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Review Article

Plant Response towards Cadmium Toxicity: An Overview

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Abstract: Cadmium (Cd) is a naturally occurring element of relatively poor abundance (64th amongst elements). It is one of the most common metal contaminant in ground water, soil and sediments due to its wide industrial application, hence posing a serious environmental concern. It exits in the soil solution primarily as Cd^{2+} but also as Cd-chelates. Cadmium usually shares natural geologic association with Zn and Hg. Due to its strong mobility and high phytoavailability in soil, Cd is readily taken up by plant roots. Cd is taken up along with other essential elements such as Calcium and Zinc through transporters. Once inside the plant, it affects several cellular processes, plant growth and metabolic pathways. It interferes with nutritional uptake and impairs the process of photosynthesis, transpiration and respiration. Cd causes oxidative stress in plants either by blocking essential functional groups in bio-molecules or by altering the antioxidant defense system. It adversely affects the enzymatic machinery associated with sugar and nitrogen metabolism. Various Cd-hyperaccumulators have been explored and exploited in view of their phytoremediating properties. The present review summarizes an overview regarding the Cd availability in environment, Cd-induced toxic symptoms in plants, effect on germination, photosynthesis, biochemical and physiological alterations and Cd-hyperaccumulation.

Key words: Cd toxicity; Physiological effects; Oxidative stress; Uptake mechanism; Cd-hyperaccumulation.

Introduction

An illegal and surplus application of phosphate fertilizers, industrial and sewage waste discharge, mining and vehicular emissions from industries have drastically mounted up heavy metal load in the agricultural soils at the lethal level (Arora *et al.*, 2008). The commercial food crops and vegetables raised in such contaminated soil accumulate toxic level of these metals thereby introducing them further in the trophic chain (soil-plant-animal) (Wuana and Okieimen, 2011). Amongst these, Cd, probably is the most ubiquitous and potent contaminant of ground water and agricultural soil owing to its high toxicity, greater solubility, strong mobility and carcinogenic properties (Tanhuanpää *et al.*, 2007). In non-polluted soil, Cd concentration ranges from 0.04mM-0.32mM while it could be assumed as moderately polluted when the range reaches up to 1mM (Sanita di toppi and Gabbrielli, 1990). It has also been categorized on the US Environmental Protection Agency's (EPA) list of priority pollutants because of its strong toxic effects (Nedelkoska and Doran, 2000). Being readily absorbed by the plants, it tends to stay primarily in roots and up to a slender extent it translocate in shoots and seeds (Chardonnens *et al.*, 1998). Its incorporation in plants has been reported to induce severe phyto-toxic effects such as it restricts the bio-synthesis of chlorophyll (Qian *et al.*, 2009), alters water status (Barceló and Poschenrieder, 1990), reduces growth, particularly roots (Zhou and Qui, 2005), interrupts mineral uptake and carbohydrate metabolism (Moya *et al.*, 1993), encourages stomatal closure (Poschenrieder *et al.*, 1989), retards the photosynthetic mechanism (Chugh and Sawhney, 1999), impairs the process of transpiration, respiration and nitrogen assimilation (Wang *et al.*, 2008) and consequently lowers biomass production.

Cadmium in the environment

Cadmium (atomic number–48) belongs to group IIB of the periodic table exhibiting chemical analogy with rest of the elements of group IIB particularly with Zinc (Zn) and Mercury (Hg). In natural aquatic medium, it generally exists in the positive valence of two and found relatively more stable in that very particular state. It releases into the environment through diverse natural and anthropogenic activities such as volcanic eruption, mining, sewage, mismanagement of industrial waste and application of phosphate fertilizers and pesticides. In contaminated

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medium, it is generally found in soluble forms or as an autonomous ion, and its movement depends upon availability of the chelating substance and other cations. A report from Kamnev and Van der Lelie (2000) suggested that globally, approx. 9.9-45.0 tons of Cd is discharged into the soil every year. To restrict Cd concentrations in edible produce, it has been recommended to be lower than 3 μg g^{-1} dry soil for agriculture and horticulture (Mengel *et al.*, 2001).

Morphological symptoms

Roots: Being susceptible to Cd-induced toxicity, root growth inhibition represents a common indication as it is characterized by high metabolic activity. Liu *et al.,* (2003) observed a diverse response pattern in the roots of *Allium* cepa, submitted to different concentration of Cd^{2+} (10^{-7}, 10^{-6}, 10^{-4}, and 10^{-2} M) as at low concentration, not much variation was recorded in the root length whereas at 10^{-5} and 10^{-4} M of Cd^{2+}, root tips displayed a slightly twisted appearance and at 10^{-3} and 10^{-2} , the root tips were unusually thick and stiff after 24 h of treatment. Varied degree of Cd exposures have been reported to induce a noteworthy inhibition on root length along with reduction in fresh and dry weight in many other plants such as *Lycopersicon esculentum* (López-Millán *et al.*, 2009), *Vicia faba* (Zhang *et al.*, 2009), *Solanum tuberosum* (Gonçalves *et al.*, 2009), *Oryza sativa* (Sun *et al.*, 2008). Greater retardation of root growth in response to Cd stress has been attributed to the tendency of Cd (II) ions towards the carboxyl groups of the cell wall (Barceló and Poschenrieder, 1990) and/or to an interaction with ~SH residues of soluble proteins (Leita *et al.*, 1993) which results in reduced cell expansion and ultimately seizes root growth/elongation.

Leaves: Salt *et al.,* (1995) reported that Cd (II) toxicity caused chlorosis in young leaves of *Brassica juncea*. Also, necrotic dots on the leaves of the Prayon ecotypes of *Thlaspi caerulescens* were found in response to 12 week exposure to 50μM Cd treatment (Cosio *et al.*, 2005) which was found further extended over the whole leaf surface with due course. Two cultivars of tomato seedlings exposed to Cd treatment (0, 0.1, 1, 5, 10μmol/L), exhibited leaf necrosis, chlorosis and reddish brown discoloration of leaf blades, which become more pronounced with extended exposure and time (Dong *et al.*, 2005). The Cd-induced growth inhibition in aerial parts of plant has been ascribed to the constrained activity of photosynthesis, diminished chlorophyll content (Lee *et al.*, 2010) as well as inactivity of both photosystem II and the enzymes of carbon reduction cycles (Greger and Ögren, 1991).

Effect on Photosynthesis

Cd, being a non-essential heavy metal and an influential enzyme inhibitor (Lockwood, 1976), has been documented to unfavorably affects the photosynthetic machinery of the plants. But despite of intensive investigations, the Cd-induced alteration in photosynthetic activity is still ambiguous because of the multiplicity of inhibitory effects and several barriers within the plant. In past, several locations have been suggested by different authors as the target sites of Cd^{2+} toxic action, for example the pigment machinery (Stiborova, 1988), electron transport pathway (Greger and Ogren, 1991), photophosphorylation (Weigel, 1985), chloroplast ultrastructure (Baszynski, 1989) and enzyme behavior (Sheoran *et al.*, 1990) etc. However, it has been already documented that photosystem II (PSII) is extremely susceptible to an inappropriate amount of $Cd^{2+}$and its activity is inhibited to a greater degree than that of PS I (Mallick and Mohn, 2003). Reported evidences suggested that extraneous Cd^{2+} level greatly reduces the P_N (net photosynthetic rate), stomatal conductance and content of photosynthetic pigments as observed in Pakchoi and mustard (Chen *et al.*, 2011), *Lepidium sativum* (Gill *et al.*, 2012), *Zinnia* (Thamayanthi *et al.*, 2011) and *Lactuca sativa* (Dias *et al.*, 2012). In *Phyllanthus*, the degree of depression in the pigments at Cd (100 μM) were about 30% for *chl* a, 48% for *chl* b and 40% for carotenoid which implied that *Chl* b was severely affected than *chl* a; hence showed an increase in *chl* a/b ratio (Rai *et al.*, 2005). The reduced carotenoid content implies that it could not assist in the process of detoxification of toxic oxidation radicals generated in response to Cd dosing. In contrast, the carotenoid content was found enhanced in lettuce plants exposed to 10 and 50μM Cd which reflected an adjustment/adaptive response activated in plants to protect the chlorophyll or the photosynthetic apparatus from the Cd-induced photo-oxidative destruction (Choudhury and Behera, 2001). Cd competitively reduces Fe uptake which thereby arrests the photosynthetic electron transport pathway followed by photosynthetic efficiency (F_V/F_M) (Krupa *et al.*, 1999). Padmaja *et al.,* (1990) proposed that Cd-induced inhibition of chlorophyll biosynthesis could be a result of diminishing level of δ-aminolevulinic acid dehydrogenase and dissociation of pigment or its precursors. In addition, a case of Barley leaves indicated that decline in the chlorophyll level and carotenoids might be due to the Cd-induced inhibition at protochlorophyllide stage which in sequence obstructs the activity of enzyme protochlorophyllide reductase (Stobart *et al.*, 1985). Additionally, decrease in the chlorophyll content in *Salvinia natans* L. plant (Mohan and Hosetti, 2006) has been suggested as a direct interference of Cd^{2+} at the sulphydryl position of all the enzymes associated with chlorophyll biosynthesis.

Effect on seed germination

Variation in seed germination ability of different cultivars against Cd stress might have been due to genetic diversity of the cultivars. A study on *Sorghum bicolor* (L.) displayed a significant decrease in germination by 13-27% after one week of exposure to different Cd concentration ranging from 0.5 mM to 3.0 mM (Kuriakose and Prasad, 2008). It has been suggested that Cd interferes with the functions of important hydrolyzing enzymes and results in impaired hydrolysis of storage product, which sequentially leads to undernourishment of germinating embryo (Kuriakose and Prasad, 2008). Similar observations were seen in case of other plant species such as Soyabean (Liu *et al.*, 2011), *Arachis hypogea* (Damodharam *et al.*, 2013) and *Zea mays* (Gupta and Abdullah, 2011) exposed to varied degree of Cd^{2+} levels. Contrastingly, an evident reverse germination rate was reported in case of *Phaseolus mungo* exposed to Cd at a dosage of 10^{-8} M and displayed slight growth enhancing effects (Siddhu and Khan, 2012).

Uptake of Cd (II)

Uptake from roots and the translocation pathway from root-to-shoot have been widely studied in variety of species but despite of that, the mechanism involved in Cd acquisition and transport into and within the cell is little known. In spite of its high mobility and toxicity at slightest concentration, the uptake potential, translocation and further accumulation of Cd^{2+} varies greatly among the plants species and even between the genotypes as it can be seen in barley (Wu and Zhang, 2002) maize (Yang *et al.*, 1995), and wheat (Hart *et al.*, 1998). Numerous cases have revealed that majority of Cd^{2+} is likely to accumulate in the roots and the fraction of it is transported to shoots and seeds. The suggested order of declining Cd content is as roots > stems > leaves > fruits > grains/seeds (Blum, 1997). In addition, Salt *et al.,* (1995) suggested that the movement of Cd from roots to shoots is possibly stimulated via xylem and triggered by transpiration from leaves. However, the bioavailability of soil-Cd^{2+} to the plants chiefly controlled by the physical, chemical and biological attributes that regulates the form of Cd ion and its solubility in the soil solution and most importantly in the rhizosphere (Evans and Bolton, 1995). In addition, other non-biotic factors which can manipulate the accessibility of Cd cation in the soil involves soil pH, clay content, carbonates, iron oxides, redox potential, type and content of organic matter, complex ligands, water content as well as soil management practices including crop rotations and soil amendments such as phosphate fertilizers, manure, sewage sludge and agriculture lime concentration. In addition, few significant factors for example plant species, crop cultivar, root activity, rooting patterns and root-associated microorganisms (mycorrhizal fungi) (Guo *et al.*, 1996) cannot be overlooked as these collectively influence the Cd accessibility to plants. Higher Cd availability to the plants typically occurs in acidic soils (Kirkham, 2006) and its solubility is boosted by the presence of root exudates (Zhu *et al.*, 1999). It has been accounted by many workers that Cd uptake and accumulation through plants roots is usually restrained by presence of other ions such as La^{3+}, Ca^{2+}, Cu^{2+}, Fe^{2+}, Zn^{2+}, or Mn^{2+} in the rhizosphere medium (Hart *et al.*, 2002; Berkelaar and Hale, 2003; Zhao *et al.*, 2006).

Moreover, it is yet to be clearly understood whether Cd cations are energetically taken up through non-specific carriers as that of Zn, Cu, or Fe or it penetrates the root cells via some particular transporters (Lombi *et al.*, 2001). However, penetration of Cd^{2+} into the root cells have been documented to be occurred through a ZIP (Zinc-regulated transporter/Iron-regulated transporter-like Protein) transporter (Verbruggen *et al.*, 2009). Moreover, the Cd^{2+} to root cells could be mediated through Cd-chelates via YSL (Yellow-Stripe 1-like) proteins (Curie *et al.*, 2009). Also, in *Arabidopsis*, ABC transporter AtPDR8 has been identified to be involved in Cd efflux across the plasma membrane of root hairs and epidermal cells (Kim *et al.*, 2007).

Influence of Cd toxicity on mineral nutrition

A homeostasis of inorganic nutrients is demanded by plants for optimal growth and development under normal and stressed conditions. In soil-plant relationship, Cd may influence physiological and biochemical mechanisms primarily by affecting composition and functions of mineral nutrients. At the root region, Cd competes for the absorption of several minerals nutrients generally those sharing similar chemical properties like Ca^{2+} and Mg^{2+}, therefore, causing mineral deficiency (Barcelo and Poschenrider, 1990). The decrease in the concentration of Fe, Mg, S and P in the leaves of Cd-sensitive cultivars under Cd stress has been shown to be a key basis for the diminishing rate of photosynthesis and reduction of cabbage growth (Sun and Shen, 2007). Gonçalves *et al.,* (2009) showed that Cd reduced the macronutrient and micronutrient contents in the *in vitro* cultured potato plantlets in both roots and shoots. On the basis of regression analysis, Dong *et al.,* (2006) showed that there exists a negative correlation between Cd and Mn which signifies an antagonistic effect of Cd on Mn absorption and translocation. Cadmium has also been shown to alter the conformation of proteins for instance enzymes, transporters or regulator protein, due to its strong propensity as ligand to sulfhydryl and carboxylic groups (Van Assche and Clijsters, 1990). Moreover, upon exposure to 1.0μM Cd in barley plant, significant decrease over control in the concentrations of P, K, Ca, Cu, Zn, Mo, Mg and B in roots was observed but contrastingly no decrease in the concentrations of these elements was noted in the shoots against the control (Guo *et al.*, 2007). Also, a substantial loss in the uptake of Ca and K in response to Cd accumulation was observed in Cd-hyperaccumulator *Atriplex halimus* subsp. *schweinfurthii* (Nedjimi and Daoud, 2009). Cd^{2+} ions interferes with homeostatic pathways for essential metal ions (Roth *et al.*, 2006) and displaces divalent cations such as Zn and Fe from proteins which causes the release of free ions and elicit oxidative burst via Fe/Cu-catalyzed Fenton reaction (Schutzendubel and Polle, 2002). However, it has been shown that severity of Cd toxicity can be minimized through the optimization of these nutrients (Jalloh *et al.*, 2009; Zhu *et al.*, 2011).

Cd-induced oxidative stress

Cd, being a redox inactive/non-redox element does not participate in Fenton-type ROS-producing reactions, however, it can indirectly activate NADPH oxidases in membranes and bring about over accumulation of $O_2^{\cdot-}$ and H_2O_2 and hydroxyl radical which eventually lead to an oxidative burst (Heyno *et al.*, 2008). These species react with lipid, protein, pigments and nucleic acids and cause lipid peroxidation, membrane damage, inactivation of enzymes, thus affecting cell viability (Gill *et al.*, 2012). It has been widely reported that over generation of H_2O_2 leads to increase leakage of ions from root or leaves in different plant species exposed to a range of Cd concentrations (Anjum *et al.*, 2011; Wang *et al.*, 2008). Exposure to Cd (500 μM) enhanced malondialdehyde (MDA), H_2O_2 content in upland cotton seedlings (Khan *et al.*, 2013). Similar upward trend in MDA and H_2O_2 was observed in *Sedum alfredii* Hance (Jin *et al.*, 2008) and *Juncus effuses* upon Cd stress (Najeeb *et al.*, 2011). Cd stress has been shown to induce the oxidation of NADPH oxidase leading to the generation of carbonyl compounds such as hydrogen peroxides, superoxide radicals and hydroxyl ions (Cho and Seo, 2005).

Cd-induced increase of cellular ROS levels is probably due to the alteration (inhibition / stimulation) of antioxidative enzymes (Schützendübel and Polle, 2002). The effect of Cd (II) on the activity of key enzymes involved in the detoxification of ROS has been profoundly studied and it has been observed to display a diverse response pattern depending on Cd concentration, period of treatment, plant tissue examined and plant species itself (Gallego *et al.*, 1999; Vitória *et al.*, 2001; Ferreira *et al.*, 2002). SODs are the group of enzymes that accelerate the dissociation of superoxide radicals to H_2O_2 (Fernández-Ocaña *et al.*, 2011). Cd-dependent reduction of SOD activity has been reported in wheat (Milone *et al.*, 2003) and pea (Romero-Puertas *et al.*, 2007) while, in other species like maize (Ekmekci *et al.*, 2008) and *Arachis hypogea* (Shan *et al.*, 2012), an increase of the activity was observed. The decrease in SOD expression most likely caused by Cd-induced Zn, Mn or Fe deficiency (Romero-Puertas *et al.*, 2007; Gonçalves *et al.*, 2009). CAT, catalyzes the decomposition of H_2O_2, decreases with increasing concentration of Cd in pea (Dixit *et al.*, 2001; Romero-Puertas *et al.*, 2007), *Salvinia natans* (Mohan and Hosetti, 2006) and *Helianthus annuus* (Gallego *et al.*, 1999). On the other hand, the activity of CAT was found enhanced in *Agropyron repens* (Brej, 1998), *Phragmites australis* (Iannelli *et al.*, 2002) and radish (Vitória *et al.*, 2003) while it was found unaltered in Soyabean leaves (Ferreira *et al.*, 2002). Being sensitive to O_2^- radical, CAT may undergo inhibition under high generation of the same (Cakmak, 2000). Also, the decline may also be attributable to detrimental effect induced by peroxisomal proteases or could be due Cd-induced photo-inactivation of enzyme (Sandalio *et al.*, 2001). Ascorbate peroxidase (APX) and Glutathione reductase (GR) are the important components of ascorbate-glutathione cycle, responsible for the elimination of H_2O_2 in different cellular compartments (Jiménez *et al.*, 1997). Cd has been shown to enhance the activity of APX in barley genotype (Tiryakioglu *et al.*, 2006) and maize (Ekmekci *et al.*, 2008). Besides, a study from Gomes-Junior *et al.,* (2006) showed that in coffee cells, the activity of APX increased at lower Cd concentration (0.05 mM) whereas it was severely inhibited by higher Cd concentration. Similar trend was observed in *Glycine max* (Balestrasse *et al.*, 2001) and *Cucumis sativus* (Zhang *et al.*, 2003). Mohan et al., (1997) suggested that increase of APX activity may be an effect of accelerated senescence and associated with enhanced formation of H_2O_2 or secondary metabolites. The reduction in APX activity at higher Cd concentration may be due to GSH depletion and a subsequent reduction in the ascorbate-glutathione cycle. GPX, similar to APX, detoxifies H_2O_2 to H_2O, but uses GSH directly as a reducing agent. Cd treatment has been documented to alter the GPX activity (Balestrasse *et al.*, 2001; Milone *et al.*, 2003; Vestena *et al.*, 2011) whereas no clear response was detected in coffee cell cultures (Gomes-Junior *et al.*, 2006) and *Arabidopsis thaliana* (Cho and Seo, 2005) exposed to Cd. Similarly, activity of GR has also been documented to be altered in response to Cd exposure such as GR activity increased in safflower (Namjooyan *et al.*, 2012) *Raphanus sativus* (Vitória *et al.*, 2001) and *Glycine max* (Ferreira *et al.*, 2002) while it was found strongly depleted in maize (Ekmekci *et al.*, 2008) and water hyacinth (Vestena *et al.*, 2011). The increased activity of GR has been explained as transcriptional or translational modification in order to maintain an adequate GR level so as to confer protection against Cd stress (Mishra *et al.*, 2006). The antioxidative defense activity has also been found to have differential response amongst the algal species as well. In marine microalgae *Nannochloropsis oculata*, the activities of APX, POX and CAT were stimulated upon Cd dosing whereas the induction level of SOD and GR were dropped (Lee and Shin, 2003). In marine microalgae *Ulva fasciata*, activities of all Fe-SOD, CAT, GR and APX were up-regulated when subjected to Cd treatment (0, 5, 10, 20 and 50μM) after 4 days (Wu *et al.*, 2009).

Under Cd stress, the formation of Cd-GSH and Cd-PC complexes reduces the free Cd concentration in the cytoplasm and assist in activation of stress-related responses in plant metabolism (Metwally *et al.*, 2005). Both AsA and GSH are not only the major cellular antioxidants and redox buffers but they also play important function in growth, development and stress responses (May *et al.*, 1998). In *Oryza sativa*, the content of GSH, PCs and –SH found progressively increased in response to increasing Cd concentration (5, 10, 20, 40, 80 mg/kg). Increase in the content of AsA and –NPSH in response to Cd were observed in barley (Tiryakioglu *et al.*, 2006) and *Bechmaria nivea* (Liu *et al.*, 2007). In contrast, studies have shown that Cd incorporation decreases AsA-GSH pools in mung bean, *Brassica* genotypes and *Pisum sativum* (Dixit *et al.*, 2001; Qadir *et al.*, 2004; Anjum *et al.*, 2011). In addition, increased generation of GSH has been noticed with increasing Cd concentrations in safflower (Namjooyan *et al.*, 2012) and *Sedum alfredii* (Sun *et al.*, 2007) while decay of GSH has been reported in *Helianthus annuus* L. (Gallego *et al.*, 2002).

Cd remediation through plants

Cd hyperaccumulation, defined as the accumulation and tolerance of up to 100 µg Cd g^{-1} in shoots by plants (Baker *et al.*, 2000). It is present only in some populations of *Thlaspi caerulescens*, *Arabidopsis halleri*, and *Thlaspi praecox*, all belonging to the *Brassicaceae* family (Verbruggen *et al.*, 2009). In general, accumulating pathway of any metal in plant system is specifically based on uptake ability and the intracellular binding sites. However, varieties of other plants have been explored *vis-à-vis* experimented considering the removal of Cd from the agricultural soil for example *Brassica juncea* L. have been found as a suitable candidate for metal removal, especially cadmium from the soil with moderately low levels of Cd infestation (Ishikawa *et al.*, 2006). In addition, crop plants like maize, rice and sugar beet have also proven their potential of being a better contender in extracting Cd from the contaminated medium (Murakami *et al*., 2009; Mojiri, 2011; Liu *et al.*, 2015). Amongst the hyperaccumulators, *Nelumbo nucifera,* a usual flora of all reservoirs, has been found to be a prospective accumulator of Cd (0.0334–0.121 ppm per week from 0.75, 1.0, 1.25 and 5% Hoagland solution) (Bandara *et al.*, 2008). More so, *Sedum alfredii* has been listed in the group of potential hyperaccumulator of Cd as 11000 mg/kg of Cd content has been recorded in leaves exposed to 600 μM of Cd (Zhou and Qui, 2005). Nevertheless, in the last few decades numerous scientists in different locations of the world has worked out the Cd bioaccumulation potential of a variety of species for instance *Pistia stratiotes* (Odjegba and Fasidi, 2004), *Tamarix smyrnensis* (Manousaki *et al.*, 2008), *Arabidopsis thaliana* (Saraswat and Rai, 2009), *Rorippa globosa* (Sun *et al.*, 2010), *Sesbania drummondi* (Israr *et al.*, 2006), *Atriplex halimus* subsp. *schweinfurthii,* (Nedjimi and Daoud, 2009).

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