



Review article

Chromium toxicity in plants

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Abstract

Due to its wide industrial use, chromium is considered a serious environmental pollutant. Contamination of soil and water by chromium (Cr) is of recent concern. Toxicity of Cr to plants depends on its valence state: Cr(VI) is highly toxic and mobile whereas Cr(III) is less toxic. Since plants lack a specific transport system for Cr, it is taken up by carriers of essential ions such as sulfate or iron. Toxic effects of Cr on plant growth and development include alterations in the germination process as well as in the growth of roots, stems and leaves, which may affect total dry matter production and yield. Cr also causes deleterious effects on plant physiological processes such as photosynthesis, water relations and mineral nutrition. Metabolic alterations by Cr exposure have also been described in plants either by a direct effect on enzymes or other metabolites or by its ability to generate reactive oxygen species which may cause oxidative stress. The potential of plants with the capacity to accumulate or to stabilize Cr compounds for bioremediation of Cr contamination has gained interest in recent years.

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Keywords: Chromium; Toxicity; Plants; Crops; Cr(III); Cr(VI); Photosynthesis; Phytoremediation; Bioremediation; Uptake; Translocation; Reactive Oxygen Species; Oxidative stress; Heavy metals

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1. Introduction

Chromium (Cr) was first discovered in the Siberian red lead ore (crocoite) in 1798 by the French chemist Vauquelin. It is a transition element located in the group VI-B of the periodic table with a ground-state electronic configuration of Ar 3d⁵4s¹. The stable forms of Cr are the trivalent Cr(III) and the hexavalent Cr(VI) species, although there are various other valence states which are unstable and short-lived in biological systems. Cr(VI) is considered the most toxic form of Cr, which usually occurs associated with oxygen as chromate (CrO₄²⁻) or dichromate (Cr₂O₇²⁻) oxyanions. Cr(III) is less mobile, less toxic and is mainly found bound to organic matter in soil and aquatic environments (Becquer et al., 2003). Contamination of soil and ground water due to the use of Cr in various anthropomorphic activities has become a serious source of concern to plant and animal scientists over the past decade.

Cr, in contrast to other toxic trace metals like cadmium, lead, mercury and aluminum, has received little attention from plant scientists. Its complex electronic chemistry has been a major hurdle in unraveling its toxicity mechanism in plants. The impact of Cr contamination in the physiology of plants depends on the metal speciation, which is responsible for its mobilization, subsequent uptake and resultant toxicity in the plant system. Cr toxicity in plants is observed at multiple levels, from reduced yield, through effects on leaf and root growth, to inhibition on enzymatic activities and mutagenesis.

2. Chromium in the environment

Chromium is found in all phases of the environment, including air, water and soil (Table 1). Naturally occurring in soil, Cr ranges from 10 to 50 mg·kg⁻¹ depending on the parental material. In ultramafic soils (serpentine), it can reach up to 125 g·kg⁻¹ (Adriano, 1986). In fresh water, Cr concentrations generally range from 0.1 to 117 µg L⁻¹, whereas values for seawater range from 0.2 to 50 µg L⁻¹. Cr concentration varies widely in the atmosphere, from background concentrations of 5.0×10⁻⁶–1.2×10⁻³ µg·m⁻³ in air samples

from remote areas such as Antarctica and Greenland to 0.015–0.03 µg·m⁻³ in air samples collected over urban areas (Nriagu, 1988). Cr(VI) is a strong oxidant with a high redox potential in the range of 1.33–1.38 eV accounting for a rapid and high generation of ROS and its resultant toxicity (Shanker et al., 2004a,b, in press).

3. Chromium as an environmental contaminant

Cr and its compounds have multifarious industrial uses. They are extensively employed in leather processing and finishing (Nriagu, 1988), in the production of refractory steel, drilling muds, electroplating cleaning agents, catalytic manufacture and in the production of chromic acid and specialty chemicals. Hexavalent chromium compounds are used in industry for metal plating, cooling tower water treatment, hide tanning and, until recently, wood preservation. These anthropogenic activities have led to the widespread contamination that Cr shows in the environment and

Table 1
Chromium concentrations in the environment

Sample type	Concentration
Natural soils	5–1000 mg kg ⁻¹ 5–3000 mg kg ⁻¹ 5–1500 mg kg ⁻¹ 30–300 mg kg ⁻¹ trace to 5.23%
Serpentine soils	634–125,000 mg kg ⁻¹
World soils	200 mg kg ⁻¹ (mean) 100–300 mg kg ⁻¹ 10–150 mg kg ⁻¹ (mean 40 mg kg ⁻¹)
US soils	25–85 mg kg ⁻¹ (mean 37 mg kg ⁻¹) 57 mg kg ⁻¹ (mean)
Canadian soils	100–5000 mg kg ⁻¹ (mean 43 mg kg ⁻¹)
Japanese soils	87 mg kg ⁻¹ (mean)
Swedish soils	74 mg kg ⁻¹ (mean)
Sediments	0–31,000 mg kg ⁻¹
Fresh water	0–117 µg L ⁻¹ (average 9.7 µg L ⁻¹)
Sea water	0–0.5 µg L ⁻¹
Air	1–545,000 ng m ³ 100 ng m ³
Plants	0.006–18 mg kg ⁻¹
Animals	0.03–1.6 mg kg ⁻¹

Modified from Zayed and Terry (2003) with permission.

have increased its bioavailability and biomobility. A detailed review on the critical assessment of Cr in the environment has been published by Kimbrough et al. (1999), Kotas and Stasicka (2000).

The leather industry is the major cause for the high influx of Cr to the biosphere, accounting for 40% of the total industrial use (Barnhart, 1997). In India, about 2000–32,000 tons of elemental Cr annually escape into the environment from tanning industries. Even if the recommended limit for Cr concentration in water are set differently for Cr(III) ($8 \mu\text{g L}^{-1}$) and Cr(VI) ($1 \mu\text{g L}^{-1}$), it ranges from 2 to 5 g/L in the effluents of these industries (Chandra et al., 1997). In the United States, $14.6 \mu\text{g L}^{-1}$ in ground water and $25.9 \text{g} \cdot \text{kg}^{-1}$ in soil have been found in the vicinity of chrome production sites (Zayed and Terry, 2003).

4. Toxic effects of chromium in plants

Chromium compounds are highly toxic to plants and are detrimental to their growth and development. Although some crops are not affected by low Cr concentration ($3.8 \times 10^{-4} \mu\text{M}$) (Huffman and Allaway, 1973a,b), Cr is toxic to most higher plants at $100 \mu\text{M} \cdot \text{kg}^{-1}$ dry weight (Davies et al., 2002). In the following sections, we review several of the metabolic and physiological processes affected by Cr in plants.

4.1. Chromium uptake, translocation and accumulation

The first interaction Cr has with a plant is during its uptake process. Cr is a toxic, nonessential element to plants; hence, they do not possess specific mechanisms for its uptake. Therefore, the uptake of this heavy metal is through carriers used for the uptake of essential metals for plant metabolism. The toxic effects of Cr are primarily dependent

on the metal speciation, which determines its uptake, translocation and accumulation (Fig. 1). The pathway of Cr(VI) transport is an active mechanism involving carriers of essential anions such as sulfate (Cervantes et al., 2001). Fe, S and P are known also to compete with Cr for carrier binding (Wallace et al., 1976).

Uptake and accumulation of Cr by various crops are well documented (Table 2). Independent uptake mechanisms for Cr(VI) and Cr(III) have been reported in barley. The use of metabolic inhibitors diminished Cr(VI) uptake whereas it did not affect Cr(III) uptake, indicating that Cr(VI) uptake depends on metabolic energy and Cr(III) does not (Skeffington et al., 1976). In contrast, an active uptake of both Cr species, slightly higher for Cr(III) than for Cr(VI), was found in the same crop (Ramachandran et al., 1980).

In 7 out of 10 crops analyzed, more Cr accumulated when plants were grown with Cr(VI) than with Cr(III) (Zayed et al., 1998). Skeffington et al. (1976) from radioactive tracer studies using ^{51}Cr reported that Cr mainly moved in the xylem of the plants. Golovatyj et al. (1999) have shown that Cr distribution in crops had a stable character which did not depend on soil properties and concentration of this element; the maximum quantity of element contaminant was always contained in roots and a minimum in the vegetative and reproductive organs. In bean, only 0.1% of the Cr accumulated was found in the seeds as against 98% in the roots (Huffman and Allaway, 1973a). The reason of the high accumulation in roots of the plants could be because Cr is immobilized in the vacuoles of the root cells, thus rendering it less toxic, which may be a natural toxicity response of the plant (Shanker et al., 2004a). Since both Cr(VI) and Cr(III) must cross the endodermis via symplast, the Cr(VI) in cells is probably readily reduced to Cr(III) which is retained in the root cortex cells under low concentration of Cr(VI) which in part explains the lower toxicity of Cr(III) (Fig. 1). Although higher vascular plants

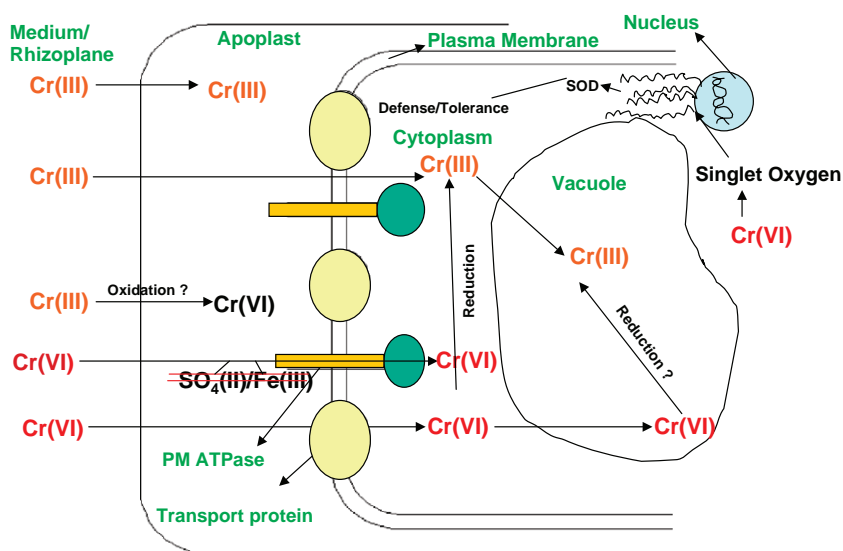


Fig. 1. Hypothetical model of chromium transport and toxicity in plant roots. Details are given in the text.

Table 2
Relationship between chromium concentration in growth medium and its uptake in crops

Cr concentration in medium	Uptake and accumulation pattern	Crop/plant	Reference
0, 5, 30, 45, 60, 75, 90, 105, 120 and 135 mg kg ⁻¹ Cr(III) and Cr(VI)	2.8 Cr(III) and 3.14 Cr(VI) µg g ⁻¹	Spinach	Singh (2001)
0, 5, 10, 20 and 40 ppm Cr(IV)	Progressive increase with more Cr in roots than shoots	Lucerne	Peralta et al. (2001)
Total Cr 1 ppm	10–200 times in roots	<i>Veronica beccabanga</i> and several hydrophytes	Zurayk et al. (2001)
0, 100, 300, 500, 1000 mg kg ⁻¹ Cr(III)	Mobile soil Cr×Plant Cr ($r=0.965$) Total soil Cr×Plant Cr ($r=0.629$)	<i>Medicago sativa</i>	Zlatareva et al. (1999)
50, 100, 200 µM Cr(VI)	Progressive increase with more Cr in roots than shoots	<i>Nelumbo nucifera</i>	Vajpayee et al. (1999)
6, 12, 24 mg L ⁻¹ Cr	Cr more in roots than shoots in A and more in shoots than roots in B	A: <i>Dactylis glomerata</i> B: <i>Medicago sativa</i>	Shanker (2003)
1 mg L ⁻¹ for 10 days Cr	Shoot: 44 mg kg ⁻¹ DW Root: 2980 mg kg ⁻¹ DW	Smart weed	Jin-Hong et al. (1999)
0.5, 1, 5, 25 µg mL ⁻¹ ⁵¹ Cr radio-labelled	Progressive increase with more Cr in roots than shoots	Rice	Mishra et al. (1997)
0, 50, 100 mg L ⁻¹ Cr(III)	roots took up more than shoots and not detected in fruits	Tomato	Moral et al. (1996)
0–200 mg kg ⁻¹	Progressive increase with more Cr in roots than shoots	Sunflower, maize and <i>Vicia faba</i>	Kocik and Ilavsky (1994)
0.25 and 1.0 mg L ⁻¹ L	75–100% steady state removal; 1–2 mg kg ⁻¹ DW at the rate of 250–667 mg day ⁻¹ m ²	<i>Lemna minor</i>	Wahaab et al. (1995)
Tannery effluent	Progressive increase with more Cr in roots than shoots, 38 ppm accumulation	<i>Eichornia crassipes</i>	Singaram (1994)
Tannery effluent 10 ppm r	38–50% removal of Cr 105–156 µg g ⁻¹ accumulation	<i>Hydrilla verticiliata</i> <i>Eichornia crassipes</i>	Vajpayee et al. (1995) Saltabas and Akcin (1994)
0, 5, 50, 150 and 300 µg mL ⁻¹ Cr(III) and Cr(VI)	70–90% accumulation in roots	<i>Allium cepa</i>	Srivastava et al. (1994)
Tannery effluent 5%, 10% and 15% 0, 2, 4, 6, 8 mg L ⁻¹	High Cr removal from 10% and 15% 6700 mg kg ⁻¹ in roots	Swiss Chard <i>Veronica beccabanga</i>	Grubinger et al. (1994) Zurayk et al. (2001)
0, 100, 500 Cr(VI) and Cr(VI)	2.4 mg kg ⁻¹ shoot and 115.6 mg kg ⁻¹ in root in A 5.8 mg kg ⁻¹ shoot and 212 mg kg ⁻¹ in root in B	A: sorghum B: sunflower	Shahandeh and Hossner, 2000a
19.2 µM Cr(VI) and 19.2 µM Cr(III)	350 mg kg ⁻¹ roots and 2 mg kg ⁻¹ shoots	Cauliflower, kale, and cabbage	Zayed et al. (1998)
0, 0.05, 0.10, 0.50, 1.00 and 5.00 ppm	11.9–32.8 ppm in tops	Soybean	Turner and Rust (1971)
0, 0.2, 2 and 10 ppm total Cr	Progressive increase with increase in C concentration	Cabbage	Hara and Sonoda (1979)

do not contain Cr(VI)-reducing enzymes, they have been widely reported in bacteria and fungi (Cervantes et al., 2001).

4.2. Growth and development

Plant growth and development are essential processes of life and propagation of the species. They are continuous and mainly depend on external resources present in soil and air. Growth is chiefly expressed as a function of genotype and environment, which consists of external growth factors and internal growth factors. Presence of Cr in the external environment leads to changes in the growth and development pattern of the plant. These effects are summarized in Table 3.

4.2.1. Germination

Since seed germination is the first physiological process affected by Cr, the ability of a seed to germinate in a

medium containing Cr would be indicative of its level of tolerance to this metal (Peralta et al., 2001). Seed germination of the weed *Echinochloa colona* was reduced to 25% with 200 µM Cr (Rout et al., 2000). High levels (500 ppm) of hexavalent Cr in soil reduced germination up to 48% in the bush bean *Phaseolus vulgaris* (Parr and Taylor, 1982). Peralta et al. (2001) found that 40 ppm of Cr(VI) reduced by 23% the ability of seeds of lucerne (*Medicago sativa* cv. Malone) to germinate and grow in the contaminated medium. Reductions of 32–57% in sugarcane bud germination were observed with 20 and 80 ppm Cr, respectively (Jain et al., 2000).

The reduced germination of seeds under Cr stress could be a depressive effect of Cr on the activity of amylases and on the subsequent transport of sugars to the embryo axes (Zeid, 2001). Protease activity, on the other hand, increases with the Cr treatment, which could also contribute to the reduction in germination of Cr-treated seeds (Zeid, 2001).

Table 3
Effects of chromium on plant growth and development

Process	Crop/plant	Effects	References
Germination	<i>E. colona</i> , bush bean, lucerne, mung bean, sugarcane	Reduced germination percentage and reduced bud sprouting	Rout et al. (2000), Peralta et al. (2001), Parr and Taylor (1982), Jain et al. (2000), Corradi et al. (1993)
Root growth	<i>Salix viminalis</i> , <i>Caesalpinia pulcherrima</i> , mung bean, rice, sorghum	Decrease in root length and dry weight, increase in root diameter and root hairs, proportional variations in cortical and pith tissue layers	Prasad et al. (2001), Iqbal et al. (2001), Panda and Patra (2000), Suseela et al. (2002) Shanker (2003)
Shoot growth	Oats, <i>Curcuma sativa</i> , <i>Lactuca sativa</i> , <i>Panicum miliaceum</i> , <i>Sinapsis alba</i>	Reduction in plant height	Anderson et al. (1972), Joseph et al. (1995), Barton et al. (2000), Sharma and Sharma (1993), Hanus and Tomas (1993), Mei et al. (2002)
Leaf growth	<i>Albizia lebbek</i> , <i>Acacia holocericra</i> , <i>Leucaena leucocephala</i> , rice, bush bean	Reduction in leaf number leaf area and biomass. Trifoliolate leaves more affected than primary leaf in legumes; scorching of leaf tip, negative effect on leaf mesostructure	Sharma and Sharma (1993), Tripathi et al. (1999), Barcelo et al. (1985), Karunyal et al. (1994), Pochenrieder et al. (1993), Shanker (2003)
Yield and dry matter production	<i>Portulaca oleracea</i> , cauliflower, cabbage, radish, bush bean, maize, finger millet, faba beans	up to 50% reduction in yield, reduced number of flowers per plant, reduced grain weight, increased seed deformity, reduced pod weight	Vajpayee et al. (2001), Zurayk et al. (2001), Chatterjee and Chatterjee, 2000, Biacs et al. (1995), Jetly and Srivastava (1995), McGrath (1982)

4.2.2. Root growth

Decrease in root growth is a well-documented effect due to heavy metals in trees and crops (Breckle, 1991; Goldbold and Kettner, 1991; Tang et al., 2001) (Table 3). Prasad et al. (2001) reported that the order of metal toxicity to new root primordia in *Salix viminalis* is Cd>Cr>Pb, whereas root length was more affected by Cr than by other heavy metals studied. Root length and dry weight of the important arid tree *Caesalpinia pulcherrima* was inhibited by 100 ppm Cr (Iqbal et al., 2001). Total root weight and root length of wheat was affected by 20 mg Cr(VI) kg⁻¹ soil as K₂Cr₂O₇ (Chen et al., 2001). Panda and Patra (2000) found that 1 μM of Cr increased the root length in seedlings growing under nitrogen (N) nutrition levels; higher Cr concentrations decreased root length in all the N treatments. Samantaray et al. (1999), in a study with chromite mine spoil soil in five cultivars of mung bean, noted that root growth was significantly affected 28 days after root emergence.

Scanning electron microscope studies of roots affected by Cr showed increased growth of root hairs and increased relative proportion of pith and cortical tissue layers (Suseela et al., 2002). General response of decreased root growth due to Cr toxicity could be due to inhibition of root cell division/root elongation or to the extension of cell cycle in the roots. Under high concentrations of both the Cr species combination, the reduction in root growth could be due to the direct contact of seedlings roots with Cr in the medium causing a collapse and subsequent inability of the roots to absorb water from the medium (Barcelo et al., 1986).

4.2.3. Stem growth

Adverse effects of Cr on plant height and shoot growth have been reported (Rout et al., 1997). When Cr was added at 2, 10 and 25 ppm to nutrient solutions in sand cultures in

oats, Anderson et al. (1972) observed 11%, 22% and 41% reduction in plant height, respectively, over control. Reduction in plant height due to Cr(VI) on *Curcumas sativus*, *Lactuca sativa* and *Panicum miliaceum* was reported by Joseph et al. (1995). Barton et al. (2000) observed that Cr(III) addition inhibited shoot growth in lucerne cultures. Sharma and Sharma (1993) reported that after 32 and 96 days, plant height reduced significantly in wheat cv. UP 2003 in a glasshouse trial when sown in sand with 0.5 μM sodium dichromate. There was a significant reduction in plant height in *Sinapsis alba* when Cr was given at the rates of 200 or 400 mg kg⁻¹ soil along with N, P, K and S fertilizers (Hanus and Tomas, 1993). The reduction in plant height might be mainly due to the reduced root growth and consequent lesser nutrients and water transport to the above parts of the plant. In addition to this, Cr transport to the aerial part of the plant can have a direct impact on cellular metabolism of shoots contributing to the reduction in plant height.

4.2.4. Leaf growth

Leaf growth, area development and total leaf number decisively determine the yield of crops (Table 3). Leaf number per plant reduced by 50% in wheat when 0.5 mM Cr was added in nutrient solution (Sharma and Sharma, 1993). Tripathi et al. (1999) found that leaf area and biomass of *Albizia lebbek* seedlings was severely affected by a high concentration (200 ppm) of Cr(VI). These authors noted that leaf growth traits might serve as suitable bioindicators of heavy metal pollution and in the selection of resistant species. Primary and trifoliolate leaves of bush bean plants grown in 1–10 μg cm⁻³ Cr showed a marked decrease in leaf area; trifoliolate leaves were more affected by Cr than the primary leaves (Barcelo et al., 1985). Dry leaf yield of bush

bean plants was found to decrease up to 45% when 100 ppm of Cr(VI) was added to soil (Wallace et al., 1976). Karunyal et al. (1994) studied the effect of tannery effluent on leaf area and biomass and reported that all the concentrations tested decreased leaf area and leaf dry weight in *Oryza sativa*, *Acacia holosericea* and *Leucaena leucocephala*.

In a study on the effect of Cr(III) and Cr(VI) on spinach, Singh (2001) reported that Cr applied at 60 mg kg⁻¹ and higher levels reduced the leaf size, caused burning of leaf tips or margin and slowed leaf growth rate. Jain et al. (2000) observed leaf chlorosis at 40 ppm Cr that turned to necrosis at 80 ppm Cr. In a study with several heavy metals, Pedreno et al. (1997) found that Cr had a pronounced effect on leaf growth and preferentially affected young leaves in tomato plants. Reduction in leaf biomass was correlated with the oxalate acid extractable Cr in *P. vulgaris* by Poschenrieder et al. (1993).

4.2.5. Total dry matter production

The first prerequisite for higher yields in plants is an increase in biomass production in terms of dry matter. Carbon compounds account for 80–90% of the total dry matter produced by plants. Higher source size and increased photosynthetic process was found to be the basis for the building up of organic substances and dry matter production under heavy-metal stress in general and Cr in particular (Bishnoi et al., 1993a,b) (Table 3).

In a study conducted on *Vallisneria spiralis* to evaluate the Cr accumulation and toxicity in relation to biomass production, it was found that dry matter production was severely affected by Cr(VI) concentrations above 2.5 µg mL⁻¹ in nutrient medium (Vajpayee et al., 2001). Zurayk et al. (2001) reported that salinity and Cr(VI) interaction caused a significant decrease in the dry biomass accumulation of *Portulaca oleracea*. Cauliflower (cv. Maghi) when cultivated at 0.5 mM Cr(VI) restricted dry biomass (Chatterjee and Chatterjee, 2000). Kocik and Ilavsky (1994) studied the effect of Cr on quality and quantity of biomass in sunflower, maize and *Vicia faba* and observed that dry matter production was not markedly affected by 200 mg kg⁻¹ Cr(VI), but uptake of Cr into plant tissue was positively correlated with their contents in the soil. There was a distinct reduction in dry biomass at flowering stage in *S. alba* when Cr(VI) was given at the rates of 200 or 400 mg kg⁻¹ soil along with N, P, K and S fertilizers (Hanus and Tomas, 1993). *P. vulgaris* and maize plants exposed to 1 µM Cr(III) showed higher root and leaf dry weight (DW) than controls, and this increase in DW was more pronounced in Fe-deficient conditions (Barcelo et al., 1993). Cabbage plants water cultured under Cr exhibited a marked reduction in dry weight of whole plant from 88.4 g plant⁻¹ in control to 28.4 g plant⁻¹ in 10 ppm Cr (Hara and Sonoda, 1979).

4.2.6. Yield

Most physiological and biochemical processes are severely affected by Cr, and as a consequence, the yield

and productivity of the crops are equally affected (Barcelo et al., 1993) (Table 3). In pot trials with soil amendment of Cr at the levels of 100 or 300 mg kg⁻¹, Golovatyj et al. (1999) reported reduction in yield of barley and maize. No harvestable yield was obtained where Cr was applied at 270 or 810 kg ha⁻¹ in carrot (Biacs et al., 1995). In wheat the number of flowers per plant decreased by >50% at 0.05 µM Cr compared with the control and even more with 0.5 µM Cr. The number of grains per plant decreased 59% from the control in 0.05 µM Cr. Grain DW was highest in the control and was reduced by 58–92% with increase in Cr level. Tillering was reduced and seed deformities increased with increase in Cr level (Sharma and Sharma, 1993). Sharma and Mehrotra (1993) found that seed DW yield was 2.11 g per plant without Cr, and 0.39 g and 0.16 g with 20 and 200 ppm of Cr, respectively. The effect of Cr on the plant processes during early growth and development culminates in reduction of yield and total dry matter as a consequence of poor production, translocation and partitioning of assimilates to the economic parts of the plant. The negative effect on yield and dry matter is essentially an indirect effect of Cr on plants. The overall adverse effect of Cr on growth and development of plants could be serious impairment of uptake of mineral nutrients and water leading to deficiency in the shoot. In addition, the normal mechanism of selective inorganic nutrient uptake may have been destroyed by oxidative damage, thus permitting larger quantities of Cr(VI) to enter the roots passively and further translocation of Cr(VI) to shoot causing oxidative damage to the photosynthetic and mitochondrial apparatus eventually reflecting in poor growth. In contrast, Cr(III) is kinetically inert to ligand substitution and therefore can form substitution inert metaloprotein complexes in vivo, thus greatly reducing its role in causing toxic symptoms. The toxicity of Cr(III) is reported to be due to indirect effects such as changes in pH and/or inhibition of ion transport.

4.3. Physiological processes

These toxic effects are summarized in Table 4.

4.3.1. Photosynthesis

Chromium stress is one of the important factors that affect photosynthesis in terms of CO₂ fixation, electron transport, photophosphorylation and enzyme activities (Clijsters and Van Assche, 1985) (Table 4). In higher plants and trees, the effect of Cr on photosynthesis is well documented (Foy et al., 1978; Van Assche and Clijsters, 1983). However, it is not well understood to what extent Cr-induced inhibition of photosynthesis is due to disorganization of chloroplast ultrastructure (Vazques et al., 1987), inhibition of electron transport or the influence of Cr on the enzymes of the Calvin cycle. Chromate is used as a Hill reagent by isolated chloroplast (Desmet et al., 1975). The more pronounced effect of Cr(VI) on PS I than on PS II activity in isolated chloroplasts has been reported by Bishnoi

Table 4
Effects of chromium on plant physiology

Process	Crop/plant	Effects	References
Photosynthesis	Wheat, peas, rice, maize, beans, sunflower	Electron transport inhibition, Calvin cycle enzyme inactivation, reduced CO ₂ fixation, chloroplast disorganization	Davies et al. (2002), Bishnoi et al. (1993a,b), Zeid (2001), Shanker (2003)
Water relations	Bush beans, sunflower, mung bean	Decreased water potential, increased transpiration rate, reduced diffusive resistance, wilting, reduction in tracheary vessel diameter	Vazques et al. (1987), Barcelo et al. (1986), Davies et al. (2002)
Mineral nutrition	Soybean, tomato, bush bean, sunflower, maize	Uptake of N, P, K, Fe, Mg, Mn, Mo, Zn, Cu, Ca, B affected	Moral et al. (1995, 1996), Khan et al. (2000)
Enzymes and other compounds	<i>Nymphaea alba</i> and various cereals and legumes	Inhibition of assimilatory enzymes, increase activity of ROS scavenging enzymes, changes in glutathione pool, no production of phytochelatins	Vajpayee et al. (2000), Panda and Patra (2000), Barton et al. (2000), Pillay (1994), Samantaray, 2002, Shanker (2003), Jain et al. (2000), Toppi et al. (2002), Bassi et al. (1990), Behra et al. (1999)

et al. (1993a,b) in peas. Nevertheless, in whole plants, both the photosystems were affected. Zeid (2001) observed in peas that Cr at the highest concentration tested (10^{-2} M) decreased photosynthesis drastically. Krupa and Baszynski (1995) explained some hypotheses concerning the possible mechanisms of heavy-metals toxicity on photosynthesis and presented a list of key enzymes of photosynthetic carbon reduction, which were inhibited in heavy-metal treated plants (mainly cereal and legume crops).

It has been noticed that the 40% inhibition of whole plant photosynthesis in 52-day-old plants at 0.1 mM Cr(VI) was further enhanced to 65% and 95% after 76 and 89 days of growth, respectively (Bishnoi et al., 1993a). Disorganization of the chloroplast ultrastructure and inhibition of electron transport processes due to Cr and a diversion of electrons from the electron-donating side of PS I to Cr(VI) is a possible explanation for Cr-induced decrease in photosynthetic rate. It is possible that electrons produced by the photochemical process were not necessarily used for carbon fixation as evidenced by low photosynthetic rate of the Cr-stressed plants. Due to the known oxidative potential of Cr(VI), it is possible that alternative sinks for electrons could have been enhanced by reduction of molecular oxygen (part of Mehler reaction) which in part explains the oxidative stress brought about by Cr(VI). The overall effect of Cr ions on photosynthesis and excitation energy transfer could also be due to Cr(VI)-induced abnormalities in the chloroplast ultrastructure like a poorly developed lamellar system with widely spaced thylakoid and fewer grana (Van Assche and Clijsters, 1983).

Bioaccumulation of Cr and its toxicity to photosynthetic pigments in various crops and trees is well documented (Barcelo et al., 1986; Sharma and Sharma, 1996; Vajpayee et al., 1999) (Table 4). Bera et al. (1999) studied the effect of Cr present in tannery effluent on chloroplast pigment content in mung bean and reported that irrespective of concentration, chlorophyll *a*, chlorophyll *b* and total chlorophyll decreased in 6-day-old mung bean seedlings

as compared to control. Chlorophyll content was high in tolerant calluses in terms of survival under high Cr concentration in a study of Cr and Ni tolerance in *E. colona* (Samantaray et al., 2001). Chlorophyll content decreased as a marked effect of various concentrations of different Cr compounds [Cr(III) and Cr(VI)] in *Triticum aestivum* (Sharma and Sharma, 1996). Cauliflower (cv. Maghi) grown in refined sand with complete nutrition (control) and at 0.5 mM each of Co, Cr and Cu showed drastic decrease in chlorophylls *a* and *b* in leaves in the order Co>Cu>Cr (Chatterjee and Chatterjee, 2000). The influence of 1 and 2 mg L⁻¹ Cr(VI) on *Salvinia minima* decreased chlorophylls *a* and *b* and carotenoid concentrations significantly (Nichols et al., 2000). The decrease in the chlorophyll *a/b* ratio (Shanker, 2003) brought about by Cr indicates that Cr toxicity possibly reduces size of the peripheral part of the antenna complex. The decrease in chlorophyll *b* due to Cr could be due to the destabilization and degradation of the proteins of the peripheral part. The inactivation of enzymes involved in the chlorophyll biosynthetic pathway could also contribute to the general reduction in chlorophyll content in most plants under Cr stress.

4.3.2. Water relations

Wilting of various crops and plant species due to Cr toxicity has been reported (Turner and Rust, 1971), but little information is available on the exact effect of Cr on water relations of higher plants (Table 4). Barcelo et al. (1985) observed a decrease in leaf water potential in Cr treated bean plants. Excess Cr decreased the water potential and transpiration rates and increased diffusive resistance and relative water content in leaves of cauliflower (Chatterjee and Chatterjee, 2000). Decreased turgor and plasmolysis was observed in epidermal and cortical cells of bush bean plants exposed to Cr (Vazques et al., 1987). Toxic levels of Cr in beans were found to decrease tracheary vessel diameter, thereby reducing longitudinal water movement (Vazques et al., 1987). Impaired spatial distribution and

reduced root surface of Cr-stressed plants can lower the capacity of plants to explore the soil surface for water. The significantly higher toxic effect of Cr(VI) in declining the stomatal conductance could be due to the high oxidative potential of Cr(VI), which in turn may be instrumental in damaging the cells and membrane of stomatal guard cells.

4.3.3. Mineral nutrition

Chromium, due to its structural similarity with some essential elements, can affect mineral nutrition of plants in a complex way. Interactions of Cr with uptake and accumulation of other inorganic nutrients have received maximum attention by researchers. Cr(III) and Cr(VI) are taken up by the plants by different mechanisms (Zaccheo et al., 1985). It has been suggested that both species can interfere with uptake of several other ionically similar elements like Fe and S (Skeffington et al., 1976). Nutrient solution with 9.6 μM Cr(VI) decreased the uptake of K, Mg, P, Fe and Mn in roots of soybean (Turner and Rust, 1971). Excess Cr interfered with the uptake of Fe, Mo, P and N (Adriano, 1986). Barcelo et al. (1985) described the inhibition of P, K, Zn, Cu and Fe translocation within the plant parts when bean plants were exposed to Cr in nutrient solutions. Sujatha et al. (1996) reported that tannery effluent irrigation caused micronutrient deficiencies in several agricultural crops.

In soil grown rye grass, the influence of Cr on mineral nutrition was highly variable and depended on the source of Cr and soil properties (Ottabong, 1989a); it was further found that differences in soluble Mn fractions, interactions with P and critical effects on the uptake of Mn, Cu, Zn, Fe and Al were influenced by Cr in rye grass (Ottabong, 1989b). Cr-induced chlorosis was also observed, whereas there was no clear correlation between leaf Fe levels and chlorosis (Ottabong, 1989c). Cr(VI)-induced decrease in Ca, K, Mg, P, B and Cu concentrations in soil-grown soybean tops was observed, but Fe, Mn and Zn uptake was not affected (Turner and Rust, 1971). In non-calcareous soils amended with Cr(III), the translocation of Fe, Zn and Mo to bean plants was decreased (Wallace et al., 1976). In contrast, other workers supplied Cr in the form of Cr(VI), Cr(III) or in the form of tannery waste to soils and found an enhancement of Fe availability and uptake by plants (Cary et al., 1977a,b; Barcelo et al., 1993).

Barcelo et al. (1985) found high correlation between chlorophyll pigments and Fe and Zn uptake in Cr-stressed plants. Moral et al. (1995) reported that the nutrient elements N, P, K, Na, Ca and Mg concentrations in stems and branches were significantly affected by the Cr treatments (50 and 100 mg L^{-1}) in tomato. Later, Moral et al. (1996) conducted a detailed study on the mineral nutrition of tomatoes under Cr stress and noted that Cr had a negative effect on Fe absorption. Competitive interaction between Cr and Cu in the roots, stems and leaves was confirmed. Mn was not clearly affected; B and Cr had synergistic interactions in roots, but an antagonistic effect in the stems and leaves. In the fruits, Cr treatment had no effect on Fe,

Mn, Cu and Zn contents. B increased with Cr concentration in the nutrient solution.

In maize (cv. Ganga 5), the effects of Cr on Fe concentration varied with plant organ and Cr level. Mn and Cu concentrations generally decreased with increasing Cr level, while Zn concentration decreased in leaves and flowers but increased in stem and roots (Sharma and Pant, 1994). In a study on Cr(III)–Fe interaction, Bonet et al. (1991) reported that Cr enhanced growth of both Fe-control and Fe-deficient plants. However, Cr concentration was correlated neither to changes of Mn, P or Fe tissue concentration nor to Cr-induced alterations of the Fe/Mn and P/Fe ratios. The reduction in the uptake of the elements S and Fe could be mainly due to the chemical similarity of these ions in solution. Dual uptake mechanisms have been reported for S, P and K (Shewry and Peterson, 1974). Hence, the competitive binding to common carriers by Cr(VI) could have reduced the uptake of many nutrients. One of the reasons for the decreased uptake of most of the nutrients in Cr-stressed plants could have been because of the inhibition of the activity of plasma membrane H^+ ATPase (Shanker, 2003) (see below). Cr treatment also markedly inhibited the incorporation of P, K, Ca, Mg, Fe, Mn, Zn and Cu in different cellular constituents in 1-year-old West Coast Tall coconut plants growing in pots (Biddappa and Bopaiah, 1989).

The reduction in N, K, P and other elements could be due to the reduced root growth and impaired penetration of the roots into the soil due to Cr toxicity. Khan et al. (2001) observed that threshold values of the concentrations of N, P and K in dry weight of rice plants showed significant decrease at 0.5 ppm Cr. Excess of Cr (0.5 mM) caused a decrease in the concentration of Fe and affected the translocation of P, S, Mn, Zn and Cu from roots to tops (Chatterjee and Chatterjee, 2000) in cauliflower. Total P in sunflower hull was highest with Cr (0.5 ppm) 30 days after flowering (Gupta et al., 2000), whereas Sharma and Sharma (1996) reported that leaf P concentration decreased with 0.25 mM Cr in wheat cv. UP2003. Cr(VI) is actively taken up and is a metabolically driven processes in contrast to Cr(III) which is passively taken up and retained by cation-exchange sites of the cell wall (Shanker et al., 2004a,in press). This in part explains the higher accumulation of Cr(VI) by the plants. In addition, it is known that P and Cr are competitive for surface sites and Fe, S and Mn are also known to compete with Cr for transport binding. Hence, it is possible that Cr effectively competed with these elements to gain rapid entry into the plant system. Poor translocation of Cr to the shoots could be due to sequestration of most of the Cr in the vacuoles of the root cells to render it non-toxic which may be a natural toxicity response of the plant. It must be noted that Cr is a toxic and nonessential element to plants, and hence, the plants may not possess any specific mechanism of transport of Cr.

4.4. Enzymes and other compounds

Chromium stress can induce three possible types of metabolic modification in plants (Table 4): (i) alteration in the production of pigments which are involved in the life sustenance of plants (e.g., chlorophyll, anthocyanin) (Boonyapookana et al., 2002); (ii) increased production of metabolites (e.g., glutathione, ascorbic acid) as a direct response to Cr stress which may cause damage to the plants (Shanker, 2003); and (iii) alterations in the metabolic pool to channelise the production of new biochemically related metabolites which may confer resistance or tolerance to Cr stress (e.g., phytochelatin, histidine) (Schmöger, 2001).

4.4.1. Nitrate reductase

Nitrate reductase (NR) activity of leaves was significantly increased over control values and negatively correlated with root and shoot length, leaf area and biomass of the plants, indicating stress due to Cr(VI) in *A. lebbek* (Tripathi et al., 1999). Cr concentrations up to 200 μM resulted in significant inhibition of NR activity in *Nelumbo nucifera* (Vajpayee et al., 1999) and *Nymphaea alba* (Vajpayee et al., 2000). Seedlings treated with 1 μM Cr resulted in increased NR activity, whereas higher Cr concentrations were toxic and reduced the enzyme activity significantly in wheat (Panda and Patra, 2000).

4.4.2. Root Fe(III) reductase

Chlorosis induced by heavy metals has been generally correlated with low plant Fe content, suggesting effects on Fe mobilisation and uptake. Under Fe-deficient conditions, dicotyledonous plants enhanced root Fe(III) reductase activity, thus increasing the capacity to reduce Fe(III) to Fe(II), the form in which roots absorb Fe (Alcantara et al., 1994). Cr is reported to affect Fe uptake in dicots either by inhibiting reduction of Fe(III) to Fe(II) or by competing with Fe(II) at the site of absorption (Shanker, 2004). Chromium application to iron-deficient *Plantago lanceolata* roots increased the activity of root-associated Fe(III) reductase. This effect was evident only with acceptors of the turbo reductase and was not observed in iron-sufficient plants (Wolfgang, 1996). In split-root experiments, which allowed only a part of the root system to receive Cr while the other portion was grown in iron-free medium, roots subjected to either treatment showed an intermediate FeEDTA reductase activity with respect to non-split control plants (Wolfgang, 1996). The addition of Cr(III) at 2 μM slightly inhibited ferric chelate reductase in roots of plants grown under iron-limited conditions; Cr(III) at 10 μM stimulated ferric chelate reductase in roots from both iron-limited and iron-sufficient media (Barton et al., 2000).

4.4.3. Plasma membrane H^+ ATPase

ATPase plays a significant role in the adaptation to heavy-metal conditions and it is regulated at the molecular and biochemical level (Dietz et al., 2001). A

toxic effect of Cr on the transport activities of plant cell plasma membrane was suggested by Zaccheo et al. (1982). After a short-term exposure to 2 μM Cr(VI), a strong inhibition of both H^+ and K^+ uptake in maize root segments was observed, while the transmembrane electric potential was unchanged (Zaccheo et al., 1985). Pillay (1994) found that ATPase activity increased at higher treatment concentrations in a study on the effects of soil Cr treatment on different metabolites and certain enzymes of *Helianthus suaveolens* and *Helianthus annuus* leaves. The inhibition of ATPase activity could be due to disruption of the membrane because of free radical formation. The decrease in ATPase activity causes a decrease in proton extrusion. This in turn could cause a decrease in the transport activities of the root plasma membrane, thus reducing the uptake of most nutrient elements. It is also possible that Cr interfered with the mechanism controlling the intracellular pH; this possibility is supported by the fact that Cr could be reduced in the cells thereby utilizing the protons (Zaccheo et al., 1985).

4.4.4. Antioxidant enzymes

Induction and activation of superoxide dismutase (SOD) and of antioxidant catalase are some of the major metal detoxification mechanisms in plants (Prasad, 1998; Shanker et al., 2003a). Gwozdz et al. (1997) found that at lower heavy metal concentrations, activity of antioxidant enzymes increased, whereas at higher concentrations, the SOD activity did not increase further and catalase activity decreased. Pea plants exposed to environmentally relevant (20 μM) and acute (200 μM) concentrations of Cr(VI) for 7 days affected total SOD activity of root mitochondria differently. At 20 μM Cr(VI), SOD activity was found to increase by 29%, whereas 200 μM Cr(VI) produced a significant inhibition (Dixit et al., 2002). A decline in the specific activity of catalase with increase in Cr concentration from 20 to 80 ppm was observed (Jain et al., 2000). Excess of Cr (0.5 mM) restricted the activity of catalase in leaves of cauliflower (Chatterjee and Chatterjee, 2000). H_2O_2 levels increased in both roots and leaves of sorghum treated with either 50 μM Cr(VI) or 100 μM Cr(III) (Fig. 2a; Table 4). A similar increase in lipid peroxidation, in terms of malondialdehyde formation, was observed with these treatments (Fig. 2b).

In *E. colona* plants supplemented with Cr at 1.5 mg L^{-1} , activities of peroxidase and catalase were higher in tolerant calluses than in non-tolerant ones (Samantaray et al., 2001). Samantaray et al. (1999) used peroxidase and catalase activities as enzyme markers for identifying Cr tolerant mung bean cultivars. In wheat cultivar cv. UP2003, the application of 0.05–0.5 mM Cr decreased activities of both enzymes (Sharma and Sharma, 1996). Sen et al. (1994) observed a decrease in catalase activity and increase in peroxidase activity at concentrations above 10 μg L^{-1} Cr(VI), whereas the enzyme activities

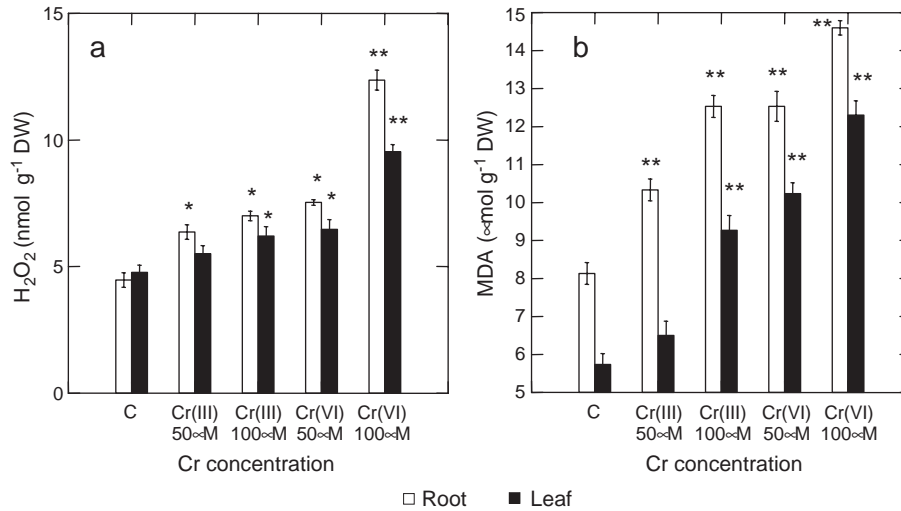


Fig. 2. Levels of H₂O₂ (a) and lipid peroxidation expressed as malondialdehyde (MDA) (b) in roots and leaves of sorghum treated with indicated concentrations of Cr(III) and Cr(VI). Data from Shanker and Pathmanabhan (2004).

were least affected by Cr(VI) at lower concentrations. The calli derived from *L. leucocephala* growing on contaminated soil when supplemented with 15 μM Cr exhibited higher catalase and peroxidase activities than those from the uncontaminated soil. This provided evidence that plant material from contaminated sources were physiologically distinct from the uncontaminated ones (Rout et al., 1999). The increase in antioxidant enzymes activity observed might have been in direct response to the generation of superoxide radical by Cr-induced blockage of the electron transport chain in the mitochondria. The higher increase noticed due to Cr(VI) indicated that Cr(VI) addition probably generates more singlet oxygen than Cr(III). The decrease in the activity of the enzyme as the concentration of the external Cr increased might be because of the inhibitory effect of Cr ions on the enzyme system itself.

4.4.5. Glutathione

Stimulation of reduced glutathione (GSH) biosynthesis was observed under stress conditions in poplar trees (Noctor et al., 1998). Toppi et al. (2002) reported that GSH levels ranged from about 30 nM SH g⁻¹ fresh weight (FW) of root extracts to 300 nM SH g⁻¹ FW of leaf extracts in maize, tomato and cauliflower plants following a Cr(VI) treatment at concentrations of 5 and 10 mg L⁻¹, these were higher than control levels. Glutathione pool dynamics of sorghum was affected, in terms of GSH and GSSG and the GSH/GSSG ratio, by Cr speciation stress (Fig. 3; Table 4), indicating that there is a possible role of this pathway in countering Cr stress (Shanker and Pathmanabhan, 2004). There was a marked decline in the GSH pool under Cr speciation stress more severely in roots (Fig. 3). Several authors have observed oxidation of different cellular thiols such as GSH and cysteine by Cr(VI) in in vitro studies

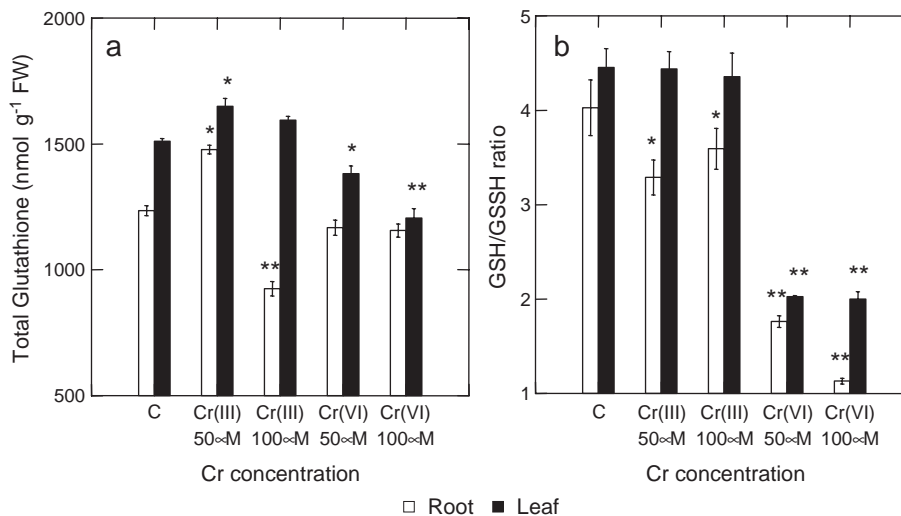


Fig. 3. Levels of total glutathione (a) and GSH/GSSG ratio (b) in roots and leaves of sorghum treated with indicated concentrations of Cr(III) and Cr(VI). Data from Shanker and Pathmanabhan (2004).

(McAuley and Olatunji, 1977a,b). Dichromate reacts with GSH at the sulfhydryl group forming an unstable glutathione–CrO₃⁻ complex (Brauer and Wetterhahn, 1991). Thiolate complexes of Cr(VI) with γ -glutamylcysteine, *N*-acetylcysteine and cysteine have also been described (Brauer et al., 1996). The interconversion of reduced and oxidised forms of glutathione to maintain redox status of the cell as well as to scavenge free radicals could have caused a decrease in GSH. Metal-binding peptides like metallothionein have been reported to have increased under Cr(VI) stress (Shanker et al., 2004b).

5. Cr plant tolerance and phytoremediation

Literature survey shows that very few workers have reported ameliorative measures for Cr toxicity in crop plants. This is largely due the reason that most of the research has been focused on enhancing phytoaccumulation of Cr by plants and trees for its use in phytoremediation. Impaired mineral nutrition due to Cr toxicity has been corrected by the application of mycorrhizal inoculation. Khan (2001) reported the potential of mycorrhizae in protecting tree species *Populus euroamericana*, *Acacia arabica* and *Dalbergia sisso* against the harmful effects of heavy metal and phytoremediation of Cr contamination in tannery effluent-polluted soils. Shanker et al. (in press) have reported the possible use of *Albizia amara* as a potential Cr phytoaccumulator. Karagiannidis and Hadjisavva Zinoviadi (1998) studied the effect of the vesicular arbuscular mycorrhizal fungus (VAMF) *Glomus mosseae* on growth, yield and nutrient uptake of durum wheat and reported that VAMF enhanced yield in wheat and simultaneously decreased the Cr content in the plant. In a study on the effects of Cr on the uptake and distribution of micronutrients (Fe, Mn, Cu and Zn) in mycorrhizal soybean and maize in sand culture, Davies et al. (2001) found that VAMF enhanced the ability of sunflower plants to tolerate Cr; similarly, Davies et al. (2002) reported that VAMF had a positive effect on tissue mineral concentration, growth and gas exchange in Cr-treated plants.

Glutathione and free amino acids are known to induce heavy-metal tolerance by antioxidant action and metal-chelating activity, respectively (Rauser, 1999). Increased S-supply resulted in an overall increase in total S, sulfate and GSH in leaves and tubers of potato. The concentrations of the total free amino acid pools in leaves and tubers showed a two- and threefold decrease, respectively, with increasing S-supply (Hopkins et al., 2000). Hence, it is possible that sulfate and iron supplementation can counter Cr toxicity in crop plants.

The poor translocation of Cr from roots to shoots is a major hurdle in using plants and trees for phytoremediation. Pulford et al. (2001) in a study with temperate trees confirmed that Cr was poorly taken up into the aerial tissues but was held predominantly in the root. These

findings mean that the prospects for using trees as phytoremediators on Cr-contaminated sites are low, their main value being to stabilise and monitor a site (Shanker et al., 2003b). This has led to research with the prospects of increasing Cr translocation by adding chemical and biological amendments to soil. It has been shown that if chromate is reduced to chromic oxide by chemical or biological methods, the inertness and insolubility of chromic oxides in soil limited the formation of chromate and reduced environmental risk (James, 1996). Mycorrhizae and organic acids (citric and oxalic) have been reported to play an important role in phytoremediation of Cr-contaminated soils by enhancing Cr uptake and increasing translocation to shoot (Chen et al., 1994; Davies et al., 2001).

Nutrient culture studies revealed a marked enhancement in uptake and translocation of chelated ⁵¹Cr in *P. vulgaris*. Cr chelated by DTPA was most effectively translocated followed by ⁵¹Cr-EDTA and ⁵¹Cr-EDDHA (Athalye et al., 1995). Significant increases in Cr accumulation from Cr(III)-treated maize plants in the presence of increasing concentrations of organic acid have been observed (Srivastava et al., 1999a). Shahandeh and Hossner (2000b) have reported a high increase in Cr uptake aided by organic acids. Srivastava et al. (1999b) found that increasing concentrations of organic acids resulted in increased uptake of Cr without affecting the distribution in plant parts. Source-to-plant transfer coefficients of Cr tended to increase with increasing concentrations of organic acids in wheat. Chaney et al. (1997) observed that phytostabilization [in situ conversion of Cr(VI) in soil to Cr(III)] appears to have strong promise with respect to chromium.

6. Concluding remarks

Having revised the overall picture of Cr toxicity in plants, it is clear that the species of Cr are toxic at different degrees at different stages of plant growth and development and also that the toxicity is concentration and medium dependent. The toxic properties of Cr(VI) originate from the action of this form itself as an oxidizing agent, as well as from the formation of free radicals during the reduction of Cr(VI) to Cr(III) occurring inside the cell. Cr(III), on the other hand, apart from generating reactive oxygen species (ROS), if present in high concentrations, can cause toxic effects due to its ability to coordinate various organic compounds resulting in inhibition of some metalloenzyme systems. The differential toxicity of these two species can be explained by (i) translocation and partitioning: Cr(VI) is actively taken up by a metabolic driven process, whereas Cr(III) is probably passively taken up and retained by cation exchange sites; in addition, Cr(VI) competes with various elements of similar electronic structure; hence, it seems that Cr(VI) has an advantage at the entry level into the plant system. However, it should be noted that Cr(III) can easily enter

the system if it is organically complexed at the rhizosphere level. (ii) Damage due to ROS production: high concentrations of ROS at cellular level cause oxidative stress which explains most of the visual Cr toxicity symptoms observed at whole plant level. However, under appropriate conditions, H_2O_2 can act as an oxidizing agent and may oxidize Cr(III) to Cr(VI), an endogenous oxidation that cannot be ruled out. On the other hand, Cr(III) can be endogenously reduced to Cr(II) by biological reductants such as cysteine and NADPH. In turn, the newly formed Cr(II) reacts with H_2O_2 producing hydroxyl radicals and causes tissue damage. Thus, one of the future challenges to understand Cr toxicity would be to unravel the complete picture of interconversion of the Cr species within the plant system, after its uptake, on a time course at environmentally relevant concentrations with emphasis at different stages of plant development. (iii) Differential defensive response: the high ROS production by Cr(VI) could set in motion a chain of signaling response at gene expression level which in turn could increase active scavenging. Higher energy allocation for active scavenging could deprive the plant of its quota of energy required for normal growth; furthermore, the absence of heavy-metal sequestering phytochelatin under Cr stress suggests that this scavenging system is more energy intensive. In contrast, a similar scenario under Cr(III) stress would not be envisaged as the oxidizing potential of Cr(III) is less and thus lesser amounts of ROS production and consequently lesser toxicity may be assigned to this Cr species.

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