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Amelioration of Cadmium Stress in Crop Plants by Nutrient Management: Morphological, Physiological and Biochemical Aspects

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ABSTRACT

Plants are sessile organisms therefore, cannot avoid adverse environmental conditions (such as soil salinity, drought, heat, cold, flooding and heavy metal contamination). These stress factors are a menace for plants, prevent them from reaching their full genetic potential and limit crop productivity worldwide. Soil contamination with heavy metals has become a world wide problem leading to losses in agricultural yield and hazardous health effects as they enter the food chain. Among heavy metals, Cadmium (Cd) is a ubiquitous environmental pollutant and is a non-essential highly toxic metal for plants. It significantly damages general plant metabolism and induces oxidative stress. In response to Cd stress, the cells of Cd-resistant plant species can produce metallothioneins, phytochelatins and stress proteins to detoxify Cd ions. The plant cells can also resort to other defense systems to detoxify Cd ions, e.g., exclusion of Cd through the action of plasma membrane, the immobilization of Cd by cell wall and compartmentalization of Cd to vacuols. It has also been found that mineral nutrient status of plants can play a critical role in increasing plant resistance to environmental stress factors. Among mineral nutrients, sulfur (S) and nitrogen (N) are major macronutrients necessary for the plant life cycle, the two processes the uptake and assimilation of S and N in higher plants are the crucial factors determining plant growth and vigor, crop yield and these nutrients play a particular role in contributing to the survival of crop plants under environmental stress conditions. In this review, we focus on the alterations in morphological, physiological and biochemical characteristics in crop plants under Cd stress. Further, the importance of plant mineral nutrients especially S and N in the amelioration of Cd stress has also been reviewed.

Keywords: abiotic stress, antioxidants, cadmium stress, nitrogen, oxidative stress, photosynthesis, pigments, sulfur, stress tolerance

Abbreviations: APX, ascorbate peroxidase; **AsA**, ascorbate; **ATP-S**, ATP-sulfurylase; **CA**, carbonic anhydrase; **CAT**, catalase; **Cd**, cadmium; **DHAR**, dehydroascorbate reductase; **γ-ECS**, γ-glutamylcysteine synthase; **GDH**, glutamate dehydrogenase; **GPX**, glutathione peroxidase; **GR**, glutathione reductase; **GS**, glutamine synthetase; **GSH**, reduced glutathione; **GSSG**, oxidized glutathione; **GSTs**, glutathione *S*-transferases; **H_2O_2**, hydrogen peroxide; **MDHAR**, monodehydroascorbate reductase; **MT**, metallothionein; **N**, nitrogen; **NR**, nitrate reductase; **PC**, phytochelatin; **S**, sulfur; **SOD**, superoxide dismutase; **TBARS**, thiobarbituric acid reactive substances

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INTRODUCTION

Various abiotic and biotic stresses are adversely affecting the plant growth, productivity and genome stability. The stress conditions such as extreme temperatures (freezing, cold, heat and global warming), water availability (drought, flooding), and ion toxicity (salinity, heavy metals) represent abiotic stresses, which result in causing massive loss of crop yield all over the world (Mahajan and Tuteja 2005; Tuteja 2007; Khan and Singh 2008; Tuteja 2009). Accor-

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ding to Bray *et al.* (2000), the relative decreases in potential maximum yields associated with abiotic stress factors vary between 54-82%. Among abiotic stresses, heavy metal contamination is a serious environmental problem that limits plant productivity and threatens human health (Wagner 1993; Sanita di Toppi and Gabbrielli 1999). The use of urban waste for the production of vegetables and other important crops in urbanized areas of Asia is a growing concern because of the contamination of soil, water and agricultural produce by heavy metals (Simmons *et al.* 2008). The agricultural soil may have toxic levels of heavy metals due to agricultural and industrial practices such as application of pesticides and chemical fertilizers, waste water irrigation, precipitation from heavy coal combustion, and smelter wastes and residues from metalliferous mining (Lombi *et al.* 2000; Xie *et al.* 2006; Verma *et al.* 2007). Although many metals are required as structural and catalytic components of enzymatic proteins involved in various physiological processes, they can still be toxic to a plant if present at higher concentrations (Clemens 2001). Plants use a variety of methods to prevent heavy metals from affecting their growth. Recently, Huang *et al.* (2009) have isolated several miRNAs from rice and suggested the role of some of them in plant responses to environmental stresses including Cd stress. The capacity of certain plants to accumulate heavy metals has long been used for phytoremediation. Chelation and sequestration of excess metal ions by binding with metal-chelating molecules such as metallothioneins (MTs), ferritin, or phytochelatins (PCs), or modulation in the ion transporters for influx or efflux of heavy-metal ions, are some of the possible strategies for counteracting heavy-metal stress (Clemens 2001). The PCs are small metal-binding peptides derived from reduced glutathione (GSH), represent one of the main metal-chelation and detoxification mechanisms and play an essential role in heavy-metal detoxification in plants (Grill *et al.* 1985).

The pollution of soil by Cd has been a major environmental concern. Cd, which is discharged into the soil to the tune of about 22,000 tons per year globally (Nriagu and Pacyna 1988), is one of the most highly toxic environmental pollutant in the atmosphere, soil and water, and in excessive amounts can cause serious problems to all organisms (Benavides *et al.* 2005). Once used, it remains embedded in a product matrix, and hence, is not directly bioavailable. It may be accumulated in all plant parts, being highly mobile in the phloem (Benavides *et al.* 2005), and can cause toxic effects on plants and to living organisms *via* food chain (Wagner 1993; Hall 2002). Cd reduces plant growth and biomass (Sandalio *et al.* 2001; Dominguez *et al.* 2003; Gianazza *et al.* 2007; Khan *et al.* 2006, 2007; Anjum *et al.* 2008a,b; Singh *et al.* 2008a,b) and causes plant death in extreme cases (Sanita di Toppi and Gabbrielli 1999). It causes inhibition of shoot and root growth (Schutzendubel *et al.* 2001), disorganization of the grana structures and reduction in the biosynthesis of chlorophyll (Padmaja *et al.* 1990; Somashekaraiah *et al.* 1992; Siedlecka and Krupa 1996; Singh and Tewari 2003). It also interferes with photosynthesis, respiration and water relations (Baszynski *et al.* 1986; Sandalio *et al.* 2001; Balakhnina *et al.* 2005; Khan *et al.* 2006, 2007; Mobin and Khan 2007; Singh *et al.* 2008a). The effect of Cd on nitrate and sulfate assimilation has been studied in several plants showing an inhibition of the nitrate uptake rate and the activity of the enzymes involved in the nitrate assimilation pathway (Hernandez *et al.* 1997; Boussama *et al.* 1999; Gouia *et al.* 2000, 2003; Ghnaya *et al.* 2005; Anjana *et al.* 2006; Hasan *et al.* 2008). Alternatively, Cd caused induction of enzymes of sulfate assimilation pathway has been studied in *Arabidopsis thaliana* (Harada *et al.* 2002), *Chlamydomonas reinhardtii* (Dominguez *et al.* 2003) and *Triticum aestivum* (Khan *et al.* 2007). Moreover, Cd can also inhibit the activity of several groups of enzymes such as those of the photosynthetic Calvin cycle (Sandalio *et al.* 2001), carbohydrate metabolism (Sanita di Toppi and Gabbrielli 1999, Verma and Dubey 2001) and phosphorus metabolism (Shah and Dubey 1998; Sharma and Dubey 2006). The toxicity symptoms observed in plants in the presence of excessive amounts of Cd are due to a range of interactions at the cellular level (Hall 2002). Besides, Cd ions interact with ligand groups of enzymes and inhibit a number of enzymes by masking the catalytically active groups thus denatures the proteins (Van Assche and Clijsters 1990; Das *et al.* 1997).

Cd is known to cause the generation of reactive oxygen species (ROS) which leads to oxidative stress in plant tissues (Sandalio *et al.* 2001; Pereira *et al.* 2002; Milone *et al.* 2003; Skorzynska-Polit *et al.* 2003/4; Romero-Puertas *et al.* 2004; Mobin and Khan 2007; Anjum *et al.* 2008a). The presence of Cd-lead high concentration of ROS causes oxidative damage to photosynthetic pigments, bio-molecules such as lipids, proteins and nucleic acids, leakage of electrolytes *via* lipid peroxidation resulting in dramatic reductions of growth and productivity, and eventually causing the death of plants. ROS are efficiently scavenged by enzymatic (superoxide dismutase, SOD; catalase, CAT; Ascorbate peroxidase, APX; guaiacol peroxidase, GOPX; glutathione reductase, GR; monodehydroascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR and glutathione-*S*-transferase, GST) and non-enzymatic antioxidants such as ascorbate (AsA) and GSH, which protect plants against oxidative damage (Foyer and Mullineaux 1994; Singh *et al.* 2008b). The response of antioxidant enzymes to Cd can vary among species and different plant tissues (Dixit *et al.* 2001; Kuo and Kao 2004; Cho and Seo 2005; Hassan *et al.* 2005; Gratao *et al.* 2006; Khan *et al.* 2007; Mobin and Khan 2007; Anjum *et al.* 2008b; Singh *et al.* 2008b). The enzymes SOD and CAT are involved in the detoxification of superoxide radicals ($O_2^{\cdot-}$) and hydrogen peroxide (H_2O_2), respectively, thereby preventing the formation of hydroxyl ($OH^{\cdot}$) radicals. Whereas, APX and GR as well as AsA and GSH, are important components of the ascorbate-glutathione cycle (AsA-GSH cycle) responsible for the removal of H_2O_2 in different cellular compartments (Foyer and Noctor 2005). AsA is the major, probably the only, antioxidant buffer in the apoplast and is an essential metabolite involved with vital cell functions. It is a key primary antioxidant that reacts directly with $OH^{\cdot}$, $O_2^{\cdot-}$, and $^1O_2$ (Chen and Gallie 2004). GSH, present in plant cell is a major non-enzymatic scavenger of ROS being itself less susceptible to attack by oxidants (Mishra *et al.* 2006). GSH is also the substrate for the biosynthesis of PCs, which are involved in heavy metal detoxification (Rauser 2000; Cobbett and Goldsbrough 2002; Hall 2002). Oxidative stress may occur as a result of an overproduction of ROS and/or of a disfunction of the scavenging systems.

The toxic effects of Cd are both acute and chronic. Therefore, for sustainable crop production, it is imperative to develop the methods or techniques for alleviating the Cd-induced growth inhibition and reducing its accumulation in plants by increasing physical and chemical fertility as well as maintaining productivity of cultivated soils by adequate and balanced supply of mineral nutrients. As Cd can induce essential nutrient deficiency and even decreased concentration of several macronutrients in plants (Jiang *et al.* 2004), it seems possible to reverse or at least partly reduce the Cd-induced growth inhibition by optimization of mineral nutrition. Increasing evidence suggest that mineral-nutrient status of plants plays a critical role in increasing plant resistance to environmental stresses (Marschner 1995; Vassilev *et al.* 2005; Anjum *et al.* 2008c, 2008d; Hassan *et al.* 2008). Of the mineral nutrients, S and N are essential for the normal growth and development of plants and their assimilation pathways are very similar and well coordinated (Brunold 1993; Takahashi and Saito 1996; Abdin *et al.* 2003; Hawkesford *et al.* 2006). Deficiency of one element was shown to repress the other pathway (Neuenschwander *et al.* 1991; Kim *et al.* 1999; Koprivova *et al.* 2000; Prosser *et al.* 2001; Hesse *et al.* 2004; Scherer 2008). S is a structural constituent of several coenzymes and prosthetic groups, such as ferredoxine, which are also important for N assimilation. Thus, S plays an important role in plant growth and in the regulation of plant development. It has also been found that S nutrition is a critical factor for the alleviation of Cd toxicity (Popovic *et al.* 1996; Chen and Huerta 1997; Hassan *et al.* 2005b; Vassilev *et al.* 2005; Anjum *et al.* 2008a, 2008b). A positive effect of S nutrition on Cd detoxification in *Beta vulgaris* plants has also been established (Popovic *et al.* 1996). It has been found that at suboptimal S nutrition Cd exposed plants preferably allocate S to PCs synthesis (McMahon and Anderson 1998). Anjum *et al.* (2008c) also reported that S supplementation increased the production of GSH content under low level of Cd which protects the *Brassica campestris* plants by improving the growth and photosynthesis. Pankovic *et al.* (2000) have shown that optimal N supply decreased the inhibitory effects of Cd on photosynthesis of sunflower plants. A proper N supply has been shown positive effects in overcoming the adverse effects caused by Cd toxicity in various crop species (Hassan *et al.* 2006). Therefore, coordination of S and N may alleviate the Cd-induced toxicity in crop plants.

In the present article, we attempt to understand the response of crop plants to Cd stress. In addition, the coordination effects of S and N nutrition in the amelioration of Cd toxicity have also been discussed.

UPTAKE, ACCUMULATION, TRANSPORT AND LOCALIZATION OF CADMIUM

Cd is taken up by plants from soil *via* the root system and to a lesser extent leaves. As soon as Cd enters the roots, it can reach the xylem through an apoplastic and/or symplastic pathway. Plants show a differing metal distribution and accumulation pattern among different parts. Most of the Cd that enters the plant system accumulates in the roots and only a small portion is translocated to the above ground parts (Schutzendubel *et al.* 2001; Vitoria *et al.* 2001; Pereira *et al.* 2002; Ramos *et al.* 2002; Kovacik *et al.* 2006; Sharma and Agrawal 2006; Mobin and Khan 2007; Ekmekci *et al.* 2007; Liu *et al.* 2007; Singh *et al.* 2008a, 2008b). The actual accumulation of Cd in plant parts depends on the plant species and soil properties (Fediuc and Erdei 2002; Arao *et al.* 2003). Substantial variability among 99 *Pisum sativum* genotypes in tolerance to Cd and uptake of different heavy metals was reported (Belimov *et al.* 2003). Zhang *et al.* (2000) reported significant difference among *Triticum aestivum* genotypes in shoot Cd concentration. Significant differences in Cd accumulation and tolerance were found in *Sedum alfredii* populations (Deng *et al.* 2007). Ten times higher Cd accumulation in the roots than above ground parts was reported in *Hordeum vulgare* plants by Vassilev *et al.* (1998). Cd was accumulated 1826 times more in the roots of *Allium sativum* than the control with the application of 10^{-2} M Cd and very low amount was transported to the bulbs and shoots (Jiang *et al.* 2001). Kovacik *et al.* (2006) reported that Cd accumulation was seven- (60 μM Cd) to 11- (120 μM Cd) fold higher in the roots than in the leaves of *Matricaria chamomilla*, whereas, only 6% of Cd was accumulated in the leaves of *Crotalaria juncea* compared to roots with 2 mM $CdCl_2$ (Pereira *et al.* 2002). The Milyang 23 rice accumulated 10-15% of the total soil Cd in its shoot (Murakami *et al.* 2007). Djebali *et al.* (2008) reported that the roots of Cd treated *Solanum lycopersicum* plants accumulated four to five fold Cd as much as mature leaves. Liu *et al.* (2007) suggested that the root tissue was a barrier to Cd uptake and translocation within rice plants. Retention of Cd in roots might be due to its cross linking with carboxyl groups of cell wall proteins (Barcelo and Poschenrieder 1990) and/or an interaction with the thiol groups of soluble proteins and non-protein thiols operating as a tolerance mechanism in root cells (Chaoui *et al.* 1997a, 1997b). Low temperature inhibits the uptake of Cd as well as its transport across plasma membrane (Hart *et al.* 1998).

The uptake of Cd by plants varies not only among plant species but also among cultivars (Salt *et al.* 1995; Arao *et al.* 2003; Metwally *et al.* 2005; Grant *et al.* 2008). Li *et al.* (1997) reported significant variation in the grain Cd level of *Helianthus annuus*, *Triticum aestivum* and *Linum usitatissimum*. Arao *et al.* (2003) found that lower level of Cd in the seeds of certain soybean varieties was due to the lower initial uptake. Studies of Cd uptake by plants have indicated that at lower Cd concentrations (2.5-90 nM), its transport across membrane is an active, energy requiring H^+-ATPase mediated process, whereas at high concentrations of Cd the uptake is a non metabolic (passive) process, involving diffusion coupled with sequestration (Grant *et al.* 1998). Although the mechanism of transport of Cd across the plasmalemma of root cells is not well understood, the electrochemical potential across the membrane appears to be an important factor (Grant *et al.* 1998). It is suggested that the uptake of cationic solutes is likely to be driven largely by the negative membrane potential across the plasma membrane, which is generated in part by metabolically dependent processes such as proton extrusion *via* the plasma membrane H^+-ATPase (Kochian 1991). Following uptake by plant roots, Cd gets accumulated in cytosol, cytosolic organelles and vacuoles. At low level of exposure, Cd forms complexes in the cytosol with GSH whereas, at higher Cd exposure levels, it is transported into the vacuoles, where it forms complexes with organic acids and PCs (Grant *et al.* 1998).

In most of the plant species much of the Cd taken up by plants is retained in root and its translocation to aerial portion is low. In *Glycine max* plants, about 98% of the accumulated Cd is strongly retained by roots and only 2% is transported to the shoot system (Cataldo *et al.* 1983). Shah and Dubey (1998) reported that localization of absorbed Cd was about 3 times in roots of rice compared to its level in shoots, when rice seedlings were raised in sand cultures for 20 d in nutrient medium containing 500 μM Cd. Movement of Cd from roots to shoots is also likely to occur *via* the xylem and is driven by the transpiration from the leaves that include metal uploading into root xylem cells, long distance transport from roots to shoots within xylem and reabsorption of metal from the xylem stream by leaf mesophyll cells (Raskin and Ensley 2000). Evidence for this was provided by Salt *et al.* (1995) who showed that ABA-induced stomatal closure reduced Cd accumulation in shoots of *Brassica juncea*. Reduced movement of Cd from roots to shoots in plants is believed to result from barrier function of root endodermis and mechanism involving sequestration and decreased xylem loading of Cd (Hart *et al.* 1998).

The casparian strips of root endodermis retard the entrance of Cd into the central cylinder (Seregin *et al.* 2004), vascular compartmentation of Cd tends to limit symplastic movement of Cd. Movement of Cd across the tonoplast occurs *via* Cd^{2+}/H^+-antiport system (Salt and Wagner 1993) as well as by PC-Cd transporter (Vogeli-Lange and Wagner 1990) that appears to be Mg-ATP dependent (Salt and Rauser 1995). The absorption of Cd by green microalgae, *Chlorella vulgaris*, *Ankistrodesmus braunii* and *Eremosphera viridis* revealed that Cd is mainly absorbed in the cell wall. The binding sites seem to be an acidic group in the cell wall structure (Geisweid and Urbach 1983). In *Eichhornia crassipes*, Cd was found to accumulate throughout the roots (Hosayama *et al.* 1994). Ammar *et al.* (2007) reported that Cd was found to be mainly accumulated in roots, but a severe inhibition of biomass production occurred in *Lycopersicon esculentum* leaves, even at its low concentration (1.0 μM). In *Solidago altissima*, Cd was found in most parts of the plant, but located mainly in the cambium, cortex and phloem tissues (Hosayama *et al.* 1994).

Most of the Cd accumulates in the vacuole within a cell. The fact that Cd is found in golgi apparatus and endoplasmmic reticulum is apparently related to metal secretion through the cell surface and into the vacuole. A small quantity of Cd reaches nuclei, chloroplast, and mitochondria and exerts toxic effects on these organelles (Miller *et al.* 1973; Malik *et al.* 1992a, 1992b). Localization of Cd in different parts of a plant appears to be maximum in roots (Hart *et al.* 1998).

MORPHOLOGICAL ALTERATIONS UNDER CADMIUM STRESS

Plant growth

The growth of whole plant or of plant parts is frequently used as an easily measurable parameter to monitor the effects of various stressors. The root system of plants acts usually as the first barrier or acceptor to heavy metals in the soil. Reduction in growth and biomass yield with increased levels of Cd in growth media arises because of altered physiological phenomena (Demirevska-Kepova *et al.* 2006). The most characteristic symptoms of Cd stress are brown and short roots, chlorosis, fewer tillers, senescence and reduced plant growth and biomass (Arduini *et al.* 1994; Wu and Zhang 2002; Wu *et al.* 2003; Cosio *et al.* 2006). In *Elodea canadensis*, a thinner stem, less expanded leaves with partial bleaching of green tissues and 40% internode shortening were observed in response Cd treatments when compared with control plants (Vecchia *et al.* 2005). Bachir *et al.* (2004) found decrease in root length, plant height and fruiting branch number in cotton with increasing Cd concentration in a pot experiment. Cd treatments inhibited the shoot and root growth and dry weight of two wheat cultivars, C-1252 and Balcali-85. The decrease was more distinct in C-1252 (Ozturk *et al.* 2003). Sandalio *et al.* (2001) reported significant reduction in root growth in *Pisum sativum* plants.

Roots of *Pisum sativum* plants were more sensitive to Cd toxicity than shoot (Metwally *et al.* 2005). Increasing concentration of Cd in liquid culture and pot experiment decreased the germination and root growth of carrot and radish plants (Chen *et al.* 2003). Rai *et al.* (2005) observed significant decrease in root and shoot length and fresh and dry weight of *Phyllanthus amarus* under Cd stress. Cd inhibited root dry mass and induced changes in biomass allocation pattern without any effect on biomass accumulation at the whole plant level in *Hordeum vulgare* (Vassilev *et al.* 2004). Leaf expansion and root growth were inhibited significantly at high Cd concentrations in *Sedum alfredii*, and Cd was suggested to suppress cell expansion and induced senescence (Zhou and Qiu 2005). Exposure to increasing Cd concentrations reduced the fresh weight of the upper part (hypocotyls+cotyledons) of the seedlings of *Brassica napus* more strongly than that of the root system, which was accompanied by higher Cd accumulation in these tissues (Filek *et al.* 2008). Ekmekci *et al.* (2007) reported that increasing Cd concentration significantly reduced the leaf and root dry weight of *Zea mays* cultivars. Prince *et al.* (2002) reported significant decrease in plant height, number of leaves and leaf yield of Cd exposed mulberry plants. Root and shoot growth of *Crotalaria juncea* seedlings was strongly inhibited by Cd concentrations above 0.2 mM $CdCl_2$ (Pereira *et al.* 2002). Di Cagno *et al.* (1999) observed Cd induced inhibition of growth parameters in *Halianthus annus* seedlings in both mature and young leaves after 7 d of exposure. The presence of Cd decreased the seedling growth of *Zea mays*, *Triticum aestivum*, *Cucumis sativus* and *Sorghum bicolor* in terms of root and shoot growth (An *et al.* 2004). Ghnaya *et al.* (2005) reported that Cd severely inhibited *Mesembryanthemum crystallinum* growth even at low concentration. Cd caused gradual decrease in plant growth of *Lemna minor* (Razinger *et al.* 2008). Increasing Cd concentration in the solution significantly decreased the shoot and root dry weight of two selected oil seed rapes and Indian mustard plants (Su and Wong 2004). Wahid *et al.* (2007) observed increased shoot Cd accumulation and leaf chlorosis with a concomitant reduction in shoot dry weight, leaf area, relative growth rate, net assimilation rate and relative leaf expansion rate in *Vigna radiata* seedlings under Cd stress. Krantev *et al.* (2008) reported that exposure of *Zea mays* plants to Cd caused a gradual decrease in the shoot and root dry weight accumulation. Ahsan *et al.* (2007) reported that increasing Cd concentration in the medium significantly decreased the germination rate, shoot elongation and biomass of *Oryza sativa*. Kuriakose and Prasad (2008) reported that at concentrations above 3.0 mM Cd, seed germination of *Sorghum bicolor* was adversely affected with a complete cessation of seedling growth.

The over all reduction in growth has been attributed to repression of the elongation and the growth rates of cells because of an irreversible inhibition exerted by Cd on proton pump (Aidid and Okamoto 1993). However, slight increase in the growth was noticed when the plants were exposed to very low Cd concentrations. Stimulatory effect of lower doses of Cd on growth was observed in *Lycopersicon esculentum* and *Solanum melongena* (Khan and Khan 1983), *Beta vulgaris* (Greger and Lindberg 1986), *Nicotiana tabacum* cells (Hirt *et al.* 1989), *Medicago sativa* seedlings (Peralta *et al.* 2000), *Hordeum vulgare* (Wu *et al.* 2003), *Miscanthus sinensis* (Arduini *et al.* 2004) and *Lycopersicon esculentum* seedlings (Dong *et al.* 2005).

PHYSIOCHEMICAL ALTERATIONS UNDER CADMIUM STRESS

Photosynthetic pigments

Chlorophylls (Chl) and carotenoids (Car) are the most abundant biological pigments in plants (Hall and Rao 1999). The presence of these pigments in plants reflects the nutritional status, growth as well as crop productivity (Seyyedi *et al.* 1999). Chlorosis and retardation of plant growth that is frequently observed in metal polluted environment indicates that an impairment of photosynthetic pigment biosynthetic pathway is among the earlier targets of heavy metal influence on plant metabolism. Lower content of photosynthetic pigments induce changes in plastid development, photosynthetic efficiency as well as in general metabolism. Better is the status of these pigments, better will be the capability of plants to fix CO_2 and hence, better will be the light harvesting capability.

Chlorophyll

Chl play a fundamental role in the process of photosynthesis because of its ability to absorb light. Baszynski *et al.* (1980) reported about the negative effect of Cd on *Lycopersicon esculentum* plants. Lately, Cd induced decrease in Chl content was observed in *Triticum aestivum* and *Cucumis sativus* (Buszek 1984; Malik *et al.* 1992a, 1992b), *Zea mays* (El-Enany 1995; Stiborova *et al.* 1986; Ekmekci *et al.* 2007; Krantev *et al.* 2008), *Phaeolus vulgaris* (Barcelo *et al.* 1988a, 1988b; Siedlecka and Krupa 1996), *Hordeum vulgare* genotypes (Wu *et al.* 2003), *Oryza sativa* (Kuo and Kao 2004), *Glycine max* seedlings (Drazic *et al.* 2004), *Matricaria chamomilla* (Kovacik *et al.* 2006), *Brassica juncea* (Mobin and Khan 2007), *Bechmeria nivea* (Liu *et al.* 2007), *Brassica campestris* (Anjum *et al.* 2008b) and *Vigna mungo* (Singh *et al.* 2008a). Following Cd treatment concentration of Chl *a* is reduced more than Chl *b* in *Phyllanthus amarus* (Rai *et al.* 2005), *Brassica juncea* plants (Mobin and Khan 2007) and *Vigna mungo* (Singh *et al.* 2008). The increased Chl *a*:*b* ratio was linked with the change in pigment composition of photosynthetic apparatus which posses lower level of light harvesting Chl proteins (Loggini *et al.* 1999). Skorzynska-Polit and Baszynski (1997) reported that Cd-induced necrosis of leaf tissues might be the reason of Cd mobilization and its transport to above ground plant parts.

Most researchers connect the reduction of Chl in Cd-treated plants with inhibition of its biosynthesis. Cd-induced inhibition of Chl biosynthesis was even suggested to be a primary event as compared to the inhibition of photosynthesis (Baszynski *et al.* 1980). Stobart *et al.* (1985) established that Cd inhibited Chl biosynthesis at two levels: in the synthesis of 5-aminolaevulinic acid (ALA) and in the formation of photoactive protochlorophyllide reductase complex. Horvath *et al.* (1996) reported that the photoconversion of protochlorophyllide was not inhibited, but Cd disturbed Chl molecules integration in stable complexes. On the other hand, Greger and Lindberg (1986) suggested that the lower Chl concentrations in plants were a result of the deficiency of Mg and Fe in the leaves of Cd-treated sugar beet plants. The decrease in Mg and Fe content in leaves as a response to Cd treatment has been established in other plant species also (Breckle and Kahle 1992; Rubio *et al.* 1994). More convincing data about the interactions between Fe deficiency (this element is a co-factor of an enzyme taking a part in Chl biosynthesis) and Chl concentrations were reported by Krupa *et al.* (1995). They showed that 50 µM Cd induced Fe deficiency and decreased Chl by 55% in bean plants. Lang *et al.* (1995) confirmed that translocation of the labeled Fe to the over-ground organs of Cd-treated *Cucumis sativus* plants was inhibited and decreased Chl. Somashekaraiah *et al.* (1992) showed that treatment of 100 µM Cd for 6 d increased the lipoxygenase activity and decreased Chl concentration in *Phaseolus vulgaris* plants.

Carotenoids

Car carry out three major functions in plants. First, they absorb light at wavelength between 400 and 550 nm and transfer it to the Chl (an accessory light-harvesting role) (Siefermann-Harms 1987). Second, they protect the photosynthetic apparatus by quenching a triplet sensitizer (Chl^3), singlet oxygen and other harmful free radicals which are naturally formed during photosynthesis (an antioxidant function) (Oelmuller 1989; Havaux *et al.* 2000; Collins 2001). Third, they are important for the photosystem (PS) I assembly and the stability of light harvesting complex proteins as well as thylakoid membrane stabilization (a structural role) (Mayfield and Taylor 1984; Siefermann-Harms 1987; Niyogi *et al.* 2001).

The influence of Cd on Car has been investigated in different plants. Cd-induced decrease in Car content in the seedlings of *Raphanus sativus*, *Ulva lactuca*, *Triticum aestivum* and *Oryza sativa* was reported by Naguib *et al.* (1982). Baszynski (1980) observed Cd induced decrease in Car content in *Lycopersicon esculentum*. The toxic effect of Cd was partially reversed by the addition of Mn; however, the Car content never reached the value of control plants. Chl and Car contents were increased initially and decreased thereafter in *Zea mays* leaves under Cd stress (Prochazkova *et al.* 2001). Baryla *et al.* (2001) reported reduced Car content in *Brassica napus* plants under Cd stress. Rai *et al.* (2005) and Singh *et al.* (2008a) reported decreased Car and Chl contents in *Phyllanthus amarus* and *Vigna mungo* plants with increasing Cd concentration, respectively. In *Brassica napus*, Cd reduced the total Chl and Car contents and increased the non-photochemical quenching (Larsson *et al.* 1998). Ekmekci *et al.* (2007) reported that the increase in Cd concentration caused loss of Car in *Zea mays* cultivars. Collin *et al.* (2008) also reported decreased concentration of Car in *Arabidopsis* plants. Car content of *Hordeum vulgare* seedlings decreased under Cd-stress (Demirevska-Kepova *et al.* 2006) or remained less affected (Clijsters and Van Assche 1985). An increase in Car content was also reported following Cd stress (Foyer and Harbinson 1994)

Photosynthesis

Cd has been shown to affect the photosynthetic functions through interacting with photosynthetic apparatus at various levels of organization and architecture *viz.*, accumulation of metal in leaf (main photosynthetic organ), partitioning in leaf tissues like stomata, mesophyll and bundle sheath cells, interaction with cytosolic enzymes and alteration of the functions of chloroplast membranes. Cd has been shown to be the most effective inhibitor of photosynthetic activity (Bazzaz *et al.* 1974; Huang *et al.* 1974), particularly the oxygen evolving reactions of PS II (Bazzaz and Govindjee 1974; Baszynski *et al.* 1980; Atal *et al.* 1991). The effects of Cd on activities of enzymes involved in photosynyhesis are shown in **Table 1**. With only small amount of Cd in chloroplasts, many direct and indirect effects are observed, resulting in strong inhibition of photosynthesis. Earlier investigations have demonstrated a marked reduction in the rate of photosynthesis by Cd in different plant species (Baszynski *et al.* 1980; Sawhney *et al.* 1990; Sheoran *et al.* 1990a, 1990b; Chugh and Sawhney 1999; Arduini *et al.* 2004; Wojcik and Tukendorf 2005; Khan *et al.* 2006, 2007; Mobin and Khan 2007; Singh *et al.* 2008a, 2008b). Deleterious effects of Cd on various facets of photosynthesis, such as Chl metabolism (Padmaja *et al.* 1990; Stobart *et al.* 1985; Sandalio *et al.* 2001; Chaffei *et al.* 2004; Hsu and Kao 2004; Vassilev *et al.* 2005), functioning of photochemical reactions (Li and Miles 1975; Skorzynska-Polit and Baszynski 1995) and the activities of the Calvin cycle enzymes (Ascencio and Cedeno-Maldonado 1979; Krupa 1999) have also been reported. Baszynski *et al.* (1980) observed that the decline in Chl content preceded that of CO_2 fixation and proposed this to be the primary cause of diminished photosynthetic activity. Cd-induced reduction in the activity of ribulose 1,5 bisphosphate carboxylase (Rubisco) has been reported in *Hordeum vulgare* (Stiborova *et al.* 1986; Vassilev *et al.* 2004), *Cajanus cajan* (Sheoran *et al.* 1990), *Triticum aestivum* (Malik *et al.* 1992b), *Pisum sativum* seedlings (Chugh and Sawhney 1999), *Zea mays* (Krantev *et al.* 2008) and *Brassica juncea* (Mobin and Khan 2007). Wahid *et al.* (2007) reported Cd induced reduction in transpiration rate, stomatal conductance and net photosynthesis due to reduced CO_2 fixation by Rubisco in *Vigna radiata* plants. Di Cagno *et al.* (2001) also observed significant reduction in CO_2 fixation rate and Rubisco activity while stomatal conductance and the Fv:Fm ratio remain unchanged in Cd-treated sunflower plants. Carbonic anhydrase (CA), a zinc metalloenzyme related to photosynthesis in higher plants, was significantly reduced by Cd in *Brassica juncea* (Mobin and Khan 2007), *Triticum aestivum* (Khan *et al.* 2008) and *Vigna mungo* (Singh *et al.* 2008a). The loss of water from crop plants is controlled mainly by the stomata on leaves that have been shown to be sensitive to various environmental factors including Cd stress (Barcelo *et al.* 1986a, 1986b). Stomatal closure to minimize water loss has been identified as an early event in plant response to Cd-induced water deficiency leading to limitations in carbon uptake by leaves (Barcelo *et al.* 1986a, 1986b; Chaves 1991; Poschenreider *et al.* 1989). In addition, conductance and index of stomata, transpiration and net CO_2 uptake are greatly reduced with elevated Cd levels in the growth media (Bindhu and Bera 2001; Balakhnina *et al.* 2005). Siedlecka and Krupa (1996) found that leaf Chl content and Hill activity decreased with increased chlorophyllase activity under Cd stress. Cd interacts with the water balance (Costa and Morel 1994) and damages the photosystem apparatus, in particularly the PS I and II (Siedlecka and Krupa 1996). In *Medicago sativa*, Becerril *et al.* (1989) found that Cd inhibited transpiration and CO_2 assimilation in a drastic manner, whereas, in *Picea abies* seedlings decreased CO_2 assimilation was mainly due to stomatal closure (Schlegel *et al.* 1987). Cd induced reduction in photosynthesis and transpiration was attributed to stomatal closure in *Beta vulgaris* (Greger and Johansson 1992). Mobin and Khan (2007) found that the Cd-induced decrease in net photosynthetic rate in non-tolerant cultivar (RH30) of *Brassica juncea* was accompanied by an increased transpiration rate and stomatal conductance but in tolerant cultivar (Varuna), it remained unaltered.

Sulfur metabolism under Cd stress

Plants can adapt to a wide range of environmental stress conditions using appropriate physiological responses. In the case of heavy metals stress, the processes consist of modulation of the activity of plasma membrane and/or vacuolar transporters and biosynthesis of intracellular metal-chelators (Clemens 2006). In this context, sulfur plays a pivotal role because sulfate transporters can mediate the entry of sulfate-analogues into the cells (Maruyama-Nakashita *et al.* 2007), and S-containing compounds like GSH, PCs and

Table 1 The effects of Cd on activities of enzymes of different metabolic processes.

Chlorophyll synthesis	ALA synthase	*Phaseolus vulgaris*	– –	Padmaja *et al.* 1990
		Hordeum vulgare	– –	Stobart *et al.* 1985
	ALA dehydratase	*Phaseolus vulgaris*	– –	Padmaja *et al.* 1990
	NADPH:protochlorophyllide oxidoreductase	*Hordeum vulgare*	– –	Stobart *et al.* 1985
		Triticum aestivum	– –	Boddi *et al.* 1995
Photosynthesis	RUBP carboxylase	*Phaseolus vulgaris*	– –	Siedlecka *et al.* 1997
		Brassica juncea	– –	Mobin and Khan 2007
		Triticum aestivum	– –	Malik *et al.* 1992b
		Cajanus cajan	– –	Sheoran *et al.* 1990
		Zea mays	– –	Krantev *et al.* 2008
		Vigna radiata	– –	Anjum *et al.* 2008
	PEP carboxylase	*Phaseolus vulgaris*	– –	Siedlecka *et al.* 1997
		Cajanus cajan	– –	Sheoran *et al.* 1990
		Zea mays	– –	Krantev *et al.* 2008
		Phaseolus vulgaris		Gouia *et al.* 2003
	Carbonic anhydrase	*Ceratophyllum demersum*	– –	Aravind and Prasad 2004
		Brassica juncea	– –	Mobin and Khan 2007
		Vigna mungo	– –	Singh *et al.* 2008
		Triticum aestivum	– –	Khan *et al.* 2007
		Brassica juncea	– –	Hayat *et al.* 2007
		Cicer arietinum	– –	Hasan *et al.* 2007
		Cicer arietinum	– –	Hasan *et al.* 2008
N metabolism	Nitrate reductase	*Sesamum indicum*	– –	Singh *et al.* 1994
	Nitrate reductase	*Vigna radiata*	– –	Wahid *et al.* 2007
		Brassica juncea	– –	Hayat *et al.* 2007
		Cicer arietinum	– –	Hasan *et al.* 2008
		Phaseolus vulgaris	– –	Gouia *et al.* 2000
	Glutamine synthatase	*Pisum sativum*	– –	Chugh *et al.* 1992
	Glutamate dehydrogenase	*Phaseolus vulgaris*	+ +	Gouia *et al.* 2000, 2003
				Hernandez *et al.* 1997
	Glutamate dehydrogenase		+ +	Boussama *et al.* 1999
				Ghnaya *et al.* 2005
S metabolism	ATP-sulfurylase	*Triticum aestivum*	+ +	Khan *et al.* 2007
	ATP-sulfurylase, APS reductase, Sulfite reductase	*Arabidopsis thaliana*	+ +	Harada *et al.* 2002
	ATP-sulfurylase, APS reductase	*Brassica juncea*	+ +	Lee and Leustek 1999
	OASTL		+ +	Barroso *et al.* 1999
	Glutamate dehydrogenase, Serine acetyltransferase and O-acetyl-L-serine (thiol)lyase	*Chlamydomonas reinhardtii*	+ +	Dominguez *et al.* 2003
	S-nitrosoglutathione reductase	*Pisum sativum*	– –	Barroso *et al.* 2006

'+' and '–' signs denote stimulatory and inhibitory effects of Cd on enzymes, respectively.

MTs often improve the tolerance of plants to several metals and metalloids through complexation and/or further sequestration of toxic forms inside cellular vacuoles (Xiang and Oliver 1998; Cobbett and Goldsbrough 2002; Hall 2002).

S is an essential macronutrient that plays a vital role in the regulation of plant growth and development (Ernst 1998; Singh 2004; Anjum *et al.* 2008c, 2008d; Bimbrow 2008; Ernst *et al.* 2008; Kumaran *et al.* 2008; Ratti and Giordano 2008). It is constituent of amino acids, Cys and Met, GSH and of varieties of other plant metabolites involved in stress tolerance (Saito 2000; Rausch and Wachter 2005; Burritt 2008; Bouranis *et al.* 2008). A significant induction in S assimilation has been reported in heavy metal-exposed higher plants (Tukendorf and Rauser 1990). Exposure of plants to Cd induces enzymes involved in the sulfate assimilation pathway (Herbette *et al.* 2006; Khan *et al.* 2007). The effects of Cd on activities of enzymes of S metabolism are shown in **Table 1**. It has been noted that genes involved in S assimilation pathway are rapidly upregulated such as *Sultr1;1* and *Sultr2;1* encoding two sulfate transporters which are up-regulated after 2 or 6 h of Cd-treatment and 12-24 h after sulfate-depletion (Takahashi *et al.* 2000; Herbette *et al.* 2006; Sarry *et al.* 2006). Nussbaum *et al.* (1988) reported that Cd accumulation increased ATP-sulfurylase (ATP-S) and adenosine 5-phosphosulfate reductase (AR) activities in *Zea mays* seedlings. Ruegsegger *et al.* (1990) showed that AR activity is induced coordinately with glutathione synthetase in Cd-treated *Pisum sativum* plants. In fact, the capacity of plants to survive in a polluted environment is partially linked to the efficiency of their reductive sulfate assimilation pathway. Upon heavy metal stress, some genes involved in the S assimilation pathway are known to be transcriptionally activated, resulting in an elevation of enzymatic activity (Schafer *et al.* 1988; Xiang and Oliver 1988; Barroso *et al.* 1999; Heiss *et al.* 1999; Lee and Leustek 1999). The involvement of S in Cd-tolerance mechanism was reported in *Arabidopsis thaliana* (Dominguez-Solis *et al.* 2001; Harada *et al.* 2002), *Brassica juncea* (Zhu *et al.* 1999a, 1999b), *Nicotiana tabacum* (Harada *et al.* 2001), *Triticum aestivum* (Khan *et al.* 2007) and *Brassica campestris* (Anjum *et al.* 2008c).

A good part of S incorporated into organic molecules in plants is located in thiol (-SH) groups in proteins (cys-residues) or non-protein thiols, GSH (Noji and Saito 2003; Tausz *et al.* 2003; De Kok *et al.* 2005; Anjum *et al.* 2008d). S being a component of PC may play an important role in their synthesis and ultimately in detoxification of Cd through the formation of Cd-binding peptides (CdBP) (Harada *et al.* 2002; Cobbett and Goldsbrough 2002). In many plants, PC synthesis is reported to be activated by heavy metal treatment and a supply of precursors, including Cys, γ-glutamylcysteine and GSH (Zenk 1996; Chen *et al.* 1997; Goldsbrough 2000; Xiang *et al.* 2001; Nocito *et al.* 2002, 2006). Studies have demonstrated the critical role of PCs in Cd detoxification and tolerance of plants to Cd (Kuboi *et al.* 1987; Howden *et al.* 1995a, 1995b; Inouhe *et al.* 2000; Harada *et al.* 2001; Ebbs *et al.* 2002; Harada *et al.* 2002; Srivastava *et al.* 2004; Wojcik *et al.* 2005; Zhang *et al.* 2007). It has been showed that PC formation was induced in the leaf, stem and root tissues of *Sedum alfredii* upon exposure to 400 µM Cd (Zhang *et al.* 2007). PCs rapidly form a low molecular weight (LMW) complex with Cd (Sanita di

Toppi 1999). These complexes acquire acid labile S at the tonoplast and form a high molecular weight (HMW) complex with a higher affinity for Cd ions (Hu *et al.* 2001). Gupta *et al.* (2002) reported an increase in Cys and GSH in the shoots of *Arabidopsis* and suggested that these changes can be expected to have a positive effect via transport on the PC/hPC synthesis and/or the other stress responses in roots in a Cd-contaminated environment.

Moreover, evidence suggests that CdS solids may be formed and coated by CdBP-Cd complexes after exposure of cultured suspension cells to high levels of Cd (Rauser 1990) and the co-occurrence of CdS and CdBP-Cd has been thought to play a role in stabilizing CdBP-Cd complexes (Rauser 1990; Wang and Evangelou 1995). As CdBP synthesis and CdS solids formation are closely dependent on S metabolism and increase the need for thiol compounds by cells, there is a need for maintaining high S ions in the roots to sustain a high S-assimilation rate during PC biosynthesis to detoxify Cd ions.

Nitrogen metabolism under cadmium stress

The presence of Cd in plants results in many physiological alterations affecting both N and carbohydrate metabolism (Greger and Bertell 1992; Hernandez *et al.* 1997; Chaffei *et al.* 2003). The nitrate assimilation process consumes about 25% of energy produced by photosynthesis (Solomonson and Barber 1990). In most of the plants nitrate reduction takes place in leaves where major part of the reducing power arises directly from light *via* ferredoxin. A high rate of CO_2 assimilation favours an efficient N assimilation and *vice versa* (Ferrario *et al.* 1998). Cd as a potential inhibitor of photosynthetic process considerably inhibits nitrate assimilation. It has been shown that enzymes of N metabolism are differentially affected by Cd stress (Chugh *et al.* 1992; Singh *et al.* 1994; Syntichaki *et al.* 1996; Boussama *et al.* 1999). The effects of Cd on activities of enzymes of N metabolism are shown in **Table 1**. Among various enzymes nitrate reductase (NR) is a key enzyme in the conversion of nitrate to nitrite, and its sustained activity is crucial to N assimilation (Srivastava 1992; Gouia *et al.* 2000; Ghnaya *et al.* 2005, 2007). NR and nitrite reductase (NiR) activities are significantly decreased by Cd, leading to reduced nitrate assimilation by plants (Ferretti *et al.* 1993; Chaffei *et al.* 2004; Rai *et al.* 1998; Khudsar *et al.* 2001; Balestrasse *et al.* 2004; Anjana *et al.* 2006; Wahid *et al.* 2007; Wang *et al.* 2008).

Cd reduces absorption of nitrate and its transport from root to shoot by inhibiting the NR activity in shoots (Hernandez *et al.* 1996). Cd treatment can also result in endogenous ammonium increase through deamination of some free amino acids and other N forms. Chaffei *et al.* (2003) demonstrated that Cd treatment produced ammonium accumulation through an increase in protease activity. Glutamine synthetase (GS) is one of the key enzymes in the main pathway of ammonium assimilation in higher plants (Lea and Miflin 2004), and deleterious effects of Cd on its activity have been observed in several species (Astolfi *et al.* 2004; Chaffei *et al.* 2004; Balestrasse *et al.* 2006), which reflects a general inhibition of primary N assimilation. In contrast, glutamate dehydrogenase (GDH), an important enzyme in the “shunt” of N metabolism, was induced under Cd stress, but the physiological role of GDH and the increase in its activity are still controversial (Hernandez *et al.* 1997; Astolfi *et al.* 2004; Chaffei *et al.* 2004; Lea and Miflin 2004; Balestrasse *et al.* 2006; Hsu *et al.* 2006). Nitrate assimilation also requires carbon skeletons, especially in the form of 2-oxoglutarate, which is produced *via* the anaplerotic pathway in the cytosol. 2-Oxoglutarate is imported into the chloroplasts (Lancien *et al.* 2000) where it serves as the NH_4 acceptor by the coupled reaction of glutamine synthase and glutamate synthase under physiological conditions (Oaks 1994; Ouariti *et al.* 1997; Gouia *et al.* 2000).

Wahid *et al.* (2007) reported that the Cd-induced inhibition of growth was mainly due to the damaged photosynthetic apparatus and disruption of the coordination between C and N metabolism in *Vigna radiata*. A high rate of CO_2 assimilation favours an efficient N assimilation and *vice versa* (Ferrario *et al.* 1998). NR and glutamine synthetase enzymes activities are sensitive to Cd stress whereas, glutamate dehydrogenase (NADH-GDH) shows a substantial rise under influence of Cd with dramatic build-up of ammonium pool (Boussama *et al.* 1999; Gouia *et al.* 2003). The induction of GDH activity by Cd results from *de novo* synthesis and/or activation of specific isoenzymes that removes excess ammonium (Syntichaki *et al.* 1996). GDH isoenzymes appear to remove in part the excess of ammonium under Cd toxicity conditions. Under physiological conditions the incorporation of ammonium into organic compounds occurs mainly *via* the GS/GOGAT cycle (Gouia *et al.* 2000). The most striking change in Cd treated plants appears to be a rapid decay of GS/Fd-GOGAT and NADH-GOGAT activities and the accumulation of ammonia (Boussama *et al.* 1999; Balestrasse *et al.* 2006). This implies a reduced capacity of GS/GOGAT cycle and induced activity of the alternative mode of ammonium assimilation by NADH-GDH pathway under Cd treatment.

N metabolism is important for the response of plants to Cd toxicity. Upon exposure to Cd, plants often synthesize a set of N-containing metabolites through N metabolism, such as proline, GSH and PCs, which play a significant role in Cd tolerance of plants (Sharma and Dietz 2006). Accordingly, plants might exhibit a higher Cd tolerance by the maintenance of normal N metabolism levels under Cd stress (Gussarsson *et al.* 1996).

YIELD CHARACTERISTICS UNDER CADMIUM STRESS

The stress factors are a menace for plants and prevent them from reaching their full genetic potential and limit the crop productivity worldwide (Mahajan and Tuteja 2005). A comparison of record yields and average yields for various crop plants indicates that crops mainly attain only 20% of their genetic potential for yield due to various biotic and abiotic stress factors. Abiotic stress is in fact the principal cause of crop failure worldwide, dipping the average yield for most major crops by more than 50-70% (Boyer 1982; Mahajan and Tuteja 2005; Khan *et al.* 2006).

Cd stress affects growth and yield through disturbances in several morpho-physiological processes and nutrient uptake. Reduction in growth and yield with increased levels of Cd in growth media arises because of increased leaf rolling and chlorosis of leaf and stem (Ghani and Wahid 2007) and reduced photosynthetic rate (Chugh and Sawhney 1999). Wahid and Ghani (2008) reported significant reduction in number of pods per plant and seeds per pod, 100-seed weight, seed yield and harvest index of *Vigna radiata* genotypes as a result of Cd toxicity. It has been suggested that although varietal difference exists, the accumuated Cd is mainly toxic to the mesophyll tissue, most probably by interfering with the uptake of essential nutrients, thereby reducing growth and yield at various stages. Cd significantly reduced the number of ear, ear weight, ear length, spikelet number, grains per ear, 1000 grain weight and grain yield of *Triticum aestivum* cultivars and the decrease was correlated with the reduced photosynthetic capacity of the cultivars (Khan *et al.* 2006, 2007).

It has been shown that Cd stress significantly reduced grain yield, panicle number per plant, spikelets per panicle, filled spikelet rate and grain weight of *Oryza sativa* genotypes and reduction in yield components of rice genotypes was proportional to grain Cd content (Cheng *et al.* 2005). Genotypic differences on the basis of biomass production, yield and yield components were observed in *Triticum aestivum* and it was noted that Cd significantly reduced the root and stem biomass and spikes per plant but the grains per ear and grain weight were not significantly reduced (Zhang *et al.* 2002). They found that the inconsistent decrease in number of grains per ear and single grain weight among wheat genotypes were because of the compensation among yield components.

Wu *et al.* (2004) reported reduction in yield of three cotton genotypes under Cd stress and found that the reduction in yield was proportional to Cd accumulation. The cotton genotype Simian 3 showed higher Cd concentration and greater decrease in yield than the other two genotypes (Zhongmian 16 and Zhonmian 16-2). Liu *et al.* (2007) noted great variation among *Oryza sativa* cultivars in their tolerance to soil Cd stress with respect to tillering, plant height, leaf area, dry matter accumulation and grain yield. The relative change in the number of grains per panicle showed a strong positive correlation with relative change in grain yield and, of the four grain yield components measured (panicles per pot, grains per panicle, filled grain percentage, weight per grain) and the reduction of grains per panicle is the main cause of grain yield loss under Cd stress.

CADMIUM-INDUCED OXIDATIVE STRESS

Plant cells are continuously exposed to various environmental and biotic stresses which lead to the increased production of ROS. The responses of plants to these excess ROS have recently been analyzed extensively at biochemical and molecular levels (Kreps *et al.* 2002; Gachomo *et al.* 2003; Kouril *et al.* 2003; Rizhsky *et al.* 2004; Kotchoni and Gachomo 2006). Under normal physiological conditions, ROS are continuously produced in the chloroplasts, mitochondria, peroxisomes as byproducts of aerobic metabolic processes like photosynthesis, respiration and photorespiration. These ROS are scavenged by both enzymatic and non-enzymatic antioxidant pathways for the maintenance of the normal plant growth (Jimenez *et al.* 1998; del Río *et al.* 2002; Mittler *et al.* 2004; Davletova *et al.* 2005; Asada 2006; Kotchoni and Gachomo 2006; Mobin and Khan 2007; Nathawat *et al.* 2007; Chalapathi Rao and Reddy 2008). The production of ROS through Cd-exposed oxidative stress is common in a variety of plants species (Sandalio *et al.* 2001; Ali *et al.* 2002; Ranieri *et al.* 2005; Smeets *et al.* 2005; Singh *et al.* 2008b). Oxidative stress occurs when there is a serious imbalance in any cell compartment between the production of ROS and antioxidant defence, leading to significant physiological challenges (Foyer and Noctor 2000). These excess ROS cause damage to proteins, lipids, carbohydrates, DNA and ultimately results in cell death (Gueta-Dahan *et al.* 1997; Fadzilla *et al.* 1997; Fahmy *et al.* 1998; Mittler *et al.* 2004; Foyer and Noctor 2005; Sairam *et al.* 2005; Shulaev and Oliver 2006; Djebali *et al.* 2008).

Photosynthesizing plants are naturally prone to oxidative stress because they have an array of photosensitizing pigments. These pigments produce and consume oxygen which can easily donate electrons to form ROS. The Chl pigments associated with the electron transport system are the primary source of singlet oxygen ($^1O_2$). It may also arise as a by product of lipoxygenase activity and is highly destructive, reacting with most biological molecules at near diffusion-controlled rates. Superoxides, produced by the transport of electron to oxygen, are not compatible with metabolism and are required to be eliminated by the antioxidative defence system while recycling of phosphoglycolate to phosphoglycerate (re-enter the Bassam-Calvin cycle) results in a considerable loss of assimilated carbon.

Cd has been found to induce oxidative stress in plants (Somashekaraiah *et al.* 1992; Piqueras *et al.* 1999; Dixit *et al.* 2001; Okamoto *et al.* 2001; Sandalio *et al.* 2001; Pereira *et al.* 2002; Milone *et al.* 2003; Wu *et al.* 2003; Skorzynska-Polit *et al.* 2003/4; Kuo and Kao 2004; Liu *et al.* 2007; Djebali *et al.* 2008; Singh *et al.* 2008a), but in contrast with other heavy metals, such as Cu, it does not seem to act directly on the production of ROS through Fenton type reactions (Salin 1988). Evidence that Cd causes the production of ROS in plants (Foyer *et al.* 1997) arised from the observations that new isozymes of peroxidases were detectable in both root and leaves of *Phaseolus vulgaris* (Van Assche and Clijsters 1990). Further evidence of the Cd-induced oxidative stress arised from the detection of lipid peroxidation, increased lipoxygenase activity, Chl degradation and inhibition or stimulation of the activity of several antioxidant enzymes (Shaw 1995a,b; Stochs and Bagchi 1995; Dixit *et al.* 2001; Iannelli *et al.* 2002; Leon *et al.* 2002; Skorzynska-Polit *et al.* 2003/4; Mobin and Khan 2007; Anjum *et al.* 2008a; Agrawal and Mishra 2009). Cd induces varying responses in plants in relation with these enzymes. The varying responses are most probably related both to the levels of Cd supplied and to concentration of thiol groups already present or induced upon treatment. All these changes lead to the alteration and the production of ROS in the plants. Cd provokes significant disturbances in the structural organization and functional activity of photosynthetic apparatus (Baszynski 1986; Krupa and Baszynski 1995; Vassilev *et al.* 1995; Dahlin *et al.* 2000). The main targets of toxic Cd effects are the pigment apparatus and photosynthetic gas exchange system (Lang *et al.* 1995; Tukendorf and Baszynski 1991; Clijsters and Van Assche 1985).

Heavy metal exposed plants adopt the process of avoidance of the production of ROS as the first line of defence against oxidative stress. Once formed, ROS must be detoxified as efficiently as possible to minimize eventual damage. Thus, the detoxification mechanisms constitute the second line of defence against the detrimental effects of ROS (Moller 2001). In fact, compounds having the property of quenching the ROS without undergoing conversion to a destructive radical can be described as antioxidant. Antioxidant enzymes are considered as those that either catalyses such reactions, or are involved in the direct processing of ROS (Medici *et al.* 2004). Hence, antioxidants (enzymatic and non-enzymatic) function to interrupt the cascades of uncontrolled oxidation (Noctor and Foyer 1998). Though, the expression for antioxidant enzymes is altered under stress conditions, their up regulation has a key role in combating the abiotic stress-induced oxidative stress. However, the level of up regulation is subject to type and magnitude of the stress. SOD, CAT, APOX, GR, MDHAR, DHAR, GOPX and GST showed great variations in their activities depending on the Cd concentration and the plant species used.

Lipid peroxidation

Photosynthesizing plants are especially at the risk of oxidative damage, because of their oxygenic conditions and the abundance of the photosensitizers and polyunsaturated fatty acids in the chloroplast envelope. It is reported that 1% of the oxygen consumed by the plants is diverted to produce activated oxygen species like $OH^\cdot$, $^1O_2$ and $O_2^{\cdot -}$ (Asada and Takahashi 1987). Free radicals and other derivatives of oxygen are inevitable by products of biological redox reactions. Their production is considered to be a universal and common feature of living world under natural conditions as a by product of respiration and photosynthesis during electron transport systems of mitochondria and chloroplast. Their concentration increases under unfavorable conditions. Intracellular structures like membranes and biomolecules like proteins, enzymes, lipids and DNA have a high degree of organization that is at the risk of being destructed by these oxidative radicals.

Lipids are most prone to oxidative damage. The peroxidation of lipids is considered as the most damaging process known to occur in every living organism (Zhang and Kirkham 1996; Hung and Kao 1998). Membrane damage is sometimes taken as a single parameter to determine the level of lipid destruction (i.e. lipid peroxidation). Now, it has been recognized that during the lipid peroxidation, products are formed from polyunsaturated precursors that include small hydrocarbon fragments such as ketones, malondialdehyde (MDA), etc and compounds related to them (de Vos *et al.* 1993; Weckx and Clijsters 1996). Some of these compounds react with thiobarbituric acid (TBA) to form coloured products called thiobarbituric acid reactive substances (TBARS) that can be measured by monitoring their absorption at around 530 nm (Gray 1978).

Plants exposed to heavy metal stress exhibited an increase in lipid peroxidation due to the generation of free radicals (Van Assche and Clijsters 1990; Shaw 1995b; Choaui *et al.* 1997; Lozano-Rodriguez *et al.* 1997; Vanaja *et al.* 2000). Increase in TBARS with increasing Cd concentration has been reported in germinating *Phaseolus vulgaris* seedlings (Somashekaraiah *et al.* 1992). This was related to blockage of electron flow in PS II by metal ions that lead to the formation of excited Chl which in turn causes the production of free radicals (Kato and Shimizu 1985). Treatment with Cd notably increased the accumulation of lipid peroxides in *Pisum sativum* (Chaoui *et al.* 1997b; Lozano Rodriguez *et al.* 1997; Dixit *et al.* 2001; Metwally *et al.* 2005), *Oryza sativa* (Ahsan *et al.* 2007; Guo *et al.* 2007), different *Hordeum vulgare* genotypes (Wu *et al.* 2003), *Helianthus annuus* (Gallego *et al.* 1996a,b; Groppa *et al.* 2001), *Arabidopsis* seedlings (Cho and Seo 2005), *Lemna minor* (Razinger *et al.* 2008), *Brassica juncea* (Mobin and Khan 2007), *Glycine max* (Balestrasse *et al.* 2004; Noriega *et al.* 2007), *Bechmeria nivea* (Liu *et al.* 2007), *Lycopersicon esculentum* (Ammar *et al.* 2007), *Brassica napus* (Filek *et al.* 2008) and *Vigna mungo* (Singh *et al.* 2008a). Contrarily, decreased rate of lipid peroxidation in peroxisomes of *Pisum sativum* plants has been reported due to Cd (Romero-Puertas *et al.* 1999). However, no lipid peroxidation was observed in the hairy roots of *Daucus carota* under Cd stress (Sanita di Toppi *et al.* 1998). Piqueras *et al.* (1999) reported an increased lipid peroxidation in BY2 cell cultures of *Lycopersicon esculentum* plants exposed to 5 mM Cd. The increase was related to a rapid generation of H_2O_2 followed by an alteration of the antioxidant system. Dixit *et al.* (2001) reported an increase in lipid peroxidation in roots and leaves of *Pisum sativum* plants exposed to varying range of Cd in hydroponic system. Okamoto *et al.* (2001) observed oxidative damage to lipids in isolated chloroplasts of unicellular alga, *Ganyaulax polyendra* under Cd stress.

Hydrogen peroxide content

H_2O_2 is produced at high flux rates by two processes associated with photosynthesis, the Mehler reaction and the Glycolate oxidase reaction of photorespiration (Foyer and Noctor 2000). In addition, there are a number of other enzymes in leaves that are capable of producing significant amounts of H_2O_2, including peroxidases, NADPH oxidases and oxalate oxidase (Berna and Bernier 1999; Bolwell 1999; Sagi and Fluhr 2001).

The accumulation of H_2O_2 after Cd exposure has been detected in the leaf of different plant species such as *Pisum sativum* (Dixit *et al.* 2001; Romero-Puertas *et al.* 2004), *Arabidopsis thaliana* (Cho and Seo 2005), *Brassica juncea* (Mobin and Khan 2007), *Vigna mungo* (Singh *et al.* 2008a). The formation of H_2O_2 after Cd exposure has also been detected in *Solanum tuberosum* tuber discs (Stroinski and Zielezinska 1997), suspension cultures of *Nicotiana tabacum* cells (Piqueras *et al.* 1999), and *Pinus sylvestris* and *Pisum sativum* roots (Schutzendubel *et al.* 2001; Romero-Puertas *et al.* 2003). Balestrasse *et al.* (2006a) also reported that Cd produced increased concentrations and *in situ* accumulation of H_2O_2 and $O_2^{\cdot -}$ in soybean leaves. Exposure to increasing Cd concentration increased the H_2O_2 content in the upper part (hypocotyls+cotyledons) and roots of *Brassica napus* (Filek *et al.* 2008). Guo *et al.* (2007) reported that exposure to 50 mM Cd significantly increased the H_2O_2 content in the roots of *Oryza sativa*. Zawoznik *et al.* (2007) reported that leaves of wild type *Arabidopsis thaliana* plants exposed to Cd showed accumulation of H_2O_2. It has also been reported that Cd increased the accumulation of H_2O_2 in soybean root tips (Yang *et al.* 2007).

Cadmium-tolerance mechanism in plants

Plants adopt several strategies such as physically avoiding the metal-contaminated environment by making exudates of complexing agents into rhizosphere region, binding metal ions in the cell wall, effluxing the metal ions from the symplasm, preventing the upward transport of metal ions to the above ground parts, transporting metal-peptide/ligand complexes into the vacuole, storing metal ions in the vacuoles by complexation with vacuolar peptides/ligands and or forming metal-resistant enzymes or metabolites to minimize metal-induced severe internal metabolic injuries (Hall 2002; McGrath and Zhao 2003; Gratao *et al.* 2005; Zhang *et al.* 2006).

Plants have evolved a complex array of mechanisms to maintain optimal metal levels and avoid the detrimental effects of excessively high concentrations (Clemens 2001). When these homeostatic mechanisms are overwhelmed, plants suffer metal-induced damage and pro-oxidant conditions within cells. However, higher plants are very well equipped with antioxidant mechanisms (Mittler *et al.* 2004; Gratao *et al.* 2006; Singh *et al.* 2008a, 2008b). Plant cells display an antioxidant network including numerous soluble and membrane compounds, particularly in mitochondria and in chloroplasts where respiratory and photosynthetic electron transfer chains, respectively, take place. Antioxidant enzymes are considered as those that either catalyze such reactions, or are involved in the direct processing of ROS (Medici *et al.* 2004). Plants possess very efficient enzymatic (SOD, CAT, APX, GR, MDHAR, DHAR, GPX, GOPX and GST) and non-enzymatic (AsA, GSH, phenolic compounds, alkaloids, non-protein amino acids and α-tocopherols) antioxidant defense systems. Components of antioxidant defense systems control the cascades of uncontrolled oxidation (Noctor and Foyer 1998) and protect plant cells from oxidative damage by scavenging of ROS.

Enzymatic antioxidant system

SOD (EC 1.15.1.1) was first isolated by Mann and Kleilin (1938) and thought to be a copper-storage protein. Subsequently, it was identified by different names, erythrocuprein, indophenol oxidase, and tetrazolium oxidase until its catalytic function was discovered by McCord and Fridovich (1969). SOD catalyzes the disproportionation of $O_2^{\cdot -}$ to H_2O_2 and molecular oxygen. It removes $O_2^{\cdot -}$ and hence decreases the risk of $OH^{\cdot}$ formation from $O_2^{\cdot -}$ *via* the metal catalyzed Haber-Weiss-type reaction.

There are three distinct types of SOD classified on the basis of the metal cofactor: the copper/zinc (Cu/Zn-SOD), the manganese (Mn-SOD) and the iron (Fe-SOD) isozymes have been reported in various plant species (Bannister *et al.* 1987; Alscher *et al.* 2002). These isozymes can be separated by native polyacrylamide gel electrophoresis. Their activity is detected by negative staining and identified on the basis of their sensitivity to KCN and H_2O_2. The Mn-SOD is resistant to both inhibitors; Cu/Zn-SOD is sensitive to both inhibitors whereas; Fe-SOD is resistant to KCN and sensitive to H_2O_2. The subcellular distribution of these isozymes is also distinctive. The Mn-SOD is found in the mitochondria of eukaryotic cells and in peroxisomes (del Río *et al.* 2003); some Cu/Zn-SOD isozymes are found in the cytosolic fractions, and also in chloroplasts of higher plants (del Río *et al.* 2002). The Fe-SOD isozymes, often not detected in plants (Ferreira *et al.* 2002) are usually associated with the chloroplast compartment when present (Bowler *et al.* 1992; Alscher *et al.* 2002). The prokaryotic Mn-SOD and Fe-SOD, and the eukaryotic Cu/Zn-SOD enzymes are dimers, whereas Mn-SOD of mitochondria are tetramers (Scandalios 1993). Peroxisomes and glyoxysomes of watermelons (*Citrillus vulgaris*) have been shown to contain both Cu/Zn- and Mn-SOD activity (Sandalio and del Río 1988), but there are no reports of extracellular SOD enzymes in plants. All forms of SOD are nuclear-encoded and targeted to their respective subcellular compartments by an amino terminal targeting sequence. Several forms of SOD have been cloned from a variety of plants (Bowler *et al*. 1992; Scandalios 1990). The response of SOD to heavy metal stress varies considerably depending upon plant species, stage of the plant development, metal in the experiment and the exposure time. SOD activity in leaves exhibited increases in activity in response to Cd, whereas in roots there was no significant variation in its activity (Vitoria *et al*. 2001). Activity staining for SOD in *Glycine max* revealed seven isozymes in leaves and eight in roots, corresponding to Mn-SOD and Cu/Zn SOD isozymes. Although a clear effect of Cd on plant growth was observed, the activities of the SOD isozymes were unaltered (Ferreira *et al*. 2002). In *Saccharum officinarum* seedlings, several isozymes have been observed, but growth in the presence of Cd did not result in any significant alteration in SOD activity (Fornazier *et al*. 2002a). In pea plants, a strong reduction in chloroplastic and cytosolic Cu/Zn SODs by Cd was reported and to a lesser extent for Fe-SOD, while Mn-SOD was only affected by the highest Cd concentration tested. This showed that Mn-SOD was the isozyme more resistant to Cd (Sandalio *et al*. 2001). In pea leaf peroxisomes, the Mn-SOD activity did not change in response to Cd treatment (Romero-Puertas *et al*. 1999). Contrarily, increases in total SOD activity were detected following the application of Cd in *Pisum sativum* (Dalurzo *et al*. 1997), *Solanum tuberosum* (Stroinski and Kozlowska 1997), *Hordeum vulgare* (Guo *et al*. 2004), *Arabidopsis thaliana* (Skorzynska-Polit *et al*. 2003/04), *Oryza sativa* (Hsu and Kao 2004), *Triticum aestivum* (Khan *et al*. 2007), *Zea mays* (Krantev *et al*. 2008a), *Brassica juncea* (Mobin and Khan 2007), *Vigna mungo* (Singh *et al*. 2008), *Cicer arietinum* (Hasan *et al*. 2008) and hyperaccumulator plants of the genus *Alyssum* (Schickler and Caspi 1999). SOD activity remained unaltered in *Helianthus annuus* (Gallego *et al*. 1996b, 1999) and declined in *Amaranthus lividus* (Bhattacharjee 1998), *Phragmites australis* (Iannelli et al. 2002), *Capsicum annuum* plants (Leon *et al*. 2002), *Glycine max* (Noriega *et al*. 2007) under Cd stress. In clonal, hydroponically grown poplar plants (*Populus* × *Canescens*, a hybrid of *Populus termula* × *Populus alba*) (Schutzendubel *et al*. 2002) and *Arabidopsis lividus* (Bhattacharjee 1998) exposed to Cd resulted in inhibition of SOD activity. Romero-Puertas *et al*. (2004) studied the involvement of H_2O_2 and $O_2^{\cdot-}$ in the signaling events that lead to the variation of the transcript levels of Cu/Zn-SOD in *Pisum sativum* plants under Cd stress.

CAT (EC 1.11.1.6) is a heme-containing enzyme that catalyzes the dismutation of H_2O_2 into water and oxygen (Frugoli *et al*. 1996). Present in all aerobic eukaryotes, this is important in the removal of H_2O_2 generated in peroxisomes (microbodies) by oxidases involved in β-oxidation of fatty acids, the glyoxylate cycle (photorespiration) and purine catabolism. CAT is one of the first enzymes isolated in a highly purified state. The isozymes of catalase have been studied extensively in higher plants (Polidoros and Scandalios 1999). Scandalios *et al*. (2000) characterized three genetically distinct CAT isozymes in maize plants. All forms of the enzyme are tetramers in excess of 220,000 kDa. Multiple forms of catalase have been described in many plants. Maize has three isoforms, *CAT 1*, *CAT 2* and *CAT 3*, that are found on separate chromosomes and are differentially expressed and independently regulated (Scandalios 1990). *CAT 1* and *CAT 2* are localised in peroxisomes and the cytosol, whereas CAT 3 is mitochondrial. Plants contain multiple CAT isozymes e.g., 2 in *Hordeum vulgare* (Azevedo *et al*. 1998), 4 in *Helianthus annuus* cotyledons (Azpilicueta *et al*. 2007) and as many as 12 isozymes in mustard (Frugoli *et al*. 1996). CAT isozymes have been shown to be regulated temporally and spatially and may respond differentially to light (Willekens *et al*. 1994; Skadsen *et al*. 1995).

The variable response of CAT activity has been observed under Cd stress. CAT activity declined in *Helianthus annuus* leaves (Gallego *et al*. 1996b), *Phaseolus vulgaris* (Chaoui *et al*. 1997b), *Phaseolus aureus* (Shaw 1995), *Pisum sativum* (Dalurzo *et al*. 1997), *Lemna minor* (Mohan and Hossetti 1997), *Amaranthus lividus* (Bhattacharjee 1998), *Glycine max* roots (Balestrasse *et al*. 2001), *Phragmites australis* (Iannelli *et al*. 2002), *Capsicum annuum* (Leon *et al*. 2002) and *Arabidopsis thaliana* (Cho and Seo 2005) under Cd stress conditions. A significant decline in CAT activity was reported after 50 μM Cd applications for 48 hours in the roots and shoots of *Bacopa monnieri* (Singh *et al*. 2006). However, CAT activity increased in *Agropyron repens* (Brej 1998), *Helianthus annus* (Gallego *et al*. 1999), *Glycine max* nodules (Balestrasse *et al*. 2001), *Oryza sativa* leaves (Hsu and Kao 2004), in tolerant varieties of *Solanum tuberosum* (Stroinski and Kozlowska 1997), in roots of *Raphanus sativus* seedlings (Vitoria *et al*. 2001), *Brassica juncea* (Mobin and Khan 2007), *Triticum aestivum* (Khan *et al*. 2007), *Vigna mungo* roots (Singh *et al*. 2008) and *Cicer arietinum* (Hasan *et al*. 2008). Azpilicueta *et al*. (2007) reported that incubation of *Helianthus annuus* leaf discs with 300 and 500 μM $CdCl_2$ under light conditions increased *CATA3* transcript level but this transcript was not induced by Cd in etiolated plants. Moreover, in roots of the transgenic CAT-deficient tobacco lines (*CAT 1AS*), the DNA damage induced by Cd was higher than in wild type tobacco (*SR 1*) roots (Gichner *et al*. 2004). Furthermore, CAT activity remained unaltered under Cd stress in *Glycine max* leaves (Ferreira *et al*. 2002).

APX (EC 1.11.1.11) is a heme protein, and its primary function is the rapid removal of H_2O_2 at the site of generation (Asada 1992). APX isozymes are distributed in at least four distinct cell compartments, the stroma (sAPX), thylakoid membrane (tAPX), the mitochondria (mAPX), and the cytosol (cAPX) (Asada 1992; Miyake and Asada 1992; Ishikawa *et al*. 1998). The various isoforms of APX respond differentially to metabolic and environmental signals (Kubo *et al*. 2000). Thylakoid membrane-bound APX is limiting factor of antioxidant systems under photo-oxidative stress in chloroplasts and the enhanced tAPX activity maintain the redox status of ascorbate under stress conditions (Yabuta *et al*. 2002). Chloroplasts contain APX in two isoforms, thylakoid-bound and soluble stromal enzymes. At least one half of the chloroplastic APX is tAPX, but the ratio of tAPX/sAPX varies according to the plant species, possibly, leaf age, but the biosynthetic ratio of the two APXs is controlled by alternative splicing (Asada 1999). Thylakoid membrane APX bind to the stroma thylakoids where the PSI complex is located, while sAPX is thought to be localized in the stroma (Asada 1999). Plants also contain the cytosolic isoforms of APX (cAPX), which has a different amino acid sequence in comparison to chloroplastic APXs, but participate in the scavenging of H_2O_2 in compartments other than chloroplasts. Chlorolastic APX is a homodimer and its electron donor is not so specific for ascorbate, unlike tAPX and sAPX (Asada 1999).

APX has an important role in the scavenging of H_2O_2 under stressed conditions but its activity depends on the Cd concentration applied. Increased leaf APX activity under Cd stress has been reported in *Ceratophyllum demersum* (Arvind and Prasad 2003), *Brassica juncea* (Mobin and Khan 2007), *Pisum sativum* (Romero-Puertas *et al*. 1999), *Phaseolus aureus* (Shaw 1995), *Phaseolus vulgaris* (Chaoui *et al*. 1997b), *Zea mays* (Krantev *et al*. 2008), *Triticum aestivum* (Khan *et al*. 2007), *Vigna mungo* (Singh *et al*. 2008a) and *Brassica campestris* (Anjum *et al*. 2008a), however, in *Hordeum vulgare* roots the APX activity was reduced at high concentration of Cd (Hegedus *et al*. 2001). Balestrasse *et al*. (2001) reported that low Cd levels led to an increased APX activity in *Glycine max* roots and nodules, but the activity decreased with high Cd concentration. The lower APX activity was also noted in *Cucumis sativus* chloroplasts with increasing Cd concentration (Zhang *et al*. 2003). Whereas, Cd induced inhibition of APX activity was also observed in clonal, hydroponically grown *Populus* × *Canescens* (Schutzendubel *et al*. 2002) and *Helianthus annuus* plants (Gallego *et al*. 1996). APX activity in *Ceratophyllum demersum* showed a very high increase in its activity in

Cd+Zn treated plants as compared to Cd or Zn alone, indicating efficient antioxidant and ROS scavenging activities by Zn against Cd induced free radicals and oxidative stress (Aravind and Prasad 2003). Khan *et al.* (2007) also reported increased APX activity in *Triticum aestivum* plants treated with Cd under low Zn levels.

GR (EC 1.6.4.2) is a flavo-protein oxidoreductase, found in both prokaryotes and eukaryotes (Mullineaux and Creissen 1997; Romero-Puertas *et al.* 2006). This enzyme was first reported in eukaryotes and yeast (Meldrum and Tarr 1935) as well as in plants (Conn and Vennesland 1951, Mapson and Goddord 1951). GR maintains the balance between reduced GSH and AsA pools, which in turn maintain cellular redox state (Lascano *et al.* 1999, 2001; Ansel *et al.* 2006; Reddy and Raghavendra 2006; Romero-Puertas *et al.* 2006; Chalapathi Rao and Reddy 2008). The enzyme protein, although synthesized in the cytoplasm, can be targeted to both chloroplast and mitochondria (Mullineaux and Creissen 1997). In higher plants, GR is involved in defence against oxidative stress, whereas GSH plays an important role within the cell system, which includes participation in the AsA-GSH cycle, maintenance of the -SH group and a substrate for GSTs (Noctor *et al.* 2002; Reddy and Raghavendra 2006). GR and GSH play a crucial role in determining the tolerance of a plant during environmental stresses (Chalapathi Rao and Reddy 2008). In almost all the biological functions, GSH is oxidized to GSSG which should be converted back to GSH in plant cell to perform normal physiological functions. Hence, rapid recycling of GSH is more essential rather than synthesis of GSH, which is a highly regulated and ATP requiring process. GR activity increases as part of the defence against Cd-exposure, which is dose-dependent and variable over time (Fornazier *et al.* 2002a). GR activity increased in the presence of Cd in *Phaseolus vulgaris* (Chaoui *et al.* 1997b), *Solanum tuberosum* (Stroinski *et al.* 1999), *Raphanus sativus* (Vitoria *et al.* 2001), *Crotolaria juncea* (Pereira *et al.* 2002), *Glycine max* (Ferreira *et al.* 2002), *Saccharum officinarum* (Fornazier *et al.* 2002b), *Capsicum annuum* (Leon *et al.* 2002), *Arabidopsis thaliana* (Skorzynska-Polit *et al.* 2003/4), *Vigna mungo* (Singh *et al.* 2008), *Triticum aestivum* (Khan *et al.* 2007) and *Brassica juncea* (Mobin and Khan 2007). In *Raphanus sativus*, it exhibited very little variation in the roots and leaves of control plants, indicating a direct correlation with Cd accumulation (Vitoria *et al.* 2001). In *Pisum sativum*, GR activity was enhanced more with 40 µM than with 4 µM Cd (Dixit *et al.* 2001). However, a decrease in GR activity after application of Cd has also been reported for a few plant species such as *Helianthus annuus* (Gallego *et al.* 1996a, 1996b), *Pisum sativum* (Dalurzo *et al.* 1997) and *Solanum tuberosum* (Stroinski and Kozlowska 1997).

MDHAR (EC 1.6.5.4) is a flavin adenin dinucleotide (FAD) enzyme that is present as chloroplastic and cytosolic isozymes which share similar properties. MDHAR exhibits a high specificity for monodehydro asorbate (MDHA) as the electron acceptor, preferring NADH rather than NADPH as the electron donor. Asada (1999) studied the multi-step reduction of FAD in detail. The first step is the reduction of the enzyme-FAD to form a charge transfer complex. The reduced enzyme donates electrons successively to MDHA, producing two molecules of ascorbate *via* a semiquinone form [E-FAD-NADP(P)$^+$]. The disproportionation by photoreduced ferrodoxin (redFd) in the thylakoids is of great importance. Since redFd (reduced ferrodoxin) can reduce MDHA more effectively than NADP$^+$, MDHAR cannot participate in the reduction of MDHA in the thylakoidal scavenging system. Therefore, MDHAR would function at a site where NAD(P)H is available, but redFd is not (Asada 1999).

MDHAR is also located in peroxisomes and mitochondria accompanying APX. MDHAR could remove and scavenge H_2O_2 in these organelles similar to that in chloroplasts, which has escaped from break down by peroxisomal CAT (del Río *et al.* 2002). Schutzendubel *et al.* (2001) have noted enhanced MDHAR activity in Cd-exposed *Pinus sylvestris* and a declined MDHAR activity in Cd-exposed poplar hybrids (*Populus* × *canescens*).

GSTs (EC 2.5.1.18) catalyze the conjugation of tripeptide GSH into a variety of hydrophobic, electrophylic and cytotoxic substrates (Marrs 1996; Hossain *et al.* 2006). Noctor *et al.* (2002) observed that GSTs can remove genotoxic or cytotoxic compounds that have potential to damage or react with genetic material (DNAs and RNAs) and protein. In fact, GSTs can reduce peroxides with the help of GSH and produce scavengers of cytotoxic and genotoxic compounds. An increased GST activity was found in leaves and roots of Cd-exposed *Pisum sativum* plants by Dixit *et al.* (2001) and in roots of *Oryza sativa* and *Phragmites australis* plants (Iannelli *et al.* 2002; Moons 2003).

H_2O_2 can be metabolized by another plant peroxidase-scavenging enzyme called glutathione peroxidase (GPX; EC 1.11.1.9) (Noctor *et al.* 2002). Millar *et al.* (2003) identified a family of seven related proteins in cytosol, chloroplast, mitochondria and endoplasmic reticulum, named AtGPX1-AtGPX7 in *Arabidopsis*. Stress increases GPX activity in cultivars of *Capsicum annuum* plants (Leon *et al.* 2002) but decreases in roots and causes no significant change in the leaves of Cd-exposed *Pisum sativum* plants (Dixit *et al.* 2001).

APX can be distinguished from plant-isolated GPOX (EC 1.11.1.7) in terms of differences in sequences and physiological functions (Chen *et al.* 1992). GPOX decomposes indole-3-acetic acid (IAA) and has a role in the biosynthesis of lignin and defence against pathogens by consuming H_2O_2. GPOX prefers aromatic electron donors such as guaiacol and pyragallol usually oxidizing ascorbate at the rate of around 1% that of guaiacol (Asada 1999).

The activity of GPOX varies considerably depending upon plant species and the concentration of Cd used. It increased in Cd-exposed plants of wheat (Milone *et al.* 2003), *Arabidopsis thaliana* (Cho and Seo 2005) and *Ceratophyllum demersum* (Arvind and Prasad 2003) and decreased in Cd-exposed *Pisum sativum* plants (Sandalio *et al.* 2001). Radotic *et al.* (2000) noted an initial increase in GPOX activity in spruce needles subjected to Cd stress and subsequent Cd-treatments caused a decline in the activity.

Non-enzymatic antioxidant system

All plants can synthesize ascorbate, which can accumulate to millimolar concentrations in both photosynthetic and non-photosynthetic tissues (Foyer *et al.* 1983). AsA is one of the most powerful antioxidants (Noctor and Foyer 1998; Smirnoff *et al.* 2001), reacts directly with OH·, O_2 and $^1O_2$ and reduces H_2O_2 to water *via* APX reaction (Noctor and Foyer 1998). AsA also acts as an electron donor in the regeneration of α-tocopherol. Under physiological conditions it exists mostly in reduced form in leaves and chloroplast and its intracellular concentration can build up to millimolar range (*viz.*, 20 mM in the cytosol and 20-300 mM in the chloroplast stroma) (Foyer and Lelandais 1996). The ability to donate electrons in a wide range of enzymatic and non-enzymatic reactions makes ascorbate the main ROS-detoxifying compound in the aqueous phase. In addition to the importance of AsA in the AsA-GSH cycle, it plays a role in preserving the activities of enzymes that contain prosthetic transition metal ions (Noctor and Foyer 1998). The ascorbate redox system consists of L-ascorbic acid, MDHA and DHA. Both oxidized forms of AsA are relatively unstable in aqueous environments while DHA can be chemically reduced by GSH to AsA (Foyer and Halliwell 1976). Evidence to support the actual role of DHAR, GSH and GR in maintaining the foliar AsA pool has been observed in transformed plants overexpressing GR (Foyer *et al.* 1995). *Nicotiana tabacum* and *Populus* × *Canescens* plants have higher foliar AsA contents and improved tolerance to oxidative stress (Aono *et al.* 1993; Foyer *et al.* 1995). Demirevska-Kepova *et al.* (2006) reported that the content of oxidized ascorbate increased during Cd exposure in *Hordeum vulgare* plants. A decrease in the AsA content in the roots and nodules of *Glycine max* under Cd stress has been observed (Balestrasse *et al.* 2001). Cd also decreases AsA content in *Cucumis sativus* chloroplast and in the leaves of *Arabidopsis thaliana*, *Pisum sativum* and *Brassica campestris* (Zhang *et al.* 2003; Skorzynska-Polit *et al.* 2003/04; Romero-Puertas *et al.* 2007; Anjum *et al.* 2008c), respectively, whereas, it remained unaffected in *Populus* × *Canescens* roots (Schutzendubel *et al.* 2002).

The tripeptide (γ-GluCysGly) GSH plays a central role in several physiological processes, including regulation of sulfate transport, signal transduction, conjugation of metabolites, detoxification of xenobiotics (Xiang *et al.* 2001) and the expression of stress-responsive genes (Mullineaux and Rausch 2005). The reduced form of glutathione, GSH, is an abundant compound in plant tissue that exists interchangeably with the oxidized form, GSSG. GSH is abundant (3-10 mM) in the cytoplasm, nuclei and mitochondria and is the major soluble antioxidant in these cell compartments. GSH has been associated with several growth and development related events in plants, including cell differentiation, cell death and senescence, pathogen resistance and enzymatic regulation (Ogawa 2005; Rausch and Wachter 2005) and its content is affected by S nutrition (Blake-Kalff *et al.* 2000). GSH is the major reservoir of non-protein sulfur. It is the major redox buffer in most aerobic cells, and plays an important role in physiological functions, including redox regulation, conjugation of metabolites, detoxification of xenobiotics and homeostasis and cellular signaling that triggers adaptive responses (Noctor *et al.* 2002; Kopriva and Koprivova 2005). It also plays an indirect role in protecting membranes by maintaining α-tocopherol and zeaxanthin in the reduced state. It can also function directly as a free radical scavenger by reacting with $O_2{\cdot}^{-}$, $^1O_2$ and $OH{\cdot}$. GSH protects proteins against denaturation caused by the oxidation of protein thiol groups under stress. In addition, GSH is a substrate for GPX and GST, which are also involved in the removal of ROS (Noctor *et al.* 2002). GSH is a precursor of PCs, which are crucial in controlling cellular heavy metal concentrations. GSH and its oxidized form, GSSG maintains a redox balance in the cellular compartments. This property of GSH is of great biological importance since it allows fine-tuning of the cellular redox environment under normal conditions and upon onset of stress, and provides the basis for GSH stress signaling. A central nucleophilic Cys residue is responsible for higher reductive potential of GSH. It scavenges cytotoxic H_2O_2, and reacts non-enzymatically with other ROS i.e. $O_2{\cdot}^{-}$, $OH{\cdot}$ and $^1O_2$ (Larson 1988).

The central role of GSH in the antioxidative defence system is due to its ability to regenerate another water soluble antioxidant, AsA, in AsA-GSH cycle (Foyer and Halliwell 1976; Noctor and Foyer 1998). The role of GSH in the antioxidant defence system provides a strong basis for its use as a stress marker. However, the concentration of cellular GSH has a major effect on its antioxidant function and it varies considerably under Cd stress. Furthermore, strong evidence has indicated that an elevated GSH concentration is correlated with the ability of plants to withstand metal-induced oxidative stress (Freeman *et al.* 2004). Xiang *et al.* (2001) observed that plants with low levels of GSH were highly sensitive to even low levels of Cd^{2+} due to limited PC synthesis. The increased demand for GSH can be met by the activation of pathways involved in S assimilation and Cys biosynthesis. Its concentration is controlled by a complex homeostatic mechanism where the availability of S seems to be required (May *et al.* 1998a,b). Manipulation of GSH biosynthesis increases resistance to oxidative stress (Youssefian *et al.* 2001; Sirko *et al.* 2004). It has been observed that upon Cd exposure, one of the main responses observed was the induction of genes involved in S assimilation–reduction and GSH metabolism in the roots of *Arabidopsis* (Herbette *et al.* 2006).

Feed back inhibition of γ-glutamylcysteine synthase (γ-ECS) by GSH has been considered as a fundamental central point for GSH synthesis. *In vitro* studies with the enzymes from tobacco and parsley cells showed that the plant γ-ECS was inhibited by GSH (Noctor and Foyer 1998). Oxidation of GSH to GSSG decreases GSH levels and allows increased γ-ECS activity under stressed conditions (Noctor and Foyer 1998).

Environmental stresses trigger an increase in ROS levels in plants and the response of GSH can be crucial for adaptive responses. Antioxidant activity in the leaves and chloroplast of *Phragmites australis* Trin. (cav.) ex Steudel was associated with a large pool of GSH, protecting the activity of many photosynthetic enzymes against the thiophilic bursting of Cd exerting a direct important protective role in the presence of Cd (Pietrini *et al.* 2003). Increased concentration of GSH has been observed with the increasing Cd concentration in *Pisum sativum* (Gupta *et al.* 2002), romaine lettuce (Maier *et al.* 2003), *Phragmites australis* (Pietrini *et al.* 2003), *Brassica juncea* (Qadir *et al.* 2004), *Pisum sativum* (Metwally *et al.* 2005), *Sedum alfredii* (Sun *et al.* 2007), *Oryza sativa* (Hassan *et al.* 2008). However, decay in GSH content in *Glycine max* roots (Balestrasse *et al.* 2001), *Helianthus annuus* leaves (Gallego *et al.* 1996b), *Zea mays* seedlings (Rauser 1990), *Pisum sativum* (Rueggsegger *et al.* 1990), *Pinus sylvestris* roots (Schutzendubel *et al.* 2001), *Cucumis sativus* chloroplast (Zhang *et al.* 2003), *Populus* × *Canescens* roots (Schutzendubel *et al.* 2002) and *Oryza sativa* leaves (Hsu and Kao 2004) has been reported under Cd stress. Furthermore, unaltered GSH content was observed in the nodules of *Glycine max* (Balestrasse *et al.* 2001). Cd-induced depletion of GSH has been mainly attributed to PC synthesis (Grill *et al.* 1985). PC-heavy metal complexes have been reported to be accumulated in the vacuole of *Nicotiana tabaccum* leaves (Vogelli-Lange and Wagner 1990) and in *Avena sativa*. These complexes have been shown to be transported across the tonoplast (Salt and Rauser 1995). The decline in the levels of GSH might also be attributed to an increased utilization for AsA synthesis or for a direct interaction with Cd (Pietrini *et al.* 2003). The variety of response to Cd-induced oxidative stress is probably related not only to the levels of Cd supplied, but also to the plant species, the age of the plant and duration of the treatment.

CO-ORDINATION OF MINERAL NUTRIENTS (SULFUR AND NITROGEN) IN PLANT GROWTH AND PRODUCTIVITY

The improvement in crop production and quality depend upon a number of plant- soil- and nutrients-associated factors i.e. balanced fertilization, optimization of nutrient replenishment, minimization of nutrient losses to the environment and the concept of co-ordination in action among plant nutrients. Among the plant nutrients, S and N are of great importance and are required by plants for maintaining normal growth and development (Bimbraw 2008; Scherer 2008). Several studies have established regulatory interactions between assimilatory sulfate and nitrate reduction in plants (Rennenberg *et al.* 1979; Reuveny *et al.* 1980; Cacco *et al.* 1983; Brunold and Suter 1984; Haller *et al.* 1986; Takahashi and Saito 1996). The two pathways are very well co-ordinated (Brunold 1993; Hawkesford *et al.* 2006). A deprivation of one leads to a reduction of the metabolism of the other (Reuveny *et al.* 1980; Prosser *et al.* 2001; Hesse *et al.* 2004; Scherer 2008). It has also been established through genetic studies that sulfate reduction is regulated by N nutrition at the transcriptional level (Koprivova *et al.* 2000).

S and N affect enzyme activity in their respective assimilatory pathways (Reuveny *et al.* 1980; Brunold and Suter 1984; Barney and Bush 1985; Bell *et al.* 1995; Ahmad *et al.* 1999). While, N directly affects the photosynthesis efficiency of the plant, S affects the photosynthesis efficiency indirectly by improving the N utilization efficiency of the plants as evident from the relationship between N content and photosynthetic rate in the leaves of S-treated and S-untreated plants (Ahmad and Abdin 2000a,b). It has also been shown in *Hordeum vulgare* that high levels of nitrate and ammonium can induce a high affinity sulfate transporter gene and hence sulfate uptake in N-fed plants suggesting that a N metabolite may affect sulfate transporter gene expression (Vidmar *et al.* 1999).

A positive interaction between S and N results in increased crop productivity (Podlesna and Cacak-Pietrzak 2008). *Brassica* genotypes require higher amounts of S in addition to N for optimum growth and yield (Aulakh *et al.* 1980; Lakkineni and Abrol 1992, 1994; Abdin *et al.* 2003; Aulakh 2003). Application of S along with N lead to enhanced biomass production and increased leaf area as both nutrients are involved in biosynthesis of proteins and several other molecules. N is a basic constituent of proteins and with the increase in the rate of N application, the N availability increases. Similarly, increased S supply increases seed yield with higher protein content. Combined application of S and N promotes the uptake of S and N, which lead to significant enhancement in seed protein and oil content in *Brassica juncea* and *Brassica campestris* (McGrath and Zhao 1996; Ahmad and Abdin 2000; Abdin *et al.* 2003). S and N relationship in terms of crop yield and quality has been established in many studies (Singh and Bairathi 1980; Sachdev and Deb 1990; Lakkineni and Abrol 1992; McGrath and Zhao 1996; Ahmad *et al.* 1998; Fismes *et al.* 2000).

CO-ORDINATION OF MINERAL NUTRIENTS (SULFUR AND NITROGEN) UNDER ENVIRONMENTAL STRESS

Plants have developed strategies resulting in optimal adaptation to environmental resources needed for growth, respiration, and propagation (Rennenberg and Brunold 1994; Brunold *et al.* 1996). Among these adaptations, strategic coordination of macronutrient assimilation, i.e. carbon, nitrogen, phosphorous, water, and sulfur [‘CHONSP’] is especially important, as these pathways are dependent on the varying availability of mineral nutrients and CO_2 and changes in light energy (Hesse *et al.* 2004). The assimilatory pathways interact in the formation of products and are regulated in a coordinated manner to balance macro- and micronutrients in possible synergistic or antagonistic effects (Brunold 1993; Leustek *et al.* 2000; Saito 2000).

As heavy metals can induce essential nutrient deficiency and even decrease the concentration of several macronutrients in plants (Siedlecka 1995), it may be possible to reverse or reduce some of the metal induced negative effects on the plants by optimization of mineral nutrition. Chen and Huerta (1997) showed that S is a critical nutritional factor for reduction of Cd toxicity. These authors observed that negative effects of Cd on growth and photosynthesis are stronger in *Hordeum vulgare* plants supplied with 0.1 mM S than in plants receiving 1 mM S. A positive effect of S nutrition on Cd detoxification in *Beta vulgaris* plants has also been established (Popovik *et al.* 1996). It has been found that at suboptimal S nutrition Cd exposed plants preferably allocate S to PCs synthesis, which may provoke S deficiency (McMahon and Anderson 1998). Probably, the improved S nutrition allows a more adequate plant defence response to Cd and also prevents S deficiency. Good S nutrition diminishes the toxicity of Cd by restoring a new steady state of the GSH level earlier than in plants grown at low S supply (McMahon and Anderson 1998). GSH represents the major pool of non-protein reduced S in plants (Kunert and Foyer 1993) and it accounts only for 2% of the total organic S content in plants ranging from 120 to 380 mmol S kg^{-1} dry matter (McMahon and Anderson 1998; Hawkesford and De Kok 2006; Sun *et al.* 2007; Ernst 2008).

GSH has critical functions aside from its role as a redox buffer. It serves as the first line of defence against the products of oxygen metabolism, ROS, and heavy metals (May *et al.* 1998a, 1998b). El-Shintinawy (1999) showed that exogenous GSH counteracted all retardation effects in soybean seedlings induced by Cd. He provided data to conclude that the dual function of GSH; first, as being an antioxidant and oxy radicals scavenger, it protects chloroplast from oxidative damage by trapping the OH·, secondly as a substrate for PCs synthesis that mainly sequesters and detoxifies excess Cd ions. When both functions are realized, repairing membrane damage and sequestration of Cd are achieved by GSH. The electron transport rate as well as photosynthetic parameters is not disturbed and this results in a photosynthetic performance similar to that in the control plants. The crucial role of plant PCs in Cd detoxification was strongly supported by the investigations on two mutants from *Arabidopsis*, *cad1* and *cad2*, which were deficient in PC and GSH biosynthesis, respectively, and are consequently more sensitive to Cd (Howden *et al.* 1995a, 1995b; Cobbett *et al.* 1998; Cobbett and Goldsbrough 2002). Inouhe *et al.* (2000) found a close relationship between high Cd sensitivity and lack of phytochelatin synthase in the cultured cells of azuki beans. In a recent study, Ranieri *et al.* (2005) reported that the leaves of *Triticum aestivum* exposed the Cd stress was counteracted by PC biosynthesis. Furthermore, Anjum *et al.* (2008c) reported that S supplementation increased the production of GSH content under low level of Cd which protects the *Brassica campestris* plants by improving the growth and photosynthesis.

Pankovic *et al.* (2000) have shown that optimal N supply decreased the inhibitory effects of Cd on photosynthesis of sunflower plants. They studied the effects of Cd on sunflower plants grown at optimal, sub-optimal and supra-optimal N supplies and found the lowest inhibition of photosynthetic activity by Cd at optimal N supply, when an investment in soluble proteins and Rubisco were at their maximum. Higher N supplies did not alleviate the toxic Cd effects; therefore the authors concluded that N nutrition can be manipulated as a means of decreasing Cd phytotoxicity. A proper N supply has positive effects in overcoming the adverse effects caused by Cd toxicity in various crop species (Hassan *et al.* 2006). Research conducted by Hassan *et al.* (2005a) has revealed that different forms of N show differential response in the alleviation of Cd toxicity in *Oryza sativa*. They concluded that among the N forms that improved growth and photosynthetic traits to a large extent was $Ca(NO_3)_2$ followed by NH_4NO_3 and $(NH_4)_2SO_4$. Beside a substantial difference was noted among N forms in their effect on Cd and N uptake $(NH_4)_2SO_4$-fed plants had less Cd and more N uptake than both $Ca(NO_3)_2^-$ and NH_4NO_3-fed plants, suggesting potential antagonist effect between Cd and ammonium-N, and synergist effect between Cd and nitrate-N.

PC biosynthesis is closely dependent on S metabolism (Leustek *et al.* 2000), synthesized from different isoforms of GSH (Grill *et al.* 1985). It is important to note here that GSH with the help of Cys takes part in the biosynthesis of PCs. In plants PCs play a crucial role in Cd detoxification (Howden *et al.* 1995a, 1995b). It complexes cations (Cd^{2+}), and makes them less harmful to plant cells (Weigel and Jager 1980). Expression of genes involved in reductive sulphate assimilation pathway and enzyme activities are stimulated by Cd (Herbette *et al.* 2006; Ernst *et al.* 2008). Cd exposure induces the activity of enzymes (γ-glutamyl-Cys synthatase, γECS and glutathione synthatase, GS) involved in the biosynthesis of GSH. Herbette *et al.* (2006) suggested that plants activate the S assimilation pathway by increasing transcription of related genes to provide an enhanced supply of GSH for PC biosynthesis to cope with Cd toxicity. In addition, when plants encounter reactive oxygen species, GSH is a direct source of electrons for stress mitigation by the enzyme GPX or an indirect means to maintain a reduced pool of AsA, another antioxidant. In fact, the biosynthesis of GSH depends on the linking and the availability of its constituent amino acids Cys, Glu and Gly. The biosynthesis of GSH in plants is well established: two sequential ATP-dependent reactions allow the synthesis of γ-glutamylcysteine (γ-EC) from L-Glu and L-Cys, followed by the formation of Gly to the C-terminal end of γ-EC (Meister 1988). These reactions are catalyzed by γ-ECS and GS (May *et al.* 1998a; Noctor *et al.* 1998). GSH contains three moles of N

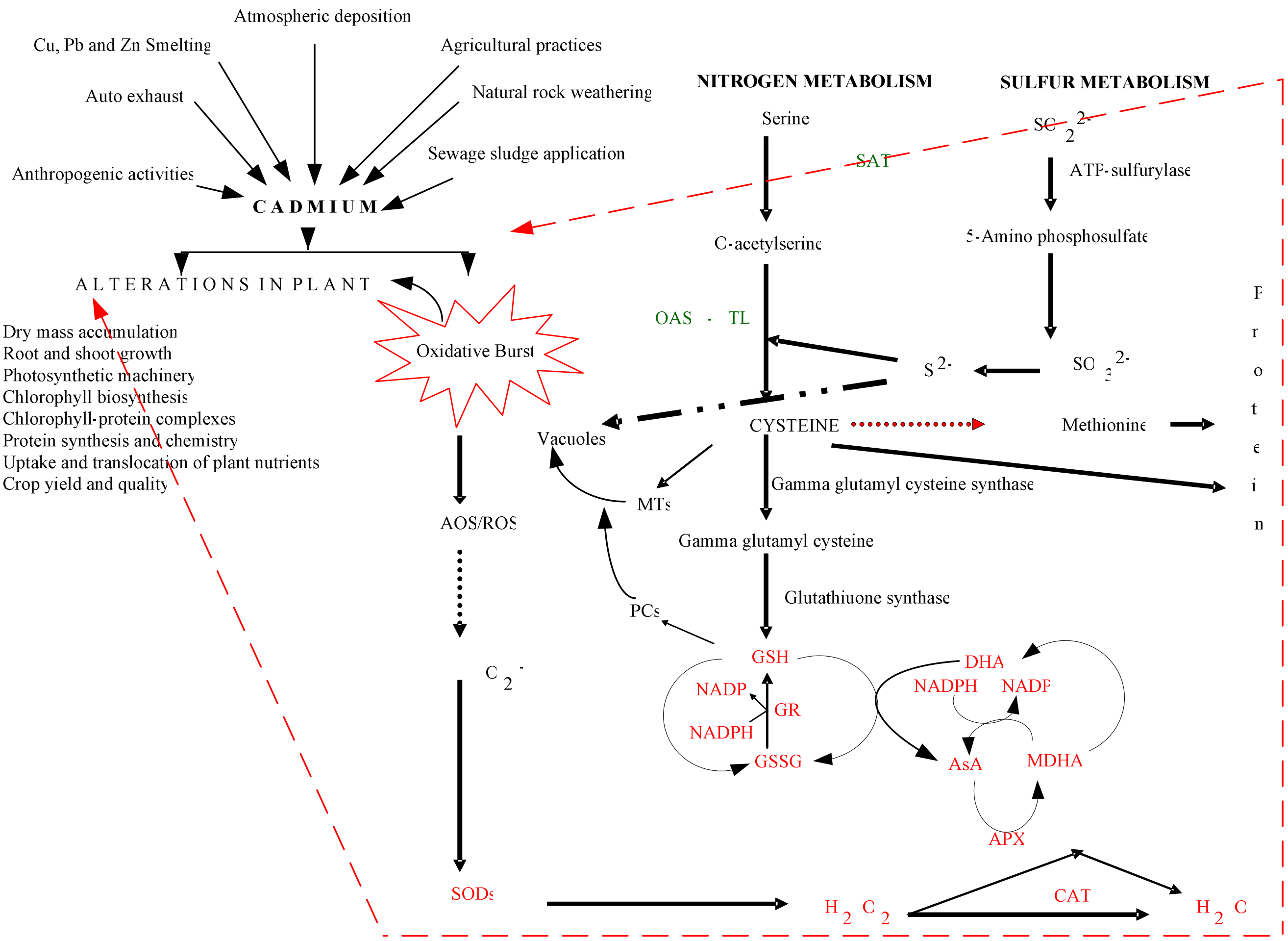

Fig. 1 Summary of sulfur and nitrogen assimilation, glutathione biosynthesis, components of ascrbate-glutathione cycle and their possible links in the control of cadmium-induced alterations and/or oxidative stress in plants. AOS, active oxygen species; ROS, reactive oxygen species; $O_2^{\cdot -}$, superoxide radicals; SODs, superoxide dismutase; H_2O_2, hydrogen peroxide; CAT, catalase; H_2O, water; APX, ascorbate peroxidase; AsA, ascorbic acid; MDHA, monodehydroascorbate; DHA, dehydroascorbate; GSH, glutathione (reduced); GSSG, glutathione (oxidised); GR, glutathione reductase; MTs, metallothioneins; PCs, phytochelatins; OSTHL, oacetylserinethiole lyase.

per mole of S and its GSH biosynthesis may depend on the availability of N precursors and thus N nutrition of plants. However, the sink strength of GSH biosynthesis for N may be low compared with the other major N sinks such as the synthesis of proteins or nucleotides (Kopriva and Rennenberg 2004). The GSH biosynthesis is, therefore, regulated not only by the dependency of Cys availability on S, N and C metabolism, but also on the availability of Glu and Gly. In this way, the co-ordinative functions of S and N may strengthen the stress tolerance ability of plants growing under abiotic stresses (**Fig. 1**).

CONCLUSION

There is a big question to answer that what might be done to decrease the environmental impacts of agriculture while maintaining or improving its productivity, stability, or sustainability? Definitely, this major challenge will have no single, easy solution. Although considerable research efforts has been made to restrict the spread and toxicity of Cd in plants, we have to have sound information regarding understanding the responses of plants to Cd-toxicity effects at physiological and molecular mechanisms, still there is a considerable room for exploring the basis of structural and functional alterations taking place in plant body. Cd toxicity in plants is observed at whole plant as well as at cellular and molecular levels, the importance of which includes perturbation of metabolic pathways. The various negative impact of Cd on plants are: 1) inhibits oxidative mitochondrial phosphorylation, 2) suppresses the elongation growth of plant cell, 3) induces oxidative stress, 4) it can affect the activities of several antioxidative enzymes, 5) affect photosynthesis by damaging photosynthesis apparatus, 6) causes the alteration of chromatin, and 7) modulates the plasma membrane ATPase activity and 8) interfere with uptake and translocation of mineral nutrients. Plants entail certain adaptive mechanisms to cope with these adverse effects of Cd which includes the synthesis of metal binding and chelating proteins and/or by enhancing different components of antioxidant defense system. Increasing evidence also suggests that mineral-nutrient status of plants plays a critical role in increasing plant resistance to environmental stress factors. Of the mineral nutrients, S and N are major macronutrients necessary for the plant life cycle, the two processes the uptake and assimilation of S and N in higher plants are the crucial factors determining plant growth and vigor, crop yield and these nutrients play a particular role in contributing to the survival of crop plants under environmental stress conditions. Sulfate assimilation is an essential pathway being a source of reduced sulfur for various cellular processes and for the synthesis of GSH, a major factor in plant stress-defense. Reports are available on the metabolic control of sulfate uptake and the mediation of further steps by Cys and GHSH and/or low levels of N. The availability of Cys is a crucial factor in GSH synthesis, but an adequate supply of Glu and Gly are also of much importance. It has also been proposed that various environmental and nutritional conditions and compounds act as molecular signals in the regulatory processes of both GSH synthesis and sulfur assimilation in plants. It has been revealed through transcriptome analyses that interactions of S, N, and C metabolism are very complex. A new perspective in this regard must be pointed out so as to dissect the mechanism(s) of regulation of sulfate and nitrate assimilation at the molecular level. The information regarding signaling molecules and pathways is still meager. Although much has been achieved in finding the majority of transcription factor genes responding to S deficiency in plants, identification of some other trans elements, molecular signals, and S-responsive elements like β-conglycinin promoter, would certainly expand our knowledge. Molecular approaches should be narrowed to manipulate sulfate and nitrate assimilatory enzymes such as ATP-sulfurylase, APS-reductase, sulfite reductase and nitrate reductase, glutamine synthetase/glutamate synthase cycle, *O*-acetyl-L-serine-sulfhydrylase, respectively. Strategies should also aim to manipulate steps of pathways leading to the production of thiols and their products in plants through overexpressing Ser acetyl transferase (SAT), γ-ECS and GSHS enzymes in respect to stress physiology. We have much information on PC biosynthesis, but through advanced molecular genetic approaches we must keep in mind the numerous other aspects of PC biosynthesis and function and the ways in which they, too, are regulated at a cellular and physiological level in response to Cd exposure. These include aspects of S assimilation, GSH and sulphide biosynthesis, PC compartmentalization, and the signal pathways through which Cd toxicity leads to gene regulation.

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