



Chromium Stress in Plants: Toxicity, Tolerance and Phytoremediation

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Abstract: Extensive industrial activities resulted in an increase in chromium (Cr) contamination in the environment. The toxicity of Cr severely affects plant growth and development. Cr is also recognized as a human carcinogen that enters the human body via inhalation or by consuming Cr-contaminated food products. Taking consideration of Cr enrichment in the environment and its toxic effects, US Environmental Protection Agency and Agency for Toxic Substances and Disease Registry listed Cr as a priority pollutant. In nature, Cr exists in various valence states, including Cr(III) and Cr(VI). Cr(VI) is the most toxic and persistent form in soil. Plants uptake Cr through various transporters such as phosphate and sulfate transporters. Cr exerts its effect by generating reactive oxygen species (ROS) and hampering various metabolic and physiological pathways. Studies on genetic and transcriptional regulation of plants have shown the various detoxification genes get up-regulated and confer tolerance in plants under Cr stress. In recent years, the ability of the plant to withstand Cr toxicity by accumulating Cr inside the plant has been recognized as one of the promising bioremediation methods for the Cr contaminated region. This review summarized the Cr occurrence and toxicity in plants, role of detoxification genes in Cr stress response, and various plants utilized for phytoremediation in Cr-contaminated regions.

Keywords: chromium (Cr); detoxification; phytoremediation; phytotoxicity

1. Introduction

Heavy metal contamination is becoming a serious environmental issue worldwide for the past few decades due to their increased concentration beyond the permissible limit. Chromium (Cr) is a naturally occurring heavy metal and the 17th most abundant element in the earth's mantle [1]. Although Cr is required in trace amounts in plants and animals, at higher concentrations it serves as a major contaminant to the environment. Natural sources, as well as various anthropogenic activities, are responsible for the release of Cr in the soil, air, and water which have ultimately led to Cr pollution globally [2]. Regarding the consequences of the contamination of food lands and the drinking system, Cr easily enters into the food chain and affects the health of all life forms directly or indirectly [3–5].

In plants, the toxic effects of Cr are also evident, showing symptoms such as delay in seed germination, damaged roots and reduction of root growth, reduced biomass, reduction in plant height, photosynthetic impairment, membrane damage, leaf chlorosis, necrosis, low grain yield and eventually plant death [6]. Cr is a fairly active metal and reacts easily with environmental oxygen. Different oxidation states of Cr have been reported ranging from 0 to +6. The trivalent Cr(III) and hexavalent Cr(VI) are the most stable forms of Cr in nature. Also, Cr(VI) shows higher toxicity than Cr(III) due to its higher solubility and



Citation: Srivastava, D.; Tiwari, M.; Dutta, P.; Singh, P.; Chawda, K.; Kumari, M.; Chakrabarty, D. Chromium Stress in Plants: Toxicity, Tolerance and Phytoremediation. *Sustainability* **2021**, *13*, 4629. https://doi.org/10.3390/su13094629

Academic Editor: Iyyakkannu Sivanesan

Received: 28 February 2021 Accepted: 16 April 2021 Published: 21 April 2021

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Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). mobility in the water system [1]. Both valence states of Cr i.e., Cr(III) and Cr(VI) are taken up by plants [7]. Cr(VI) is actively taken up into the plant cells by sulfate carriers [8]. On the other hand, Cr(III) enters passively by the cation exchange sites of the plant cell walls [9]. Moreover, the carboxylic acids present in the root exudates facilitate the Cr solubilization, and thus its uptake into the plants [10].

Phytoremediation is a rapidly growing field of research for heavy metal contaminated regions. There are various processes of phytoremediation such as phytovolatilization, phytoextraction, phytostabilization, and hyperaccumulation [11,12]. Numerous research studies have shown that many plant species are capable of effectively removing Cr from contaminated regions which could be useful for the phytoremediation process [13]. Cr hyperaccumulators, with their associated microflora, have been used around the industrial effluent sites to remove the excess toxic Cr, as well as organic matters. Plant-microbe interaction is also one of the efficient strategies for Cr detoxification due to its high efficiency, low cost, and eco-friendly nature [14,15]. At the molecular level, various pathways involved in Cr detoxification have been deciphered to provide tolerance in response to Cr toxicity. Cr stress activates Reactive Oxygen Species (ROS) signaling, antioxidant responses, defense proteins such as phytochelatins (PCs), metallothionine (MTs), and glutathione-Stransferases (GSTs) followed by phytosequestration and compartmentalization thereby accelerating the bio-accumulating potential of the plants [16–18]. One approach could be developing transgenics by upregulating genes responsible for Cr uptake, transport, and sequestration to enhance the tolerance and accumulation rate of the plant.

Taking all into consideration, this review addresses Cr sources, effects, uptake, translocation, and subcellular distribution in plants. We also discussed Cr detoxification remedies in plants through phytoremediation and biotechnological approaches. Also, the molecular events underlying Cr toxicity and the defense signal transduction have been discussed. Overall, the review summarizes the recent development of sustainable approaches for Cr detoxification in the environment.

2. Cr Occurrence and Sources

The distribution of Cr(III) and Cr(VI) containing compounds in the environment depends on the presence of oxidizing or reducing compounds, redox potential, the formation of Cr(III) complexes or insoluble Cr(III) salts, the kinetics of the redox reactions, pH, and the total chromium concentration [2]. In the environment, Cr(VI) occurs mostly as chromate ions (Cr₂O₄ and Cr₂O₇) or chromic acid (H₂CrO₄), whereas Cr(III) occurs in the form of oxides, hydroxides(Cr(OH)_n⁽³⁻ⁿ⁾⁺), and sulfates [2,9]. The chemical structure of various existing forms of Cr(VI) and Cr(III) in the environment has been given in Figure 1. Cr is also found in the air where it occurs in the form of aerosols. Cr(VI) has been reported to be 0.01–30% of the total Cr present in the air. Tobacco smokes result in a total Cr level of around 1000 ng/m³ in indoor air, i.e., 10–400 times higher than outdoor levels [2]. The average level of Cr in surface water, seawater, and rainwater is around 0.001–0.010 mg/L, 0.00004–0.0005 mg/L, and 0.0002–0.001 mg/L, respectively [2,5].

Both natural, as well as anthropogenic sources, contribute to total Cr toxicity in the environment. Mineral leaching accounts for the natural origin of Cr in groundwater that is dominated by Cr(VI). However, above 70% of total Cr in the environment is due to the anthropogenic pollutants from effluent streams from paper and pulp mills, non-ferrous base metal smelters, leather tanning industries, refineries, releases from thermal generating stations, and urban stormwater runoff [2]. Among all sources, tanning industries play a vital role as they use $Cr_2(SO_4)_3$ as a tanning agent, of which 30–40% is unused and discharged into the environment via tannery effluent [19]. This inefficient usage of Cr brings about water defilement, carrying 500–1000 mg/L Cr from the current high-exhaust chrome tanning approaches and as high as 1500–3000 mg/L Cr from the conventionalmethodologies [20].



Figure 1. The chemical structures of existing forms of Cr(VI) (**A**–**D**) and Cr(III) (**E**–**G**) in the environment. Abbreviations: Cr, Chromium; O, Oxygen; H, Hydrogen; Pb, Lead; S, Sulphur.

In nature, Cr(III) predominates in soil and occurs in small amounts in rocks. Worldwide, the average concentration of Cr in the soil is dependent on the bedrock and range between 10–100 mg/kg with an average concentration of 60 mg/kg [21,22]. The estimated acceptable level of Cr in the soil for environmental safety and human health is 64 mg/kg that is difficult to maintain because of the discharge of the anthropogenic pollutants [23]. Cr(III) is present in the form of chromite [FeCr(III)₂O₄], bentorite Ca₆(Cr,Al)₂(SO₄)₃, and vauquelinite (CuPb₂CrO₄PO₄OH) in rocks from where it can be released into groundwater via weathering and erosion [1]. However, Cr(VI) seldom occurs naturally and is released from anthropogenic sources. The only natural source of Cr(VI) is an uncommon mineral, crocoite (PbCrO₄). High Cr(VI) concentration in California (0.006–0.036 mg/L in aquifer) [24], Italy (0.005–0.073 mg/L in groundwater) [25], Mexico (270–4120 mg/kg in rocks) [26], Zimbabwe (310-8600 mg/kg in soil) [27], Brazil (0.0025-0.11 mg/L in groundwater) [28], Indonesia (50-90 mg/kg in river sediment) and Japan (510-1420 mg/kg in river sediment) [29] were reported owing to the contact of water with ultramafic rocks and soil such as ophiolites, dunites, and serpentinite. Cr emitted into the air through sources such as Cr-based automotive catalytic convertors, tobacco smoke, and coal combustion also end up in soils [9].

Food is also a source of Cr exposure to the living population, containing a total Cr level spanning between <0.0005 to 1.3 mg/kg. However, fresh food is reported to be very low in Cr i.e., 0.02–0.05 μ g/kg. As the food is recognized as a reducing medium, the total Cr found in it can be classed as Cr(III). Food items such as meat, seafood, fish, cereal products, black pepper, tea, cheese, some fruits, vegetables, and wheat germ have high Cr content (>0.1 mg/kg). Beer, spirits, and wine have total Cr concentrations of around 0.45, 0.135, and 0.30 mg/L respectively. Utensils, especially made up of stainless steel, can also add to total Cr concentrations in food [2].

3. The Effects of Cr on Plants

Oxidation state is the deciding factor of the toxicologic or physiologic effects of Cr. Higher concentrations of Cr(III) might be inhibitory to plant growth and development. On the contrary, Cr(VI) is highly toxic for plants and inhibits various morphological, physiological, and metabolic activities in plants, and may even lead to their complete damage [30,31].

3.1. Effects on Seed Germination

Seed germination in a Cr enriched environment depends on the plant's ability to withstand Cr toxicity. Excess Cr limits the seed germination rate of *Cucumis melo* L. (>10 mg/L Cr(III) in culture medium) [32], *Hibiscus esculentus* (>50 mg/kg Cr(VI) in soil) [6], *Triticum aestivum* (>25 mg/L Cr(VI) in the nutrient solution) [33], and *Echinochola colona* (2.5 mg/L Cr(VI) in the nutrient solution) [34]. Two freshwater plants, *Lemna minor*, and *Pistia stratiotes* when grown in nutrient solution containing 1, 5, or 10 mg/L of Cr(VI) resulted in retardation of the growth [35]. The seed germination of *Salvia sclarea* L. was inhibited when treated with different concentrations of Cr(VI) ranging from 1–10 mg/L [36].

3.2. Effects on Shoot Growth

Cr exposure affects the shoot length and biomass of the plant [37]. With the increase in Cr(VI) concentration, the shoot length of *Helianthus annus* L. was found to be decreased [38]. In *Allium cepa*, Cr(III) concentration higher than 100 mg/L, reduced the shoot growth [39]. In *Citrus aurantium* L., an increase in Cr(III) concentration in the soil resulted in 39.3% and 90.4% reduced shoot length at 50 mg/kg and 200 mg/kg of Cr, respectively [40]. The small stem with a slow growth rate was observed in *Camellia sinensis* on exposure to 600 mg/kgCr(III) [41]. It was reported that a lower Cr(VI) concentration (0.05 mg/L) increases the shoot length, while a higher Cr(VI) concentration (1 mg/L) retarded the shoot length and weight of *Myriophyllum spicatum* [30].

3.3. Effects on Root Growth

Being a primary organ for nutrient uptake, the roots are directly associated with Cr uptake and thus serve as a principal site of Cr toxicity in plants. In a greenhouse experiment, root growth of sour orange seedlings was analyzed under 50–200 mg/kg Cr(III) concentrations and the significant reduction in the root length was found at 200 mg/kg Cr(III) [40]. In *Pistia stratiotes*, Cr at low concentration (0.25 mg/L) promotes root length, laminal length, and breadth as compared to control but at higher concentration (2.5 mg/L), the root length was found to be decreased [42]. *C. sinensis* roots were severely affected on high Cr concentration (600 mg/kg) leading to a reduction in roots dry weight [41]. Cr(VI) at a concentration of 6, 12, 18, and 24 mg/kg caused a reduction in root length and root dry weight in *T. aestivum* [43]. Sundaramoorty et al. [44] reported decreased root growth of field grown *Oryza sativa* L. treated with 200 mg/L Cr(VI) in distilled water. Also, the thin and brittle roots of *Pisum sativum* were observed under high Cr(VI) concentration (>1000 mg/L) [45].

3.4. Effects on Total Leaf Area

Plant takes up Cr via the root and it gets transported to the upper plant parts via various transporters. The leaf is one of the important organs of a plant that performs photosynthesis. The total leaf area is one of the determining factors for photosynthesis. The Cr(VI) toxicity affects the total leaf area and also showed a 50% reduction in leaf number per plant in *O. sativa* [44]. *Brassica oleracea* showed a decrease in leaf size, wilting, and chlorosis when grown in refined sand with complete nutritional media under 0.5 mM Cr(III) toxicity [46]. In *Lolium perenne* L., a noticeable wilting has been observed under 0.50mM Cr(VI) prepared in nutrient media [47]. Leaf chlorosis and leaf necrosis have been reported in *Saccharum officinarum* on Cr(VI) exposure of 40 mg/kg and 80 mg/kg, respectively [48]. *Phaseolus vulgaris* showed a reduction in leaf biomass under 0.01 mM Cr(III) treatment in nutrient solution [49]. The decreased number of leaves was reported in *Prosopis laevigatar* under 3.4 mM Cr(VI) toxicity in nutrient media [50].

3.5. Effects on Grain Yield

The yield and productivity of crops are affected by Cr exposure as it exerts an adverse impact on biochemical and physiological processes. The reduction in yield of *Hordeum vulgare* and *Zea mays* was observed at a concentration of 100 or 300 mg/kg of Cr [51]. In *Daucus carota*, no harvestable yield was obtained on 270 or 810 kg/ha of Cr(VI) applica-

tion [52]. In *O. sativa*, Cr(VI) application under 200 mg/L caused a decrease in grain weight and 80% loss [44].

3.6. Anatomical Changes

Cr induces structural and ultrastructural alterations in plant organs. In *Vigna radiata*, Cr exposure led to change in the epidermis, cortex, and stele in its stem [53]. The addition of 0.60 mM Cr(VI) in nutrient solution media caused less wax deposition and wide stomatal opening in the leaves of *Phyllanthus amarus* [54]. The number of palisade and spongy parenchyma cells were found to be decreased in fronds of *Pteris vittata* at 500 mg/kg of Cr(VI) and 1000 mg/kg of Cr(III) [55]. The roots of *Scirpus lacustris* L. showed an increase in pith and cortical tissue layer proportion under two different concentrations of Cr(IV) i.e., 4 and 8 mg/L [56]. *Mentha aquatica* roots showed structural changes such as damaged root cap, loss of root hairs, inhibition in lateral roots formation on exposure of Cr(VI) at a concentration of 20 or 40 mg/L [57].

3.7. Physiological Changes

Exposure of the elevated concentration of heavy metals leads to degradation of photosynthetic pigments that are responsible for deficiency in light-harvesting capacity. The 0.05 mg/L of Cr(VI) exposure resulted in a reduction in photosynthetic rate in *M. spicatum* [58]. Some species like *Citrus aurantium* [40], *Najas indica, Vallisneria spiralis*, and *Alternanthera sessilis* showed decrease in chlorophyll (Chl) content under Cr toxicity [30]. In *T. aestivum*, net photosynthetic rate (Pn) was reduced with a gradual increase in Cr exposure time. Less chlorophyll content was found in Cr(VI) treated wheat in comparison to control plants. Interestingly, it was due to the more reduction in Chl b than Chl a content [59]. However, in the case of *Chlorella pyrenoidosa*, both Chl a and b content were decreased under 0.1–50 mg/L of Cr(VI) [60]. The light-harvesting complex of the photosystem II was extensively affected in *T. aestivum* after treatment with 0.10 mM, 0.20 mM, and 0.30 mM of Cr(VI) [61].

In higher plants, Cr inhibits mitochondrial electron transport leading to higher ROS generation that causes oxidative stress, pigment, and chloroplast alterations [62]. Chromosomal impairment by Cr(VI) treatments (0.01 mM and 0.1 mM) has been reported in *Amaranthus viridis* plant tissues, where it regulated the activity of calmodulin that was further responsible for the activation of many key enzymes such as phospholipase and nicotinamide adenine dinucleotide kinase, involved in the chromosomal movement [63]. Furthermore, Cr has also been observed to affect the concentrations of free polyamines in *Avena sativa, Brassica napus*, and *H. vulgare* seedlings after treatment with 100 mg/L of Cr(III) for 1–14 days [62,64].

Wilting caused by Cr has been reported in various crops and plant species, but the effect of Cr on water relations of higher plants is less studied. Chatterjee and Chatterjee reported a decrease in water potential, transcription rate, and relative water content in *B. oleracea* leaves, grown in refined sand in a glass house with 0.5 mM of Cr(VI) toxicity [46]. In *Spinacea oleracea* leaves, the decrease in water potential and increase in diffusive resistance led to a decrease in physiological availability of water under 0.10 and 0.40 mM of Cr(VI) toxicity [65]. Essential nutrients uptake was reduced in *Spartina argentinensis* on Cr(III) exposure at 1500 mg/kg [66]. Longitudinal water movement was found to be reduced in beans due to a decrease in tracheary vessel diameter on high Cr(VI) level (0.096 mM) [67].

3.8. Effects on Nutrient Balance

The soil-plant transfer index of Cr(VI) is comparatively higher than Cr(III) due to its better adsorption and high solubility in the cells [68]. Cr(VI) modulates the intracellular concentration of essential nutrients viz phosphorus (P), calcium (Ca), manganese (Mn), magnesium (Mg), potassium (K), and iron (Fe) in plants [69]. It has also been reported that mycorrhizal fungi as well as organic acid such as citric acid increases the uptake of Cr(VI) in plants [70]. The field-grown *O. sativa* irrigated with different concentrations of

Cr(VI), (50–500 mg/kg) showed a gradual decrease in uptake of macronutrients (K, P, and nitrogen (N)) and micronutrients manganese (Mn), zinc (Zn), copper (Cu) with increased Cr concentration [44,71]. In contrast, Mg concentration increased in nucleus and mitochondria with an increase in Cr(VI) concentration in *O. sativa*, showing a positive correlation [72]. Dube et al. [73] demonstrated that Cr(VI) exposure increased the accumulation of P, Mn, and Zn while decreased sulfur (S) and Cu content in *Citrullus vulgaris*. *Zea mays* roots showed a decrease in Cu absorption on Cr(VI) exposure [74]. In *B. oleracea*, a high concentration of Cr(VI) (0.5 mM) affected the Fe concentration and translocation of Zn, Cu, S, P, Mn from the roots to other plant parts [46].

3.9. Molecular Changes

The molecular changes after the Cr stress were explored through comparative transcriptome analyses in several plants to get insight of the underlying mechanism during Cr stress. Previous reports showed that the application of Cr modulates several biological processes to lessen the phytotoxicity of Cr stress. A recent microarray analysis on Cr(III) and Cr(VI) treated *O. sativa* seedlings showed that Cr stress induces the transcript levels of different antioxidant enzymes ascorbate peroxidase (APX), superoxide dismutase (SOD), peroxidase (POD), and glutathione peroxidase (GPX) coding genes in treated plants in comparison to control plants [75]. Likewise, Dubey et al. [17] observed the differential expression pattern of numerous genes (1138 up-regulated and 1610 down-regulated) in *O. sativa* roots exposed with 0.10 mM Cr(VI). Among all the up-regulated genes, most of the genes were related to secondary metabolites biosynthesis, transporters, and xenobiotics biodegradation. Interestingly, this study also showed the modulation of the sucrose degradation pathway which could be salvage machinery in response to Cr stress. On the other hand, Cr stress also stimulates the expression of microRNAs. Some Cr(VI)-responsive miRNAs have been identified in *Raphanus sativus* and *O. sativa* [76,77].

4. Cr Uptake and Translocation in Plants

The uptake of Cr and its translocation to various parts of the plant have lately grasped immense attention worldwide not only because of its role in human metabolism but also due to its carcinogenic repercussions. To date, the mechanism of Cr uptake in plants has not been distinctly explained as it is not involved in plant metabolism. The primary source of Cr uptake is the root of the plant that rely upon the plant type and Cr speciation i.e., Cr(III) and Cr(VI) [7]. Also, Cr uptake from aqueous media depends upon pH, Cr concentration, salinity, and presence of dissolved salts [78]. Studies also suggested that the formation of Cr-organic ligand complexes enhances the Cr uptake in plants [79].

Plants uptake Cr(III) through a passive mechanism by diffusion at the cation exchange site of the cell wall [9]. Cr(VI) has a structural similarity with phosphate and sulfate and thus its uptake occurs through phosphate and sulfate transporters via an energy-dependent active process [80]. It has been reported that active transport of Cr(VI) results in its immediate conversion to Cr(III) in roots by the action of ferric reductase enzymes [81]. This converted Cr(III) binds to the cell wall thereby inhibiting its further transport in the different plant tissues [82].

In transgenic *Nicotiana tabacum*, an increase in MSN1 (a putative yeast transcriptional activator) expression resulted in elevated uptake and tolerance of both Cr and S [7]. Further studies in *N. tabacum* suggested an increase in the expression of sulfate transporter 1 (*NtST1*) upon Cr stress, indicating that both S and Cr are taken up through the sulfate transporter. Sulfate transport in prokaryotic organisms generally takes place through ABC transporter [83]. On the contrary, in the case of eukaryotic organisms, various sulfate transporters with a varying affinity for the substrates have been identified. Six plasma membrane sulfate transporters have been identified in *Chlamydomonas reinhardtii* belonging to Na⁺/SO₄²⁻ and H⁺/SO₄²⁻ transporter family. It has been suggested that these transporters might be involved in the transportation of Cr in plants [84]. Among all heavy metals, Cr is found to be the least mobile element in the plant roots. Till now, various

studies have shown that the maximum accumulation of Cr occurs in roots as compared to other plant parts [7]. For instance, the study of Zayed et al. [81] showed 100 fold higher Cr accumulation in roots than in shoots of vegetable crops due to the formation of insoluble Cr compounds in roots. Similarly, more Cr was found to be accumulated in roots of *P. sativum* and *S. oleracea* L. cv. Banarasi as compared to leaves and stems. Notably, the bean plants showed 98% Cr accumulation in roots and only 0.1% accumulation in seeds under Cr toxicity [85]. Another study performed in Lolium perenne showed 10 times higher accumulation of Cr in roots as compared to leaves when treated with 0.50 mM of Cr(VI) [47]. In Iris pseudacorus, elevated Cr concentration was found in the cell wall of the root as well as in cytoplasm and intracellular spaces of the rhizome [86]. Cr accumulation in the roots of T. aestivum, A. sativa, and Sorghum bicolor was more as compared to the shoots [87]. The translocation of Cr from roots to aerial parts of the plant is limited but it depends upon the chemical form of Cr. Notably, the exogenous application of EDTA (Ethylenediaminetetraacetic acid) enhances the Cr uptake and its translocation from root to upper part of the plant [21]. The Fe hyperaccumulators viz. S. oleracea, and Brassica rapa subsp. rapa could efficiently translocate Cr to aerial parts of the plants whereas non-Fe accumulating plants such as Lactuca sativa and B. oleracea var. capitata were least effective in Cr translocation [88]. The study in Z. mays also suggested that the presence of Fe in the medium results in decreased Cr(VI) translocation [74].

5. Molecular Approaches of Cr Detoxification in Plants

Generally, the plants have developed two important strategies i.e., avoidance and tolerance to mitigate the harmful effects of Cr. In the case of tolerance, the defense responsive genes/proteins play a significant role during Cr uptake, translocation, chelation, and its vacuolar sequestration. According to Marieschi et al. [89], S starvation activates the Cr(VI) detoxification or tolerance through overall decrease in Cr(VI) uptake in wild type *Scenedesmus acutus* strain. Under S-starved condition, the Cr(VI) uptake was reduced due to activation of "high affinity sulfate transporters" that enhanced the uptake of S over Cr(VI). In addition, S-starvation activated the S-uptake/assimilation pathway resulting in the production of S-containing molecules (GSH, PCs, or MTs) which ultimately aids in Cr(VI) tolerance in these cells.

5.1. Avoidance

The preliminary step to avoid Cr stress is to impede Cr ion uptake in the root thus preventing its further translocation. In the case of Cr accumulating aquatic and terrestrial plant species, Cr ion binds to the cell wall which comprises pectic sites, callose, and mucilage thereby causing reduction of Cr translocation into the cytosol [90]. Additionally, binding of Cr ions to the secondary cell wall occurs due to the presence of lignin [91]. A previous study showed the deposition of callose in the cell wall of *O. sativa* as well as the elevated expression of proteins related to the cell wall structure which signified the importance of the cell wall as a barrier to reduce Cr translocation [92].

5.2. Antioxidant Response

Cr toxicity results in the generation of ROS by the Fenton and Haber-Weiss reactions [93], followed by modulated antioxidant enzyme activities in plants. The higher activities of antioxidant enzymes *viz*, POD, catalase (CAT), APX, and SOD safeguard the plants from ROS generated by Cr stress. Interruption of free radical chain reaction by these antioxidant enzymes inhibits or reduces the oxidative process. Studies in *Z. mays*, *Solanum lycopersicum*, and *B. oleracea* upon Cr (VI) treatments showed increased glutathione (GSH) levels in roots as well as leaves [16]. Additionally, increased GSH production upon Cr treatment has also been observed in *O. sativa*, *Actinidia deliciosa* (A.Chev.) C.F.Liang & A.R.Ferguson, *Salvinia natans*, *P. stratiotes*, *Brassica napus*, *Salvinia rotundifolia*, and *Salvinia minima* [7]. On the contrary, *Jatropha curcas* showed decreased GSH activity under Cr toxicity [94]. In response to Cr stress, there is an elevation in the level of glutathione reductase (GR), one of the important enzymes of the Ascorbate-Glutathione pathway [95]. GR behaves as a metal chelator, ROS scavenger, as well as a substrate for PCs biosynthesis. Recent studyon *Miscanthus sinensis* showed over-expression of 36 proteins involved in oxidative stress, metabolism, molecular chaperones, etc. upon exposure of 0.50–1 mM Cr [96].

5.3. Compartmentalization and Sequestration

To avert Cr toxicity after its uptake, the plants have developed various mechanisms to accumulate Cr ions in certain cell types/intracellular compartments where Cr can impose the least harm. This ultimately prevents the entry of Cr ions into metabolically active compartments *viz*. chloroplast and mitochondria [95]. A study on *Leersia hexandra* showed Cr accumulation as well as sequestration primarily inside the cell wall of the roots and secondarily in the vacuoles of the leaves [97]. An ultrastructural localization analysis in *R. sativus* showed that Cr get accumulated as inclusion bodies in the cell wall of root cortical cells [98]. The localization and speciation study of Cr in a medicinal plant, *Coptis chinensis* Franch, showed the highest Cr accumulation in roots followed by rhizome and least in the petiole. This study also showed the Cr distribution in the vascular cylinder, outer cortex, and periderm of the accumulating cell [99].

5.4. Reduction of Cr(VI) to Cr(III)

The reduction of Cr(VI) to Cr(III) by chemical or enzymatic method decreases Cr toxicity in plants. This reduction can occur chemically with the help of glutathione, cysteine, sulfite, and thio-sulfates which occur in the plant cell [100]. On the other hand, an enzymatic reduction is done by various rhizospheric bacteria viz, *Staphylococcus arlettae*, *Ochrobacterium intermedium*, *Pseudomonas* sp., *Bacillus* spp., *Mesorhizobium* spp. and *Cellulosimicrobium cellulans* KUCr3 [95]. These rhizospheric bacteria have soluble and membrane-bound reductases which use chromate as the terminal electron acceptor in the electron transfer chain [101].

5.5. Detoxification Genes/Proteins in Plants

5.5.1. Phytochelatins

Phytochelatins are cysteine-rich polypeptides that are produced by PC-synthase utilizing GSH as a substrate. PCs play an important role in the detoxification and homeostasis of heavy metals including Cr. During Cr detoxification, the Cr (VI) reduced to Cr(III) further forms a complex with PCs. These PC-Cr complexes are further transported to the vacuoles [102]. Initial studies suggested that Cr was unable to activate detoxification by phytochelatins [17]. But later on, it was reported that Cr toxicity results in the production of PCs both in the roots and shoots of the plant. Studies showed that Cr detoxification in *Vigna radiata, Brassica juncea, Helianthus annuus, Xanthoria parietina, R. sativus, Z. mays, S. lycopersicum, and B. oleracea,* and *O. sativa* occurs by the production of PCs [7]. Recent studies also showed that the addition of silicon reduces Cr toxicity by increasing the concentration of PCs and GSH under Cr stress [103].

5.5.2. Metallothioneins

Metallothioneins are low molecular weight cysteine-rich proteins, localized in the golgi apparatus membrane, which play an important role in Cr detoxification in plants. Although, the role of MTs in Cr detoxification has not been studied broadly as compared to other heavy metals; however, a study in two *S. bicolor* cultivars K-10 (susceptible) and CO-27 (tolerant) upon Cr stress showed increased expression of *MT3* gene in the tolerant cultivar as compared to the susceptible one [104]. Few studies suggested that MTs may bind to Cr ions making them non-toxic and thereby providing tolerance to plants against Cr. A recent study in *O. sativa* seedlings under Cr stress provided evidence that *OsMTs* help in Cr detoxification by scavenging ROS and stimulating metal chelation. Also, these

specific *OsMT* genes were differentially expressed in roots and shoots under both Cr(VI) and Cr(III) treatments [18].

5.5.3. Glutathione-S-Transferases

Glutathione-S-Transferases belong to a predominant multifunctional enzyme family that can conjugate with GSH resulting in cellular detoxification of various substrates [105,106]. GSH is a low molecular weight tri-peptide (γ -glutamate-cysteine-glycine; γ -Glu-Cys-Gly) which provides tolerance against Cr stress by regulating peroxide reduction, thiol-disulphide status, and scavenging free radical [107]. A genome-wide transcriptome analysis of O. sativa treated with 0.10 mM Cr(VI) showed the differential expression of a number of genes related to glutathione metabolism, transport, and signal-transduction pathways in treated plants in comparison to control plants. Out of these, six genes were tau class GSTs (OsGSTU5, OsGSTU6, OsGSTF10, OsGSTU30, OsGSTU37, and OsGSTU41) that showed the highest expression in O. sativa roots under Cr(VI) stress [17]. Another study suggested that OsGSTU30 and OsGSTU41 were root-specific OsGSTs and over-expressing these genes in Schizosaccharomyces pombe resulted in elevated Cr(VI) tolerance. Further inhibiting the γ -Glu-Cys-Gly synthesis and decreasing cellular GSH concentration in S. pombe abolished the tolerance of OsGSTs against Cr(VI) stress suggesting a conserved role of tau class of GSTs in O. sativa for Cr(VI) detoxification and homeostasis [108]. Additionally, OsGSTU30 was functionally characterized by developing overexpressing lines of OsGSTU30 in A. thaliana, which enhanced Cr(VI) tolerance. It was also found that OsGSTU30 has dual enzymatic activities i.e., GST as well as glutathione peroxidase (GPX) under Cr(VI) stress [109]. The proposed model for Cr uptake, translocation, and detoxification has been given in Figure 2.



Figure 2. A schematic model showing chromium uptake, translocation and detoxification in plants. Abbreviations: Cr(VI) and Cr(III), Chromium; GSH, Glutathione; PC, Phytochelatin; PCS, Phytochelatin synthase; GST, Glutathione-S-transferase; ROS, Reactive Oxygen Species.

6. Phytoremediation Approach for Cr Detoxification

Research in the past few decades identified tolerant and hyperaccumulator plants to study their mechanism and usage for the phytoremediation process. To date, nearly 500 plant species belonging to more than 45 families have been identified. Most of the tolerant hyper-accumulator plants transformed the toxic metals into lesser toxic and immobile forms [110]. The mechanism behind the Cr hyper-accumulators mostly involves the function of high-affinity ligands such as amino acids, peptides, and organic acids which chelates the metal ions and sequesters them into the vacuole. The important factors governing the hyper-accumulation of Cr as well as other heavy metals comprise the increased rhizospheric metal mobilization by organic acids; absorption using the different family of transporters and then translocating it into shoot via xylem loading, finally detoxifying it via chelation and compartmentalization within the vacuoles [111].

6.1. Phytoremediation by Hyperaccumulating Plants

An environmentally sustainable way of rehabilitation of contaminated soil and wastewater by phytoremediation can be a very efficient and cost-effective strategy to combat the toxicity of Cr. Numerous research studies showed that many plant species are capable of effectively removing Cr from contaminated regions which could be useful for the phytoremediation process. A novel Cr-hyperaccumulating plant, *Lonicera japonica* Thunb, is traditionally used in Chinese medicine and can offer great opportunities in the phytoremediation process. The mechanism of Cr tolerance mainly involved the increased production of oxalic acid, anthocyanin and carotene in these plants [112]. The macrophyte *Callitriche cophocarpa* is an effective biosorbent for Cr removal from concentrated solutions, typical for industrial effluents [113]. Eze et al. [114] showed that the Cr removal capability of *Vigna unguiculata* was significantly higher than *Arachis hypogea* which makes them a better candidate for phytoremediation of Cr contaminated soils. *V. unguiculata* accumulated Cr from the soil into their roots, not in aerial parts.

Nayak et al. [115] showed that the hyper-accumulating capability of *Vetiveria zizanoides* could be enhanced by inoculating the native V. zizanioides with Bacillus cereus T1B3 strain. Similarly, Colocasia esculenta showed effective removal of Cr(VI) in water from wetlands due to the high accumulation of Cr(VI) in the roots part compared to the other parts [116]. The Cr accumulation potential of four weed species like Parthenium, Cannabis, Euphorbia, and Rumex was investigated which showed that Cannabis and Parthenium have higher accumulation capability than *Rumex* and *Euphorbia* due to having bio-concentration BCF > 1 [117]. A report from Sajad et al. [118] stated that to cope with the high Cr concentration in contaminated regions, the hyper-accumulators Cannabis sativa and Allium griffithianum efficiently accumulated a higher concentration of Cr ranging from 568.33 to 1233.3 mg/kg. Singh et al. [119] showed that Spirodela polyrrhiza (L.) Schleid accumulated a high amount of Cr on exposure to tannery effluent making it a prospective contender for tannery waste water remediation and also in exploration of Cr hyperaccumulation. Some plants like Canna indica L. and Hydrocotyle umbellata L. have good potential and are effective in remediating Cr in an artificial wetland system and contaminated waste water, and Canna indica being a comparatively higher accumulator [120]. The detailed study of Chrysopogon zizanioides L.Roberty showed that it accumulates a higher concentration of toxic Cr by evolving mechanisms for detoxification, elevating the levels of antioxidant enzymes, photosynthetic pigments, and malondialdehyde content [121].

Levizou et al. [122] conducted a pot experiment outdoor and found that *Origanum vulgare* has an exceptional capacity to bioaccumulate Cr in both the aerial part and the root when grown in Cr contaminated soils. The hybrid Napier grass (*Pennisetum americanus* L. × *Pennisetum purpureum* Schumach) could also be applicable for Cr phytostabilization which had bioaccumulation factor (BAF) > 1 and transfer factor (TF) < 1 [123]. Afonso et al. [124] found that *Solanum viarum* Dunal species accumulate high Cr in their biomass and can be potentially applicable in phytoremediation and treatment of areas contaminated with heavy metals such as Cr. The *Cassia tora* proved to be a potential phytoremediator

of Cr from contaminated sites due to its high bioaccumulation activity, high tolerance, and transportation index concluding its utilization for the phytostabilization program to lessen the toxicity of Cr from chromite overburdened mining sites [125]. *Arundo donax* L. an energy crop has shown tolerance to moderate concentrations of heavy metals and confers hyperaccumulating potential for Cr [126]. Recently, Mohanty et al. [127] identified the native Cr hyperaccumulators in contaminated regions of South Kaliapani chromite mine area in India. The highest Cr concentrations were recorded in roots of *Diectomis fastigiata* (2371 mg/kg dry matter) and shoots of *Vernonia cinerea* (5500 mg/kg dry matter) showing their Cr phytoremediation capability. Besides, *Callitriche cophocarpa* Sendtn was introduced into the heavily polluted watershed with sediments to demonstrate its outstanding hyperaccumulation properties towards Cr [128].

A study found that the common water hyacinth *Eichhornia crassipes* has efficient Cr removal capability, where they conducted a small-scale hydroponic experiment with different metal concentrations for one month period. The accumulation of Cr was significantly higher in the roots compared to shoot [129]. *Cirsium vulgare* plant is an effective accumulator for Cr and can be effectively used for the phytoremediation of the Cr-contaminated soils [130]. An aquatic macrophyte *Ipomoea aquatica* could effectively remove Cr within a relatively short period and being a fast-growing species could be a suitable candidate for phytoremediation of Cr contaminated water bodies [131].

6.2. Cr Detoxification Using Anti-Oxidant Machinery and Other Innovative Strategies

Ipomonea aquatica could be used to potentially remediate high Cr contaminated wastewater [132]. Further, Sabir et al. [11] reported that the fast-growing, tolerant, hyperaccumulating *I. aquatica* plants possessing bio-accumulation and translocation factor >1 and showed the capability to phytoremediate Cr. A previous study reported the usefulness of *Lemna minuta* Kunth for the spontaneous removal of Cr(VI) suggesting a high potential or usage in the treatment of effluents. They also found that there were minimal changes in the anti-oxidant machinery when treated with Cr compared to control [133]. An innovative Cr detoxification system has been established, where iron-biochar nano-complex was used to immobilize the bioavailable mobile fraction and the hyperaccumulator *Leersia hexandra* for uptake, along with microbial consortium for assisting the plant. With this system *L. hexandra* could accumulate Cr from 147.5 to 785.0 mg/kg biomass of plant tissue [134].

Notably, the chemically modified *Salvia moorcroftiana* leaves could be used as biomass for biosorptive detoxification of aqueous solutions by removing Cr(IV) ions via endothermic and non-spontaneous thermodynamic processes [135]. This could be a better alternative due to its high biosorption potency and low cost, thus, can be used for detoxification of water contaminated Cr(IV) and other heavy metals like Pb(II) (lead) and Cd(II) (cadmium). In a greenhouse experiment, two free-floating macrophytes, *Eichhornia* sp. and *Pistia* sp. was found to be effectively used in the remediation of Cr(VI) contaminated aquatic bodies due to their tolerance by increasing anti-oxidant activity and accumulation [136]. *Gomphrena celosoides* have considerable Cr accumulating capability due to increased proline and antioxidant enzyme activities [137]. *Melia azedarach* L. has a high bioaccumulation capacity of Cr and Cd in root tissues due to increased activity of non-enzymatic antioxidants such as GSH, soluble protein, and proline in the plant in detoxification of metal-induced ROS generation [12]. *Calotropis procera* accumulates a high concentration of Cr and also has increased activities of SOD, CAT, and GR upon Cr exposure, hence, can be used for the phytoremediation of Cr polluted arid soil [138].

6.3. Phytostabilization and Phytoextraction for Cr Tolerance

The phytoextraction/phytostabilization capabilities for metal detoxification have been found in various plants. *Conocarpus erectus* showed immense potential for phytostabilization of Cr in contaminated soil [139]. *Sesbania sesban* has a high bioaccumulation capacity of Cr and also high tolerance index and transportation index compared to *Brachiaria mutica*, thus, can be recommended as a phytostabilizer to reduce toxic Cr from chromite contami-

nated mining sites [140]. A widely studied model plant *Mesembryanthemum crystallinum* L. has high tolerance capacity against various biotic and abiotic stresses and it is suitable for bio-reclamation of contaminated soils due to considerable phytoremediation capabilities and unique growth potential. This plant is also especially capable of efficient phytoextraction from chromate-contamination due to its vigorous growth without exhibiting any physiological or anatomical disorders [141]. Thus, it was confirmed that this plant could perform as excellent decontamination for the Cr heavy metal under controlled (pH, redox potential, water disturbances) conditions. The summary of various plant species which have been discovered for their role in Cr detoxification from the last decade has been listed in Table 1.

Family	Plant	Habitat	Tolerance Mechanism	References
Aizoaceae	Mesembryanthemum crystallinum L.	Large, mat-forming annual with sprawling stems	Phyto-extraction	[141]
Amaranthaceae	Gomphrena celosoides Mart.	Perennial herb	Increased proline and antioxidant enzyme activities	[137]
Amaryllidaceae	Allium griffithianum Boiss.	Perennial herb	Hyper-accumulation	[118]
Apocynaceae	Calotropis procera (Aiton) W.T. Aiton	Large shrub or small tree	Increased activities of superoxide dismutase (SOD), catalase (CAT), and glutathione reductase (GR)	[138]
Araceae	Colocasia esculenta (L.) Schott	Fast growing, herbaceous	High accumulation of Cr(VI)	[116]
	Lemna minor L.	Free floating aquatic plants	Increased anti-oxidant activity, Phyto-extraction	[142]
	<i>Lemna minuta</i> Kunth	Small aquatic floating plant	Increased anti-oxidant activity	[133]
	Pistia stratiotes L.	Aquatic plant	Anti-oxidant activity and accumulation	[136]
	Spirodela polyrrhiza (L.) Schleid	Aquatic weed	Hyper-accumulation	[119]
Araliaceae	Hydrocotyle umbellata L.	Creeping, aquatic herb	Hyper-accumulation	[120]
	Cirsium vulgare (Savi) Ten.	Annual or biennial, herbaceous plant	Hyper-accumulation	[130]
	Dicoma niccolifera Wild	Terrestrial	Hyper-accumulation	[13]
Asteraceae	Gynura pseudochina (L.) DC.		Cr VI reduction	[143]
Tisteraceae	Helianthus annuus L.	Annual forb	Hyper-accumulation	[144]
	Parthenium hysterophorus L.	Annual, erect, herbaceous Hyper-accumulation	[117]	
	Vernonia cinerea (L.) Less.	Perennial herb	51	[127]
Brassicaceae	Brassicanapus L.	Annual or biennialherb	Gentle Remediation Options (GROs)	[139]
Callitraceae	Callitriche cophocarpa Sendtn.	Aquatic macrophyte	Cr VI reduction	[145]
Cannabaceae	Cannabis sativa L.	Annual, herbaceous, flowering	Hyper-accumulation	[117,118]
Cannaceae	Canna indica L.	Long-lived, perennial herb	Hyper-accumulation	[120]
Commeliniaceae	<i>Tradescantia pallida</i> (Rose) D.R. Hunt	Succulent perennial herb	Increased anti-oxidant activity	[146]
Convolvulaceae	Ipomoea aquatica Forssk.	Semi-aquatic, tropical plant	Hyper-accumulation	[131]
Euphorbiaceae	Euphorbia helioscopia L.	Desert, herbaceous spurge	Hyper-accumulation	[117]
	Rumex dentatus L.			
Fabaceae	Arachis hypogea L.	Annual herb	Hyper-accumulation	[114]
	Cassia tora L.	Annual under shrub		[140]
	Medicago sativa L.	Perennial flowering plant	High proline and GST accumulation	[147]
	<i>Medicago truncatula</i> Gaertn.	Small annual legume	Regulating the sulphur transport and metabolism	[14]
	Sesbaniasesban (L.) Merr.	Fast-growing, perennial legume tree	Phyto-stabilizer	[125]
	<i>Vigna unguiculata</i> (L.) Walp.	Annual, herbaceous legume	Hyper-accumulation	[114]

Table 1. List of chromium tolerant plant species, their habitats and tolerance mechanisms.

Family	Plant	Habitat	Tolerance Mechanism	References
Lamiaceae	Origanum vulgare L.	Mediterranean, perennial herb	Hyper-accumulation	[122]
	Salvia moorcroftiana Wall.ex Benth.	White-woolly perennial herb	Biosorptive detoxification	[135]
Plantaginaceae	Callitriche cophocarpa Sendtn.	Water-submerged, macrophyte	Hyper-accumulation	[128]
	Arundo donax L.	Tall perennial cane	Hyper-accumulation	[126]
Poaceae	Brachiaria mutica (Forssk.) Stapf	Evergreen, perennial grass	Phyto-stabilizer	[125]
	<i>Chrysopogon</i> <i>zizanioides</i> (L.) Roberty	Perennial, bunch-grass	Hyper-accumulation	[121]
	<i>Diectomis fastigiata</i> (Sw.) P. Beauv.	Tropical grass		[127]
	Triploid hybrid Napier grass (diploid <i>Pennisetum americanus</i> L. X tetraploid elephant grass <i>Pennisetum purpureum</i> Schumach)	Waste lands, roadside, tropical grass		[123]
	Leersia hexandra Sw.	Aquatic perennial grass	Iron-biochar nano-complex & hyperaccumulator	[134]
	<i>Miscanthus sinensis</i> Andersson (1855)	Herbaceous perennial plant	Hyper-accumulation	[97]
	Oryza sativa L.	Flooded, arable land	Hyper-accumulation	[18]
	Phragmites australis (Cav.)Trin. ex Steud.	Perennial grass	Cr III precipitation	[148]
			Cr VI reduction	[144]
	Phragmites communis (Trin.)	Wetland grass	Producing indole acetic acid, siderophores etc.	[15]
	Spartina argentinensis (Trin.) Merr.	Perennial grass	Hyper-accumulation	[66]
	Vetiveria zizanoides (L.) Roberty			[115]
	Eichhornia crassipes Mart.	Aquatic, flowering plant	Hyper-accumulation	[129]
Pontederiaceae		Aquatic plant	Anti-oxidant activity and accumulation	[136]
		Free floating, perennial aquatic plant	Increased anti-oxidant activity	[149]
Pteridaceae	Pteris vittata L.	Fern species	Hyper-accumulation	[150]
Rubiaceae	Genipa americana L.	Wood plant	Hyper-accumulation	[151]
Salviniaceae	Salvinia minima Baker 1886	Aquatic macrophyte	Increased anti-oxidant activity	[152]
Solanaceae	Solanum viarum Dunal	Perennial shrub	Hyper-accumulation	[124]

Table 1. Cont.

7. Concluding Remark and Future Prospect

Cr affects various life forms by altering its physiological and metabolic pathways. On exposure with Cr, the plant remodulates its genetic and transcriptional regulation for better adaptation. Until now, only limited studies on molecular pathways and signaling have been discovered to confer tolerance against Cr toxicity in plants. Further research is required to know the various transporters for Cr uptake and its translocation inside the plant through which the complete metabolic machinery could be understood. A handful of the phytoremediation experiments are generally performed at a lab scale in controlled hydroponic settings with different concentrations of Cr. Results showed significant reduction and removal in toxic Cr concentration but these data are limited by the fact that in vitro conditions are quite different from the outside ecosystem. Hence, the tolerant native plants need to be screened that are better adapted and can bioremediate Cr from the Cr-contaminated regions. Author Contributions: Conceptualization, D.S. and M.T.; investigation, D.S., M.T., P.D., P.S., K.C. and M.K.; data curation, D.S., M.T., P.D., P.S., K.C. and M.K.; writing—original draft preparation, D.S., M.T., P.D., P.S., K.C. and M.K.; writing—review and editing, D.C., D.S. and M.T.; visualization, D.C.; supervision, D.C. All authors have read and agreed to the published version of the manuscript.

Funding: This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: Authors acknowledge Director, CSIR-National Botanical Research Institute for providing facilities and support during the study. This manuscript bears CSIR-NBRI Communication number CSIR-NBRI_MS/2021/04/04.

Conflicts of Interest: The authors declare no conflict of interest.

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