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Chromium Toxicity in Crop Plants: Mechanisms, Physiological Responses, and Remediation Strategies: A Review

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ABSTRACT

Chromium (Cr) contamination has emerged as a serious environmental concern driven by rapid industrialization and diverse anthropogenic activities. Chromium enters agricultural soils and water systems primarily through effluents from leather tanning, electroplating, metal processing, pigment manufacturing, and mining operations. Among its various oxidation states, hexavalent chromium [Cr(VI)] is considerably more toxic, mobile, and bioavailable than its trivalent counterpart [Cr(III)], with Cr(VI) being absorbed more readily by plants and forming free radicals during intracellular reduction. Elevated chromium concentrations adversely affect seed germination, plant growth, photosynthesis, mineral nutrition, water relations, and cellular metabolism across diverse crop species including wheat, rice, maize, sunflower, and legumes. A key mechanism underlying this phytotoxicity is the induction of oxidative stress via the generation of reactive oxygen species (ROS), including superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($OH^·$), leading to membrane damage through lipid peroxidation, protein degradation, and DNA alterations. In response, crop plants deploy a range of physiological and biochemical defenses, most notably the upregulation of antioxidant enzyme systems including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX). Certain plant species capable of accumulating and tolerating chromium, such as Brassica juncea, Helianthus annuus, Sorghum bicolor, and Vetiveria zizanioides, hold significant promise for phytoremediation applications. Recent advances have identified novel amelioration strategies including the application of nanoparticles, plant growth regulators, chelating agents, and beneficial microorganisms that enhance chromium tolerance and remediation efficiency. This review synthesizes current knowledge on the sources, environmental distribution, uptake mechanisms, physiological and biochemical impacts, and remediation strategies associated with chromium toxicity in crop plants, with emphasis on molecular mechanisms and practical applications for sustainable agriculture.

KEY WORDS: *Chromium toxicity, Heavy metals, Oxidative stress, Crop plants, Phytoremediation, Chromium uptake, Antioxidant enzymes, ROS generation*

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1. Introduction

Heavy metal contamination has become one of the most pressing environmental concerns worldwide, threatening agricultural productivity, food security, and ecosystem health [1], [2]. Among the metals of greatest concern, chromium (Cr) stands out for its widespread release

into the environment through both industrial and agricultural activities, with particular emphasis on its accumulation in agricultural soils and subsequent entry into the food chain [2], [3]. Although chromium occurs naturally in rocks, soils, and volcanic emissions at background concentrations typically ranging from 10 to 50 mg kg^{-1}, anthropogenic inputs have substantially elevated its concentrations across terrestrial and aquatic ecosystems, often exceeding safe thresholds for plant growth and human health [2], [4].

Chromium exists predominantly in two stable oxidation states: trivalent chromium [Cr(III)] and hexavalent chromium [Cr(VI)], which exhibit markedly different chemical properties, mobility, and biological effects [2], [5]. Cr(VI) is highly soluble, mobile, and readily absorbed by plant roots, rendering it considerably more toxic than Cr(III), which is relatively immobile and less bioavailable under typical environmental conditions [2], [6]. The critical distinction between these forms lies in their redox chemistry: Cr(VI) acts as a strong oxidizing agent and forms free radicals during its intracellular reduction to Cr(III), thereby generating reactive oxygen species (ROS) that cause extensive cellular damage [2], [7]. This oxidative stress mechanism underlies much of the phytotoxicity observed in chromium-exposed plants [7], [8].

The progressive accumulation of chromium in agricultural soils poses a growing threat to crop productivity, with documented adverse effects on major food crops including wheat (*Triticum aestivum*), rice (*Oryza sativa*), maize (*Zea mays*), sunflower (*Helianthus annuus*), and various legume species [1], [3], [4], [9]. Chromium toxicity manifests across multiple levels of biological organization, from molecular alterations in gene expression and protein synthesis to whole-plant effects on growth, development, and yield [6], [10], [11]. Understanding these multifaceted impacts is essential for developing effective strategies to mitigate chromium toxicity and restore contaminated agricultural lands [12], [13].

Recent advances in plant molecular biology, proteomics, and metabolomics have provided unprecedented insights into the mechanisms of chromium toxicity and tolerance, revealing complex networks of stress-responsive genes, metabolic pathways, and defense systems [6], [10], [11]. Simultaneously, innovative remediation approaches combining phytoremediation with microbial inoculants, nanoparticles, and plant growth regulators have shown promise for enhancing chromium removal from contaminated soils while maintaining agricultural productivity [9], [13], [14]. This review synthesizes current knowledge on chromium toxicity in crop plants, integrating mechanistic understanding with practical applications for sustainable agriculture and environmental restoration [1], [2], [12].

2. Sources of Chromium Contamination

Chromium contamination in agricultural and natural environments originates from a broad range of industrial activities that have intensified with global industrialization [2], [15]. Key anthropogenic sources include leather tanning industries, which are among the largest contributors of chromium pollution due to the extensive use of chromium salts in the tanning process, electroplating operations that generate chromium-rich effluents, stainless steel manufacturing and other metallurgical processes, textile dyeing industries, pigment production facilities, mining and ore processing activities, coal combustion in power plants, and the discharge of untreated or inadequately treated industrial wastewater into agricultural irrigation systems [2], [4], [15].

In developing countries in particular, the release of inadequately treated industrial effluents has contributed substantially to chromium accumulation in agricultural lands, with documented cases of soil chromium concentrations exceeding 500 mg kg^{-1} in areas adjacent to industrial zones [1], [4]. Tannery effluents represent a particularly severe source of contamination, often containing chromium concentrations ranging from 2,000 to 5,000 mg L^{-1}, which when used for irrigation can rapidly elevate soil chromium levels beyond phytotoxic thresholds [2], [15]. Similarly, electroplating industries discharge effluents containing 100 to 1,000 mg L^{-1} chromium, primarily in the highly toxic hexavalent form [2].

Agricultural practices can also contribute to chromium accumulation through the application of chromium-contaminated sewage sludge, industrial compost, and certain phosphate fertilizers that contain chromium as an impurity [2], [4]. The long-term irrigation of agricultural fields with chromium-contaminated groundwater or surface water further exacerbates soil contamination, creating a persistent environmental problem that threatens both crop production and food safety [1], [15]. The spatial distribution of chromium contamination is typically heterogeneous, with highest concentrations observed in topsoil layers (0-20 cm depth) where most crop roots are concentrated, thereby maximizing plant exposure to this toxic element [4].

3. Chromium Uptake and Translocation in Plants

Chromium is not an essential nutrient for plants, and consequently, no dedicated transporters exist for its uptake [2], [16]. Instead, chromium enters plant tissues via transport systems evolved for structurally similar essential ions, exploiting the molecular mimicry between chromate [CrO_4^{2-}] and sulfate [SO_4^{2-}], phosphate [PO_4^{3-}], and iron carriers [2], [5], [16]. Of

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the two dominant oxidation states, Cr(VI) in the form of chromate anion is absorbed more readily than Cr(III), which exists as cationic species with limited mobility in soil solution and restricted entry through root cell membranes [2], [5], [6].

The uptake of Cr(VI) occurs primarily through sulfate transporters located in root cell plasma membranes, as the tetrahedral chromate ion closely resembles sulfate in size and charge [2], [16]. This non-selective uptake mechanism explains why chromium accumulation in plants is often inversely related to sulfate availability in the growth medium [16]. Once absorbed, Cr(VI) is rapidly reduced to Cr(III) within plant tissues through both enzymatic and non-enzymatic pathways involving ascorbate, glutathione, and other cellular reductants, with this reduction process generating reactive oxygen species as toxic byproducts [2], [7], [8].

Following uptake, chromium tends to accumulate predominantly in root tissues, with only limited translocation to shoots and reproductive organs, resulting in root-to-shoot translocation factors typically ranging from 0.1 to 0.5 in most crop species [1], [3], [4], [5]. This restricted translocation pattern reflects the plant's defense strategy to minimize chromium transport to photosynthetically active and reproductive tissues [5], [16]. Studies on wheat, rice, and maize have demonstrated that 60-80% of total plant chromium remains sequestered in roots even after prolonged exposure [3], [4], [10]. To mitigate internal toxicity, plants often sequester chromium within root vacuoles through the action of tonoplast-localized transporters, thereby restricting its movement to more metabolically active tissues and reducing interference with essential cellular processes [5], [16].

However, significant interspecific variation exists in chromium uptake and translocation patterns, with hyperaccumulator species such as *Leersia hexandra* and certain *Brassica* species exhibiting enhanced translocation to aerial parts, a trait that makes them particularly valuable for phytoremediation applications [2], [23]. Recent transcriptomic and proteomic studies have identified specific transporter genes and proteins that are differentially regulated under chromium stress, including members of the ABC transporter family, metal tolerance proteins (MTPs), and natural resistance-associated macrophage proteins (NRAMPs), which collectively modulate chromium uptake, sequestration, and detoxification [6], [10], [11].

4. Effects of Chromium on Seed Germination and Plant Growth

Chromium toxicity exerts pronounced inhibitory effects across multiple stages of plant development, beginning with seed germination and extending through vegetative growth to reproductive maturity [1], [3], [4]. Reductions in seed germination percentage, germination

rate, root elongation, shoot growth, biomass accumulation, and yield attributes have been widely documented across diverse crop species [1], [3], [4], [5].

In sunflower (*Helianthus annuus*), chromium application at concentrations ranging from 50 to 500 mg kg^{-1} soil significantly decreased germination percentage, with the highest concentration reducing germination by approximately 40% compared to control plants [1]. Similarly, studies on wheat seedlings exposed to 10, 50, and 100 ppm chromium demonstrated progressive reductions in seedling vigor, with germination inhibition reaching 80% at the highest concentration [28]. The inhibitory effects on germination are attributed to chromium interference with water imbibition, disruption of enzyme activities involved in reserve mobilization, and direct toxicity to embryonic tissues [1], [4].

Root growth is typically the most severely impaired parameter under chromium stress, as roots represent the primary site of chromium contact and uptake from contaminated growing media [3], [4], [5]. In mung bean (*Vigna radiata*) grown in chromium-contaminated soil, root length decreased progressively with increasing contamination levels, with plants in 100% waste soil (5.433 mg kg^{-1} available chromium) showing 60% reduction in root length compared to controls [29]. Maize seedlings exposed to chromium stress exhibited significant reductions in both root and shoot length, with root growth being more sensitive than shoot growth across all tested concentrations [4], [12]. This differential sensitivity reflects the direct exposure of roots to soil chromium and the plant's ability to restrict chromium translocation to aerial parts [5].

Chromium toxicity also severely impacts plant biomass accumulation, with reductions in both fresh weight and dry weight reported across numerous crop species [1], [3], [4], [5]. In sunflower, chromium treatments (50-500 mg kg^{-1}) caused dose-dependent decreases in plant biomass, with the highest concentration reducing dry biomass by approximately 65% [1]. Rice seedlings exposed to hexavalent chromium showed significant reductions in shoot and root fresh weight, with proteomic analysis revealing alterations in proteins involved in cell wall synthesis, cytoskeleton organization, and cell division [20]. The growth inhibition is mechanistically linked to chromium-induced disruptions in cell division, cell elongation, and overall metabolic efficiency [4], [20].

At the cellular level, chromium exposure causes ultrastructural alterations including disruption of cell wall integrity, plasma membrane damage, organelle degradation, and accumulation of electron-dense chromium deposits in root cells [24]. Sweet potato (*Ipomoea batatas*) plants exposed to chromium exhibited severe ultrastructural damage including swollen mitochondria,

disrupted chloroplast thylakoid membranes, and accumulation of lipid droplets and starch granules, indicative of metabolic dysfunction [24]. These cellular-level changes provide mechanistic insight into the macroscopic growth reductions observed under chromium stress [20], [24].

5. Physiological Effects of Chromium Toxicity

5.1 Photosynthesis

Chromium impairs photosynthetic efficiency through several interconnected mechanisms, including reduction in chlorophyll content, structural damage to chloroplast ultrastructure, inhibition of electron transport chain components, suppression of Calvin-Benson cycle enzyme activities, and reduced CO_2 assimilation capacity [1], [5], [8], [18], [30]. These effects collectively diminish the plant's capacity for carbon fixation and energy production, ultimately limiting growth and productivity [1], [8].

Chlorophyll degradation is one of the most consistent responses to chromium stress across crop species [1], [3], [5], [18]. In sunflower, chromium treatments (50-500 mg kg^{-1}) caused significant reductions in total chlorophyll content, with the highest concentration decreasing chlorophyll by approximately 55% compared to controls [1]. Similarly, maize plants exposed to chromium stress showed dose-dependent decreases in chlorophyll a, chlorophyll b, and total chlorophyll content, with concurrent increases in chlorophyllase activity suggesting active chlorophyll degradation [18]. The reduction in chlorophyll content is attributed to chromium interference with chlorophyll biosynthesis, particularly through inhibition of δ-aminolevulinic acid synthesis and disruption of magnesium insertion into the porphyrin ring [8], [18].

Chromium stress severely impairs photosystem function and electron transport processes [8], [30]. In pepper (*Capsicum annuum*), Cr(VI) stress severely impaired photosynthetic performance by disrupting photosystem efficiency, suppressing Calvin-Benson cycle enzyme activities, and reducing ATP and NADPH production, leading to excessive reactive oxygen species accumulation [30]. Studies on tomato plants demonstrated that chromium exposure decreased the maximum quantum yield of photosystem II (Fv/Fm), effective quantum yield (ΦPSII), and photochemical quenching coefficient, indicating damage to the photosynthetic apparatus [8]. The application of 5-aminolevulinic acid was shown to alleviate these effects by protecting photosystem II and enhancing chlorophyll synthesis [8].

At the ultrastructural level, chromium causes severe damage to chloroplast structure, including disruption of thylakoid membrane organization, swelling of grana stacks, accumulation of

plastoglobuli, and reduction in starch grain number [20], [24]. Rice seedlings exposed to hexavalent chromium exhibited chloroplast degradation with disorganized thylakoid membranes and reduced grana stacking, correlating with decreased photosynthetic efficiency [20]. Sweet potato plants showed similar chloroplast damage along with accumulation of electron-dense deposits, likely representing chromium-protein complexes [24].

The Calvin-Benson cycle, responsible for carbon fixation, is also significantly impaired under chromium stress [30]. In pepper plants, Cr(VI) stress suppressed the activities and gene expression of key Calvin cycle enzymes including ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), fructose-1,6-bisphosphatase, and sedoheptulose-1,7-bisphosphatase, leading to reduced carbon assimilation [30]. The application of the synthetic strigolactone analog rac-GR24 markedly restored photosynthetic carbon metabolism by enhancing these enzyme activities and preserving chloroplast function [30]. Proteomic studies have identified numerous photosynthesis-related proteins that are downregulated under chromium stress, including components of photosystem I and II, ATP synthase subunits, and RuBisCO subunits, providing molecular evidence for the observed physiological impairments [10], [20].

5.2 Water Relations

Chromium stress also disrupts plant-water dynamics, adversely affecting water uptake, stomatal conductance, relative water content, transpiration rate, and overall water use efficiency [1], [5]. These disruptions in water relations compound growth inhibition and may exacerbate nutrient deficiencies under field conditions [1], [5].

Studies on sunflower demonstrated that chromium treatments significantly reduced relative water content and increased water saturation deficit, indicating impaired water balance [1], [5]. The reduction in water uptake is attributed to chromium-induced damage to root cell membranes, disruption of aquaporin function, and reduced root hydraulic conductivity [5]. Additionally, chromium accumulation in root tissues can cause physical blockage of xylem vessels through the formation of chromium-protein precipitates, further restricting water transport to aerial parts [5].

Stomatal function is also compromised under chromium stress, with reports of both stomatal closure (as a stress response) and impaired stomatal regulation [5], [18]. In maize, chromium exposure led to decreased stomatal conductance and transpiration rate, which while potentially reducing water loss, also limited CO_2 uptake for photosynthesis, thereby contributing to

reduced photosynthetic efficiency [18]. The disruption of water relations is closely linked to chromium-induced oxidative stress, as ROS accumulation can damage membrane lipids and proteins involved in water transport and regulation [7], [8].

5.3 Mineral Nutrition

Chromium interferes with the uptake and utilization of essential macronutrients and micronutrients, including nitrogen (N), phosphorus (P), potassium (K), iron (Fe), magnesium (Mg), calcium (Ca), and zinc (Zn) [1], [2], [5]. The resulting nutrient imbalances further impair physiological function and growth, creating a cascading effect that amplifies the overall toxicity response [1], [5].

In sunflower, chromium treatments (50-500 mg kg^{-1}) significantly reduced the concentrations of nitrogen, phosphorus, potassium, and magnesium in plant tissues, with the highest chromium level causing 40-50% reductions in these essential nutrients [1]. The interference with nutrient uptake occurs through multiple mechanisms: competitive inhibition at transporter sites (e.g., chromate competing with sulfate and phosphate transporters), chromium-induced damage to root cell membranes affecting nutrient permeability, disruption of root architecture reducing absorptive surface area, and chromium-induced alterations in rhizosphere pH and microbial communities affecting nutrient availability [2], [5], [16].

The reduction in iron uptake and utilization is particularly significant, as iron deficiency symptoms (chlorosis) are commonly observed in chromium-stressed plants [2], [5]. Chromium can interfere with iron transport proteins and disrupt iron homeostasis mechanisms, leading to functional iron deficiency even when soil iron levels are adequate [5]. Similarly, magnesium deficiency induced by chromium stress contributes to chlorophyll degradation, as magnesium is the central atom in the chlorophyll molecule [1], [18]. The complex interactions between chromium and essential nutrients highlight the multifaceted nature of chromium toxicity and the importance of maintaining balanced mineral nutrition in contaminated soils [1], [2], [5].

6. Biochemical and Molecular Responses

Chromium exposure triggers oxidative stress by overproducing reactive oxygen species (ROS), including superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($OH\cdot$), which cause extensive cellular damage through lipid peroxidation, protein oxidation, and DNA damage [2], [7], [8], [16], [29]. The generation of ROS occurs primarily during the intracellular reduction of Cr(VI) to Cr(III), a process that involves electron transfer reactions

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producing free radicals as intermediates [2], [7]. Additionally, chromium-induced disruption of electron transport chains in mitochondria and chloroplasts contributes to ROS overproduction [7], [8].

Lipid peroxidation, measured as malondialdehyde (MDA) content, is a widely used biomarker of oxidative damage in chromium-stressed plants [7], [8], [16], [18], [28], [29]. In wheat seedlings exposed to chromium (10-100 ppm), lipid peroxidation increased significantly in a dose-dependent manner, with the highest concentration causing a 250% increase in MDA content compared to controls [28]. Similarly, mung bean plants grown in chromium-contaminated soil exhibited elevated lipid peroxidation levels, indicating membrane damage and loss of cellular integrity [29]. Green gram (*Vigna radiata*) exposed to chromium showed progressive increases in peroxide content and lipid peroxidation with increasing chromium concentrations [16].

To counteract the resulting cellular damage, plants activate a suite of antioxidant defense enzymes—notably superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX)—that collectively help restore and maintain cellular redox homeostasis under chromium stress [7], [8], [13], [16], [18], [28]. The response patterns of these enzymes vary with chromium concentration, exposure duration, and plant species [13], [16], [18].

Superoxide dismutase (SOD), which catalyzes the dismutation of superoxide radicals to hydrogen peroxide and oxygen, typically shows increased activity under moderate chromium stress but may decline at very high concentrations [16], [18], [28]. In wheat seedlings, SOD activity initially increased at 10 ppm chromium but declined at 50 and 100 ppm, suggesting that the antioxidant system was overwhelmed at higher concentrations [28]. Maize plants exposed to chromium showed enhanced SOD activity as a primary defense response, with activity levels correlating with chromium tolerance [18].

Catalase (CAT) and various peroxidases (POD, APX) are responsible for scavenging hydrogen peroxide, preventing its conversion to highly reactive hydroxyl radicals [7], [8], [16]. In wheat, CAT activity declined under chromium stress, while POD activity increased dramatically (370% increase at 100 ppm), suggesting a compensatory mechanism where peroxidases assume a greater role in H_2O_2 detoxification when catalase is inhibited [28]. Green gram showed increased POD activity under chromium stress, contributing to oxidative stress mitigation [16]. Tomato plants treated with 5-aminolevulinic acid exhibited enhanced

activities of SOD, CAT, POD, and APX, which correlated with improved chromium tolerance and reduced oxidative damage [8].

Beyond enzymatic antioxidants, plants also accumulate non-enzymatic antioxidants including ascorbate, glutathione, proline, and phenolic compounds under chromium stress [7], [8], [13]. Sunflower plants exposed to chromium accumulated proline as an osmolyte strategy, which not only helps maintain osmotic balance but also acts as a ROS scavenger and stabilizer of proteins and membranes [1]. The glutathione system plays a crucial role in chromium detoxification through direct reduction of Cr(VI) to Cr(III) and conjugation of chromium with glutathione for sequestration in vacuoles [7], [13].

Recent advances in omics technologies have provided unprecedented insights into the molecular responses to chromium stress [6], [10], [11]. Transcriptomic analysis of rice roots exposed to Cr(VI) revealed differential expression of thousands of genes involved in stress response, detoxification, antioxidant defense, and metabolic reprogramming [10]. Key upregulated genes included those encoding glutathione S-transferases, metallothioneins, heat shock proteins, and transcription factors regulating stress responses [10]. Metabolomic profiling identified significant alterations in amino acid metabolism, organic acid accumulation, and secondary metabolite biosynthesis, reflecting comprehensive metabolic reprogramming under chromium stress [6], [10].

Proteomic studies have identified numerous proteins that are differentially expressed under chromium stress, including those involved in antioxidant defense, protein folding and degradation, energy metabolism, and signal transduction [11], [12], [20]. In maize leaves, short-term chromium stress altered the expression of 42 proteins, with upregulation of stress-responsive proteins and downregulation of photosynthesis-related proteins [12]. Rice seedlings showed similar proteomic alterations, with increased abundance of detoxification enzymes and decreased abundance of metabolic enzymes [20]. These molecular studies provide mechanistic insights into chromium toxicity and tolerance, identifying potential targets for genetic improvement of chromium resistance [6], [10], [11].

7. Chromium Toxicity Symptoms in Plants

Chromium toxicity manifests through a characteristic set of visible symptoms that reflect the underlying physiological and biochemical disruptions [1], [3], [4], [5], [24]. These symptoms include reduced seed germination, stunted growth, leaf chlorosis (yellowing), necrosis (tissue death), root browning and reduced root proliferation, diminished biomass production,

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premature senescence, and in severe cases, plant death [1], [3], [4], [24], [29].

Chlorosis is one of the earliest and most prominent visual symptoms, typically appearing first in younger leaves due to chromium-induced disruption of chlorophyll synthesis and iron uptake [1], [5], [18]. As stress intensifies, chlorosis progresses to necrosis, with brown or black necrotic lesions appearing on leaf margins and interveinal areas [5], [24]. In sweet potato plants, chromium exposure caused severe phenotypic alterations including leaf curling, wilting, and extensive necrosis, along with root discoloration and reduced root branching [24].

Root symptoms are particularly pronounced, with chromium-exposed roots exhibiting brown to black discoloration, reduced lateral root formation, thickening and brittleness, and in some cases, formation of root galls or nodule-like structures [4], [5], [24], [29]. Mung bean plants grown in chromium-contaminated soil showed progressive reductions in root length and fresh weight with increasing contamination levels, with roots appearing stunted and discolored [29]. These root symptoms reflect the high chromium accumulation in root tissues and the direct toxic effects on root cell division and elongation [4], [5].

At the whole-plant level, chromium toxicity results in overall growth retardation, with plants appearing stunted with reduced leaf area, shortened internodes, and delayed developmental transitions [1], [3], [4]. Sunflower plants exposed to chromium (50-500 mg kg^{-1}) showed dose-dependent reductions in plant height, leaf number, and overall vigor, with the highest concentration causing severe stunting and premature senescence [1]. The severity of these symptoms varies with chromium concentration, exposure duration, plant species, and the inherent tolerance mechanisms of the plant in question [1], [3], [4], [5].

Ultrastructural examination reveals cellular-level symptoms including disruption of cell wall integrity, plasma membrane damage, organelle degradation (particularly chloroplasts and mitochondria), accumulation of electron-dense chromium deposits, and formation of abnormal cellular inclusions [20], [24]. Sweet potato plants showed severe ultrastructural damage including swollen mitochondria with disrupted cristae, chloroplasts with disorganized thylakoid membranes, and accumulation of lipid droplets and starch granules indicative of metabolic dysfunction [24]. These cellular symptoms provide mechanistic insight into the macroscopic toxicity symptoms observed in chromium-stressed plants [20], [24].

8. Phytoremediation of Chromium-Contaminated Soils

Phytoremediation has gained recognition as an environmentally sustainable, cost-effective, and aesthetically acceptable strategy for managing chromium-contaminated soils [1], [2], [12],

[13], [23], [25]. This approach utilizes plants' natural abilities to absorb, accumulate, stabilize, or transform contaminants, offering advantages over conventional remediation methods such as soil excavation, chemical treatment, or thermal desorption [2], [12], [13].

Plant species with high chromium accumulation capacity and tolerance can be strategically deployed to extract (phytoextraction) or stabilize (phytostabilization) chromium in situ [1], [2], [23], [25]. Among the most promising candidates identified to date are *Brassica juncea* (Indian mustard), *Sorghum bicolor* (sorghum), *Helianthus annuus* (sunflower), *Vetiveria zizanioides* (vetiver grass), *Leersia hexandra* (southern cutgrass), *Eichhornia crassipes* (water hyacinth), *Medicago sativa* (alfalfa), and various species of *Brassica* [1], [2], [23]. Sunflower varieties demonstrated high chromium uptake potential, accumulating significant amounts of chromium in both roots and shoots, indicating their suitability as phytoremediation tools for contaminated soil [1]. Studies have shown that certain plant species can accumulate chromium concentrations exceeding 1,000 mg kg^{-1} dry weight in their tissues without severe toxicity symptoms, qualifying them as chromium hyperaccumulators [2], [23].

The efficacy of phytoremediation can be further enhanced by integrating complementary strategies including the inoculation of beneficial rhizospheric microorganisms, application of chelating agents to increase chromium bioavailability, use of nanoparticles to improve plant tolerance, and application of plant growth regulators to enhance biomass production [9], [13], [14], [15], [25]. Arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) have shown particular promise in improving chromium tolerance and uptake [9], [13], [30]. These beneficial microorganisms enhance plant growth under stress conditions, improve nutrient acquisition, produce phytohormones, and in some cases, directly transform chromium to less toxic forms [9], [13].

Recent studies have demonstrated the effectiveness of various amelioration strategies for enhancing chromium tolerance and remediation efficiency [8], [9], [13], [14], [15], [17], [19], [21]. The application of nanoselenium inhibited chromium toxicity in wheat plants by modulating the antioxidant defense system, ascorbate-glutathione cycle, and glyoxalase system, while also reducing chromium uptake [15]. Similarly, iron nanoparticles combined with *Staphylococcus aureus* alleviated chromium stress in rice plants by enhancing antioxidant enzyme activities and reducing oxidative damage [9]. The synthetic strigolactone analog rac-GR24 mitigated Cr(VI) toxicity in pepper by limiting chromium uptake and restoring photosynthetic carbon metabolism [30].

Chelating agents such as EDTA (ethylenediaminetetraacetic acid) and DTPA (diethylenetriaminepentaacetic acid) have been used to enhance chromium bioavailability and uptake, though their application requires careful management to prevent excessive chromium mobilization and potential groundwater contamination [3], [25]. A comparative study of chromium stress in wheat and rice seedlings demonstrated that DTPA and EDTA chelation significantly increased chromium bioaccumulation and altered antioxidant responses, with species-specific differences in tolerance mechanisms [3].

Exogenous application of organic compounds has also shown promise in alleviating chromium toxicity [17], [19], [21]. Salicylic acid-mediated enhanced regulation of oxidative and glyoxalase defense systems, combined with reduced chromium uptake, contributed to alleviation of Cr(VI) toxicity in plants [17]. Glycinebetaine application alleviated chromium toxicity by elevating antioxidant enzyme activities and suppressing chromium uptake and oxidative stress in wheat [21]. These findings highlight the potential for integrating multiple amelioration strategies to optimize phytoremediation efficiency while maintaining plant health and productivity [13], [17], [21].

Genetic variation in chromium tolerance among crop cultivars presents opportunities for breeding or selecting chromium-resistant varieties for cultivation in contaminated areas [3], [6], [13]. Integrative metabolomic and transcriptomic analyses of contrasting rapeseed cultivars revealed distinct mechanisms of hexavalent chromium toxicity and tolerance, with tolerant cultivars exhibiting enhanced antioxidant capacity, more efficient chromium sequestration, and better maintenance of metabolic homeostasis [6]. Such studies provide valuable insights for developing genetically improved chromium-resistant crop varieties through conventional breeding or genetic engineering approaches [6], [13].

9. Future Perspectives

Advancing our understanding of chromium toxicity and its remediation will require sustained interdisciplinary effort integrating plant physiology, molecular biology, soil science, microbiology, and environmental engineering [6], [10], [11], [12], [13]. Priority areas for future research include elucidating the molecular mechanisms underlying chromium tolerance, particularly the identification and characterization of key genes, transcription factors, and regulatory networks controlling chromium uptake, translocation, sequestration, and detoxification [6], [10], [11].

Developing genetically improved chromium-resistant crop varieties through conventional

breeding, marker-assisted selection, or genetic engineering represents a promising avenue for sustainable agriculture in chromium-affected regions [6], [13]. The identification of quantitative trait loci (QTL) associated with chromium tolerance and the cloning of major tolerance genes would facilitate the development of molecular markers for breeding programs [6], [13]. Additionally, genetic engineering approaches such as overexpression of genes encoding metal chelators (metallothioneins, phytochelatins), antioxidant enzymes, or chromium efflux transporters could enhance chromium tolerance in crop plants [13].

Optimizing microbe-assisted phytoremediation strategies requires better understanding of plant-microbe interactions under chromium stress, identification of the most effective microbial strains for different soil types and chromium concentrations, and development of efficient inoculation methods for field applications [9], [13]. The use of synthetic microbial consortia combining multiple beneficial functions (chromium reduction, plant growth promotion, stress tolerance enhancement) may offer superior performance compared to single-strain inoculants [9], [13].

Evaluating sustainable remediation technologies at the field scale is essential for translating laboratory and greenhouse findings to practical applications [12], [13], [25]. Long-term field trials are needed to assess the effectiveness, economic feasibility, and environmental safety of various phytoremediation approaches under realistic agricultural conditions [12], [13]. Such studies should consider factors including seasonal variations, crop rotation systems, biomass disposal methods, and potential risks of chromium entry into the food chain [12], [13].

Conducting comprehensive food safety assessments in chromium-affected agricultural systems is crucial for protecting human health [2], [12]. Research is needed to quantify chromium accumulation in edible plant parts, assess the bioavailability of plant-accumulated chromium to humans, establish safe threshold levels for chromium in food crops, and develop strategies to minimize chromium transfer from soil to edible tissues [2], [12]. Additionally, investigating the effects of food processing and cooking on chromium speciation and bioavailability would provide valuable information for risk assessment [2].

Emerging technologies such as nanotechnology, synthetic biology, and precision agriculture offer new opportunities for managing chromium contamination [9], [14], [15]. Nanoparticles can be engineered to enhance plant tolerance, improve nutrient delivery, or directly remediate chromium through adsorption or reduction mechanisms [9], [15]. Synthetic biology approaches could enable the design of novel chromium-sensing and detoxification systems in

plants or microorganisms [13]. Precision agriculture technologies including remote sensing, GIS mapping, and site-specific management could optimize remediation efforts by identifying contamination hotspots and tailoring interventions to local conditions [12].

10. Conclusion

Chromium is a highly toxic environmental pollutant with far-reaching consequences for plant growth, physiology, biochemistry, and agricultural productivity [1], [2], [3], [4], [5]. Cr(VI) is of particular concern given its high mobility, solubility, bioavailability, and oxidative potential in biological systems, with its toxicity primarily mediated through the generation of reactive oxygen species during intracellular reduction to Cr(III) [2], [7], [8]. The multifaceted impacts of chromium toxicity span from molecular alterations in gene expression and protein synthesis to whole-plant effects on germination, growth, photosynthesis, water relations, mineral nutrition, and yield [1], [3], [4], [5], [6], [10], [11].

Although plants possess intrinsic antioxidant mechanisms including enzymatic (SOD, CAT, POD, APX) and non-enzymatic (ascorbate, glutathione, proline) defense systems to partially offset chromium-induced oxidative damage, excessive chromium accumulation can overwhelm these defenses and severely compromise plant development [7], [8], [13], [16], [18], [28]. The severity of chromium toxicity varies with concentration, exposure duration, plant species, and developmental stage, with roots being particularly vulnerable due to their direct contact with contaminated soil [1], [3], [4], [5].

The deployment of chromium-tolerant plant species, in combination with phytoremediation technologies and microbial inoculants, offers a viable and ecologically sound approach to restoring contaminated ecosystems and safeguarding sustainable agricultural production [1], [2], [9], [12], [13], [23], [25]. Recent advances in understanding the molecular mechanisms of chromium toxicity and tolerance, coupled with innovative amelioration strategies involving nanoparticles, plant growth regulators, chelating agents, and beneficial microorganisms, have opened new avenues for managing chromium contamination in agricultural systems [6], [8], [9], [10], [11], [13], [14], [15], [17], [19], [21], [30].

Future research should focus on translating mechanistic insights into practical applications, developing genetically improved chromium-resistant crop varieties, optimizing integrated remediation strategies for field-scale implementation, and ensuring food safety in chromium-affected agricultural regions [6], [12], [13]. By integrating fundamental research with applied technologies and adopting a holistic approach to chromium management, it is possible to

mitigate the adverse impacts of chromium contamination while maintaining agricultural productivity and environmental quality [2], [12], [13].

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