Cadmium Phytotoxicity: Responses, Mechanisms and Mitigation Strategies: A Review

Abdul Wahid, Muhammad Arshad and Muhammad Farooq

Abstract Contamination of soils with cadmium is a critical factor affecting soil properties and plant growth. Cadmium is toxic to most plants in trace amounts, while other plants show varying tendencies to grow under relatively high cadmium levels. Some plants can bind the absorbed cadmium to their cell walls. Roots, being directly exposed, always accumulate greater amounts of cadmium than shoots. Effects of cadmium toxicity on above-ground parts include plant stunting, leaf rolling, chlorosis and necrosis, diminished stomatal conductance and gas exchange, perturbed leaf water and nutrient status, hormonal imbalance, production of oxidative stress, and enhanced peroxidation of membrane lipids. Plants use various mechanisms to cope with cadmium, which include synthesis of metal chelating proteins, expression of enzymatic and nonenzymatic antioxidants, organic acids, and plant root–mycorrhizal association. Cadmium toxicity can be alleviated by the exogenous use of metal chelators, and organic and inorganic sources. Finding strategies to bind cadmium in soil systems and better understanding of species diversity for cadmium tolerance, cadmium-responsive genes, and the molecular basis of cadmium-tolerance may be important strategies for coping with this ever-increasing problem.

Keywords Cadmium · Phytoavailability · Oxidative stress · Chelation · Genotypic variability · Nutrients

Contents

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1 Introduction

Heavy-metal pollution is an ever-increasing worldwide issue (Kashem and Singh, 1999; Yagdi et al., 2000; Jamali et al., 2007). Heavy metals, including cadmium, mercury, copper, and zinc, accumulate in soils and plants in variable quantities and create a range of agricultural and human health-related issues. Major soil pollutants and their sources include pesticide and fertilizer use, solid waste and sludge disposal, and processes including electroplating, batteries, welding, smelting, and pigments (Lugon-Moulin et al., 2006). In many countries, wastewater is used for irrigation, which is a main cause of the accumulation of even essential micronutrients to phytotoxic levels in soils. Thus, to lower the damaging effects of toxic metals on plants, a suitable pretreatment of wastewater and soils prior to its use is imperative (Ghafoor et al., 1997; Ye et al., 2000).

Cadmium is an important toxicant in affecting plant productivity (Prasad, 1995; Thiebeauld et al., 2005; Wahid and Ghani, 2008) and has a long biological half-life (Himly et al., 1985). Uninterrupted application of industrial wastewaters for irrigation over the past few decades has led to the accumulation of heavy metals in upper soil strata, which is not only phytotoxic (Helal et al., 1998) but also reduces the bioavailability of essential metals (Ghafoor, 2000). Cadmium is a nonessential element and is released into the environment from various industries like power stations, heating systems, metal industries, and urban traffic. Its wide use in industries constitutes an important source (Sanita di Toppi and Gabbrielli, 1999). It never occurs in isolation in natural environments, rather it is often found in association with lead and zinc as a guest metal. Therefore, greater accumulation of cadmium in plants appears due to its accompaniment of other metals (Baker et a1., 1994). A nonpolluted soil contains 0.04–0.32 μM cadmium, while its concentration in moderately polluted soil solutions varies from 0.32 μM to $\sim$1 mM (Wagner, 1993). In water, however, cadmium concentrations vary from none to about 0.01 μg/L (Anonymous, 2006).

Cadmium toxicity in plants is observed at the whole plant, as well as at cellular and molecular levels; the most important of which includes perturbation of metabolic pathways such as photosynthesis, energy transduction, protein synthesis, and nutritional disorders. Plants entail certain adaptive mechanisms to cope with these adverse effects, including the synthesis of metal binding and chelating proteins, antioxidants, and osmoprotectants. Furthermore, the adverse effects of cadmium can be alleviated by employing breeding and selection strategies, functional genomics approaches, exogenous use of organic and inorganic chemicals, and membrane stabilizers. This review emphasizes important effects, mechanisms, and some mitigation strategies employed to overcome the adverse impacts of cadmium on plants.

2 Cadmium in the Soil System

Physico-chemical properties of soil and soil solution greatly affect the phytoavailability of cadmium (Cao et al., 2007). However, data pertaining to the effects of added cadmium on the properties of soil are scarce. This is most likely due to the fact that cadmium is toxic to plants in very low amounts and plants can not thrive in heavily cadmium-contaminated soils, which may alter their physiological properties. The available literature shows that soil properties, including chemical form and speciation, valence state, solubility characteristics, interactions with essential metals, presence of cadmium-chalators, ascorbate, metallothionein, and cadmium-complex formation are important (Mengel et al., 2001). Stimulation of oxygen consumption on soil incubation with 0.01 and 10 mg cadmium per kg soil has been shown to uncouple respiratory phosphorylation (Naidu and Reddy, 1988). It has been shown that growing crops on heavy-metal dredged sediments can modify their physico-chemical state by lowering the pH, enhancing redox potential by mechanical action of root, production of soluble organic compounds, and promoting microbial activity. These processes enhance the mobility and bioavailability of already existing heavy metals, which may be a great threat to upcoming vegetation as well as the environment (Marseille et al., 2000).

At higher cadmium levels, a substantial accumulation of nitrite nitrogen (NO_2–N) suggests that cadmium is toxic to soil nitrification (Rother et al., 1982). Ammonium nitrogen (NH_4^+–N) lowers the soil pH upon dissociation of nitrogen from proton (H^+) and enhances the bioavailability of cadmium (Lorenz, 1994; Mengel et al., 2001). Other studies show that the combined effects of a range of soil properties, particularly cation exchange capacity (CEC), organic matter, and pH, control the concentration of cadmium in solution, and its sorption and desorption in soil (Gray et al., 1999). Of these, soil pH is more important; acidic pH enhances—while alkaline pH lowers—its phytoavailability (Guo et al., 2007). By contrast, chelating agents in the organic matter may chelate cadmium and allow the soil microflora to flourish (Jones et al., 1987). In addition to chelating agents, the addition of phosphate as KH_2PO_4 increases the soil pH, negative charge, and adsorption by the soil, and enhances soluble and exchangeable cadmium-fraction, resulting in its poor phytoavailability (Bolan et al., 2003).

3 Cadmium Phytotoxicity Responses

Cadmium does not have any beneficial physiological role in plants, but when accumulated, it affects all aspects of growth and development (Fig. 1). The most frequently observed effects of cadmium-phytotoxicity are inhibition of root elongation, perturbation of water relations, suppression of photosynthetic activity, a decline in biomass production, and even the plant death. It is strongly phytotoxic and produces a vast array of changes at morpho-anatomical, physiological, and biochemical levels. These effects are strongly dependent upon the stage of plant growth, the level of cadmium applied, and the physico-chemical nature of the plant growth medium (Table 1).

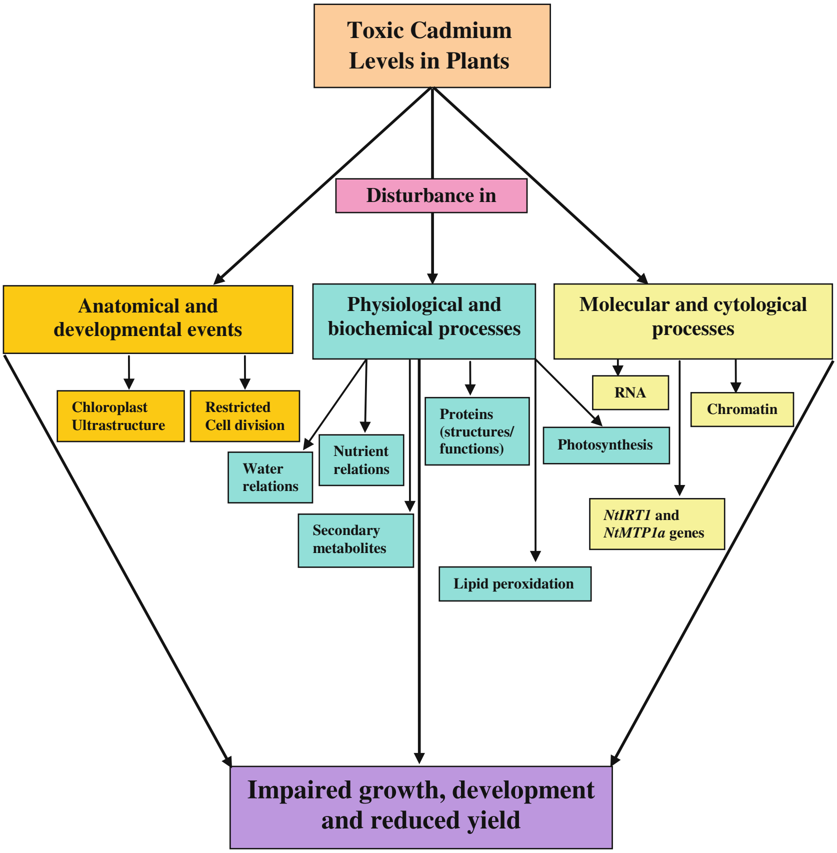

Fig. 1 Proposed mechanisms of damage by toxic levels of cadmium in plants. The cadmium adversely affects the plant growth and development and these effects are evident on the physiological, biochemical, and developmental phenomena of plants

Table 1 Phytotoxic concentrations of cadmium in plant species and their growth stages. The phytotoxic levels of cadmium vary greatly with plant species and cadmium accumulation in various plant parts is highly linked to the levels of cadmium in the growth medium

Plant species	Plant part analyzed	Growth medium	Maximum cadmium concentration (on dry weight basis)	Reference
Cape gooseburry (*Physalis peruviana*)	Leaf	Nutrient solution (200 mg/L cadmium; pH 5.5)	~3.0 mg/kg	Thiebeuld et al. (2005)
As above	Root	As above	~70 mg/kg	As above
Pepino (*Solanum muricatum*)	Leaf	As above	~35.0 mg/kg	As above
	Root	As above	~120 mg/kg	As above
Pepper (*Capsicum annuum*)	Leaf	As above	~33.0 mg/kg	As above
	Root	As above	~110 mg/kg	As above
Tobacco (*Nicotiana tabacum*)	Leaf	As above	~31.0 mg/kg	As above
	Root	As above	~75 mg/kg	As above
Tomato (*Lycopersicon esculentum*)	Leaf	As above	~15.0 mg/kg	As above
	Root	As above	~82 mg/kg	As above
Tomato	Shoot	Nutrient solution (50 µM $CdCl_2$)	~65 µmol/g	Mediouni et al. (2006)
	Root	As above	~25 µmol/g	As above
Greengram (*Vigna* sp.)	Root	Soil	~2.2 µg/g	Wani et al. (2007)
	Shoot	As above	~0.8 µg/g	As above
	Grain	As above	~0.5 µg/g	As above
Spinach (*Spinacea oleracea*)	Shoot	Cd-polluted soil	2.81 µg/g	Helal et al. (1998)
	Root	As above	12.10 µg/g	As above
Willows (*Salix* sp.) clones	Leaves	Cd-contaminated soil (Cambisol)	47–89 mg/kg	Tlustos et al. (2007)
As above	Twigs	As above	18–40 mg/kg	As above

Table 1 (continued)

Plant species	Plant part analyzed	Growth medium	Maximum cadmium concentration (on dry weight basis)	Reference
As above	Leaves	Cd-contaminated soil (Chernozem)	0.93–3.66 mg/kg	As above
As above	Twigs	-do-	0.91–2.18 mg/kg	As above
As above	Leaves	Cd-contaminated soil (Fluvisol)	9.51–101 mg/kg	As above
As above	Twigs		6.24–53.2 mg/kg	As above
Maize (*Zea mays*)	Seedling shoot	Black soil	~42 mg/kg	Cao et al. (2007)
As above	Seedling root	As above	~140 mg/kg	As above
Soybean (*Glycine max*)	Seedling shoot	As above	~70 mg/kg	As above
As above	Seedling root	As above	~155 mg/kg	As above
Chamomile (*Matricaria chamomilla*)	Shoot	Nutrient solution	~550 µg/g	Kovacik et al. (2006)
As above	Root	As above	~4500 µg/g	As above
Almond (*Prunus dulcis*)	Leaves	Nutrient solution	~75 µg/g	Nada et al. (2007)
As above	Root	As above	~3200 µg/g	As above
Barley (*Hordeum vulgare*)	Glum	Nutrient solution	~7 mg/kg	Chen et al. (2007b)
As above	Awn	As above	~21 mg/kg	As above
As above	Rahis	As above	~13 mg/kg	As above
As above	Stem	As above	~39 mg/kg	As above
As above	Grain	As above	~14 mg/kg	As above
As above (cv. Hamidiye)	Shoot	As above	138 mg/kg	Tiryakioglu et al. (2006)

Table 1 (continued)

Plant species	Plant part analyzed	Growth medium	Maximum cadmium concentration (on dry weight basis)	Reference
As above	Root	As above	3743 mg/kg	As above
As above (cv. Tokak)	Shoot	As above	110 mg/kg	As above
As above	Root	As above	3164 mg/kg	As above
Phyllanthus amarus	Aerial parts	Loam soil (pH 7.7)	85 ppm	Rai et al. (2005)
As above	Root	As above	65 ppm	As above
Wheat (*Triticum aestivum*) cv. PBW343	Leaf	Soil	~60 μg/g	Khan et al. (2007)
As above	Root	As above	~330 μg/g	As above
As above cv. WH542	Leaf	As above	~90 μg/g	As above
As above	Root	As above	~580 μg/g	As above
Sunflower (*Helianthus annuus*)	Young leaf	Nutrient solution	42.43 μg/g	Di Cagno et al. (1999)
As above	Mature leaf	As above	37.06 μg/g	As above
As above	Stem	As above	25.02 μg/g	As above
As above	Root	As above	240.82 μg/g	As above
Durum wheat (*Triticum turgidum* var *Durum*); a low Cd line	Shoot	As above	~0.6 μg/g	Hart et al. (2006)
As above	Root	As above	~9.0 μg/g	As above
As above; a high Cd line	Shoot	As above	~1.1 μg/g	As above
As above	Root	As above	~6.0 μg/g	As above
Arabidopsis halleri	Shoot	As above	~3000 mg/kg	Zhao et al. (2006)
As above	Root	As above	13000 mg/kg	As above

3.1 Morphology, Growth and Yield Responses

Cadmium is one of the most toxic and mobile metallic elements in soil (Pinto et al., 2004). It is a potential contaminant of the soil and environment. Its salts are highly water-soluble and cadmium in ionic form is highly mobile within the phloem and, therefore, easily translocated to various plant parts (Mengel et al., 2001; Pinto et al., 2004). A high mobility of cadmium in the phloem is due to its properties, such as a high affinity and binding with the sulphydryl group of amino acids and some proteins in the sieve tube (Reid et al., 2003). It diminishes the elongation of both shoot and root, and dry matter production by plants, primarily due to hampered photosynthetic activity (Azevedo et al., 2005b). Plant species and even genotypes differ in their ability to absorb, transport, and accumulate cadmium in a number of species, including cotton (Wu et al., 2004), pea (Metwally et al., 2005), lupin (Brennan and Mann, 2005), salix (Tlustos et al., 2007), mungbean (Wahid and Ghani, 2008), *Avena strigosa* and *Crotalaria juncea* (Uraguchi et al., 2006), and many other plant species (Table 1).

The symptoms visible on plant parts directly indicate the intensity of prevailing stress. Visual cadmium-toxicity symptoms on plants are leaf rolling, chlorosis of leaf and stem, leaf necrosis, tip-burning, plant-stunting, browning of roots and yellowing of leaves (Baryla et al., 2001; Mishra et al., 2006; Ghani and Wahid, 2007; Wahid et al., 2007b), impaired growth, and decline in yield due to higher cadmium tissue concentrations (Schützendübel and Polle, 2001; Dhir et al., 2004; Wu et al., 2006). Such effects appear due to iron and phosphorus deficiencies or reduced manganese transport (Godbold and Hüttermann, 1985; Alcantara et al*.*, 1994). Uptake of cadmium from the substrate and its accumulation in the plant is quite fast, and toxicity symptoms are discernible within 48 h of exposure (Tiryakioglu et al., 2006). Plant stunting due to cadmium-stress occurs mainly due to diminished water uptake (Costa and Morel, 1993; Perfus-Barbeoch et al., 2002) and reduced leaf gas exchange. (Chugh and Sawhney, 1999). These effects can be of immense help in the diagnosis of stress effects and in adopting appropriate strategies to increase stress tolerance and, ultimately, selection of promising germ plasm (Wu et al., 2006; Wahid and Ghani, 2008).

Species and cultivars display marked differences for cadmium accumulation and tolerance (Table 1). These differences are evident from physiological processes like decline in production of reactive oxygen species and enhanced antioxidative defense (Tiryakioglu et al., 2006). Inter- and intraspecific variations in cadmium concentration have been found in certain crops at various growth stages (Florijin and Van Beusichem, 1993; Li et al., 1995; Metwally et al., 2005). For example, comparison of two *Nicotiana* species revealed that *Nicotiana rustica* was more tolerant of cadmium than *Nicotiana tabacum* due to a difference in zinc homeostasis and root growth (Bovet et al., 2006). In maize and soybeans, seed germination did not prove a good indicator of cadmium toxicity; while the roots of both these plants showed greater sensitivity to cadmium than shoots (Cao et al., 2007). In mungbean, postgermination mortality (instead of germination) was considered as an important cadmium-phytotoxicity effect (Ghani and Wahid, 2007). Comparison of three ornamental species revealed that, on a dry weight basis, African marigold (*Tagetes erecta*) proved the most tolerant, scarlet sage (*Salvia splendens*) was the most sensitive, and sweet hibiscus (*Abelmoschus manihot*) showed high sensitivity with 50% inhibition in seed germination (Wang and Zhou, 2005). Significant differences have been reported for wheat genotypes in shoot cadmium concentration (Zhang et al., 2002). Cadmium is accumulated by many cereals, potatoes, vegetables, and fruits, and humans get at least 70% of it from plant food (Jackson and Alloway, 1991; Wagner, 1993).

Greater final economic yield is an index of metal tolerance by tolerant plant species. Studies show that cadmium applied to green gram plants at the rate of 24 mg/kg soil diminished the seed yield by 40%, while 50% diminution in nodule leghaemoglobin protein occurred at 12 mg/kg soil. This led to a substantial diminution of total grain protein (Wani et al., 2007).

In summary, although differences exist, most crop species and varieties are sensitive to cadmium stress. The cadmium toxicity effects are evident in terms of injury symptoms on the above-ground parts, reduced growth, and yield.

3.2 Anatomical and Developmental Responses

As an initial target, roots show wide-ranging responses to excesses of cadmium (Wojcik and Tukiendorf, 2005). Histolocalization experiments involving transmission electron microscopy (TEM) indicate the presence of cadmium deposits in the vacuoles of the exodermal cells in *Phragmites australis*. This shows that roots, as a tolerance mechanism, store the cadmium in the vacuole to protect the cytoplasm from its adverse effects (Ederli et al., 2004). Suzuki (2005) reported that cadmium causes cell death in the elongation zone of *Arabidopsis* roots. During incubation of the roots for two weeks in a sublethal level of cadmium, cells became deformed with irregularly thickened walls. These cells exhibited the accumulation of some chemical in the endodermis, pericycle, and cambium. Although a clear mechanism causing such changes could not be ascertained, it seemed that cadmium restricted the mitosis of the root cells (Vernoux et al., 2000). In addition to causing anatomical changes, cadmium alters the developmental phenomena at both the cellular and tissue levels. It induced the production of root hairs 2–4 mm behind the root tip, caused premature development of the root, hastened xylogenesis, and ultimately the production of shortened root, primarily by elevated hydrogen peroxide production and peroxidase activity in the early metaxylem and vascular bundles (Durcekova et al., 2007).

Detrimental effects of cadmium have also been reported in the cellular ultrastructures. Applied cadmium led to the disorganization of the chloroplast ultrastructure with an increase in the plastoglobulii and formation of vesicles in the vacuole. It caused the senescence of peroxisomes and induced a metabolic transition from peroxisomes to glyoxysomes (McCarthy et al., 2001).

In short, higher levels of cadmium have substantial influence in producing anatomical and developmental changes in the cells and tissues, including the disruption of organelles structure.

3.3 Cell and Tissue Localization

Having been taken up by the root and translocated to various cells and tissues within the plant, cadmium concentrates there and causes injury. Cadmium-tolerant tobacco species (*Nicotiana rustica*) indicated greater labeled cadmium (^{109}Cd) content in the roost than the leaves, the major part of which was stored in the distal part as a tolerance strategy (Bovet et al., 2006). Studies employing the use of analytical electron microscopy, x-ray spectromicroscopy and energy-dispersive x-ray microanalysis revealed the localization of cadmium in vascular bundles and linked to the cell wall of the S-ligands and pericycle in the root of *Arabidopsis thaliana*. However, leaf trichomes represented major compartments of cadmium accumulation (Wojcik and Tukiendorf, 2004; Isaure et al., 2006). Although in *Phragmites australis* roots a high dose of cadmium did not reveal any ultrastructural changes, histochemical localization exhibited the deposition of cadmium in the parenchyma cells below the exodermis (Ederli et al., 2004). However, in a study on the ultrastructure of *Arabidopsis thaliana* roots using energy-dispersive x-ray microanalysis, cadmium was found to deposit with phosphorus in the apoplast (Cd/P) and sulfur in the symplast (Cd/S), suggesting its precipitation with phytochelatins.

In endodermis, cadmium was sequestered as fine granular deposits in the cytoplasm (symplast). The passage cells appeared to play a role in the cadmium transport from pericycle to the stele for its entry again into the apoplast. In the leaves, the cadmium was detected in the tracheids but not the mesophyll cells. This indicated cadmium retranslocation from the shoot to the root (Van Belleghem et al., 2007). In the willow (*Salix viminalis*), major cadmium deposition took place in a pectin-rich layer of collenchyma cell walls in the veins, accelerated senescence of the mesophyll cells in the leaf blade, and caused tannin-plugging and necrosis in the leaf edges surrounding the mesophyll and upper epidermis (Vollenweider et al., 2006).

Many studies show that roots, because they are directly exposed, accumulate greater quantities of cadmium. In *Phaseolus vulgaris*, a greater cadmium accumulation in the root had no marked effect on the plastid ultrastructure. Younger leaves, compared to primary leaves, indicated a greater disruption of chloroplast structure and function (Barcelo et al., 1988). This indicated that when cadmium is transported to the shoot, photosynthetic (mesophyll) cells are more prone to cadmium toxicity where it is deposited, causing oxidative damage and enhancing senescence (Baryla et al., 2001; Vollenweider et al., 2006; Wahid and Ghani, 2008). In summary, cadmium is accumulated and deposited both in shoot and root tissues, where it interferes with physiological phenomena, and disrupts cellular structures.

3.4 Physiological and Biochemical Responses

Cadmium has two major effects on plant systems: inactivation of macromolecules and cellular structures, and induction of oxidative stress (Stroinski, 1999). Decline in growth and yield with elevated levels of cadmium in growth media have been attributed to factors like reduced photosynthetic rate (Verma and Dubey, 2002).

Nonetheless, mechanisms of cadmium toxicity are still the subject of intensive research, as discussed in the next sections.

3.4.1 Photosynthesis

It has been reported that all aspects of photosynthesis, including light and dark reaction and assimilate partitioning, are sensitive to cadmium excesses. It disturbs the chloroplast metabolism, either by inhibiting chlorophyll biosynthesis, enhancing its degradation at the heme level, or hampering photochemical and carboxylation reactions (de Filippis and Zeigler, 1993; Vassilev et al., 2003, 2005) by affecting the activities of chloroplastic enzymes (Chugh and Sawhney, 1999). Although all photosynthetic enzymes are affected, the enzymes of light reactions are specifically influenced (Kupper et al., 2007).

Among the light reactions of photosynthesis, applied cadmium readily and pronouncedly affects photosystem-II activity over short exposure periods in *Thlaspi caerulescence* (Kupper et al., 2007), and both photosystem-I and II over long periods of exposure in peas (Chugh and Sawhney, 1999). A greater arrest in the photosystem-II activity compared to photosystem-I was associated with greater reactive oxygen species generation and diminished antioxidant activities in *Riccia* (Prasad et al., 2004). However, in two maize cultivars, the photosystem-II activity was declined due to oxidative damage but did not cease, although there was a considerable loss in the levels of chlorophylls and carotenoids (Ekmekci et al., 2008).

Applied cadmium reduced the carbonic anhydrase activity and photosynthetic pigments in the leaves, and nitrate reductase activity and carbohydrate content in the root (Hayat et al., 2007) and leaves (Mobin and Khan, 2007), although lower levels enhanced carotenoid content (Prasad et al., 2004). Photosynthesis in sunflowers is mainly altered by cadmium-induced oxidative damage to chloroplastic membranes due to hampered Rubisco activity that diminishes photochemical and nonphotochemical quenching, and quantum efficiency of photosystem-II and CO_2 assimilation (Di Cagno et al., 2001).

Among gas-exchange parameters, stomatal conductance and its indices, transpiration and net photosynthetic rate, are greatly affected by cadmium (Sanita di Toppi et al., 1999; Balakhnina et al., 2005; Wahid et al., 2008). Reduction in transpiration rate of cadmium-treated plants might be due to stomatal closure. Although cadmium declines the stomatal conductivity, a beneficial aspect of such an effect might be associated with a limited transport of cadmium with reduced transpirational flow (Bindhu and Bera, 2001; Wahid et al., 2007b).

In summary, cadmium affects all the aspects of photosynthesis—light reactions of photosynthesis, particularly photosystem-II activity, and enzymes of dark reactions are specific targets of cadmium toxicity.

3.4.2 Water and Nutrient Relations

As a result of cadmium effects on root structure and functions, hampered water and nutrient status of plants is an immediate response. Available evidence suggests that cadmium permeates the cytosol through calcium channels on the plasmalemma and changes the cell-water relationship (Perfus-Barbeoch et al., 2002; Teresa Milone et al., 2003). Acquisition of essential nutrients in appropriate amounts is important to plant growth, since they constitute either structural or functional components of cells (Epstein and Bloom, 2005).

Elevated cadmium levels substantially influence plant mineral nutrition, and a negative correlation has been reported for the uptake and distribution of various macro- and micronutrients in various plant parts (Shukla et al., 2003; Drazic et al., 2004; Adhikari et al., 2006; Ghnaya et al., 2007; Wahid et al., 2008). Cadmium-induced leaf chlorosis appears due to the antagonistic effect of cadmium on the uptake of iron, phosphorus, manganese, zinc, and copper, causing their deficiencies particularly in the cadmium-sensitive varieties (Alcantara et al., 1994; Epstein and Bloom, 2005; Chen et al., 2007a). It appears that the same metal transporters are employed for cadmium as for other metal ions (Sharma et al. 2004). Root membrane transporters involved in the uptake of potassium, calcium, and magnesium are the first targets of cadmium toxicity (Mengel et al., 2001). In cadmium-tolerant but non-hyperaccumulator *Matricaria chamomilla*, plants low levels of cadmium promoted potassium uptake, but higher levels stimulated potassium leakage from the root (Kovacik et al., 2006). This implied that changes in both water and nutritional relations are primarily due to altered root structure and functions.

3.4.3 Antioxidants and Other Enzyme Functions

Enzymes, as biochemical catalysts, are vital for metabolic functions in the cells. Like other metals, cadmium has a well-marked inhibitory effect on the activities of enzymes. Applied cadmium enhances the activities of glyoxylate cycle enzymes in the pea leaf peroxysomes, as well as activities of leucine-aminopeptidase and endopeptidase isozymes, which displayed senescence symptoms on the leaves (McCarthy et al., 2001). It reduces ATPase activity of the plasma membrane fraction of roots, leading to hampered transport and transfer processes at the root surface (Fodor et al., 1995; Obata and Umebayashi, 1997; Hall, 2002; Astolfi et al., 2005). In the root, nodules, and leaves of soybeans, cadmium completely inhibited the δ-aminolevunic acid dehydratase activity and led to a build up of δ-aminolevunic acid levels in these parts.

Exposure of sunflower plants to cadmium levels enhanced the arginine decarboxylase and ornithine decarboxylase activities, which enhanced the level of putrescine and spermine and diminished spermine and proline contents (Groppa et al., 2007). This accumulation resulted in the enhanced thiobarbituric acid reactive substances (TBARS) and diminished expression and activities of antioxidants, although S-adenosyl-L-methionine played a protective role against δ-aminolevunic acid induced oxidative damage (Leon et al., 2002; Mediouni et al., 2006; Noriega et al., 2007). Cadmium produces alterations in the functions of membranes by altering their lipid composition (Ouariti et al., 1997) and making them more permeable to solute leakage (Azevedo et al., 2005a). Studies suggest that such changes occur due to cadmium-produced oxidative damage to the membrane lipids due to the production of free radical or diminished antioxidant activities (Foranzier et al., 2002; Cho and Seo, 2004). The senescence observed in soybean nodules treated with cadmium has also been attributed to the oxidative damage (Balestrasse et al., 2004).

Cadmium is assumed to be involved directly or indirectly in the formation of free radicals, thereby causing oxidative stress (Fig. 2). Higher concentrations of cadmium in the cytosol leads to the generation of reactive oxygen species in plants (Benavides et al., 2005; Smeets et al., 2005). A balance between the steady-state levels of different reactive oxygen species are determined by the interplay between different reactive oxygen species-producing and scavenging mechanisms. The physiological condition of the plant and the integration of different environmental, developmental and biochemical stimuli are important in this regard (Asada and Takahashi, 1987; Asada, 1999; Polle, 2001). Induction of antioxidants is a protective response against oxidative damage (Schützendübel et al., 2001; Sandalio et al., 2001). A variety of antioxidants, including superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase, and thioredoxin are the peroxiredoxin family of proteins (Bowler et al., 1992; Asada, 1999; Mittler, 2002). These protein antioxidants are supplemented with nonprotein scavengers, including intracellular ascorbate and glutathione. (Noctor and Foyer, 1998) to scavenge the reactive oxygen species, including superoxide and hydrogen peroxide, which enhance membrane permeability (Mobin and Khan, 2007). In *Bacopa monnieri* and potato tubers, the level of glutathione changes due to declined glutathione reductase activity (Stroinski et al., 1999; Mishra et al., 2006) or superoxide dismutase activity in *Brassica juncea* (Mobin and Khan, 2007). In maize, on the other hand, there was no change in the superoxide dismutase, ascorbate peroxidases, or glutathione reductase activities, but there was an increase in peroxidase activity under cadmium stress.

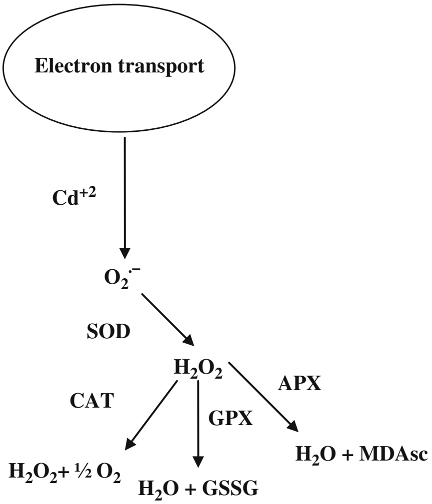

Fig. 2 Generation of reactive oxygen species by cadmium, and their scavenging mechanism by antioxidants (Modified from Pinto et al., 2003)

4 Cadmium Tolerance and Detoxification Mechanisms

When present at supraoptimal levels in the soil, cadmium is inevitably taken up by the roots and damages various plant organs and tissues (Sections 3.1. and 3.2.). Chemical and biological metal-binding capacity of the soil can reduce the uptake of cadmium. Plants can synthesize many metabolites, including phytochelatins, metallothioneins, and organic acids, which can bind and inactivate cadmium (Costa and Morel, 1993; Sanita di Toppi et al., 1999; Rauser, 1999; Schat et al., 2002; Clemens and Simm, 2003). However, their induction and synthesis demand some lag period, while the plant still experiences the toxic effects of metals (Wahid, 2008). Therefore, plant tolerance to metal toxicity cannot solely be attributed to the formation of complexes with the chelating metabolites. Phytohormones are also assumed to play an important role in the adaptation of plants to metal toxicity (Prasad, 1995). In view of this, cadmium tolerance in plants can be related to mechanisms occurring in soils and whole plants—cellular, physiological, and biochemical.

4.1 Soil Mechanisms

There are various mechanisms through which cadmium can be detoxified in the soil. Cadmium immobilization, involving fixation by solidification or stabilization through physical, chemical, or biological means, can prevent its migration into the groundwater (Lothenbach et al., 1999). Soil washing is another promising technique that involves the transfer of heavy metals into a wash solution either by desorption or solubilization (Semer and Reddy, 1996). Organic ligands such as organic acids and amino acids in soil may bind and chelate the cadmium and other heavy metals in the soil, thereby making them unavailable for soil microflora or absorption by the root (Mengel et al., 2001; Collins et al., 2003). Heavy metal ions, even under soil conditions of low pH or low organic matter, can quite often bind to soil particles in significant amounts. This binding affinity of cations also restricts cation movement into the xylem of vascular plants. A general solution to this problem is chelation, which is generally understood as a process of cation binding to a compound, resulting in a neutrally-charged complex that can move more freely via a variety of substrates.

Bioremediation in the rhizosphere may be another important strategy in coping with metal toxicity. High organic carbon and microflora of soil encourage degradation of organic chemicals in the soil. Available evidence shows that arbuscular mycorrhizal fungi facilitate cadmium uptake by bean and maize up to 41%, but this varies with soil pH and cadmium concentration (Guo et al., 1996). In a study, Heggo et al. (1990) found that arbuscular mycorrhizal fungi increased cadmium uptake in soybeans when the soil cadmium concentration was low, and vice versa. Although the mechanisms behind these phenomena are elusive, the arbuscular mycorrhizal fungi appear to offer potential for phytoextraction.

4.2 Whole Plant Mechanisms

Cadmium accumulates in many cereals, potatoes, vegetables, and fruits (Wagner, 1993; Jamali et al., 2007). Therefore, the tolerance of crops to cadmium toxicity may be related to their ability to absorb and accumulate cadmium in various parts (Leon et al., 2002). Difference in grain accumulation of two near-isogenic lines of durum wheat was due to diminished capacity for transport from root to shoot of the low cadmium-accumulating isoline. Furthermore, root phytochelatin synthesis had no influence on the shoot accumulation of cadmium in both the isolines (Hart et al., 2006). Application of higher levels of cadmium induced changes in stomatal openings and closings, and deposition of wax on both the leaf surfaces (Rai et al., 2005).

Normally, cadmium ions are retained in the root, and only small amounts are transported to the shoot (Cataldo, 1981). *Matricaria chamomilla* showed seven- to eleven-fold higher accumulations of cadmium in the roots. However, it was not classified as a hyper-accumulator and was found unsuitable for phytoremediation (Kovacik et al., 2006). On the contrary, Moral et al. (1994) reported that cadmium was easily transported to the aerial parts of tomato plants but was not detected in the fruit. In general, the content of cadmium in different plants declined in the following order: roots > stems > leaves > fruits > seeds (Blum, 1997). In cotton, the cadmium accumulation was in the following order: root > petiole > xylem > fruiting branch, leaf > phloem in vegetative organs and seed coats, seed nut > boll shell > fiber in reproductive organs (Wu et al., 2004). Exposure of potatoes to radioactive cadmium (^{109}Cd) showed that basal roots retained a greater proportion of the absorbed cadmium, while tubers and associated stolons contributed only a minor fraction at the vegetative stage. Short-term experiments using foliar cadmium application showed that newly absorbed cadmium was rapidly sequestered by the stem, which acted as a transitional storage pool. During long-term study, the leaves constituted a major pool, indicating redistribution of the absorbed cadmium within the plant body (Reid et al., 2003). Studies at reproductive stage of barley revealed that cadmium was partitioned into various parts of the spike and the partitioning was in the order: awn > stem > grain > rachis > glum. However, awn-removal and stem girdling decreased the amount of cadmium in the grain, implying their role in controlling cadmium translocation to grains (Chen et al., 2007b).

In summary, as a tolerance mechanism, plants partition cadmium in various parts, including roots, above-ground vegetation, and reproductive parts.

4.3 Cellular Mechanisms

To detoxify cadmium effects and protect the physiologically active sites from cadmium damage, plants have four general cellular strategies: (1) metal binds to the cell wall, (2) transport across cell membranes is reduced, (3) compartmentalization, and (4) chelation (Prasad, 1995; Dan et al., 2002; Clemens, 2006). Most plants utilize one or more of these strategies.

4.3.1 Cell Wall Binding

Preventing cadmium ions from entering the cytosol by the plant cell walls could theoretically represent the best detoxification mechanism (Ernst et al., 1992; Blaudez et al., 2000). Cell walls of the root can act as a first barrier against cadmium stress in immobilizing excesses of cadmium (Nishizono et al., 1989). Available evidence suggests that cadmium binds to the secondary wall and middle lamellae in maize roots (Kahn et al., 1984). On the other hand, in bush bean, cadmium was mainly bound to pectic sites and hystidyl groups of the cell wall in roots and leaves (Leita et al., 1996). In white lupin, the cell wall was found to retain up to 47% of the absorbed cadmium in leaves, 51% in stems, and 42% in the root, and this accumulation was related well to enhanced phytochelatins synthesis, particularly in the roots. This implied that cell-wall binding is a major detoxification mechanism (Vazquez et al., 2006).

4.3.2 Reduced Transport

Although not fully established, the transport of cations across cell membranes is achieved by transporters. Molecular studies led to the cloning of copper, zinc, and iron transporters from *Arabidopsis thaliana* (Salt et al., 1998). Blocking the transcription of gene coding for transporters could enhance the tolerance of plants to heavy metals (Prasad, 1995). Subsequent to metal uptake into the root symplasm, the movement of metals from roots into the xylem is governed by: (1) sequestration of metals inside root cells, (2) symplastic transport into the stele, and (3) release into the xylem (Clemens et al., 2002). During transport, cadmium is transferred to phloem and rapidly distributed throughout the plant (Reid et al., 2003).

Various transporters are involved in heavy metal resistance; the most important of these are a family of ATP-binding cassette transporters reported from bacteria, yeast, plants, and animals that transport a wide variety of materials across the cellular membranes (Higgins, 1992). A p-type pump, ZntA, from *Escherichia coli* (Sharma et al., 2000), and two ATP-binding cassette transporters from yeast (Ortiz et al., 1995; Li et al., 1997) make complexes of cadmium with phytochelatins, and transport into the vacuole. Among plant ATP-binding cassette transporters, only AtMRP3 (Bovet et al., 2003) and AtATM3 (Kim et al., 2006) have been reported to sequester cadmium into the vacuole. Bovet et al. (2003) reported the greater synthesis of four putative sequences coding for *ATMRPs* genes after cadmium treatment in *Arabidopsis thaliana*. Furthermore, phytochelatins, glutathionein, and oxidative stress were consistent with these transporters' gene expression. Another ATP-binding cassette transporter is AtPDR8, which when overexpressed in the transgenic *Arabidopsis thaliana* plants, conferred resistance against cadmium. Use of radioactive cadmium provided evidence that AtPDR8 was an efflux pump of cadmium ions or cadmium conjugates at the plasmalemma of *Arabidopsis thaliana* (Kim et al., 2007).

4.3.3 Compartmentalization

Free and complexed cadmium is sequestered in the vacuole of root cells in most species. It is actively transported from the cytosol into the vacuole across the tonoplast via proton/cadmium (H^+/Cd^{2+}) antiport or an ATP-dependent phytochelatin transporter. A gene coding for a phytochelatin-transporter (*hmt1*) was isolated in yeast (Salt and Wagner, 1993). When overexpressed in plants, this gene allowed for enhanced production of phytochelatin (PC) transporters, which boosted the ability of a plant to sequester PC-cadmium complexes in the vacuole (Ortiz et al., 1995). One recurrent mechanism for detoxifying heavy metals in plants and other organisms is the chelation of metal by a ligand and, in some cases, the subsequent compartmentalization of the ligand-metal complex. Vacuolar compartmentalization prevents the free movement of cadmium in the cytosol and forces it into a limited area (Sanita di Toppi and Gabbrielli, 1999). Several studies suggest that the vacuole is the main accumulation site for a number of heavy metals, including zinc and cadmium (Ernst et al., 1992; Benavides et al., 2005). Several metal-binding ligands, including organic acids, amino acids, and polypeptides, have been recognized in plants (Rauser, 1999).

4.3.4 Chelation

Several chelators are known to perform the function of chelation. Among the natural chelators, phytochelatins and metallothioneins are the main metal-chelating proteins expressed in plants. Of these, phytochelatins are small polypeptides produced in plants by enzymes, which are expressed in response to heavy metals or oxyanions (Prasad, 1995; Clemens, 2006). A majority of the reports show that phytochelatins constitute a major cadmium-detoxification system in plants. They are accumulated in both shoot and root; however, their predominant synthesis in either tissue depends upon the tendency of the species to biosynthesize them (Clemens and Simm, 2003; Rauser, 2003; Clemens, 2006). Use of buthionine sulfoximine—an inhibitor of glutathione synthesis—revealed the formation of cadmium-phytochelatins complexes and cadmium detoxification in *Arabidopsis thaliana* (Wojcik and Tukiendorf, 2004). Alternatively, the role of phytochelatins in the sequestration of cadmium by the transporters at plasmalemma and tonoplast is a likely mechanism in plants (Gadapati and Macfie, 2006). In *Schizosaccharomyces pombe*, however, it is shown that absorbed sulfate after being assimilated with cysteine is incorporated into phytochelatins that bind cadmium and are transported to the vacuole by an ATP-binding cassette transporter (Hmt1) as a low molecular-weight complex, which with the availability of more sulfur-containing compounds is converted to a high molecular-weight complex (Fig. 3). Studies on maize roots show that, over a short-term cadmium-stress period, low molecular-weight cadmium-phytochelatin complexes predominated in the apices, with high molecular-weight ones in the mature zone of maize roots. However, this binding of cadmium is in a dynamic state and depends upon the treatment and its amount in the tissue (Rauser, 2003).

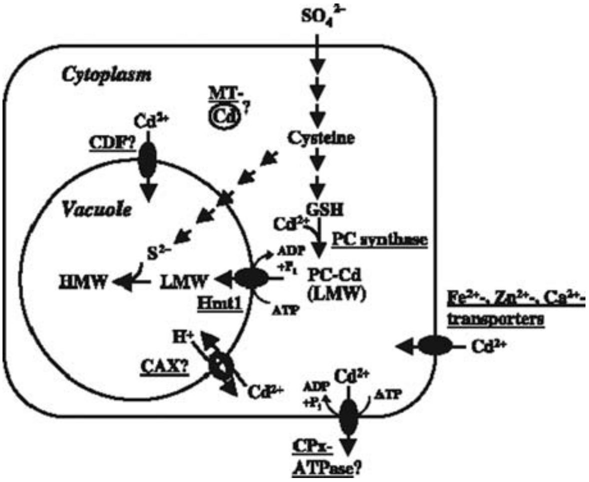

Fig. 3 Possible mechanisms for the detoxification of Cd by phytochelatins (PC). Abbreviations: GSH (glutathione), LMW (low molecular weight complex), HMW (high molecular weight complex), CAX (protein mediating pH dependent high affinity for Ca^{2+} uptake through tonoplast), CDF (cation diffusion facilitator protein), Hmt1 (ABC-type transporter at tonoplast for transport of PC-Cd LMW). Reproduced with permission from Blackwell

Studies show that phytochelatin accumulation has a protective role in physiological phenomena against cadmium toxicity. In addition to phytochelatin involvement in photosynthetic processes, their enhanced accumulation has been suggested as phytoremediation through its antioxidative mechanism (Mishra et al., 2006). A greater effect of cadmium on the chlorophyll fluorescence parameters of maize leaf segments was considerably offset by cadmium-induced phytochelatins and thiol(-SH)-specific molar ratios (Drazkiewicz et al., 2003). Contrary to this, it has been shown that phytochelatin-accumulation has a negative correlation with chlorophyll content in *Brassica juncea* and *B. napus*. Although phytochelatins appear to be mainly responsible for modulating a cadmium-phytotoxicity response of plants, a recent study suggests that in the cadmium hyper-accumulating *Sedum alfredii* plant, cadmium leads to a greater accumulation of glutathione (GSH) rather than phytochelatins—the activity of which is consistent with GSH accumulation (Sun et al., 2007).

Unlike phytochelatins, metallothioneins are found both in animals as well as plants. They are gene-encoded polypeptides with an apparent molecular mass of 8–14 kDa (Robinson et al., 1993), and thought to be aggregates of phytochelatins (Prasad, 1995). In the plant kingdom, metallothionein-like proteins are reported in a number of plant species (Wojcik and Tukiendorf, 2005; Clemens, 2006). Metallothioneins behave similar to phytochelatins, and metal complexation is often shared by both, as observed in *Datura* and maize (Rivai, et al., 1990). Introduction of mammalian metallothionein into *Brassica campestris, B. napus*, and *Nicotiana tabacum* conferred cadmium tolerance by promoting complexation and minimizing translocation of cadmium via xylem to shoots (Maiti et al., 1989).

Cysteine is an important amino acid, which is a precursor and an integral component for the biosynthesis of glutathione, phytochelatins, and thiolate peptides involved in the detoxification and transport of cadmium and many other heavy metals to vacuoles (Cobbett, 2000). Therefore, enhanced synthesis of cysteine is imperative for efficient heavy-metal detoxification. Genetic transformation in *Arabidopsis thaliana* using *Atcys-3A* construct expression cytosolic O-acetylserine(thiol)lyase (OASTL) indicated that the tranformant in the presence of cadmium indicated significantly higher cysteine biosynthesis than the wild type, which was responsible for enhanced tolerance and accumulation of cadmium in the leaves (Dominguez-Soils et al., 2004).

In summary, the synthesis of chelating proteins constitutes a major cadmium-detoxification mechanism. The major roles of phytochelatins remain the protection of photosynthetic machinery and membrane structure from cadmium damage.

4.3.5 Complexation

Organic acids have great potential to form complex with heavy metals. In this regard, both citric acid and malic acid have been shown to complex heavy metals in plant roots (Benavides et al., 2005). After the loss of H^+, each acid contains a COO^- group, which binds to the cation. Plants secrete acids that aid in the uptake of nonbioavailable metals (Larsen et al., 1998). These acids protect cellular function when the acid-cadmium complex is brought into the root. Citric acid metal complexes have been shown to translocate via the xylem (Senden et al., 1990). Genetic alteration of plants for producing higher levels of endogenous citric acid or malic acid may lead to enhanced phytoextraction of the metals, including cadmium.

4.4 Physiological Mechanisms

Heavy metal accumulation influences various metabolic functions in plants. However, plants show some adaptive physiological mechanisms for cadmium tolerance as detailed in the following section.

4.4.1 Water and Nutrient Transport

Cadmium has been shown to interfere with the transport of water, and uptake and the distribution of several macro- and micronutrients in plant roots (Gussarson et al., 1996; Hernandez et al., 1996; Das et al., 1997). Some evidence suggests that under excessive transpiration rates, cadmium permeates the cytosol through calcium channels on the plasmalemma, and hampers the cell water status (Perfus-Barbeoch et al., 2002; Teresa Milone et al., 2003).

Data suggest that cadmium can alter the uptake of minerals by plants either by reducing the availability of minerals in the soil or through a reduced population of soil microbes (McGrath et al., 2001). Cadmium has been shown to interfere with the transport and distribution of several macro- and micronutrients in plants roots (Gussarson et al., 1996; Hernandez et al., 1996; Das et al., 1997). Ederli et al. (2004) showed that *Phragmites australis* roots could tolerate higher levels of cadmium by accumulating in parenchymatous cells below the endodermis. Substantial declines in nitrate reductase activity, nitrogen fixation, and primary ammonia assimilation in nodules were found in legumes due to cadmium application (Balestrasse et al., 2004). In the cadmium-hyperaccumulator *Arabidopsis halleri*, the use of radioisotopes indicted that cadmium and zinc employed the same transporter, but that cadmium detoxification did not follow the zinc-detoxification mechanism (Zhao et al., 2006).

4.4.2 Photosynthesis and Assimilate Partitioning

Photosynthesis represents a key metabolic pathway in plants in the production of energy-rich organic compounds. The assimilation of these high-energy compounds in growth phenomena requires a balanced supply of reducing powers. The maintenance and activity of photosystem-II is of vital importance in the regulation of electron transport. An increasing number of studies show that photosystem-II is highly sensitive to stressful conditions, including that of cadmium toxicity (Chugh and Sawhney, 1999; Prasad et al., 2004; Ekmekci et al., 2008); however, understanding the precise mechanisms of cadmium toxicity on various aspects of photosynthesis is still the subject of intensive research. Pulse-chase labeling experiments employing [^{35}S]methionine indicated a great effect of cadmium on the synthesis, degradation, and assembly of D1 protein, which appeared to be due to an unknown primary effect of cadmium on the photosystem-II apparatus (Geiken et al., 1998). In wheat, an efficient sulfur assimilation and antioxidative system was helpful in protecting the photosynthetic ability and maintaining high-yield potential under cadmium stress (Khan et al., 2007).

4.4.3 Membrane Damage and Antioxidative Defense

As discussed earlier (Section 3.5.3.), one of the most pronounced effects of cadmium toxicity is the production of reactive oxygen species, which leads to peroxidation of membrane lipids and disrupts the normal membrane functions. Among various reactive oxygen species, generation of hydrogen peroxide is more damaging due to its relatively longer life (Foyer and Noctor, 2005). Mitochondria and peroxisomes of mesophyll and guard cells produce hydrogen peroxide catalyzed by the enzyme NADP-oxidase, which is localized on the tonoplast of the bundle sheath and plasma membrane of mesophyll cells, where it is involved in the production of activated oxygen and hydrogen peroxide (Hsu and Kao, 2004; Romero-Puertas et al., 2004). Tobacco cell death during exposure to cadmium chloride was accompanied by successive waves of reactive oxygen species generation, which differed in their nature and subcellular localization. These were (a) NADPH-oxidase dependent accumulation of hydrogen peroxide, (b) accumulation of activated oxygen in mitochondria, and (c) a wave of reactive oxygen species consisting of fatty acid hydroperoxide, which was concomitant with cell death (Garnier et al., 2006). This was confirmed from the fact that cell line gp3, impaired in NADPH-oxidase activity, was unable to accumulate hydrogen peroxide. Nevertheless, the cell death appeared to be due to cell poisoning by cadmium (Garnier et al., 2006). Thus, inhibition of the activity of NADP-oxidase can reduce the content of NADP-oxidase. Treatment of detached rice leaves with diphenyleneiodonium chloride and imidazole, inhibitors of NADP-oxidase, prevented cadmium chloride-induced hydrogen peroxide production, suggesting that cadmium chloride toxicity was primarily due to generation of hydrogen peroxide (Hsu and Kao, 2007b).

Glutathione reductase (GR) is an important antioxidant enzyme that exists in various isoforms, is expressed in various tissues, and prevents oxidative damage to plants subjected to a variety of stresses including cadmium toxicity. In the roots (but not the shoots) of wheat, no change in mRNA and protein expression occurred, but occurrence of posttranslational modification was evident. These changes induced distinctive isoforms and up-regulated the GR activity as a defense mechanism against oxidative stress (Yannarelli et al., 2007).

4.4.4 Modulation of Hormonal Levels

Hormones play important roles in the adaptation of plants to stressful environments (Wahid et al., 2007a). Cadmium causes the senescence of cells via intricate mechanisms. It may lead to enhanced biosynthesis of ethylene and reactive oxygen species and a decline in nitric oxide, which promote cellular senescence. The synthesis of jasmonic acid and salicylic acid may regulate the cellular response to combat cadmium damage (Rodriguez-Serrano et al., 2006). Accumulation of abscisic acid and diminution of cytokinins has been reported in the plants treated with toxic metals (Poschernirieder et al., 1989; Prasad, 1995). In an attempt to elucidate the role of abscisic acid in cadmium tolerance, Shanti and Kumar (2002) noted that seed germination and seedling growth of abscisic acid-deficient and abscisic acid-insensitive mutants were comparable to wild-type plants of *Arabidopsis thaliana*, which suggested no mediatory role of abscisic acid in cadmium tolerance (Sharma and Kumar, 2002).

5 Mitigation of Cadmium Toxicity Effects

The toxic effects of cadmium are both acute and chronic. For sustainable crop production, it is imperative that strategies may be adopted to alleviate the effects of cadmium toxicity. In this regard, some research efforts have been undertaken that are summarized in Table 2 and briefly described in the next section.

Ethylene diamine tetra acetic acid is a synthetic chelator, and has been shown to substantially lower the cation exchange capacity (CEC) of soil. It has been used frequently since the 1950s to alleviate iron deficiency and improve phytoextraction of metal contaminants, such as lead, from soil (Jorgenson, 1993). Invariably, a sudden rise in bioavailable metals with the applied ethylene diamine tetra acetic acid may be fatal to plants. This can be overcome by growing plants up to advanced stages and then adding ethylene diamine tetra acetic acid. In this way, the metal becomes more bioavailable and is taken up in large quantities by the plant for a short time before the plant dies. Thus, large amounts of metal can be extracted from soil and

Table 2 Effectiveness of some organic and inorganic sources on the alleviation of cadmium's pytotoxic effects. The ameliorative action of various sources is quite diversified and depends upon the plant species

Plant species	Amelioration source	Mode of application	Effective concentration	Major effect	Approximate improvement	Reference
Rice (*Oryza sativa*)	Salicylic acid	Seed presoaking	100 µM for 16 h	Induction of antioxidants	2–20%	Panda and Ratra (2007)
Soybean (*Glycine max*)	$Ca(OH)_2$	Sand culture	200 ppm	Non-availability of Cd	10–19%	Chaney et al. (1977)
Mustard (*Brassica juncea*)	Phosphate as KH_2PO_4	Soil culture	10 mg P/kg soil	Immobilization of Cd in soil	Up to 88%	Bolan et al. (2003)
Alfalfa (*Medicago sativa*)	Salicylic acid	Seed imbibition	10 µM for 3 h	Improved Mg and Ca status of shoot and root	22–40%	Drazic et al. (2006)
Rice	Polyamines (spermidine & spermine)	Pretreatment of detached leaves	5 mM for 6 h in dark	Reduction in H_2O_2 and MDA increase in ascorbic acid reduced glutathione production	4–43%	Hsu and Kao (2007b)
Kidney bean (*Phaseolus vulgaris*)	Lanthanum chloride	Foliar spray	10 mg/L	Improved membrane permeability, chlorophyll content, activities of catalase and peroxidase and reduced Cd uptake	3.5–37.5%	Xiaohua and Qing (2006)
Corn (*Zea mays*)	As above	As above	20 mg/L	As above	2.1–14.5%	As above
Barley (*Hordeum vulgare*)	Fe (Fe tartarate)	Nutrient solution	250 µM	Antagonistic effect of Fe on Cd uptake	Significant	Sharma et al. (2004)

this strategy is referred to as “chelator-assisted phytoextraction” (Salt et al., 1998). A related compound, ethylene glycol tetra-acetic acid, has also been shown to be quite effective in enhancing cadmium bioavailability for phytoextraction (Blaylock et al., 1997).

The genotypic flexibility of species and cultivars for cadmium accumulation and tolerance (Section 3.1.) can be exploited to breed and select desired materials. Breeding for cadmium tolerance is a long-term and cost-intensive venture, while selection of the desired material can be made in a short span of time. Exogenous use of osmoprotectants and other organic and inorganic compounds, including monosaccharides, quaternary ammonium compounds, amino acids, organic acids, ascorbate, polyamines, and growth regulators, etc., is an effective approach to combatting cadmium toxicity. Exogenous application of glucose and reduced forms of glutathione were effective in enhancing photosynthetic oxygen evolution and reducing the tissue content of cadmium (El-Naggar and El-Sheekh, 1998). Soybean plants treated with sodium naphthenate diminished 40% of intracellular cadmium in roots, stems, and leaves (on average), resulting in alleviation of cadmium toxicity with the activity of nitrate reductase and photosynthetic pigments (Ewais, 1997; Kevresan et al., 2004). Likewise, exogenous application of ascorbate was beneficial in enhancing the activities of antioxidative enzymes and alleviating oxidative damage and improving light harvesting under cadmium stress in barley (Wu and Zhang, 2004).

Plant-growth regulators function as signal molecules under a variety of stresses (Taiz and Zeiger, 2006). Studies show that use of salicylic acid, either as a presowing seed treatment in alfalfa (Drazic et al., 2006) and rice (Panda and Patra, 2007), or as its supplementation to soybean seedlings in nutrient solutions (Drazic and Mihailovic, 2005), was effective in lowering cadmium-induced oxidative damage in rice leaves and improving the growth and homeostasis of potassium, magnesium, and calcium. In another study, barley grains soaked with salicylic acid exhibited little effect in the absence of cadmium, but promoted root and shoot length and fresh and dry weight, and inhibited lipid peroxidation in roots in the presence of cadmium (Metwally et al., 2003). Polyamines, mainly spermidine and spermine, alleviated the cadmium toxicity on detached rice leaves by curtailing the cadmium uptake and production of hydrogen peroxide and malondialdehyde (Hsu and Kao, 2007a). *Brassica juncea* fed with 0.01 μM 28-homobrassinolide in nutrient solution and subsequently treated with cadmium levels enhanced the activities of antioxidants both in the shoot and root and contents of proline in the aerial parts. This suggested the role of 28-homobrassinolide in inducing cadmium tolerance in this plant species (Hayat et al., 2007).

Although cadmium has an antagonistic effect on the acquisition and transport of mineral nutrients (Section 4.4.1.), available evidence suggests that exogenous supply of some nutrients and inorganic sources can alleviate the cadmium phytotoxicity. However, the mitigatory roles of various nutrients may be different. For instance, lime (calcium hydroxide) has long been known to prevent the phytotoxic effect of cadmium (Chaney et al., 1977). Supplementing with 30 mM of calcium in the nutrient solution restored root elongation of *Arabidopsis* by diminishing up to 70% of the cadmium content of the seedlings compared to that treated with cadmium alone. This happened because calcium was able to compete and alleviates cadmium toxicity through competition for influx (Suzuki, 2005). Among other nutrients, application of phosphorus mitigated the phytotoxic effect of cadmium and promoted dry matter yield of mung bean (Panwar et al., 1999) and soybean (Arao and Ishikawa, 2006). Similar effects of zinc were also reported in wheat and barley plants exposed to cadmium in vivo (Zhao et al., 2005; Chen et al., 2007a). In durum and bread wheat, necrotic patches developed on the leaf base and sheath due to cadmium toxicity were offset by the external supply of zinc (Koleli et al., 2004). Hassan et al. (2005) reported that the application of increased levels of sulfur to cadmium-stressed rice cultivars reduced the activity of superoxide dismutase and growth with a concomitant decline in malondialdehyde and tissue content of cadmium. The supply of magnesium in nutrient solution alleviated the cadmium toxicity by lessening chlorosis, the cadmium content of tissue, and enhancing potassium and zinc content in shoots and roots (Kashem and Kawai, 2007). Exogenously applied lanthanum was beneficial in improving root structure, chlorophyll content, and photosynthetic capacity and activities of antioxidants, while reducing membrane permeability and malondialdehyde in cadmium-treated kidney beans and corn (Xiaohua and Qing, 2006).

In short, application of some synthetic metal chelators and organic acids is important in alleviating the cadmium phytotoxicity in soils. For plants, exogenous applications of nutrients, polyamines, and plant-growth regulators can induce cadmium tolerance in plants by improving mineral homeostasis, antioxidant defense, and membrane properties.

6 Conclusion

Cadmium is a great threat to soil processes, plant growth, and productivity around the globe. Plant responses to cadmium toxicity are elicited at morphological, physiological, and biochemical levels. These include stunted growth, changes in the structure and function of organelles, diminished photosynthesis, effects on the membrane transporters, modulation of metabolic pathways and altered gene expression. Plants display a range of mechanisms to cope with the adverse effects of cadmium—the most important of these include reduced uptake from the soil, binding of the absorbed cadmium to cell walls, storage intcellular compartments, and detoxification by metal chelating and complexing, such as organic acids, phytochelatins, and metallothioneins. Cadmium toxicity can be overcome by the use of metal chelators in the soil, thereby reducing its bioavailability to plants. Breeding and selection of plants showing reduced ability to accumulate cadmium in the cells and tissues, and/or its efficient binding, complexation, and compartmentation, seed and foliar application of osmoprotectants, mineral nutrients, and plant-growth regulators are among the important strategies for mitigating cadmium toxicity on plants. Concerted research efforts on finding novel compounds with the ability to bind and inactivate cadmium, earmarking plant species capable of effectively binding or excluding metal at root levels with their lowered tendency to transport to shoot, and partitioning to grain are desirable. This will be beneficial for more economical utilization of such plant species, and their sustainable production in marginally cadmium-contaminated soils.

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