Chromium-Induced Reactive Oxygen Species Accumulation by Altering the Enzymatic Antioxidant System and Associated Cytotoxic, Genotoxic, Ultrastructural, and Photosynthetic Changes in Plants

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Abstract: Chromium (Cr) is one of the top seven toxic heavy metals, being ranked 21st among the abundantly found metals in the earth’s crust. A huge amount of Cr releases from various industries and Cr mines, which is accumulating in the agricultural land, is significantly reducing the crop development, growth, and yield. Chromium mediates phytotoxicity either by direct interaction with different plant parts and metabolic pathways or it generates internal stress by inducing the accumulation of reactive oxygen species (ROS). Thus, the role of Cr-induced ROS in the phytotoxicity is very important. In the current study, we reviewed the most recent publications regarding Cr-induced ROS, Cr-induced alteration in the enzymatic antioxidant system, Cr-induced lipid peroxidation and cell membrane damage, Cr-induced DNA damage and genotoxicity, Cr-induced ultrastructural changes in cell and subcellular level, and Cr-induced alterations in photosynthesis and photosynthetic apparatus. Taken together, we conclude that Cr-induced ROS and the suppression of the enzymatic antioxidant system actually mediate Cr-induced cytotoxic, genotoxic, ultrastructural, and photosynthetic changes in plants.

Keywords: reactive oxygen species; antioxidants; cytotoxicity; genotoxicity; photosynthesis

1. Introduction

Chromium (Cr), heavy metal with a range of oxidation numbers [Cr(II) to Cr(VI)], which is placed in the group (VI-B) of transition elements in the modern periodic table [1]. Chromium, which is the hard silver color metal with 7.19 g/cm³ density, 51.10 g/M molecular weight, and 24 atomic number, has been ranked 21st among the most abundantly found metals on the earth’s crust [2]. The trivalent [chromite; Cr(III)] and the hexavalent [chromate; Cr(VI)] are the most stable naturally found Cr species [3]. Hexavalent form of Cr is a potentially strong oxidizing agent, and higher water solubility, mobility, and bioavailability make it the most toxic form of Cr as compared to other Cr species [4]. The oxygenated environment can convert Cr(III) into Cr(VI), the factors that are involved in maintaining the proper ratio of these Cr forms are oxygen concentration, pH, complexing factors, and reducing agents [5].

Chromium extraction from the mines has been excessively increased due to its increasing use in various industries [2]. Kazakhstan, South Africa, China, and India are the world-leading Cr using countries [2,6,7]. Leather tanning, metallurgy, electroplating, alloying, ceramic glazes, wood preservation, water corrosion inhibition, refractory bricks, pressure-treated lumber, textile dyes, and mordant, pigments and paints production, and paper and pulp production industries contribute
to the hyperaccumulation of Cr in the environment. Furthermore, anthropogenic activities, such as the dumping of Cr-contaminated liquids and solids wastes, are the reason for the hyperaccumulation of Cr in the environment [8–11]. The emission of Cr from the cooling towers of the industries and the dust rising from the roads and roadsides are considered to be the most important Cr sources [12,13].

Increased Cr accumulation in the agricultural land causes damage to the plant growth and development at the organ, cellular, or even genetic level [14]. Cr-induced phytotoxicity is mostly mediated via induced reactive oxygen species (ROS), which cause the cellular and extracellular damage in plants [8]. In the current study, we reviewed Cr-induced ROS, associated cellular, and ultra-structural damages in plants.

2. Chromium-Induced Oxidative Stress in Plants

Plants that are exposed to unfavorable conditions produce reactive oxygen species (ROS) as a defense mechanism [15,16]. The hyperaccumulation of ROS generates endogenous stress that can damage plant growth and development [8]. Hydrogen peroxide (H₂O₂), superoxide anion (O₂⁻), singlet oxygen (¹O₂), hydroxyl ion (HO⁻), peroxyl (RO²⁻), alkoxyl (RO⁻), and organic hydroperoxide (ROOH) are the various ROS that are found in plants [2,17,18]. Reactive oxygen species are produced in the mitochondria, peroxisome, and chloroplast as a byproduct of various biochemical reactions [18–21]. Plants mechanisms that are in the regulation of ROS level include ROS biosynthesis, enzymatic, and/or non-enzymatic ROS scavenging [8]. Heavy metals, such as lead (Pb), cadmium (Cd), aluminum (Al), nickel (Ni), and Cr, are reported for the enhancement in ROS productions and accumulation [8,19,22]. Various plant species that are exposed to toxic Cr level or industrial wastes containing the toxic oxygen (¹O₂).

### Table 1. Accumulations and investigations of various ROS species in numerous plant species exposed to Cr(VI) and/or Cr(III).

| Plant Species                   | Common Name          | ROS Types               | Cr(VI) Concentration | References |
|---------------------------------|----------------------|-------------------------|----------------------|------------|
| Arabidopsis thaliana            | Arabidopsis          | O₂⁻, H₂O₂               | 100–400 µM           | [8,23]     |
| Zea mays                        | Sunflower            | O₂⁻, OH⁻, H₂O₂          | 20 mg/L & 20 mg/Kg   | [24–26]    |
| Brassica juncea                 | Indian mustard       | O₂⁻, H₂O₂, OH⁻          | 100–300 µM & 100–300 mg/Kg | [27–32]    |
| Glycine max                     | Soybean              | H₂O₂                    | 400 mg/kg & 500 mg/kg Cr(III) | [23]       |
| Oryza sativa                    | Rice                 | O₂⁻, H₂O₂               | 80–200 µM            | [34–37]    |
| Amaranthus cruentus             | Green & Blood        | O₂⁻, H₂O₂               | 50 µM                | [38]       |
| Chenopodium quinoa              | Quinoa               | H₂O₂                    | 5 mM Cr(III)         | [39]       |
| Cucumis sativus                 | Cucumber             | O₂⁻, H₂O₂               | 200 µM               | [40]       |
| Brassica napus                  | Oilseed rape         | O₂⁻, H₂O₂, OH⁻          | 400 µM               | [41,42]    |
| Brassica campestris             | Cabbage              | O₂⁻                     | 1 mg/L               | [43]       |
| Pisum sativum                   | Pea                  | O₂⁻, H₂O₂               | 100 µM               | [44]       |
| Allium cepa                     | Onion                | O₂⁻, H₂O₂, OH⁻          | 200 µM               | [45]       |
| Matricaria chamomilla           | Chamomile            | H₂O₂                    | 120 µM Cr(III)       | [46]       |
| Lens culinaris                  | Lentil               | H₂O                    | 250 µM               | [47]       |
| Raphanus sativus                | Radish               | O₂⁻, H₂O₂               | 1.2 mM               | [48]       |
| Pistia Striatotes               | Lettuce              | H₂O₂                    | 10 mM                | [49]       |

Chromium-induced ROS accumulation mediates various physiological, biochemical, molecular, and developmental changes in plants [41]. These alterations in the physiological and biochemical process may be provoked by directly interacting with enzymes, lipids, proteins, and genetic material (DNA and/or RNA), or by Cr-induced ROS accumulation [8,50,51]. Cr direct interaction or Cr-induced ROS both mediated membrane damage, degradation and deactivation of genetic material, proteins, and enzymes, which resulted in the growth inhibition by the suppression cell division or activation programmed cell death [8,52,53].
Chromium-induced ROS mediates ultra-structural alteration in various plant tissues and irreversibly degrades biomolecules, except for DNA, cysteine, and methionine, which can be restored, in a dose-dependent and tissue-specific manner [23,45,49,54]. Reactive oxygen species are produced during the reduction reaction of Cr(VI) to Cr(III) and Fenton reaction. The catalytic power of Cr(III) is greater than iron (Fe), copper (Cu), cobalt (Co), manganese (Mn), and zinc (Zn) in the Fenton reaction [2,45,54,55]. The Cr involvement in such reactions is not well studied and some other intermediates and factors may also be involved in the Cr-induced ROS generation [8]. ROS mediated various physiological, biochemical, molecular, and ultrastructural changes, as shown in Figure 1.

**Figure 1.** Cr(VI)-induced ROS mediated alteration in plants: Cr(VI)-induces ROS accumulation by suppressing enzymatic antioxidant system, which damages cellular and subcellular membranes; induces ultrastructural changes in cell organelles such as mitochondria, plastids, and thylakoids; inhibits protein and enzymes at transcriptional or post-transcriptional level as well as degrades various enzymes and proteins; and DNA damages. All of these alterations inhibit photosynthesis and trigger and enhance necrosis, apoptosis, and programmed cell death, and significantly inhibit plant growth and development. Superoxide (O$_2^-$), hydrogen peroxide (H$_2$O$_2$), hydroxyl ion (HO$^-$), and singlet oxygen ($^1$O$_2$). Ascorbate peroxidase (APX), catalase (CAT), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), glutathione reductase (GR), glutathione S-transferase (GST), monodehydroascorbate reductase (MDHAR), peroxidase (POD), and superoxide dismutase (SOD). T-bars represent inhibition or suppression of the target, arrows represent promotion or upregulation of the target, and bold arrows represent the ultimate downstream result or impact of the process.

### 3. Chromium-Mediated Alteration in the Enzymatic Antioxidant System

Plants have developed a complex and well-organized enzymatic antioxidant system to deal with access ROS, produced by various endogenous and exogenous stimuli, including toxic Cr levels [8]. Superoxide (O$_2^-$) is converted to H$_2$O$_2$ by superoxide dismutase (SOD). H$_2$O$_2$ is converted by ascorbate peroxidase (APX), peroxidase (POD), and catalase (CAT) to H$_2$O [8,56]. Furthermore, to minimize the Cr, cadmium (Cd), bisphenol A (BPA), and other abiotic stresses mediated oxidative stress, plants use the enzymatic antioxidant system, which includes, SOD, APX, POD, CAT, glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), and glutathione S-transferase (GST) [8,17,21,50,57,58]. Previous studies have reported that Cr-induces the alteration in the production and accumulation of enzymatic antioxidant system for the regulation and scavenging Cr-induced ROS have been summarized in Table 2.
Table 2. Chromium-modulated antioxidant enzymes in various plant species. Ascorbate peroxidase (APX), catalase (CAT), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), glutathione reductase (GR), glutathione S-transferase (GST), monodehydroascorbate reductase (MDHAR), peroxidase (POD), and superoxide dismutase (SOD).

| Plant Species | Common Name | Enzymes | Cr(VI)       | References |
|---------------|-------------|---------|--------------|------------|
| Helianthus annuus | Sunflower | CAT, SOD, POD, APX | 20 mg/kg | [25,26] |
| Triticum aestivum | Wheat & Barley | CAT, APX | 22 mg/kg | [59] |
| Hordeum vulgare | Black Barley | CAT, APX | 225 µM | [81] |
| Brassica oleracea | Cauliflower | CAT, SOD, POD | 200 µM | [60] |
| Pennisetum alopecuroides | Fountain Grass | CAT, SOD, POD | 1500 mg/kg | [61] |
| Sorghum bicolor | Sorghum | CAT, SOD, APX, GR, GST | 64 ppm | [62] |
| Brassica juncea | Indian Mustard | CAT, SOD, POD, GR, GPX, CAT, SOD, POD, APX, MDHAR, DHAR | 300–500 µM | [17,63] |
| Solanum melongena | Eggplant | APX, GST, GR | 25 µM | [64] |
| Amaranthus viridis & | Green & Blood | CAT, SOD, POD, GST | 50 µM | [38] |
| Amaranthus cruentus | Amaranth | CAT, SOD, POD | 100–250 µM | [65,66] |
| Zea mays | Maize | APX, CAT, SOD, POD | 100–250 µM | [65,66] |
| Hibiscus cannabinus | Kenaf | CAT, SOD, POD | 1.5 Mm Cr(III) | [67] |
| Oryza sativa | Rice | APX, CAT, SOD, POD, GR | 20–100 µM | [68,69] |
| Vigna radiate | Mung Bean | CAT, SOD, POD | 500 µM | [70] |
| Brassica chinensis | Pakchoi | CAT, SOD, POD | 100 µM & 200 mg/kg | [71,72] |
| Setaria italic | Foxtail Millet | CAT, SOD, POD, APX | 1000 µM | [73] |
| Solanum nigrum & | Black Nightshade & | SOD, POD | 500 µM Cr(III) | [74] |
| Parthenium hysterophorus | Santa-maria | SOD, POD | 250 µM | [75] |
| Brassica rapa | Turnip | SOD, APX | 500 µM | [76] |
| Brassica napus | Canola | CAT, SOD, POD, APX | 1 mg/l | [43] |
| Brassica campestris | Cabbage | SOD, POD | 100 µM | [77] |
| Cotton | Cotton | CAT, SOD, POD, APX | 400 mg/kg | [78] |
| Corchorus olitorius | Tossa Jute | CAT, SOD, POD, APX, GR | 8 mM | [80] |
| Brassica napus | Canola | CAT, SOD, POD, APX | 225 µM | [81] |

4. Chromium-Induced Lipid Peroxidation

Lipid peroxidation is initiated by the increased ROS accumulation through the decomposition of membrane lipids and proteins, and it is one of the primary reasons for abiotic stress-induced cell damages [82]. Chromium stress has been reported for the induced ROS production, and it has been also reported for biological membrane damage [2]. One of the lipid peroxidation products, called malondialdehyde (MDA), which is considered as an oxidative damage indicator, has been greatly studied in the heavy metals mediated damage of biological membrane, including Cr [8,82]. Chromium-induced ROS mediated lipid peroxidation in various plant species, including economically important crops, has been summarized in Table 3.
Table 3. Chromium-induced lipid peroxidation indicators in various plant species. Thio-barbituric acid reactive substances (TBARS) and malondialdehyde (MDA).

| Plant Species        | Common Name           | LPO    | Cr(VI)  | References |
|----------------------|-----------------------|--------|---------|------------|
| Arabidopsis thaliana | Arabidopsis           | MDA    | 400 µM  | [8]        |
| Zea mays             | Maize                 | MDA    | 100–300 µM | [27,28,31,32,65] |
| Triticum aestivum    | Wheat & Barley        | MDA    | 22 µM   | [59]       |
| Hordeum vulgare      | Tomatoes              | MDA    | 24.66 mg/L | [83]       |
| Oryza sativa         | Rice                  | MDA, TBARS | 20–200 µM & 20 mg/L | [35,36,69,82,84,85] |
| Linum albuminum      | Floating Plant        | MDA    | 70 µg/L Cr(III) | [86]       |
| Citrus reticulata    | Kinnow                | MDA    | 750 µM  | [87]       |
| Sorghum bicolor      | Sorghum               | MDA    | 64 ppm  | [62]       |
| Helianthus annuus    | Sunflower             | MDA    | 20 mg/kg | [25]       |
| Brassica juncea      | Indian Mustard        | MDA    | 100–500 µM & 100 mg/Kg | [17,63,88,89] |
| Solanum melongena    | Eggplant              | MDA    | 25 µM   | [64]       |
| Tradescantia pallida | Rose                  | MDA    | 20 mg/L | [90]       |
| Amaranthus viridis & | Green & Blood         | MDA    | 50 µM   | [38]       |
| Amaranthus cruentus  | Amaranth              | MDA    | 50 µM   | [38]       |
| Pteris vittata       | Chinese Brake         | TBARS  | 5 mM    | [91]       |
| Chenopodium quinoa   | Quinoa                | MDA    | 5 mM Cr(III) | [39]       |
| Saccharum spp. Hybrid| Sugarcane             | MDA    | 50 ppm  | [92]       |
| Cucumis sativum      | Cucumber              | MDA    | 200 µM  | [40]       |
| Pisum sativum        | Pea                   | MDA    | 100 µM  | [44]       |
| Brassica napus       | Turnip                | MDA    | 250 µM Cr(III) | [75]       |
| Brassica napus       | Canola                | MDA    | 50–100 µM | [79,93,94] |
| Brassica oleracea    | Cauliflower           | MDA    | 250 µM  | [95]       |
| Salvinia minima      | Floating Fern         | MDA    | 20 mg/L | [96]       |
| Tradescantia pallida | Wandering Jew         | TBARS  | 20 mg/L | [97]       |
| Gossypium hirsutum   | Cotton                | MDA    | 100 µM  | [77]       |
| Triticum aestivum    | Wheat                 | MDA    | 200 µM  | [98]       |
| Allium cepa          | Onion                 | MDA    | 200 µM  | [45]       |
| Raphanus sativus     | Radish                | MDA    | 125 m   | [80]       |
| Miscanthus sinensis  | Chinese Reed          | MDA    | 1000 µM | [99]       |
| Brassica rapa        | Rapseseed             | TBARS  | 480 µM Cr(III) | [100]      |

5. Chromium-INDUCED DNA DAMAGE and Genotoxicity

Genotoxicity is one of the most serious threats of heavy metals toxicity to living organisms [101,102]. DNA damage can have serious consequences, such as deregulation or mutagenesis of the cell replication process, leading to tumor formation, and ultimately cell death [101,103,104]. Heavy metals cause DNA damage either by direct interaction with DNA or by induced ROS accumulation, which is considered to be one of the main internal causes of DNA damage (Figure 1). Heavy metals not only induce DNA damage, but also interrupt DNA damage repair mechanisms [101,102].

In contrast to other heavy metals, which are directly interacting with DNA, Cr-induces ROS mediated genotoxicity [105]. Chromium-induced genotoxicity and carcinogenic effects are greatly investigated in yeast and animal cells. Its carcinogenic effects have been also reported in the workers, working in the Cr mines and Cr consuming industries [101,104–106]. In vivo and in vitro investigations revealed that Cr(VI) produces various types of structural alterations in genetic materials, including inter-DNA strand cross-links, DNA chromosomal protein cross-links, and nucleotide strand breaks [105,107,108].

Chromium-DNA adducts (association of Cr with phosphodiester backbone of DNA), which are mainly reported in mammalian cells, being considered the primary cause of Cr(VI) induced mutagenicity [105,109]. Cr(VI)-mediated genotoxicity has been reported in humans, rats, fish, fish cell lines, yeast, and bacteria [105,108,110–113]. Some studies have reported that Cr(III) is also interacting with DNA to form a covalent bond with the phosphate backbone [105]. Cr(III) also interacts with the DNA base pairs’ stacking mode, which leads to DNA lesion, cleavage, and the DNA single/double-strand breakage [105,108]. Cr(VI)-induced ROS mediates these various DNA degradations [45]. The current study reviews chromium-induced chromosomal fragmentation and bridging, alteration in DNA methylation, DNA mutation, increase in percent tail DNA, tail moment, and percent DNA damage in tail length, chromosome aberrations or micronuclei formations,
DNA inter/intrastrand crosslinks, protein-DNA crosslinks, DNA-single/double-strand breaks, DNA adducts, DNA transcription, and replication dysfunction, abnormal DNA repair mechanisms, changes in signaling pathways for survival, genomic instability, oxidized bases, instability of microsatellites, and genetic/epigenetic alteration in different plant species (Table 4).

6. Chromium-Induced Ultrastructural Changes

6.1. Cr-Induced Necrosis and Cellular Injury

Chromium-induced cytotoxicity affects essential micronutrient absorption, lipid peroxidation, cell cycle arrest and ultimate cell death in plants [8,22,56,87]. Toxic Cr levels also mediate the stomatal abnormalities, such as the decreased size of stomatal aperture, swelling of guard cells, changes in membrane permeability level, ion flux, and osmotic pressure [22,87,114,115]. These stomatal aberrations significantly influence the a, b, and total chlorophyll contents, stomatal conductance, photosynthetic rate, respiration, and transpiration rate [87,114,115]. Trichomes, which are unicellular outgrowths on the leaf, play a defensive role in plants under stress conditions [116,117]. Metal ions’ active transport regulates the number and distribution of trichomes, and an increased trichome number has been noticed in the plants exposed to toxic Cr(VI) levels [22].

Exposure to high Cr-concentration causes mitochondrial damages, such as outer membrane rupture, swelling, deformed or altered internal cristae, dense electron accumulated materials, and spherical morphology [23,118,119]. It has been also reported that mitochondria were underdeveloped in the Brassica napus seedlings that were exposed to 400 µM Cr as compared seedlings exposed to control conditions [41,120]. The ultrastructural investigations also revealed that Cr(VI) stress alters plastid structure, more specifically, chloroplast, with a spherical and contracted morphology [120–123]. The irregular shape and size of the chloroplast with contained large plastoglobuli and starch grains were reported in Spirodela poyrhiza seedlings that were exposed to high Cr(VI)-level [23]. Cell membrane injury, disruption of cytoplasm, and vacuole upon Cr exposure are frequently reported [23,120,121]. Table 5 summarizes the ultrastructural changes reported in the different plant species exposed to Cr-stress.

Table 4. Chromium-induced genotoxicity in various plant species.

| Plant Species     | Common Name | Genotoxicity                                | Cr- Type          | References       |
|-------------------|-------------|--------------------------------------------|-------------------|------------------|
| Glycine max       | Soybean     | DNA damage, Micronucleus, Chromosomal      | Cr(VI)/(III)      | [22]             |
|                   |             | fragmentation & bridging, Increase in %    |                   |                  |
|                   |             | tail DNA, tail moment and Tail length      |                   |                  |
| Vicia faba        | Faba Bean   | DNA damage, Chromosomal fragmentation &    | Tannery solid     | [124–127]        |
|                   |             | bridging, Increase in % tail DNA, tail    | waste & Cr(VI)    |                  |
|                   |             | moment and Tail length                     |                   |                  |
| Allium cepa       | Onion       | Aberrations, Micronuclei, Chromosomal      | Tannery solid     | [45,125,127–129] |
|                   |             | fragmentation & bridging                   | waste, Tannery    |                  |
|                   |             |                                             | effluent & Cr(VI)|                  |
| Hordeum vulgare   | Barley      | Chromosomal aberrations                    | Cr(VI)            | [130]            |
| Vicia sativa      | Vetch       | Chromosomal aberration                     | Wastes, Cr(VI)/(III) | [125,127,131]   |
|                   |             | Chromosomal fragmentation & bridging       |                   |                  |
| Raphanus sativus  | Radish      | Chromosomal aberration                     | Cr(VI)/(III)      | [125]            |
| Zea mays          | Maize       | Chromosomal aberration                     | Cr(VI)/(III)      | [125]            |
| Brassica napus    | Oilseed Rape| Methyltion changes, mutation                | Cr(VI)            | [127,132]        |
| Arabidopsis thaliana | Arabidopsis | DNA mutation                               | Cr(VI)            | [127,133]        |
Table 5. Chromium-induced ultra-structure variation in numerous plant species. Epi-C-wax (epicuticular wax), TRICH (trichome), CW (cell wall), MITO (mitochondria), CM (cell membrane), THY (thylakoid), THY-O (thylakoid orientation), PG (plastoglobuli), SG (starch grains), GB (Golgi bodies), ER (endoplasmic reticulum), CHLP (chloroplast), I-cristae (interior Cristae), T-nuclei (tubular nuclei), T-stroma (translucent stroma), ML (middle lamella), NM (nuclear membrane), and PT (Plant tissue used).

| Plant Species | Common Names | PT | Effect                                                                 | Cr-Type     | References        |
|---------------|--------------|----|----------------------------------------------------------------------|-------------|-------------------|
| Glycine max   | Soybean      | L  | Loss of Epi-C-wax increased TRICH-number                              | Cr(VI)/(III)| [22]              |
| Brassica napus| Oilseed rape | L & R | Alteration in CW, MITO, CM, THY, PG, SG, GB, ER, Irregular nucleus, THY disappeared, Increased SG number/size. | Cr(VI)      | [41,42,120,134]   |
| Triticum aestivum| Wheat & Barley | L  | Damaged CHLP, THY; Increased PG, Swollen MITO; altered I-cristae CW/CW not distinguishable, Disarranged CHLP structure, Undeveloped nucleus, damaged NM, Swollen/distorted THY, Increased PG, Large SG Swollen CHLP; grana/stroma/lamellae, Reduced grana/CHLP, Increased SG, Matrix zone expanded. | Cr(VI)      | [59]              |
| Nicotiana tabacum| Tobacco      | L & R | Undeveloped nucleus, damaged NM, Swollen/distorted THY, Damaged CHLP, MITO, Altered THY-O, Increased PG, Large SG Swollen CHLP, Grana/stroma/ lamellae, Reduced grana/CHLP, Increased SG, Matrix zone expanded. | Cr(VI)      | [122,123]         |
| Oryza sativa  | Rice         | L  | Damaged CHLP, grana, THY, Increased number/size of SG; large PG Swollen CHLP; Grana/stroma/ lamellae, Reduced grana/CHLP, Increased SG, Matrix zone expanded. | Cr(VI)      | [35,135]          |
| Arabidopsis thaliana| Arabidopsis | R  | Altered MITO with no/reduced I-cristae Swollen CHLP, increased PG, Disintegrated/disappeared THY, MITO, Increased SG | Cr(VI)      | [23,47,136]       |
| Eichhornia crassipes| Water Hyacinth | L  | Damaged THY, MITO, CHLP (structure/distribution), grana Damaged CHLP, grana, THY, Increased number/size of SG; large PG Swollen CHLP, grana, CHLP, Increased SG, Matrix zone expanded. | Cr(VI)      | [137]             |
| Salvinia minima| Floating Fern| L  | Altered MITO with no/reduced I-cristae Swollen CHLP, increased PG, Disintegrated/disappeared THY, MITO, Increased SG | Cr(VI)      | [96]              |
| Taraxacum officinale| Dandelion   | C  | Altered MITO with no/reduced I-cristae Swollen CHLP, increased PG, Disintegrated/disappeared THY, MITO, Increased SG | Cr(VI)      | [138]             |
| Hordeum vulgare| Barley       | L & R | Reduced vacuole size/number, Increased vacuolar size, Cr-presence in CW, Vacuoles, Nucleus disruption/disappearance Abnormal shaped reduced grana/CHLP, altered THY, MITO; reduced cristae numbers Swollen CHLP, CHLP- envelop breakage, decreasing cristae, MITO vacuolization. | Cr(VI)      | [139]             |
| Solanum lycopersicum| Tomatoes     | P  | Grana/CHLP, altered THY, MITO; reduced cristae numbers Swollen CHLP, CHLP- envelop breakage, decreasing cristae, MITO vacuolization. | Cr(III)     | [140]             |
| Potamogeton crispus| Curled Pondweed | L  | Reduced cristae numbers Swollen CHLP, CHLP- envelop breakage, decreasing cristae, MITO vacuolization. | Cr(VI)      | [141]             |

6.2. Electron-Dense Material Deposition in the Subcellular Compartments

Plants restrict the accumulation of heavy metals in the less sensitive organelles to avoid damage to the more sensitive organelles at the cellular level [16,142,143]. The precipitation of electron-dense granules in subcellular compartments, especially in the cell wall, is the first line cellular defense mechanism, against toxic heavy metals [23,144,145]. The electron-dense deposition in the interspace between the cell wall and cell membrane, vacuoles, plastids, between the cisternae of endoplasmic reticulum, and cytoplasm in the seedlings of Arabidopsis that were exposed to Cr(VI) have been previously reported [23,136]. The deposition of electron-dense material in the pectic middle lamella instead of cellulosic/hemicellulosic components of Arabidopsis root tip cells has been also reported [23].
There is a prominent difference in the degree of Cr(VI)-induced damages among the different cellular compartments of plants [23,47,136]. The cellular compartments, such as mitochondria, plastids, Golgi bodies, and vacuoles, were severe; cytoplasm, cell membrane, endoplasmic reticulum (ER) were mild; cell wall and nuclei were moderately damaged in the seedlings of Arabidopsis that were exposed to high Cr(VI) levels [23], as shown in Table 5.

7. Chromium-Mediated Changes in Photosynthesis and Photosynthetic Apparatus

Various heavy metals that influence plant biochemical, physiological, and metabolic processes affect photosynthesis and photosynthetic apparatus, leading to reduced plant growth and yield [3,8,19,23]. The effect of Cr on the photosynthesis and photosynthetic apparatus has been greatly studied in different plant species, and it mainly influences the enzymatic activities, electron transport chain, CO₂ fixation, photosynthetic phosphorylation, and structure of plastids [35,65,146,147]. In various plant species Cr-reduced chlorophyll contents, carotenoids, and photosynthetic activities have been greatly investigated, as summarized in Table 6. The structural changes in the chloroplast could be one of the factors that are involved in the defective photosynthesis [2]. Chromium-induced chloroplast ultrastructural changes mediate the suppression of photosynthesis in various plant species, as summarized in Table 5. Chromium-reduced alterations in the volume and auto-fluorescence of chloroplast [127], altered thylakoid arrangement, chloroplast membrane distortion, and negatively affected light/dark reactions have also been reported [2,22,96,148]. Electron transport chain inhibition might be due to the Cr-induced redox changes in the Fe and Cu carriers or binding of Cr to cytochrome groups to inhibit its oxidative activity [149–151].

Furthermore, high Cr-level mediates ROS accumulation, which is an alternative sink for the electron, being involved in the suppression of photosynthesis [8,127,152]. Heavy metals-induced ROS modulated alteration in the photosynthesis and photosynthetic machinery is intensely studied [60,76]. Destabilization and degradation of antenna complex proteins, Mg⁺ substitutions with H⁺ ion, and thylakoid membrane damage are the main steps in ROS assisted pigment-protein structure and function retardation [2,153]. The Cr(VI)-induced degradation of a chlorophyll biosynthesis key enzyme delta-aminolaevulinic acid dehydratase, and its competing capability with Mg and Fe translocation to leaves are involved in the decreased photosynthetic pigments and photosynthesis [81,154]. High Cr-level in the soil greatly influences macro/micronutrient uptake. As Cr has no specific uptake channels, it is competing with essential elements for the uptake channels [155,156].
Table 6. Chromium-induced alteration in photosynthesis and photosynthetic apparatus in various plant species. Chl a (Chlorophyll a), Chl b (Chlorophyll b), Chl t (total chlorophyll), Chl f (chlorophyll fluorescence), Trmmol (transpiration rate), Cond (stomatal conductance), photo (photosynthetic rate), PSII (photosystem II), Ci (intercellular CO₂), ΦPSII (effective quantum of yield of photosystem II), qP (photochemical quenching), NPQ (non-photochemical quenching), PN (net CO₂ assimilation rate), ETR (electron transportation rate), pigment (photosynthetic pigments).

| Plant Species                   | Common Name          | Alteration in Photosynthetic Parameters                                                                 | Cr(VI)   | References                             |
|---------------------------------|----------------------|---------------------------------------------------------------------------------------------------------|----------|-----------------------------------------|
| Arabidopsis thaliana &          | Arabidopsis & Indian Mustard | Reduced chl a, b, and t Reduced chl a, Reduced Chl t, Carotenoids, and net photo, b, and t, Gas exchange | 400 µM   | [8] & [58,88,89,157]                   |
| Brassica juncea                 |                      |                                                                                                         | 100–300 µM & 100 mg/Kg                             |          |
| Helianthus annuus               | Sunflower            | Reduced chl a, b, t, gas exchange, and carotenoid levels                                              | Tannery effluent & 20 mg/kg                         | [26,158] |
| Citrus reticulate              | Kinnow Mandarin     |                                                                                                         | 0.75 mM  | [87]                                    |
| Cypersus alternifolius & Coix lacryma-jobi & |          | Inhibition in photosynthetic capacities                                                              | 40 mg/L  | [159]                                   |
| Solanum melongena               | Eggplant             | Reduced pigments, photo, photochemistry of PSII                                                      | 25 µM    | [64]                                    |
| Oryza sativa                    | Rice                 | Reduced Chl a, b, and carotenoids, Reduced Fv/Fm                                                    | 80–200 µM | [34,35]                                |
| Zea mays                        | Maize                | Inhibition photochemistry of PSII Alteration in Fv/Fm, Fv/F0, and qP                                 | Tannery effluent & 150–250 µM                       | [29,147,160] |
| Amaranthus viridis & Amaranthus cruentus & | | Reduced chl f parameters, and Cr(III)                                                                    | 50 µM    | [38]                                    |
| Nicotiana tabacum               | Tobacco              | Reduced Chl a, b, carotenoids, photo, gas exchange, Fv/Fm fluorescence                                | 50 µM    | [122]                                   |
| Sesbania grandiflora            | Hummingbird Tree     | Reduced Chl t                                                                                           | 1.92 mM/Kg | [161]                               |
| Lactuca sativa                  | Lettuce              | Decreased levels Chl a, ΦPSII, qP, NPQ, Pn and RuBisCO activity                                         | 200 mg/L | [162]                                   |
| Triticum aestivum               | Wheat                | Decline active reaction centers of PSII, ETR, and PSII heterogeneity                                   | 300 µM   | [163]                                   |
| Humulus scandens                 | Asian Hop            | Decreased chl f parameters, chl t, and PSII reaction                                                  | 300 mg/kg Cr(III)                                  | [164]     |
| Cucumis sativus                 | Cucumber             | Decline in Fm, Fv, Fv/Fm, Fm/F0, and Fv/F0                                                           | 200 µM   | [40]                                    |
| Lemna minor                     | Duckweed             | Decreased in Fv/Fm, chl b                                                                              | 6 mg/L   | [165]                                   |
| Pisum sativum                   | Pea                  | Decreased pigments and Fv/Fm, Fv/F0 and qP, and NPQ increased                                          | 100 µM   | [44]                                    |
| Raphanus sativus, Solanum       | Radish, Tomato & Spinach | Reduced photosynthetic activity and Chl t                                                             | 100 mg/kg | [166]                                   |
| lycopersicum & Spinacia oleracea & | |                                                                                                         |          |                                         |
| Brassica napus Solanum          | Rapseseed            | Reduced chl t, and carotenoid                                                                           | 500 µM   | [76]                                    |
| lycopersicum & Solanum melongena & | |                                                                                                         | 7.5 ppm  | [155]                                   |

8. Strategies to Overcome Cr-Uptake and Phytotoxicity

Chromium (III) has an essential role in the human metabolic process [102]. However, none of the Cr species have been reported to be essential in plants, thus there is no specialized mechanism for Cr-uptake in plants [23]. In plants, Cr-uptake, which depends on the Cr-type and plant species, is carried out through essential nutrients uptake channels [167]. Plants uptake Cr(III) by passive mechanism, while the uptake of Cr(VI), which has a structural resemblance with sulfate and phosphate, takes palace by the active mechanism through sulfate and phosphate channels [2,28,167]. The restriction of Cr(VI)-uptake and no change in Cr(III)-uptake by the treatment of exogenous metabolic inhibitors confirmed the active
and passive uptake mechanisms of these Cr species, respectively [2,89]. The molecular mechanism for Cr uptake and translocation is elusive and further studies are required.

Heavy metal ATPase (HMA), cation diffusion facilitator (CDF), superfamily of ATP binding cassette (ABC), natural resistance-associated macrophage protein (NRAMP), and ZRT IRT-like proteins (ZIP) are some of the gene families that are involved in the transportation of metals and heavy metals in plants [18]. Further investigations regarding the possible role of these gene families in Cr-uptake and translocation will increase our understanding of the Cr-transportation mechanism in plants. Some of the studies reported that Cr is sharing the iron, sulfate, and phosphate transport pathways in plants [55]. Thus, plants that are exposed to a toxic level of Cr-concentrations are also experiencing starvation of essential elements [168,169]. As Cr-competes with some essential metals for the uptake, these essential elements enriched environment can reduce Cr-uptake, transport, and toxicity in plants.

Iron enriched growth medium significantly reduced Cr(VI)-uptake and translocation in plants [170]. The pretreatment of seeds with salicylic acid, application of auxin and ethylene inhibitors to growth media, treatment of polyamine-brassinosteroid, 24-epibrassinolide, and plant growth-promoting bacteria reduce Cr-uptake, translocation, and toxicity [8,30,42,48,68,123,171]. The natural selection of Cr-tolerant varieties, conventional breeding, and targeted genes mutation can be used for the control of Cr-phytotoxicity and damage to yield of economically important crops.

9. Conclusions

Plants exposed to toxic Cr-level mediate high ROS accumulation by either oxidation and interconversion of one Cr form to other or by the inhibition enzymatic antioxidant system. Cr-induced ROS mediates DNA damage and genotoxicity, cytotoxicity, ultrastructural damages, and alteration in photosynthesis and photosynthetic apparatus. These alterations include necrosis, programmed cell death, cell cycle arrest, and suppression of cell division that ultimately reduce plant growth, development, and yield, as shown in Figure 1.

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