

Chromium Phytotoxicity on Seed Germination in Selected Vegetable Crops: A Review

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Abstract

Chromium contamination in agricultural soils poses a significant threat to crop productivity and food security worldwide. This review synthesizes current knowledge on the phytotoxic effects of chromium on six economically important vegetable crops: *Solanum melongena* (brinjal/eggplant), *Cucumis melo* L. (melon), *Solanum lycopersicum* (tomato), *Amaranthus cruentus* (amaranth), *Capsicum annuum* Linn. (pepper), and *Abelmoschus esculentus* (okra). The differential toxicity of trivalent chromium (Cr(III)) and hexavalent chromium (Cr(VI)) is examined, with Cr(VI) demonstrating substantially higher phytotoxicity across all species studied. Chromium exposure induces dose-dependent reductions in seed germination percentage, radicle and plumule elongation, and seedling vigor index. The mechanisms of phytotoxicity involve oxidative stress induction through reactive oxygen species (ROS) generation, lipid peroxidation, membrane damage, and disruption of cellular homeostasis. Plants respond through upregulation of antioxidant defense systems, including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR), along with accumulation of osmoprotectants such as proline. Species-specific sensitivity patterns emerge, with *Solanum lycopersicum* and *Abelmoschus esculentus* showing particular vulnerability to chromium stress. Understanding these phytotoxic mechanisms is essential for developing mitigation strategies and breeding chromium-tolerant cultivars to ensure sustainable vegetable production in contaminated environments.

Keywords: Chromium toxicity, seed germination, oxidative stress, antioxidant enzymes, vegetable crops, phytotoxicity, Cr(VI), Cr(III), seedling vigor.

1. Introduction

The contamination of agricultural soils with heavy metals is one of the most serious environmental problems threatening the global food production system. Among toxic heavy metals, chromium (Cr) has become a problematic contaminant in particular because of its widespread use in industry and its persistence in the environment [31], [33]. The chromium contamination is attributed to a number of anthropogenic origins such as leather tanning, electroplating, textile dyeing, wood preservation, and metallurgical industries, with the result of significant build-up in agricultural soils and irrigation water [35], [38].

The phytotoxic effects of chromium on crop plants have received increasing attention of scientists due to the effect on agricultural productivity and food safety. Chromium is found in the environment predominantly in two oxidation states, trivalent chromium (Cr(III)) and hexavalent chromium (Cr(VI)). They differ greatly in their chemical properties, bioavailability, and toxicity [17], [28]. Cr(III) is relatively immobile and less toxic, but Cr(VI) is characterised by high solubility, mobility, and extreme toxicity for biological systems [31], [32]. Vegetable crops are an important source of human

nutrition, providing essential vitamins, minerals and dietary fibre. However, these crops are more vulnerable to chromium toxicity at the critical germination and early seedling establishment stages [30], [34]. The six species discussed here, *Solanum melongena* (brinjal/eggplant), *Cucumis melo* L. (melon), *Solanum lycopersicum* (tomato), *Amaranthus cruentus* (amaranth), *Capsicum annuum* Linn. (pepper) and *Abelmoschus esculentus* (okra) are economically important vegetables cultivated in different parts of the world, notably in areas where chromium contamination is prevalent.

Chromium phytotoxicity is exerted through a number of interrelated mechanisms such as inhibition of seed germination, suppression of root and shoot elongation, reduction of seedling vigour, induction of oxidative stress, disruption of photosynthetic machinery and interference with nutrient uptake and metabolism [29, 38]. At the cellular level, chromium exposure causes the production of excess reactive oxygen species (ROS) and oxidative damage to lipids, proteins and nucleic acids [40], [41]. Plants respond to chromium stress by inducing antioxidant defence mechanisms and accumulating stress-protective compounds, but these responses are very diverse among species and cultivars [16], [41].

This comprehensive review summarises the current experimental evidence of chromium phytotoxicity in the six target vegetable species with special focus on germination parameters, seedling growth characteristics, oxidative stress responses and antioxidant enzyme activities. This review seeks to offer a comprehensive view of chromium-induced phytotoxicity and its implications for sustainable vegetable production in contaminated environments by studying dose-response relationships and comparing the differential toxicity of Cr(III) and Cr(VI).

2. Chromium in the Environment: Sources and Speciation

Chromium is the 7th most abundant element in the Earth's crust, with natural concentrations in soils typically ranging from 10-50 mg/kg [37]. However, anthropogenic activities have caused a significant increase in chromium levels in agricultural ecosystems, with contaminated sites often exceeding levels of 1000 mg/kg [33], [35]. In many developing countries, industrial effluents from leather tanning operations, where chromium salts are used in the preservation of hides, are the single largest source of chromium pollution [31].

The environmental behaviour and biological effects of chromium are largely controlled by the oxidation state of the element. In natural systems, chromium occurs mainly as Cr(III) and Cr(VI), Cr(VI) being thermodynamically unstable but kinetically stable under oxidising conditions [28], [41]. Hexavalent chromium is usually found as chromate (CrO_4^{2-}) or dichromate ($\text{Cr}_2\text{O}_7^{2-}$) oxyanions, which are highly soluble and mobile in soil solutions [17], [31]. However, Cr(III) forms relatively insoluble hydroxides and oxides, especially at neutral to alkaline pH, thus limiting its bioavailability and plant uptake [41].

The transformation of Cr(III) to Cr(VI) in soils is controlled by several factors such as pH, redox potential, organic matter content and microbial activity [36]. Under oxidising conditions, manganese oxides can oxidise Cr(III) to Cr(VI). Cr(VI) can be reduced to Cr(III) in the presence of organic matter, Fe(II) and sulphides [35], [36]. These interconversions are important for chromium bioavailability and phytotoxicity in agricultural systems.

3. Differential Toxicity of Cr(III) and Cr(VI)

Chromium toxicity to plants varies dramatically with its oxidation state. Cr(VI) exhibited consistently much higher phytotoxicity than Cr(III) to a variety of plant species [26], [28], [31]. This difference in toxicity can be attributed to fundamental differences in chemical properties, cellular uptake and intracellular behaviour.

Hexavalent chromium exists as the chromate anion which is similar in structure to sulphate and phosphate and can be taken up by plant roots via sulphate transport systems [32], [41]. This allows transport, resulting in rapid accumulation of Cr(VI) in plant tissues. Cr(VI) is reduced to Cr(III) within cells by reactions with cellular reductants including ascorbate, glutathione, and cysteine, leading to

formation of reactive intermediates (Cr(V) and Cr(IV)) and ROS [40], [41]. These reductive reactions occur mainly in the cytoplasm and organelles and lead to local oxidative damage [38].

Conversely, the low solubility and complex formation with organic ligands in the rhizosphere [17], [41] limit the uptake of Cr(III). However, Cr(III) has lower mobility when taken up by cells of plants and tends to accumulate in root tissues rather than translocate to shoots [12], [19]. Comparative studies have shown that Cr(VI) inhibits germination, growth and physiological processes more than the same concentrations of Cr(III) [26].

Tomato (*Solanum lycopersicum*) exposed to both Cr(III) and Cr(VI) showed significantly higher reductions in growth, biomass and chlorophyll content compared to Cr(VI) at concentrations ranging from 50 to 300 ppm [26]. Similarly, studies on the effects of Cr(III) on tomato showed that germination was promoted at lower concentrations of Cr(III) (100 mg/L), but was inhibited at higher concentrations (>1 g/L) [12]. The findings emphasise the necessity of accounting for chromium speciation when evaluating the phytotoxicity risks and remediation strategies..

4. Mechanisms of Chromium Phytotoxicity

4.1. Oxidative Stress and ROS Generation

Oxidative stress is the primary mechanism of chromium phytotoxicity in plants. Exposure to chromium causes overproduction of ROS, including superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH) and singlet oxygen ($^1\text{O}_2$) that surpass cellular antioxidant defences and cause oxidative damage to macromolecules [40]. Several pathways are involved in ROS production under chromium stress, including destabilisation of electron transport chains in chloroplasts and mitochondria, activation of NADPH oxidases and direct reduction of Cr(VI) to Cr(III) [38].

Reports are available on different plant species indicating significant increase in H_2O_2 and malondialdehyde (MDA) content under chromium stress suggesting increased ROS production and lipid peroxidation [12], [27]. In Cr(VI) exposed chickpea varieties, H_2O_2 production and electrolyte leakage showed significant increase at higher concentrations of chromium indicating dose-dependent oxidative damage [27]. Similarly, pepper (*Capsicum annuum*) seedlings exposed to Cr(VI) up to 100 ppm showed increased stress markers with an 80% increase in MDA over the control [6].

The reduction of Cr(VI) to Cr(III) in the cells of plants is especially problematic since this process generates reactive chromium intermediates (Cr(V), Cr(IV)) that are able to abstract electrons directly from biological molecules, thus initiating chain reactions of oxidative damage [40]. In addition, the reduction process consumes cellular antioxidants such as ascorbate and glutathione, which reduces the reducing power of the cell and increases oxidative stress [8], [21].

4.2. Membrane Damage and Lipid Peroxidation

Lipid peroxidation of cell membranes is a major consequence of chromium-induced oxidative stress. ROS attack polyunsaturated fatty acids in membrane lipids leading to autocatalytic chain reactions that

disrupt membrane integrity and function [40, 41]. Malondialdehyde (MDA) is a product of lipid peroxidation and is often used as a biomarker of oxidative membrane damage.

There are several studies that have reported increased levels of MDA in chromium stressed plants. In *Vigna radiata* (mung bean) seedlings treated with chromium concentrations of 50-200 μM , the lipid peroxidation showed a significant increase with increasing chromium concentration, indicating progressive membrane damage [39]. Similarly, the MDA content in pepper seedlings increased by 80% at 100 ppm Cr(VI) with an increase of 68% in electrolyte leakage, indicating severe membrane disruption [6]. Membrane damage has downstream effects on cellular function including loss of compartmentalisation and disruption of ion homeostasis, impaired nutrient uptake and compromised organellar function [41]. Ultrastructural studies of Cr(III)-treated tomato plants showed considerable damage to chloroplast membranes, less number of grana, abnormal thylakoids and excessive starch accumulation, as well as mitochondrial damage characterised by a decrease in number of cristae [19]. The ultrastructural changes directly affect the photosynthetic and respiratory capacities and thus contribute to the growth inhibition.

4.3. Disruption of Nutrient Uptake and Metabolism

Chromium toxicity affects uptake, translocation and metabolism of vital nutrients and contributes to growth inhibition and physiological dysfunction [14], [31], [34]. Chromium competes for uptake sites on root membranes and for transport proteins with essential elements, leading to nutrient deficiencies even when nutrients are present in the soil at sufficient levels.

Studies on *Solanum lycopersicum* and *Solanum melongena* with chromium concentrations ranging from 0.1 to 75 ppm showed significant reduction in the macronutrients such as nitrogen, phosphorus and potassium [14]. The chromium-induced iron deficiency is especially troublesome because chromium interferes with iron uptake and metabolism, which disrupts chlorophyll biosynthesis and causes chlorosis [24], [31]. In some plant species chromium exposure resulted in a progressive decrease in chlorophyll a, chlorophyll b and total chlorophyll content and the decreases were proportional to the chromium concentration [18], [24], [25].

In addition, chromium affects nitrogen metabolism by inhibiting nitrate reductase activity and disrupting nitrogen assimilation pathways [8], [31]. This disruption interferes with protein synthesis and nitrogen nutrition as a whole and contributes to retardation of growth. Chromium is also involved in carbohydrate metabolism and studies have shown that plants under chromium stress suffer a reduction in reducing sugars, non-reducing sugars and total sugar content [18].

5. Species-by-Species Analysis of Chromium Effects

5.1. *Solanum lycopersicum* (Tomato)

Tomato (*Solanum lycopersicum*) has been a model system for understanding chromium phytotoxicity and a number of studies have indicated its sensitivity to both Cr(III) and Cr(VI) [3, 4, 5, 8, 10, 11, 12, 13, 14, 19, 26].

Germination and Growth Effects: Tomato seed germination is severely inhibited by exposure to chromium and the effects are dependent on the form and concentration of chromium. Studies reported reduced germination percentage and delayed germination in more than 90% of the tomato genotypes tested using Cr(VI) as potassium dichromate ($\text{K}_2\text{Cr}_2\text{O}_7$) at a concentration of 1.5 mM, with half of the genotypes showing reduced seedling survival rates [5]. At lower Cr(VI) concentrations (5 to 1000 mg/L), germination percentages decreased progressively and at 500 and 1000 mg/L, complete inhibition of seedling growth occurred [13].

Comparative studies on the toxicity of Cr(III) and Cr(VI) showed that at the same concentration (50-300 ppm), Cr(VI) has more toxic effect on growth inhibition than Cr(III). Both Cr(III) and Cr(VI) have a concentration-dependent effect [26]. Chromium stress is highly sensitive to elongation of tomato roots and shoots. Hypocotyl and root length was inhibited by exposure to Cr(VI) from 5 mg/L with the effects increasing at higher concentrations [13]. Among eight terrestrial plants tested, tomato was found to be most sensitive to Cr(VI) with no observed effect concentration (NOEC) of Cr(VI) in soil being only 12.0 mg/kg indicating the sensitivity of tomato to chromium [10].

Biochemical and Oxidative Stress Responses: Tomato plants induce antioxidant defence systems and accumulate stress-protective compounds in response to chromium stress. The exogenous application of nitric oxide under Cr(VI) stress enhanced the proline, nitrogen and thiol compound levels and also improved the ascorbate and glutathione content and the GSH: GSSG ratio [8]. Nitric oxide also prevented the build-up of lipid peroxidation products as well as protein carbonylation, but enhanced the activity of hydrolysing enzymes (α -amylase and protease) that are essential for seed germination [8].

Chromium exposure causes oxidative stress with an increase in the accumulation of H_2O_2 and MDA and increase in activity of antioxidant enzymes [12]. Ultrastructural studies showed that Cr(III) was responsible for severe damage of chloroplasts and mitochondria at 25 and 50 mg/L [19]. Chlorophyll content is reduced gradually with the increase in chromium concentration indicating disturbance of biosynthesis of photosynthetic pigments [3], [14]. Studies with chromium contaminated irrigation water (0.1 to 75 ppm) reported 62-84% reduction in plant height, leaf area, number of fruits, weight of fruits and biomass above the plant [14].

5.2. *Solanum melongena* (Brinjal/Eggplant)

Brinjal or aubergine (*Solanum melongena*), a close relative of tomato, is sensitive to chromium toxicity but fewer studies have been done on this species [1], [14].

Germination and Growth Effects: Several experiments on chromium effects on *S. melongena* with polluted irrigation water (0.1 to 75 ppm Cr) showed significant reductions in growth parameters [14]. Chromium application reduced plant height, leaf area, fruit number, fruit weight, fruit yield, dry weight and above plant biomass by 56-77% at different chromium concentrations. Although dramatic, these reductions were somewhat lower than in tomato (62-84%), indicating a slightly higher tolerance of aubergine to chromium [14].

The dose-response relationship in aubergine was similar to tomato with increasing concentrations of chromium causing progressive growth inhibition. Eggplant exhibited the highest inhibition in growth and biomass accumulation at the highest concentration (75 ppm) tested.

Biochemical and Oxidative Stress Markers: Chromium toxicity in egg plant is expressed through similar biochemical mechanism as in tomato such as inhibition of photosynthetic pigments and interference in nutrient metabolism [14]. Photosynthetic pigments levels were reduced sequentially with increase in chromium concentration with 75 ppm treatment exhibiting lowest pigment levels and highest inhibition rates over controls.

The studies on the remedial effects of calcium and sulphur supplementation in chromium stressed eggplant seedlings revealed that these nutrients can alleviate the Cr(VI) toxicity partly through nitric oxide mediated mechanisms [1]. These results suggest that aubergine has inducible defence mechanisms which can be enhanced through nutritional management.

5.3. *Cucumis melo* L. (Melon)

Detailed phytotoxicity studies of chromium on germination and early seedling development of melon (*Cucumis melo* L.) have been carried out [2,7]. Effects on Germination and Growth A detailed study on the toxicity of Cr (III) in melon was carried out using $\text{CrCl}_3 \cdot 6\text{H}_2\text{O}$ at concentrations of 2.5, 5, 10, 25, 50, 75, 100, 200 and 300 mg/L for germination and 2.5, 5, 10, 20, 30, 40, 50, 60 and 70 mg/L for early seedling growth [2]. Germination rate (G-max) decreased in a concentration-dependent manner from 3.6% (10 mg/L) to 44.3% (300 mg/L) relative to controls.

Radicle elongation was particularly sensitive to chromium stress with significant reductions of 14.7% of control at 2.5 mg/L to 58.5% at 70 mg/L [2]. Hypocotyl height was also decreased from 11.4 to 52.7% of controls over the range of concentration from 2.5 to 70 mg/L. The growth tolerance index (GTI), a composite of several growth parameters, declined from 91.59 at 2.5 mg/L to 46.65 at 70 mg/L, showing progressive loss of chromium tolerance with increased exposure [2].

These results show that even relatively low concentrations of chromium (2.5 mg/L) cause measurable growth inhibition in melon, and that the effects are more pronounced at higher concentrations.

The higher sensitivity of root elongation than germination percentage indicates that chromium affects mostly post-germination developmental processes rather than the initial seed activation.

5.4. *Capsicum annuum* Linn. (Pepper)

The phytotoxicity of chromium to pepper (*Capsicum annuum* L.) was studied with special attention to the effects of Cr(VI) and the oxidative stress responses [6], [15], [21].

Germination and Growth Effects: Studies on Cr (VI) toxicity in pepper seedlings showed significant dose-dependent reduction in growth parameters [6], [15]. The plant growth and physiological responses were severely impaired by increasing concentrations of Cr(VI) up to 100 ppm. Pepper demonstrated significant differences in aboveground and underground dry weight at low Cr (VI) concentrations as compared to control groups, and the root-to-crown dry weight ratio tended to increase with the rise in Cr (VI) concentration [15].

Pepper weight, chlorophyll content and chlorophyll a/b ratio were significantly decreased with the increase of Cr(VI) concentration [15]. The reductions indicate that chromium interferes in both processes of growth and photosynthetic capacity in pepper and are more severe at higher levels of exposure.

Biochemical and Oxidative Stress Responses Pepper exhibits robust antioxidant enzyme responses to chromium stress, which are concentration-dependent. Peroxidase (POD) activity was increased dominantly and superoxide dismutase (SOD) activity was little inhibited at low concentrations of Cr(VI) [15]. However, the increase of Cr (VI) concentration decreased the SOD activity and the POD activity showed a maximum at 20 mg/L and then decreased with the increase of Cr (VI) concentration [15].

A detailed study of pepper plants treated with Cr (VI) up to 100 ppm has shown drastic increase in stress parameters and antioxidant enzyme activities [6]. The increased proline content (94%), MDA (80%) and electrolyte leakage (68%) over controls indicated severe oxidative stress and membrane damage. In response, the activities of antioxidant enzymes (CAT, APX, POD, GPX, SOD and GR) were strongly induced at 100 ppm, indicating the activation of multiple antioxidant defence pathways [6].

A study on H_2S -mediated chromium tolerance in pepper showed that nitric oxide assisted in stress relief by controlling the subcellular chromium distribution and boosting the ascorbate-glutathione cycle [21]. The results suggest that pepper can activate complex signalling pathways to alleviate chromium stress.

5.5. *Abelmoschus esculentus* (Okra)

Okra (*Abelmoschus esculentus* L. Moench), commonly known as lady's finger, has been investigated for chromium phytotoxicity and the morphological, physiological and biochemical responses have been documented in detail [18], [25].

Germination and Growth Effects Studies on the effects of hexavalent chromium on okra using potassium dichromate ($\text{K}_2\text{Cr}_2\text{O}_7$) tested concentrations of 2.5, 5, 10, 25, 50, 75 and 100 mg/L [18].

Morphological parameters showed progressive decline under chromium treatments. With the increase in chromium concentration, the root and shoot length decreased progressively.

Control plants had root lengths of 8.36, 15.5, and 17.5 cm/plant at 25, 50, and 75 days after sowing (DAS), respectively [18]. Under the treatment of chromium at less than 50 mg/L the minimum root lengths significantly dropped to 3.40, 9.20 and 11.20 cm/plant at the same time points with the reduction of about 59%, 41% and 36% respectively. Similarly, the control shoot length was 26.0, 37.5 and 58.5 cm/plant at 25, 50 and 75 DAS, while the least shoot length under 50 mg/L chromium was reduced to 9.64, 21.5 and 38.5 cm/plant, with reduction of 63%, 43% and 34% [18].

Another study on the effects of Cr(VI) on germination and growth of okra was performed using a range of concentrations from 0.5 to 100 mg/kg in soil [25]. Germination was not affected at 0.5-25 mg/kg but it was significantly reduced by 42.22 and 48.88% at 50 and 100 mg/kg, respectively. With increasing chromium levels, seedling vigour index decreased from 1672.66 in controls to 333.18 at 50 mg/kg [25]. This dramatic 80% reduction in vigour index indicates that moderate to high concentrations of chromium inhibit okra seedling establishment considerably.

Biochemical and Oxidative Stress Responses Okra shows significant biochemical responses to chromium stress with significant changes in photosynthetic pigments, proteins, amino acids and carbohydrates [18], [25]. The chlorophyll a, chlorophyll b, total chlorophyll and carotenoid contents were decreased with chromium exposure with lowest values obtained at 50 mg/L: 0.1694, 0.1095, 0.2973 and 0.2590 mg/g fresh weight at 75 DAS, respectively [18].

The protein content was reduced under chromium stress with the minimum values in leaf (0.8973 mg/g), stem (0.6294 mg/g) and root (1.2973 mg/g fresh weight) tissues at 75 DAS under 50 mg/L treatment [18]. The amino acid content also decreased with minimum values of 1.874 (leaf), 0.5470 (stem), and 1.4076 mg/g fresh weight (root) at 25 DAS under 50 mg/L chromium [18].

Total chlorophyll content showed dramatic reduction under chromium stress, from 14.85 ± 0.03 mg/g fresh weight in controls to 1.38 ± 0.01 mg/g at 50 mg/kg, which represented a 91% reduction [25]. At 50 mg/kg, chlorophyll a decreased from 5.71 ± 0.03 to 0.19 ± 0.01 mg/g (97% reduction) and chlorophyll b decreased from 9.13 ± 0.00 to 1.18 ± 0.00 mg/g (87% reduction) [25]. These drastic reductions in photosynthetic pigments are responsible for the considerable growth inhibition observed in chromium-stressed okra plants.

5.6. *Amaranthus cruentus* (Amaranth)

Despite the economic and nutritional importance of amaranth species, specific research on chromium phytotoxicity in *Amaranthus cruentus* remains limited in the available literature. While general reviews of chromium toxicity in plants acknowledge amaranth species as potential subjects [16], [31],

detailed experimental data on germination parameters, growth responses, and biochemical changes specific to *A. cruentus* under chromium stress are not well documented in the current body of research.

The lack of species-specific data for *A. cruentus* represents a significant knowledge gap, particularly given that amaranth species are increasingly cultivated as nutritious leafy vegetables and grain crops in regions where soil contamination is prevalent. Based on general patterns observed in other dicotyledonous vegetable crops, *A. cruentus* would be expected to exhibit dose-dependent reductions in germination and seedling growth under chromium stress, along with activation of antioxidant defense systems. However, the magnitude of these responses and the critical threshold concentrations for toxicity in this species remain to be determined through targeted experimental studies.

6. Antioxidant Enzyme Responses and Defense Mechanisms

Plants have evolved complex antioxidant defence systems for dealing with oxidative stress caused by heavy metals such as chromium [40]. These defence mechanisms consist of enzymatic and non-enzymatic components that act synergistically to scavenge ROS and maintain cellular redox homeostasis.

Enzymatic Antioxidants: The major antioxidant enzymes induced by chromium stress are superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX) and glutathione reductase (GR) [40]. SOD catalyses the dismutation of superoxide radicals into H_2O_2 and oxygen, which is the first line of defence against ROS. Cat and other peroxidases then convert H_2O_2 to water and oxygen, which prevents Fenton reactions from forming hydroxyl radicals.

In general, antioxidant enzyme activities were found to increase under moderate chromium stress but decreased at very high concentrations when cellular damages were too severe, as demonstrated in studies on different species [20], [27], [39]. SOD and POD activities increased by 48.06% and 35.88% respectively in Pusa 2085 variety and CAT activity increased by 56.09% at 120 μM in chickpea varieties subjected to Cr(VI) (0-120 μM) [27]. Likewise, pepper seedlings treated with 100 ppm Cr(VI) had high induction of CAT, APX, POD, GPX, SOD and GR activities [6].

APX and GR are key enzymes of the ascorbate-glutathione cycle, which is involved in the tolerance to chromium stress [21], [40]. APX reduces H_2O_2 to water using ascorbate and produces dehydroascorbate, and GR regenerates reduced glutathione from oxidised glutathione (GSSG) to maintain the cellular reducing environment. Studies on pepper demonstrated that hydrogen sulfide-mediated chromium tolerance is linked to the upregulation of the ascorbate-glutathione cycle and the involvement of nitric oxide in this protective mechanism [21].

Non-Enzymatic Antioxidants: Non-enzymatic antioxidants like ascorbate, glutathione, proline and phenolic compounds complement the enzymatic defences [40].

Accumulation of proline is a common response to chromium stress and has several protective roles such as osmotic adjustment, scavenging of ROS and stabilisation of proteins and membranes [27], [39]. Proline content increased up to 71.56% in roots of chickpea exposed to 120 μM Cr(VI) [27]. Pepper showed 94% increases in proline at 100 ppm Cr(VI) [6].

Major cellular reductants, including glutathione and ascorbate, directly scavenge ROS and serve as substrates for antioxidant enzymes [8], [40]. Glutathione and ascorbate levels are frequently increased in plants under Cr stress. However, under severe stress, these compounds may be depleted due to their overconsumption during Cr(VI) reduction and ROS scavenging. Studies on tomato demonstrated that treatment with nitric oxide resulted in increase of ascorbate and glutathione content and improved the ratio of GSH:GSSG under Cr(VI) stress, thus improving the stress tolerance [8].

Response Patterns: Dose-Dependent The correlation between chromium concentration and antioxidant enzyme activity is usually biphasic [20], [39]. At low to moderate concentrations of chromium, enzyme activities increase in an adaptive response to oxidative stress. However, enzyme activities may plateau or even decline at high concentrations as cellular damage becomes severe and protein synthesis is impaired. In *Vigna radiata* seedlings treated with 50-200 μM chromium, lipid peroxidation increased significantly with increasing chromium concentration, while antioxidant enzyme activities (SOD, CAT, APX and GR) increased to fight the oxidative damage [39].

7. Dose-Response Relationships Across Chromium Concentrations

Data on dose-response relationships are required to evaluate the phytotoxic risk of chromium and to define safe threshold concentrations in agricultural soils. A number of consistent trends were observed among the species investigated concerning the relationship between chromium concentration and phytotoxic effects.

Threshold concentrations: Most of the vegetable species show minor effects at very low concentrations of chromium (< 5 mg/L or mg/kg). Toxicity is observed at moderate concentrations (5-50 mg/L) and severe at high concentrations (> 50 mg/L) [2], [18], [23], [25]. Threshold concentrations are highly variable among species and depend on chromium form, exposure time and growth conditions.

For tomato, the most sensitive species among eight tested terrestrial plants, the no observed effect concentration (NOEC) for Cr(VI) in soil was as low as 12.0 mg/kg [10]. Conversely, okra did not exhibit significant effects on germination at soil concentrations as high as 25 mg/kg, but significant inhibition was observed at 50 and 100 mg/kg [25]. Melon exhibited measurable growth inhibition at a concentration as low as 2.5 mg/L Cr(III) and the effects increased progressively to 300 mg/L [2].

Concentration-Dependent Effects The toxicity of chromium was observed to be dose dependent in all the species and parameters studied.

The higher concentrations inhibited germination, growth and physiological processes in increasing order [2], [9], [22], [23]. Studies on the effect of hexavalent chromium on germination of crop seeds in solution culture indicated that low concentrations of Cr(VI) (< 1 mg/L) had no significant difference from controls in terms of germination indices, while higher concentrations progressively inhibited germination [9]. Importantly, the effects of Cr(VI) on shoot and root growth were significantly greater than on germination rate and inhibition rates were found to be extremely significantly positively correlated with Cr(VI) concentration [9].

Comparative studies with different plant species exposed to 0, 100, 200 and 300 mg/L Cr(VI) demonstrated that all concentrations had a detrimental effect on seed germination and viability, with the seedling responses being more pronounced than germination due to the impermeability of the seed coat and selectivity of the embryo [23]. Species exhibited different tolerance [23] and Cr(VI) accumulation caused inhibition of root and shoot length.

Species Sensitivity Distribution: Based on the available data, the relative sensitivity of the six target species to chromium toxicity can be tentatively ranked as follows: *Solanum lycopersicum* (most sensitive) > *Abelmoschus esculentus* > *Cucumis melo* > *Capsicum annuum* > *Solanum melongena* > *Amaranthus cruentus*. However, this ranking should be taken with caution as studies employed different Cr forms, concentrations, exposure methods, and assessment parameters.

Critical concentrations for soils for agriculture from an agricultural point of view, the available evidence suggests that soil chromium concentrations should be below 10-20 mg/kg to reduce the risk of phytotoxicity to sensitive vegetable crops [10], [22]. Most vegetable species are likely to experience considerable growth inhibition and yield losses at concentrations above 50 mg/kg [18, 25].

8. Conclusion and Future Perspectives

This extensive review summarises the current knowledge of chromium phytotoxicity in six economically important vegetable crops and the consistent pattern of dose-dependent growth inhibition, oxidative stress induction and antioxidant defence activation across species. Several major conclusions can be drawn from the available evidence.

First of all, hexavalent chromium (Cr(VI)) is far more toxic than trivalent chromium (Cr(III)) for all the species studied due to differences in bioavailability, cellular uptake and intracellular behaviour [26], [28], [31]. The differential toxicity has important implications for risk assessment and remediation strategies and highlights the need to consider chromium speciation rather than total chromium content in the assessment of contamination risks.

Second, chromium phytotoxicity is mediated by several integrated mechanisms, oxidative stress being the main cause of cellular damage [40]. Excessive generation of ROS overwhelms antioxidant defences and leads to lipid peroxidation, membrane damage, protein oxidation and nucleic acid damage.

Plants respond with a coordinated upregulation of antioxidant enzymes (SOD, CAT, POD, APX, GR) and accumulation of non-enzymatic antioxidants (proline, glutathione, ascorbate), but these defences are overwhelmed at high concentrations of chromium.

Thirdly, germination and early seedling growth are critical vulnerability windows for chromium toxicity with effects on root and shoot elongation often more pronounced than effects on germination percentage itself [2], [9], [23]. The pattern suggests that chromium is involved primarily in post-germination developmental processes such as cell division, cell elongation and differentiation. The seedling vigour index, combining germination and growth parameters, is a sensitive indicator of chromium phytotoxicity [25].

Fourth, there are species-specific sensitivity patterns, with *Solanum lycopersicum* (tomato) and *Abelmoschus esculentus* (okra) being especially sensitive to chromium stress [10], [18], [25]. Knowledge of these differential sensitivities can help guide decisions on crop selection in contaminated areas and can inform breeding programs aimed at development of chromium tolerant cultivars.

While much progress has been made in understanding chromium phytotoxicity, there are still some major gaps in knowledge. Research on *Amaranthus cruentus* is notably absent, constituting a major gap especially in view of the expanding cultivation of amaranth species. Most studies have been aimed at the short-term effects on germination and early seedling growth and there is little information on the effects of chronic exposure during the whole life cycle. Future studies using omics approaches are needed to understand the molecular mechanisms of chromium tolerance including identification of specific genes, transcription factors and signalling pathways.

From a practical perspective, a number of management strategies can be implemented for reducing chromium phytotoxicity in agricultural settings, including remediation of contaminated soils, choice of relatively tolerant crop species and cultivars, management of soil pH and redox conditions, application of organic matter and beneficial amendments, use of clean irrigation water, and breeding of chromium-tolerant cultivars using conventional and molecular approaches.

Future research should be aimed toward fully characterising the effects of chromium on under-researched species such as *Amaranthus cruentus* and toward long-term studies on the effects of chronic exposure on yield and produce quality. Molecular and genomic studies should be conducted to identify genes and mechanisms conferring tolerance. The variation between genotypes within species should be assessed, as should the accumulation of chromium in edible parts of plants and the associated risks to food safety. Practical mitigation methods should be developed and validated and species-specific threshold values for chromium in soil should be established for regulatory purposes.

To summarise, chromium contamination poses a major threat to vegetable production systems throughout the world, and there are documented phytotoxic effects on germination, growth, and physiological processes in a number of economically important species. Understanding the mechanisms of chromium toxicity and plant defence responses is essential for developing effective strategies to ensure sustainable vegetable production in contaminated environments.

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