage as ROS, reduced photosynthesis and carbon fixation. Compromised primary metabolism negatively feedbacks the plant growth, result into loss of potential crop yield.
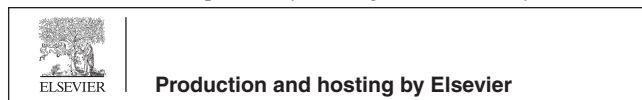
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1. Introduction to cadmium enrichment in agriculture

The non-judicial use of phosphate fertilizers, industrial and sewage waste water, mining and industrial and vehicular emissions from industries, mining and transport vehicles significantly adds the heavy metals (HMs) in agricultural soils at toxic level (Arora et al., 2008; Wuana and Okieimen, 2011), particularly the nearby urban and peri-urban farmlands. The leafy vegetables and food crops grown in such soils accumulate toxic level of these toxic metals to add them further in the trophic chain (soil–plant–animal) (Wuana and Okieimen, 2011). Among the heavy metals, Cd is the most abundant, and readily taken up toxic HM by the crop plants; therefore, of great concern (Arora et al., 2008). Its normal concentration in soil ranges from 0–1 mg/kg, while 1–3 mg/kg indicates slight contamination (Rodriguez-Flores and Rodriguez-Castellon, 1982). The Cd polluted soil may comprise 3–10 mg/kg of soil Cd (Rodriguez-Flores and Rodriguez-Castellon, 1982) to a lethal level of < 100 mg/kg in sewage sludge treated soils as shown in the study by NEERI (1999–2002). Cd over-accumulate in plant (Wuana and Okieimen, 2011) with an enrichment ratio (ER) ranging from 1–10. FAO/WHO recommended maximum tolerable intake of Cd of 400–500 µg per week or equal 70 µg per day. Alternatively studies reveal that 60–80% of HM toxins found in human bodies in urban areas were the results of consuming contaminated foods rather than air pollution.

2. Cadmium causes nutrient deficiency signaling

Cd induced oxidative signals at root membranes get intensified at toxic Cd level to elicit PCD. Leakage of energy pool as reactive oxygen species (ROS) alters the growth metabolism toward defense metabolism constraining the primary metabolism, particularly the enzymes of Krebs cycle and photosynthesis (Fig. 1). Furthermore, the nutrients availability for soil-nutrient-plant system relies on several factors. Soil often preconditioned with chemical fertilizers, waste water, manures, liquid fertilizers, sewage sludge etc. adds a voluminous amount of toxic HMs including Cd (Wahid et al., 2009). Cd taken up by plants transferred to particular organs (Kabata-Pendias and Pendias, 2001) induces chlorosis, necrosis, vein reddening, and root and shoot growth retardation, besides reduced nutrient uptake (Sanita di Toppi and Gabbrielli, 1999; Mohamed et al., 2012). Cd competes for plant nutrient status and subsequently alters its physiology. This is particularly important during studying the physiologically effect of P and Ca (Wang, 1987) and other important micronutrients e.g. Zn (Kim et al., 1988). Yang et al. (1996) reported various effects of Cd on the uptake of Fe, Zn, Mn, Cu, P, K, Ca, Mg and S.

At the root region Cd competes for absorption of several mineral nutrients generally those sharing similar chemical properties like Ca^{2+} and Mg^{2+}, therefore, causing mineral deficiency (Barcelo and Poschenrieder, 1990). The reduction of K, Ca and Mg in the tissue due to high concentrations of Cd has been reported in cucumber and tomato plants (Burzynski, 1988). An antagonism between Zn and Cd and their active absorption were also observed in lettuce roots (Costa and Morel, 1994). Moreover, other mineral nutrients such as nitrates, sulfates etc. which do not share chemical characterisity with Cd, has also been restricted by the presence of Cd. Since the plant development responses are quite plastic and opinioned to be controlled by availability of soil nutrient status. The nutritional signal seems to be sensed and coordinated with hormonal signals (Krouk et al., 2011). Soil nitrogen and phosphorus have been evidenced to control the internal hormonal level of plants to interplay with nutritional provisions and efficiency. Molecular switches tightly control the plant growth based upon nutritional cues. Substituting nitrate (NO_3^-) to ammonium (NH_4^+) supplement triggers a decrease in shoot growth within hours (Walch-Liu et al., 2000). Alternatively, N metabolism of plants plays a central role in HM responses. Plants sensitivity to Cd is affected by both the form supplied (Xie et al., 2009) and availability of N (Finkemeier et al., 2003). Sulfate salts have also been reported to afford protection to Cd toxicity by enhancing sulfate uptake, leading to an increased glutathione synthesis, a precursor of PCs (Van de Mortel et al., 2008).

3. Cadmium induces oxidative signaling

The free state of HMs is never tolerated in the biological system as they have shown to elicit futile reactions generating toxic free radicals (Lindh, 2007) or altering membrane potential and enzyme activities (Schützendübel and Polle, 2002; Fediuc et al., 2005; Janicka-Russak et al., 2008). Apoplastic low pool of thiol buffers and ROS-sensors instantaneously led to outburst of ROS initiating defense or death responses (-apoptosis) depending upon the extent of ROS leaked (Foyer and Noctor, 2005; Keunen et al., 2011). Upsurge of ROS is optimally regulated through sub-cellular pool of antioxidants
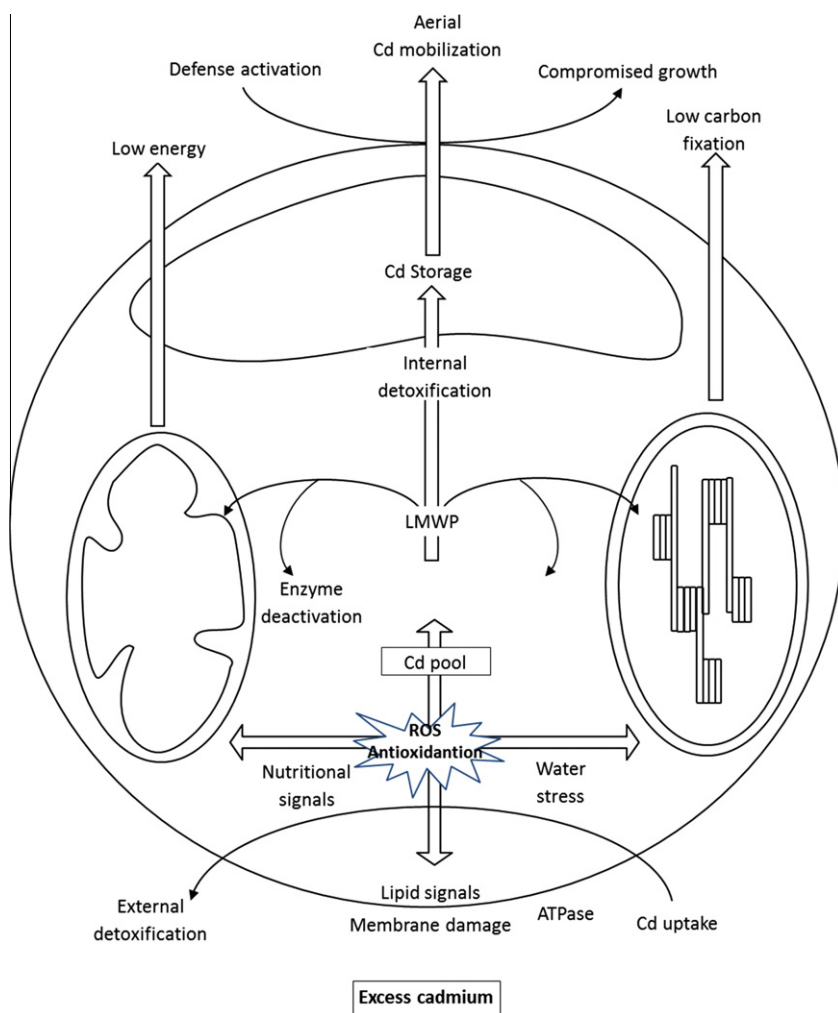
Figure 1   Cadmium uptake and processing in plant.

Table 1   Cadmium in soil environment initiates physiological constraints and subsequent consequences.

Cd in environment	Consequences
Phase I	
Enrichment in plant	Accumulation
Nutritional competition	Nutritional deficiency symptoms
Disturbed osmolality	Altered water potential
Binding to proteins (membrane proteins/enzymes)	Altered physiology (stressed state)
Phase II	
Defense activation	Response
Accumulation of osmolytes	Induction of homeostasis restoration
Expression of chelates	Detoxification of free Cd
Anti-oxidation	ROS management compartmentation
Redirection of Cd	
Phase III	
Phytohormones	Enhanced response
Temporal/spatial regulation of defense molecules	Systemic defense activation
Up-expression/activation of antioxidant system	Decline of oxidative/stressed state
Regulation of hierarchical expression of enzymes	Elicitation of secondary metabolism
Co-ordination of primary and sec. metabolism promotion	Maintaining house-state and growth

to protect the tissue from oxidative damage (Milone et al., 2003; Gill and Tuteja, 2010) which is regulated via systemic network of plant hormones (Overmyer et al., 2003). Superoxide dismutase (SOD) is the first enzyme in the ROS detoxifica-
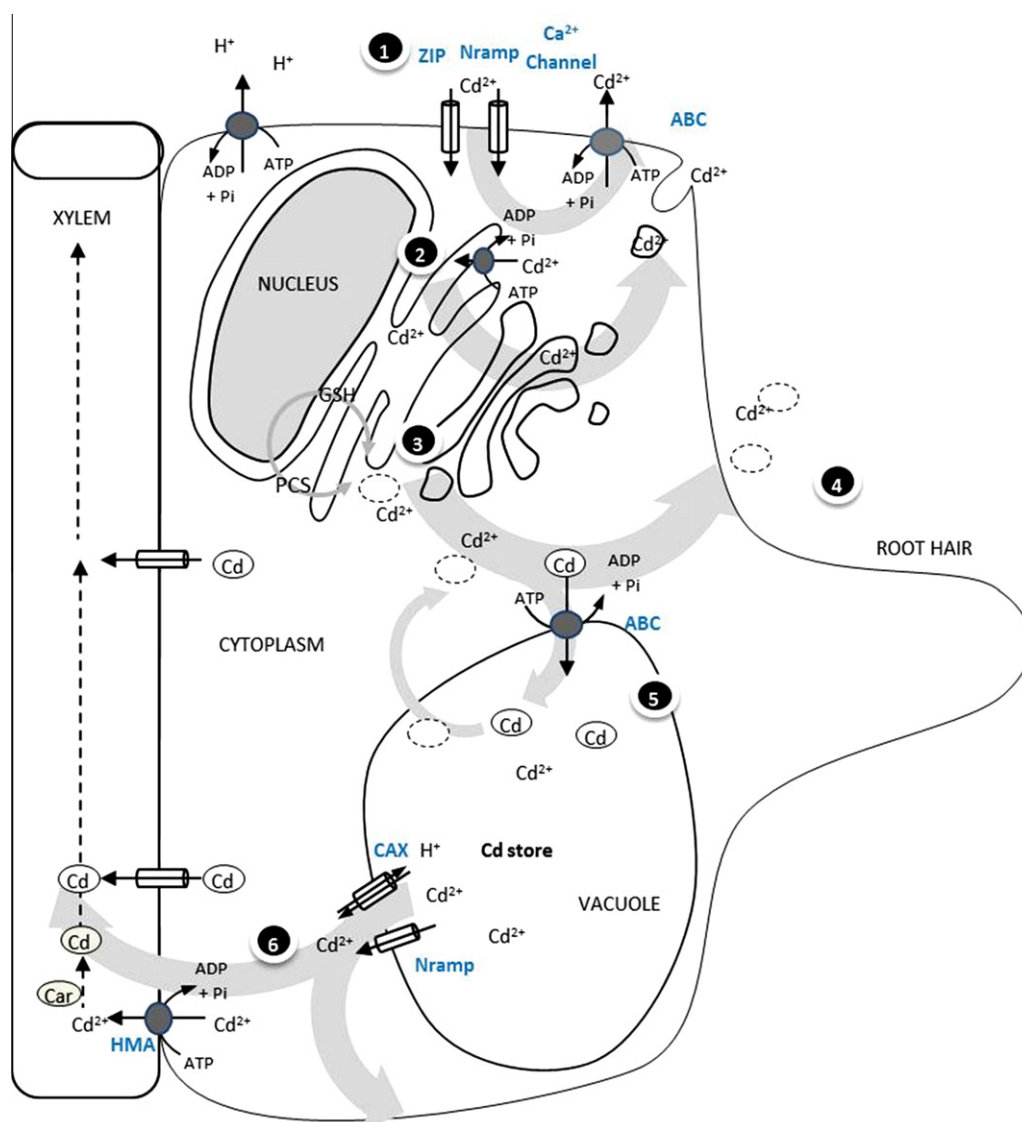
Figure 2   Mechanisms to counter excess cadmium in root epidermal cells.

tion process converting O^{2-} radicals into H_2O_2 at a very rapid rate (Foyer and Noctor, 2005). Cd was found to result in oxidative stress (Hendy et al., 1992) by either inducing oxygen free radical production (Demirevska-Kepava et al., 2006) or by decreasing concentrations of enzymatic and non-enzymatic antioxidants (Milone et al., 2003). These non-enzymic antioxidant molecules include ascorbate, glutathione, tocopherol, etc., while enzymes include peroxidases (POX), catalases (CAT) and SOD (Milone et al., 2003; Mohamed et al., 2012).

4. Cadmium uptake, accumulation and transport

To cope up with toxic metal reactions and maintaining the level of essential metals within the nontoxic range, plants induce a variety of mechanisms on very first sensing at root hairs (Table 1). Uptake of essential divalent cations is a natural phenomenon to drive normal metabolic processes drawn by the plasma membrane H^+-ATPase mediated acidification of rhizospheric soil. *AHA2* gene putatively encodes this proton pump (Fox and Guerinot, 1998). In acidic soils, however,

HM problem is much more exaggerated. Excess soil HMs including nonessential divalent cations (e.g. Cd) get enriched excessively through non-specificity of transporters and channels that led to uptake and transport the essential mineral HMs. No report is available indicating specific mechanism that is involved for the uptake or transport of Cd in plant kingdom or its involvement in plant metabolism as a moiety of metalloprotein. The only exceptions are the marine diatoms where Cd has shown its involvement in the activity of carbonic anhydrase and photosynthesis (Morant-Manceau et al., 2007). Cd is known to compete with several essential metal ions. It is reported that plants accumulate a variety of cations under iron-deficiency including Cd (Wuana and Okieimen, 2011). Cd can be easily transported within plants (Epstein and Bloom, 2005) in the form of metallo-organic complexes. The mechanisms of uptake, translocation and deposition depend upon the bio-availability of soil, pH, temperature, redox potential and concentration of other elements. Cd can easily penetrate the root system of xylem through the apoplastic and/or symplastic pathway (Salt and Rauser, 1995) and reach tissues of aerial

parts of the plants (Yang et al., 1998). Soil HM status or Cd enrichment is sensed at root epidermal cells. When Cd enters first into the roots it primarily damages the root system (Sanita di Toppi and Gabbrielli, 1999). This damage could result from oxidation of membrane proteins/thiols, inhibition of pumps and channels or altered membrane fluidity (Meharg, 1993). Damaged plasma membrane initiates lipid induced signals to control GABA based cytosolic acidification, or intracellular depleted thiol pool induces ROS based signals. Cd stress induced depletion in GSH/GSSG ratio has been observed in different plant species (Romero-Puertas et al., 2007). The distribution and accumulation of Cd within plant tissue are gated at various key points. The regulatory proteins, which open the door for Cd or work as vehicle to Cd transport have been studied governing plant Cd localization. These key points are as follows (Fig. 2).

4.1. Root plasma membrane facing apoplastic space

Absorption of Cd could also occur as inorganic complexes of Cd such as $CdCl^+$, $CdCl_2$, $CdSO_4$, etc. or as organic complexes such as phytometallophore complexes (McLaughlin et al., 1996). Cd, the potent antagonist of Zn and Cu, also competes with Fe and Ca transporters and channels to get pass to the cytoplasm. Cd absorption across the plasma membrane of root cells is controlled by the electrochemical potential difference between the activity of Cd^{2+} in the cytosol and that in the root apoplasts. The large negative membrane potential alone provides more than enough energy to drive Cd^{2+} uptake even at low concentrations of Cd^{2+} (Costa and Morel, 1993).

Cd has been shown to be transported through several Fe and Zn transporters collectively known as ZIP (ZRT, IRT-like Proteins). The cation transporter; IRT1 (iron-regulated transporter) is one of the member of this group up-expressed in the iron deficient roots of *Arabidopsis*. Several divalent metal ions (e.g. Cd, Co, Mn, and Zn) could be transported via IRT1 (Hall and Williams, 2003). Besides, ZIPs; Nramps, LCT1 and Ca^{2+} channels facilitate the uptake of Cd^{2+} within the cytoplasm (Connolly et al., 2002). The plasma membrane-localized enzyme; FRO2 is known for the Fe(III)-chelate reductase activity induced in the roots of *Arabidopsis* under iron deficient conditions (Robinson et al., 1999). Overexpression of ferritin also induces Cd uptake (Sappin-Didier et al., 2005). Sufficient amount of excess Cd load is actively effluxed through ABC transporters located at the plasma membrane of root epidermis. ABC transporters are suggested to confer HM resistance and even iron homeostasis (Chen et al., 2007). Kim et al. (2007) have implicated the role of PDR8 in Cd^{2+} and Pb^{2+} resistance. PDR8 over-expresser plants have comparatively reduced Cd levels in their roots and shoots and were resistant to Cd^{2+}. Also ATPase ZntA overexpression conferred reduced Cd^{2+} accumulation and enhanced tolerance in *Arabidopsis* (Lee et al., 2003).

4.2. Vacuolar sequestration

Plant vacuoles serve various purposes including the accumulation of toxic secondarily produced metabolites or those eventually taken up through soil mineral solutions. Cd appeared to be complexed to the cell wall surrounding root apoplast, effluxed or checked at very first entrance while majority of Cd entered is channelized to the root vacuoles or of older leaves. AtMTP1 and ShMTP encode Zn and Mn transporters, putatively involved in sequestering metals to the root vacuole to confer higher tolerance (Van der Zaal et al., 1999). Cytosolic low molecular weight proteins (LMWPs) transport Cd-complexes to vacuoles. LMWPs are recycled subsequently. Cation/H^+ antiporters located at tonoplast constitute the system for Cd^{2+} sequestered from the cytoplasm to the vacuole (Vogelilange and Wagner, 1990). CAX (CAtion eXchangers) transporters are vacuolar Ca^{2+}/H^+ antiporters. Salt and Wagner (1993) and Korenkov and co-workers (2007) demonstrated vacuolar Cd^{2+}/H^+ antiport activity in plants while Shigaki and Hirschi (2000) have shown the catalysis of Cd^{2+} and with protons at vacuolar membrane via CAX transporters. Comparative and overexpression studies with *CAX4* and *CAX2* genes in *Nicotiana tobaccum* have shown a high transport activity of Cd^{2+} through root tonoplast vesicles therefore, affecting root to shoot distribution and level of uptake of Cd responsible for this distribution (Korenkov et al., 2007). NRAMP (Natural Resistance Associated Macrophage Protein) transporters are distributed ubiquitously in plants. Fe transport NRAMP genes also confer Cd^{2+} uptake activity when expressed in *Saccharomyces cerevisiae*. NRAMP4 as well as NRAMP3 are localized in the vacuolar membrane (Thomine et al., 2003; Lanquar et al., 2005).

4.3. Cellular detoxification

Plants' provision for detoxification mechanisms employs chelating compounds such as glutathiones (GSH), PCs, MTs and other cystein-rich membrane proteins (Clemens et al., 2001; Cobbett and Goldsbrough, 2002). These either detoxify the cellular pool of free toxic metals to sequester in vacuole or transport to sink. Another group of Cys-rich chelater is MTs, the low molecular peptides induced against HMs (Cobbett and Goldsbrough, 2002). MTs also reduce cytosolic toxicity load of free HMs. MT overexpressing plants for instance; tobacco, *Arabidopsis thaliana*, *Vicia faba* also favored metal detoxification via MTs (Lee et al., 2004). MTs increased tolerance to Cd and other HMs in different transgenic plants overexpressing PCs supported the role of PCs in stress resistance (Mohamed et al., 2012). Metal complexation to the PCs in the cytosol also lowers its toxicity (Cobbett, 2000). Cd is chelated with glutathione and PCs (Mohamed et al., 2012; Cobbett, 2000) which complex with Cd to sequesters it in vacuole or expel in apoplasts through facilitated membrane pumps. The PCs are expressed constitutively and their expression is enhanced under HM stress (Cobbett and Goldsbrough, 2002) for instance under excess Cd (Wang et al., 2009). The high level of PCs determines the root to shoot transport of Cd, therefore, maintain low pool of Cd in the shoot as compared to the root (Mohamed et al., 2012).

4.4. Extracellular soil detoxification

Exudation of organic chelates and LWMPs also detoxifies HMs extra-cellularly. Different amino acids and carboxylic acid viz. citric, malic and histidine are exuded from the roots to bind and detoxify HMs in soil, therefore, playing an important role in tolerance (Rauser, 1999; Clemens et al., 2001). Kramer et al. (1996) reported a 36-fold increase of HMs

content in xylem sap when *Alyssam lesbiacum*, a Ni hyper-accumulator species was exposed to Ni. Phytosiderophores (PSPs) in monocots are commonly exuded for Fe acquisition. YSL, the member of OPT family transporting oligopeptide is another important plasma membrane localized protein transporting Fe(III)-PSPs (Curie et al., 2001).

4.5. Golgi–Endoplasmic reticulum secretory pathway

The evidence of Golgi–Endoplasmic reticulum secretory network to exocytose waste vesicular cargo of excess metals to confer tolerance is studied (Peiter et al., 2007) but not fully investigated yet as a plant mechanism to get rid of excess metal. Cytosolic excess HMs are taken up into the labyrinth of endoplasmic reticulum and Golgi vesicles through MTPs (metal transporter proteins). In yeast ATX1 delivers Cu into the Golgi vesicle. Ubiquitous metallo-chaperone ATX1 has its homologs in plants, microbes and animals transferring Cu through P-type ATPase across membrane (Huffman and O'Halloran, 2000). This ATPase (Ccc2) in yeast is involved in transferring Cu into lumen of Golgi vesicles (Culotta et al., 1997). The *Arabidopsis* Homolog of Ccc2, RAN1 pumps Cu into Golgi vesicles (Hirayama et al., 1999). Possibly vesicular transport of excess HMs is effluxed through the plasma membrane.

4.6. Xylem loading to sinks

The regulation of long distance Cd transport to the aerial part is also an important determinant of resistant approach. Several transporter families aid to this necessity to cope with Cd toxicity. NRAMP (natural resistance-associated macrophage protein) family is another important family of metal transporters to mobilize Cd. NRAMP and CAX export vacuolar Cd to cytosol from where Heavy Metal transporting ATPases (HMAs) and unknown other transporters load Cd to xylem. Eight *HMA* genes identified in rice and *A. thaliana* (Baxter et al., 2003) suggested the role of this class in HMs xylem loading in plants. The class of HMAs transporting divalent cations also transports Cd along with Zn, Co and Pb hydrolyzing ATP (Verret et al., 2005). HMA4 overexpressed in both the root and shoot of Cd/Zn hyperaccumulators (Courbot et al., 2007) contributes the tolerance to genotypes. The OPT members e.g. OPT6, are also able to transport Cd–Glutathione (Cd–GSH) complexes and GSH derivatives (Cagnac et al., 2004). Ligands and carriers (Car) Cd-complexes are carried to sink tissues.

5. Cadmium toxicity induced metabolic alterations and manifestations

5.1. Hormonal signaling and cross talk

Cd accumulation triggers the production of ROS altering activity of antioxidant enzymes (Romero-Puertas et al., 2007). Plant defense system counters HM stress through altering hormonal regulation (Hsu and Kao, 2008; Krouk et al., 2011). This regulation includes the detoxification and sequestration mechanisms, regulation of redox status and replenishing basal nutrient supply (Mohamed et al., 2012). The change in hormone profile is often evident from the key enzymes of biosynthetic pathway (Fediuc et al.,

2005) or mutant study. The signals within the cell join through phosphorylation of an array of kinases and phosphatases (e.g. MAPK). This stress, in part, could also be contributed through Cd competed reduced availability of P for phosphorylation-relay-signals (Jonak et al., 2004). Heavy metal (HM) stress signals besides phosphorylation cascades transduced through Ca–calamudulin system, or ROS signaling to converge at transcriptional regulation (Romero-Puertas et al., 2007; Tamas et al., 2008). Several transcriptional factors have been identified induced in response to Cd applications (Van de Mortel et al., 2008) which share the culminating pathways of other related abiotic stresses (Singh et al., 2002).

Crucial role of certain plant hormones has been suggested in plants in response to different environmental stresses including HM stress (Hsu and Kao, 2008). The treatment with Cd, Cu, Fe, and Zn led to the increase of ethylene. Increased activity of ACC synthase and up-regulation of its transcription in particular treating with Cd and Cu were also reported (Maksymiec et al., 2007). The jasmonic acid content in *Arabidopsis*, *Oryza* and bean get increased when treated with Cd or Cu. Cd has been shown to increase abscisic acid (ABA) contents in plants (Poschenrieder et al., 1989; Fediuc et al., 2005). Cd-induced ABA accumulation was observed in rice leaves (Hsu and Kao, 2008) and roots of *Typha and Phragmites* plants (Fediuc et al., 2005). Cd has also been shown to stimulate SA accumulation in the roots. Cd-induced increases in ABA and salicylic acid (SA) contents were observed in citrus leaves but not in the roots (López-Climent et al., 2011). Cd treatment following the application of SA partially protected the barley seedlings against HM toxicity (Maksymiec et al., 2007). Salicylic acid mediates the H_2O_2 accumulation in rice leaves and protects against Cd toxicity (Chao et al., 2009). In cell cultures exposed to Cd an increase in NO production was observed in pea roots (Bartha et al., 2005) and soybean (Kopyra et al., 2006). However, long exposure led to reduction in NO production (Rodríguez-Serrano et al., 2009) and lateral root induction (Lombardo et al., 2006). Exogenous application of NO has shown to augment HM stress (Wang and Yang, 2005; Laspina et al., 2005) and is assumed through activation of antioxidant system (Wang and Yang, 2005; Rodríguez-Serrano et al., 2009; Singh et al., 2008).

5.2. Biochemical changes

It has been shown that the excess HMs cause cell death in plants by inactivating enzymes, through metal sensitive groups, and rendering them to be catalytically inactive (Fediuc et al., 2005). The presence of Cd decreased nodulation and nitrogenase activity in *Trifolium repens* (McGrath et al., 1988), *Phaseolus vulgaris* (Dewdy and Ham, 1997), *Pisum sativum* (Dhingra and Priefer, 2006), mungbean (Wahid et al., 2007), and chickpea (Hasan et al., 2008). Nitrogen assimilation in pea plants was severely affected on exposure to Cd (Dhingra and Priefer, 2006). A positive correlation was observed between leghemoglobin content and nitrogenase activity (Dakora, 1995) and both these parameters exhibited a parallel decrease in the presence of Cd (Fernandez-Pascual et al., 1996).

Nitrate reductase (NR), the primary enzyme in the nitrate assimilation pathway, is the limiting factor in plant growth

and development (Solomonson and Barber, 1990) and its level is influenced by a variety of environmental factors (Murphy et al., 1997). The presence of Cd in the soil retarded the assimilation of NO₃ in *Silene vulgaris* (Mathys, 1975), pea (Burzynski, 1988), tomato (Quariti et al., 1997), bean (Gouia et al., 2003) and in *Cicer arietinum* (Hasan et al., 2008).

The decreased activity of carbonic anhydrase in plants (Siedlecka et al., 1997) could be coupled with Cd induced stomatal closure (Poschenrieder et al., 1989). The plants exposed to HMs seem to induce accumulation of free proline. Among the four tested HMs that induce proline accumulation Cd was the strongest inducer (Saradhi and Saradhi, 1981). An increase in constitutive proline levels has been observed in a copper-tolerant ecotype of *Armeria meritima* exposed to Cd (Farago, 1981). Cd induced proline in rice (Roy et al., 1992), *Armeria moritima* (Farago, 1981), and sunflower (Kastori et al., 1992) and *Hordeum vulgare* (Tamas et al., 2008) and in *Cicer arietinum* (Hasan et al., 2008). In addition, proline could be involved in metal chelation in the cytoplasm (Farago and Mullen, 1979).

5.3. Photosynthesis and carbon fixation efficiency

Cd is an effective inhibitor of photosynthesis (Chugh and Sawhney, 1999; Vassilev et al., 2005; Mohamed et al., 2012). A linear relationship between photosynthesis and inhibition of transpiration was observed in clover, lucerne, and soybean that suggest Cd inhibited stomatal opening (Barcelo and Poschenrieder, 1990). Cd damages the photosynthetic apparatus, in particular the light harvesting complex II and photosystems I and II (Krupa et al., 1993; Siedlecka et al., 1997). The inhibition of root Fe(III) reductase induced by Cd leads to Fe(II) deficiency which seriously affects photosynthesis (Alkantara et al., 1994). Cd also causes alteration in leaf gas exchange (Costa and Morel, 1994; López-Climent et al., 2011) stomatal closure in higher plants (Poschenrieder et al., 1989) and an overall inhibition of photosynthesis (Ekmekci et al., 2008; Mohamed et al., 2012). In *A. thaliana* Cd altered the activity of photosynthetic apparatus (Mohamed et al., 2012) while decreased the potential quantum yield of PSII (Maksymiec et al., 2007). Similarly, the synthesis and level of pigments are decreased in other plant species under the influence of Cd (Ekmekci et al., 2008; Mohamed et al., 2012).

5.4. Vegetative growth and potential yield

The presence of Cd in the soil retards the growth of many crop plants; to name some are soybean (Dewdy and Ham, 1997), *Corchorus olitorius* (Mazen, 2004), *Medicago sativa* (Drazic et al., 2006), maize (Krantev et al., 2008) and chickpea (Hasan et al., 2008). High concentrations of Cd decreased the cell growth as well as the plant yield (Prasad, 1995; Yang et al., 1998). The interaction of *Rhizobium* in the nodules of chickpea was found to be very sensitive to HMs resulting in a decrease in dry mass of chickpea and green gram (Woolhouse, 1983; Rana and Ahmad, 2002). An increase in Cd concentration decreased the fresh mass in mung bean (Wahid and Ghani, 2007), *Medicago sativa* (Drazic et al., 2006), and maize (Ekmekci et al., 2008). Moreover, a marked decrease in root and shoot mass was observed when treated with low concentrations of Cd in *Brassica juncea* (Mohamed et al., 2012), *Vigna ambacen-*

sis (Al-Yemeni, 2001) and wheat (Milone et al., 2003). Phytotoxicity of the metal in other crop plants has been observed in the form of a loss in protein levels (Krantev et al., 2008). Moreover, the grains developed on the plants grown under Cd stress had lower protein content (Salgare and Acharekar, 1992). Hasan et al. (2008) reported lower seed protein content in chickpea plants grown under Cd stress.

6. Conclusion

Cd, the most abundant and a highly toxic nonessential HM is well known for its negative influence on the enzymatic systems of cells, oxidative stress and inducing nutritional deficiency in plants. Nutritional deficiency and breakdown of photosynthetic efficiency have been perceived as major checkpoints of growth. Nonspecific enrichment of least or non-essential HMs (e.g. Cd) prove futile for the plant system, channelized into plant body through various mechanisms of their entry. Their pooling and mobilization into resistant and sensitive genotypes elucidate the key events of physiological and biochemical perturbations. Cd interruptions at electron transport chain of major membranous organelles and cytosolic depletion of LMWP pool induce the defense metabolism at the cost of primary metabolism. Plant hormones' cross talk orchestrates the plant basal defense detoxifying, sequestering or expelling these toxic molecules to manifest optimal vegetative growth.

Acknowledgements

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