International Journal of
Molecular Sciences

MDPI

Review

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

Abdul Wakeel [1], Ming Xu [1,*] and Yinbo Gan [2,*]

[1] Key Laboratory of Geospatial Technology for the Middle and Lower Yellow River Regions, College of Environment and Planning, Henan University, Kaifeng 475004, China; awzju@yahoo.com
[2] Zhejiang Key Lab of Crop Germplasm, Department of Agronomy, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou 310058, China
* Correspondence: mingxu@henu.edu.cn (M.X.); ygan@zju.edu.cn (Y.G.)

Received: 26 December 2019; Accepted: 17 January 2020; Published: 22 January 2020

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/cm^3 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 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 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 (H_2O_2), superoxide anion (O_2^-), singlet oxygen ($^1O_2$), hydroxyl ion (HO^-), peroxyl (RO^-), 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 level of Cr, showed induced ROS accumulation, as summarized in Table 1.

Table 1. Accumulations and investigations of various ROS species in numerous plant species exposed to Cr(VI) and/or Cr(III). Superoxide (O_2^-), hydrogen peroxide ($H_2O_{2)}$, hydroxyl ion (HO^-), and singlet oxygen ($^1O_2$).

Plant Species	Common Name	ROS Types	Cr(VI) Concentration	References
Arabidopsis thaliana	Arabidopsis	O_2^-, H_2O_2	100–400 µM	[8,23]
Helianthus annuus	Sunflower	O_2^-, OH^-, H_2O_2	20 mg/L & 20 mg/Kg	[24–26]
Zea mays	Maize	O_2^-, H_2O_2, OH^-	100–300 µM & 100–300 mg/Kg	[27–32]
Brassica juncea	Indian mustard	$^1O_2$, O_2^-, H_2O_2, OH^-	300 µM	[17,33]
Glycine max	Soybean	H_2O_2	400 mg/kg & 500 mg/kg Cr(III)	[22]
Oryza sativa	Rice	O_2^-, H_2O_2	80–200 µM	[34–37]
Amaranthus viridis & *Amaranthus cruentus*	Green & Blood amaranth	O_2^-, H_2O_2	50 µM	[38]
Chenopodium quinoa	Quinoa	H_2O_2	5 mM Cr(III)	[39]
Cucumis sativus	Cucumber	O_2^-, H_2O_2	200 µM	[40]
Brassica napus	oilseed rape	O_2^-, H_2O_2, OH^-	400 µM	[41,42]
Brassica campestris	Cabbage	O_2^-	1 mg/L	[43]
Pisum sativum	Pea	O_2^-, H_2O_2	100 µM	[44]
Allium cepa	Onion	O_2^-, H_2O_2, OH^-	200 µM	[45]
Matricaria chamomilla	Chamomile	H_2O_2	120 µM Cr(III)	[46]
Lens culinaris	Lentil	H_2O	250 µM	[47]
Raphanus sativus	Radish	O_2^-, H_2O_2	1.2 mM	[48]
Pistia Stratiotes	Lettuce	H_2O_2	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.

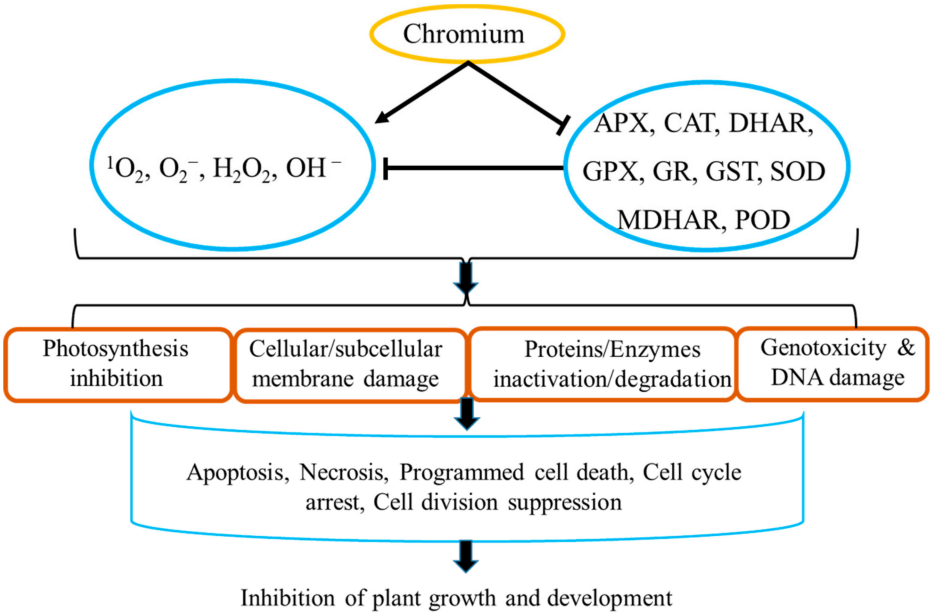

Figure 1. Cr(VI)-induced ROS mediated alteration in plants: Cr(VI)-induces ROS accumulation by suppressing enzymatic antioxidant system, which damages cellular and subcellular membranes; induces ultrastructural changes in cell organelles such as mitochondria, plastids, and thylakoids; inhibits protein 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_2O_2), hydroxyl ion (HO^-), and singlet oxygen ($^1O_2$). 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_2O_2 by superoxide dismutase (SOD). H_2O_2 is converted by ascorbate peroxidase (APX), peroxidase (POD), and catalase (CAT) to H_2O [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 *Hordeum vulgare*	Wheat & Barley	CAT, APX	22 mg/kg	[59]
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	GR, GPX, CAT, SOD, POD, APX, MDHAR, DHAR	300–500 µM	[17,63]
Solanum melongena	Eggplant	APX, GST, GR	25 µM	[64]
Amaranthus viridis & *Amaranthus cruentus*	Green & Blood Amaranth	CAT, SOD, POD, GST	50 µM	[38]
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 & *Parthenium hysterophorus*	Black Nightshade & Santa-maria	SOD, POD	500 µM Cr(III)	[74]
Brassica rapa	Turnip	SOD, APX	250 µM	[75]
Brassica napus	Rapeseed	CAT, SOD, POD, APX	500 µM	[76]
Brassica campestris	Cabbage	SOD, POD	1 mg/L	[43]
Gossypium hirsutum	Cotton	CAT, SOD, POD, APX	100 µM	[77]
Corchorus olitorius	Tossa Jute	CAT, SOD, POD, APX, GR	400 mg/kg	[78]
Brassica napus	Canola	CAT, SOD, POD, APX	50 µM	[79]
Raphanus sativus	Radish	CAT, SOD, POD	8 mM	[80]
Hordeum vulgare	Barley	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 *Hordeum vulgare*	Wheat & Barley	MDA	22 mg/kg	[59]
Solanum lycopersicum	Tomatoes	MDA	24.66 mg/k	[83]
Oryza sativa	Rice	MDA, TBARS	20–200 µM & 20 mg/L	[35,36,69,82,84,85]
Limnobium laevigatum	Floating Plant	MDA	70 µg/L Cr(III)	[86]
Citrus reticulata Blanco	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 & *Amaranthus cruentus*	Green & Blood 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 sativus	Cucumber	MDA	200 µM	[40]
Pisum sativum	Pea	MDA	100 µM	[44]
Brassica rapa	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	TBARS	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 napus	Rapeseed	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 t (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	Cr(VI)/(III)	[22]
Vicia faba	Faba Bean	Micronucleus, Chromosomal fragmentation & bridging, Increase in % tail DNA, tail moment and Tail length	Tannery solid waste & Cr(VI)	[124–127]
Allium cepa	Onion	DNA damage, Chromosomal Aberrations, Micronuclei, Chromosomal fragmentation & bridging	Tannery solid waste, Tannery effluent & Cr(VI)	[45,125,127–129]
Hordeum vulgare	Barley	Chromosomal aberrations	Cr(VI)	[130]
Vicia sativa	Vetch	Chromosomal aberration, Chromosomal fragmentation & bridging	Wastes, Cr(VI)/(III)	[125,127,131]
Raphanus sativus	Radish	Chromosomal aberration	Cr(VI)/(III)	[125]
Zea mays	Maize	Chromosomal aberration	Cr(VI)/(III)	[125]
Brassica napus	Oilseed Rape	Methylation 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 *Hordeum vulgare*	Wheat & Barley	*L*	Damaged CHLP, THY; Increased PG, Swollen MITO; altered I-cristae	Cr(VI)	[59]
Nicotiana tabacum	Tobacco	*L* & *R*	CW/CM not distinguishable, Disarranged CHLP structure, Undeveloped nucleus, damaged NM, Swelled/distorted THY,	Cr(VI)	[122,123]
Oryza sativa	Rice	*L*	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)	[35,135]
Arabidopsis thaliana	Arabidopsis	*R*	T-nuclei, GB disintegrated, spherical MITO, plastids; T-stroma; damaged MIOT, plastids; increased SG, amorphous material deposition in CW, ML, vacuoles, collapsed vacuoles, cytoplasm contained opaque lipid,	Cr(VI)	[23,47,136]
Eichhornia crassipes	Water Hyacinth	*L*	Damaged THY, MITO, CHLP (structure/distribution), grana	Cr(VI)	[137]
Salvinia minima	Floating Fern	*L*	Damaged CHLP, grana, THY, increased number/size of SG; large PG	Cr(VI)	[96]
Taraxacum officinale	Dandelion	*C*	Altered MITO with no/reduced I-cristae	Cr(VI)	[138]
Hordeum vulgare	Barley	*L* & *R*	Swollen CHLP, increased PG, Disintegrated/disappeared THY, MITO, Increased SG size/number, Increased vacuolar size, Cr-presence in CW, Vacuoles, Nucleus disruption/disappearance	Cr(VI)	[139]
Solanum lycopersicum	Tomatoes	*P*	Abnormal shaped reduced grana/CHLP; altered THY, MITO; reduced cristae numbers	Cr(III)	[140]
Potamogeton crispus	Curled Pondweed	*L*	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, CO_2 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 leaf 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 CO_2), Φ_{PSII} (effective quantum of yield of photosystem II), qP (photochemical quenching), NPQ (non-photochemical quenching), P_N (net CO_2 assimilation rate), ETR (electron transportation rate), pigment (photosynthetic pigments).

Plant Species	Common Name	Alteration in Photosynthetic Parameters	Cr(VI)	References
Arabidopsis thaliana & *Brassica juncea*	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 100–300 µM & 100 mg/Kg	[8] & [58,88,89,157]
Helianthus annuus	Sunflower	Reduced chl a, b, t, gas exchange, and carotenoid levels	Tannery effluent & 20 mg/kg	[26,158]
Citrus reticulate	Kinnow Mandarin	Decreased chl t, photosynthetic activity, Trmmol, Cond, and water use efficiency	0.75 mM	[87]
Cyperus alternifolius & *Coix lacryma-jobi*	Umbrella Palm & Adlay Millet	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 F_v/F_m	80–200 µM	[34,35]
Zea mays	Maize	Reduced carotenoids, chl a, b, and t, Photo, Trmmol, Ci, Water use efficiency and intrinsic, Alteration in F_v/F_m, F_v/F_0, F_m/F_0, and qP	Tannery effluent & 150–250 µM	[29,147,160]
Amaranthus viridis & *Amaranthus cruentus*	Green & Blood Amaranth	Inhibition photochemistry of PSII	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, Φ_{PSII}, qp, NPQ, P_N 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 lycopersicum* & *Spinacia oleracea*	Radish, Tomato & Spinach	Reduced photosynthetic activity and Chl t	100 mg/kg	[166]
Brassica napus	Rapeseed	Reduced chl t, and carotenoid	500 µM	[76]
Solanum lycopersicum & *Solanum melongena*	Tomato & Eggplant	Reduced pigments	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.

Funding: The research was supported by The National Key Research and Development Program of China [2016YFD0100701, 2018YFA0606500, 2017YFA0604300], National Natural Science Foundation of China [Grant No. 31570183, 31529001].

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

References

1. Sinha, V.; Pakshirajan, K.; Chaturvedi, R. Chromium tolerance, bioaccumulation and localization in plants: An overview. *J. Environ. Manag.* **2018**, *206*, 715–730. [CrossRef] [PubMed]
2. Shahid, M.; Shamshad, S.; Rafiq, M.; Khalid, S.; Bibi, I.; Niazi, N.K.; Dumat, C.; Rashid, M.I. Chromium speciation, bioavailability, uptake, toxicity and detoxification in soil-plant system: A review. *Chemosphere* **2017**, *178*, 513–533. [CrossRef] [PubMed]
3. Ashraf, A.; Bibi, I.; Niazi, N.K.; Ok, Y.S.; Murtaza, G.; Shahid, M.; Kunhikrishnan, A.; Li, D.; Mahmood, T. Chromium(VI) sorption efficiency of acid-activated banana peel over organo-montmorillonite in aqueous solutions. *Int. J. Phytoremediat.* **2017**, *19*, 605–613. [CrossRef] [PubMed]
4. Sultana, M.-Y.; Akratos, C.S.; Pavlou, S.; Vayenas, D.V. Chromium removal in constructed wetlands: A review. *Int. Biodeterior. Biodegrad.* **2014**, *96*, 181–190. [CrossRef]
5. Mandiwana, K.L.; Panichev, N.; Kataeva, M.; Siebert, S. The solubility of Cr(III) and Cr(VI) compounds in soil and their availability to plants. *J. Hazard. Mater.* **2007**, *147*, 540–545. [CrossRef] [PubMed]
6. Pandey, B.; Agrawal, M.; Singh, S. Ecological risk assessment of soil contamination by trace elements around coal mining area. *J. Soils Sediments* **2016**, *16*, 159–168. [CrossRef]
7. Ghosh, I.; Ghosh, M.; Mukherjee, A. *Remediation of Mine Tailings and Fly Ash Dumpsites: Role of Poaceae Family Members and Aromatic Grasses. In Enhancing Cleanup of Environmental Pollutants*; Springer: Cham, Germany, 2017; pp. 117–167.

8. Wakeel, A.; Ali, I.; Wu, M.; Kkan, A.R.; Jan, M.; Ali, A.; Liu, Y.; Ge, S.; Wu, J.; Gan, Y. Ethylene mediates dichromate-induced oxidative stress and regulation of the enzymatic antioxidant system-related transcriptome in *Arabidopsis thaliana*. *Environ. Exp. Bot.* **2019**, *161*, 166–179. [CrossRef]
9. Elsawy, E.E.T.; El-Hebeary, M.R.; El Mahallawi, I.S.E. Effect of manganese, silicon and chromium additions on microstructure and wear characteristics of grey cast iron for sugar industries applications. *Wear* **2017**, *390–391*, 113–124. [CrossRef]
10. Florea, C.D.; Carcea, I.; Cimpoesu, R.; Toma, S.L.; Sandu, I.G.; Bejinariu, C. Experimental Analysis of Resistance to Electrocorosion of a High Chromium Cast Iron with Applications in the Vehicle Industry. *Rev. Chim.* **2017**, *68*, 2397–2401.
11. Bharagava, R.N.; Mishra, S. Hexavalent chromium reduction potential of Cellulosimicrobium sp isolated from common effluent treatment plant of tannery industries. *Ecotoxicol. Environ. Saf.* **2018**, *147*, 102–109. [CrossRef]
12. Byrne, P.; Taylor, K.G.; Hudson-Edwards, K.A.; Barrett, J.E.S. Speciation and potential long-term behaviour of chromium in urban sediment particulates. *J. Soils Sediments* **2017**, *17*, 2666–2676. [CrossRef]
13. Yang, L.; Zhu, G.; Pan, H.; Shi, P.; Li, J.; Liu, Y.; Tong, H. Surface dust heavy metals in the major cities, China. *Environ. Earth Sci.* **2017**, *76*, 757.
14. Wakeel, A.; Ali, I.; Upreti, S.; Ullah, A.; Liu, B.; Khan, A.R.; Huang, L.; Wu, M.; Gan, Y. Ethylene mediates dichromate induced inhibition of primary root growth by altering AUX1 expression and auxin accumulation in *Arabidopsis thaliana*. *Plant Cell Environ.* **2018**, *41*, 1453–1467. [CrossRef] [PubMed]
15. Cui, W.; Wang, H.; Song, J.; Cao, X.; Rogers, H.J.; Francis, D.; Jia, C.; Sun, L.; Hou, M.; Yang, Y.; et al. Cell cycle arrest mediated by Cd-induced DNA damage in Arabidopsis root tips. *Ecotoxicol. Environ. Saf.* **2017**, *145*, 569–574. [CrossRef] [PubMed]
16. Gielen, H.; Vangronsveld, J.; Cuypers, A. Cd-induced Cu deficiency responses in *Arabidopsis thaliana*: Are phytochelatins involved? *Plant Cell Environ.* **2017**, *40*, 390–400. [CrossRef] [PubMed]
17. Al Mahmud, J.; Hasanuzzaman, M.; Nahar, K.; Rahman, A.; Hossain, M.S.; Fujita, M. Maleic acid assisted improvement of metal chelation and antioxidant metabolism confers chromium tolerance in *Brassica juncea* L. *Ecotoxicol. Environ. Saf.* **2017**, *144*, 216–226. [CrossRef] [PubMed]
18. Shahid, M.; Dumat, C.; Khalid, S.; Niazi, N.K.; Antunes, P.M.C. Cadmium Bioavailability, Uptake, Toxicity and Detoxification in Soil-Plant System. In *Reviews of Environmental Contamination and Toxicology*; DeVoogt, P., Ed.; Springer: Cham, Germany, 2017; Volume 241, pp. 73–137.
19. Abbas, G.; Murtaza, B.; Bibi, I.; Shahid, M.; Niazi, N.K.; Khan, M.I.; Amjad, M.; Hussain, M.; Natasha. Arsenic Uptake, Toxicity, Detoxification, and Speciation in Plants: Physiological, Biochemical, and Molecular Aspects. *Int. J. Environ. Res. Public Health* **2018**, *15*, 59. [CrossRef] [PubMed]
20. Chen, Q.; Wu, K.; Tang, Z.; Guo, Q.; Guo, X.; Wang, H. Exogenous ethylene enhanced the cadmium resistance and changed the alkaloid biosynthesis in *Catharanthus roseus* seedlings. *Acta Physiol. Plant.* **2017**, *39*, 267. [CrossRef]
21. Hasanuzzaman, M.; Nahar, K.; Gill, S.S.; Alharby, H.F.; Razafindrabe, B.H.N.; Fujita, M. Hydrogen Peroxide Pretreatment Mitigates Cadmium-Induced Oxidative Stress in *Brassica napus* L.: An Intrinsic Study on Antioxidant Defense and Glyoxalase Systems. *Front. Plant Sci.* **2017**, *8*, 115. [CrossRef]
22. Balasaraswathi, K.; Jayaveni, S.; Sridevi, J.; Sujatha, D.; Aaron, K.P.; Rose, C. Cr-induced cellular injury and necrosis in *Glycine max* L.: Biochemical mechanism of oxidative damage in chloroplast. *Plant Physiol. Biochem.* **2017**, *118*, 653–666. [CrossRef]
23. Eleftheriou, E.P.; Adamakis, I.-D.S.; Panteris, E.; Fatsiou, M. Chromium-Induced Ultrastructural Changes and Oxidative Stress in Roots of *Arabidopsis thaliana*. *Int. J. Mol. Sci.* **2015**, *16*, 15852–15871. [CrossRef] [PubMed]
24. Farid, M.; Ali, S.; Rizwan, M.; Ali, Q.; Saeed, R.; Nasir, T.; Abbasi, G.H.; Rehmani, M.I.A.; Ata-Ul-Karim, S.T.; Bukhari, S.A.H.; et al. Phyto-management of chromium contaminated soils through sunflower under exogenously applied 5-aminolevulinic acid. *Ecotoxicol. Environ. Saf.* **2018**, *151*, 255–265. [CrossRef] [PubMed]
25. Farid, M.; Ali, S.; Akram, N.A.; Rizwan, M.; Abbas, F.; Bukhari, S.A.H.; Saeed, R. Phyto-management of Cr-contaminated soils by sunflower hybrids: Physiological and biochemical response and metal extractability under Cr stress. *Environ. Sci. Pollut. Res.* **2017**, *24*, 16845–16859. [CrossRef] [PubMed]
26. Farid, M.; Ali, S.; Rizwan, M.; Ali, Q.; Abbas, F.; Bukhari, S.A.H.; Saeed, R.; Wu, L. Citric acid assisted phytoextraction of chromium by sunflower; morpho-physiological and biochemical alterations in plants. *Ecotoxicol. Environ. Saf.* **2017**, *145*, 90–102. [CrossRef] [PubMed]

27. Kharbech, O.; Houmani, H.; Chaoui, A.; Corpas, F.J. Alleviation of Cr(VI)-induced oxidative stress in maize (*Zea mays* L.) seedlings by NO and H2S donors through differential organ-dependent regulation of ROS and NADPH-recycling metabolisms. *J. Plant Physiol.* **2017**, *219*, 71–80. [CrossRef]
28. Anjum, S.A.; Ashraf, U.; Khan, I.; Tanveer, M.; Shahid, M.; Shakoor, A.; Wang, L. Phyto-Toxicity of Chromium in Maize: Oxidative Damage, Osmolyte Accumulation, Anti-Oxidative Defense and Chromium Uptake. *Pedosphere* **2017**, *27*, 262–273. [CrossRef]
29. Singh, V.P.; Kumar, J.; Singh, M.; Singh, S.; Prasad, S.M.; Dwivedi, R.; Singh, M.P.V.V.B. Role of salicylic acid-seed priming in the regulation of chromium(VI) and UV-B toxicity in maize seedlings. *Plant Growth Regul.* **2016**, *78*, 79–91. [CrossRef]
30. Islam, F.; Yasmeen, T.; Arif, M.S.; Riaz, M.; Shahzad, S.M.; Imran, Q.; Ali, I. Combined ability of chromium(Cr) tolerant plant growth promoting bacteria (PGPB), and salicylic acid (SA) in attenuation of chromium stress in maize plants. *Plant Physiol. Biochem.* **2016**, *108*, 456–467. [CrossRef]
31. Singh, S.; Srivastava, P.K.; Kumar, D.; Tripathi, D.K.; Chauhan, D.K.; Prasad, S.M. Morpho-anatomical and biochemical adapting strategies of maize (*Zea mays* L.) seedlings against lead and chromium stresses. *Biocatal. Agric. Biotechnol.* **2015**, *4*, 286–295. [CrossRef]
32. Maiti, S.; Ghosh, N.; Mandal, C.; Das, K.; Dey, N.; Adak, M.K. Responses of the maize plant to chromium stress with reference to antioxidation activity. *Braz. J. Plant Physiol.* **2012**, *24*, 203–212. [CrossRef]
33. Handa, N.; Kohli, S.K.; Thukral, A.K.; Arora, S.; Bhardwaj, R. Role of Se(VI) in counteracting oxidative damage in *Brassica juncea* L. under Cr(VI) stress. *Acta Physiol. Plant.* **2017**, *39*, 51. [CrossRef]
34. Chen, Q.; Zhang, X.; Liu, Y.; Wei, J.; Shen, W.; Shen, Z.; Cui, J. Hemin-mediated alleviation of zinc, lead and chromium toxicity is associated with elevated photosynthesis, antioxidative capacity; suppressed metal uptake and oxidative stress in rice seedlings. *Plant Growth Regul.* **2017**, *81*, 253–264. [CrossRef]
35. Ma, J.; Lv, C.; Xu, M.; Chen, G.; Lv, C.; Gao, Z. Photosynthesis performance, antioxidant enzymes, and ultrastructural analyses of rice seedlings under chromium stress. *Environ. Sci. Pollut. Res.* **2016**, *23*, 1768–1778. [CrossRef] [PubMed]
36. Zeng, F.; Wu, X.; Qiu, B.; Wu, F.; Jiang, L.; Zhang, G. Physiological and proteomic alterations in rice (*Oryza sativa* L.) seedlings under hexavalent chromium stress. *Planta* **2014**, *240*, 291–308. [CrossRef]
37. Ngoc-Nam, T.; Huang, T.-L.; Chi, W.-C.; Fu, S.-F.; Chen, C.-C.; Huang, H.-J. Chromium stress response effect on signal transduction and expression of signaling genes in rice. *Physiol. Plant.* **2014**, *150*, 205–224.
38. Bashri, G.; Parihar, P.; Singh, R.; Singh, S.; Singh, V.P.; Prasad, S.M. Physiological and biochemical characterization of two Amaranthus species under Cr(VI) stress differing in Cr(VI) tolerance. *Plant Physiol. Biochem.* **2016**, *108*, 12–23. [CrossRef]
39. Scoccianti, V.; Bucchini, A.E.; Iacobucci, M.; Ruiz, K.B.; Biondi, S. Oxidative stress and antioxidant responses to increasing concentrations of trivalent chromium in the Andean crop species Chenopodium quinoa Willd. *Ecotoxicol. Environ. Saf.* **2016**, *133*, 25–35. [CrossRef]
40. Tripathi, A.; Tripathi, D.K.; Chauhan, D.K.; Kumar, N. Chromium(VI)-induced phytotoxicity in river catchment agriculture: Evidence from physiological, biochemical and anatomical alterations in *Cucumis sativus* (L.) used as model species. *Chem. Ecol.* **2016**, *32*, 12–33. [CrossRef]
41. Gill, R.A.; Zang, L.; Ali, B.; Farooq, M.A.; Cui, P.; Yang, S.; Ali, S.; Zhou, W. Chromium-induced physio-chemical and ultrastructural changes in four cultivars of *Brassica napus* L. *Chemosphere* **2015**, *120*, 154–164. [CrossRef]
42. Gill, R.A.; Zhang, N.; Ali, B.; Farooq, M.A.; Xu, J.; Gill, M.B.; Mao, B.; Zhou, W. Role of exogenous salicylic acid in regulating physio-morphic and molecular changes under chromium toxicity in black- and yellow-seeded *Brassica napus* L. *Environ. Sci. Pollut. Res.* **2016**, *23*, 20483–20496. [CrossRef]
43. Qing, X.; Zhao, X.; Hu, C.; Wang, P.; Zhang, Y.; Zhang, X.; Wang, P.; Shi, H.; Jia, F.; Qu, C. Selenium alleviates chromium toxicity by preventing oxidative stress in cabbage (*Brassica campestris* L. ssp. Pekinensis) leaves. *Ecotoxicol. Environ. Saf.* **2015**, *114*, 179–189. [CrossRef] [PubMed]
44. Tripathi, D.K.; Singh, V.P.; Prasad, S.M.; Chauhan, D.K.; Dubey, N.K. Silicon nanoparticles (SiNp) alleviate chromium(VI) phytotoxicity in *Pisum sativum* (L.) seedlings. *Plant Physiol. Biochem.* **2015**, *96*, 189–198. [CrossRef] [PubMed]
45. Patnaik, A.R.; Achary, V.M.M.; Panda, B.B. Chromium(VI)-induced hormesis and genotoxicity are mediated through oxidative stress in root cells of *Allium cepa* L. *Plant Growth Regul.* **2013**, *71*, 157–170. [CrossRef]

46. Kovacik, J.; Babula, P.; Klejdus, B.; Hedbavny, J. Chromium Uptake and Consequences for Metabolism and Oxidative Stress in Chamomile Plants. *J. Agric. Food Chem.* **2013**, *61*, 7864–7873. [CrossRef]
47. Eleftheriou, E.P.; Adamakis, I.-D.S.; Fatsiou, M.; Panteris, E. Hexavalent chromium disrupts mitosis by stabilizing microtubules in *Lens culinaris* root tip cells. *Physiol. Plant.* **2013**, *147*, 169–180. [CrossRef]
48. Choudhary, S.P.; Kanwar, M.; Bhardwaj, R.; Yu, J.-Q.; Lam-Son Phan, T. Chromium Stress Mitigation by Polyamine-Brassinosteroid Application Involves Phytohormonal and Physiological Strategies in *Raphanus sativus* L. *PLoS ONE* **2012**, *7*, e33210. [CrossRef]
49. Upadhyay, R.; Panda, S.K. Influence of Chromium Salts on Increased Lipid Peroxidation and Differential Pattern in Antioxidant Metabolism in *Pistia stratiotes* L. *Braz. Arch. Biol. Technol.* **2010**, *53*, 1137–1144. [CrossRef]
50. Gill, S.S.; Tuteja, N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol. Biochem.* **2010**, *48*, 909–930. [CrossRef]
51. Zhang, M.; Smith, J.A.C.; Harberd, N.P.; Jiang, C. The regulatory roles of ethylene and reactive oxygen species (ROS) in plant salt stress responses. *Plant Mol. Biol.* **2016**, *91*, 651–659. [CrossRef]
52. Pourrut, B.; Shahid, M.; Douay, F.; Dumat, C.; Pinelli, E. Molecular mechanisms involved in lead uptake, toxicity and detoxification in higher plants. In *Heavy Metal Stress in Plants*; Springer: Berlin/Heidelberg, Germany, 2013; pp. 121–147.
53. Shahid, M.; Austruy, A.; Echevarria, G.; Arshad, M.; Sanaullah, M.; Aslam, M.; Nadeem, M.; Nasim, W.; Dumat, C. EDTA-enhanced phytoremediation of heavy metals: A review. *Soil Sediment Contam. Int. J.* **2014**, *23*, 389–416. [CrossRef]
54. Panda, S.K. Chromium-mediated oxidative stress and ultrastructural changes in root cells of developing rice seedlings. *J. Plant Physiol.* **2007**, *164*, 1419–1428. [CrossRef] [PubMed]
55. Singh, H.P.; Mahajan, P.; Kaur, S.; Batish, D.R.; Kohli, R.K. Chromium toxicity and tolerance in plants. *Environ. Chem. Lett.* **2013**, *11*, 229–254. [CrossRef]
56. Kim, Y.-H.; Park, S.C.; Yun, B.-W.; Kwak, S.-S. Overexpressing sweetpotato peroxidase gene swpa4 affects nitric oxide production by activating the expression of reactive oxygen species- and nitric oxide-related genes in tobacco. *Plant Physiol. Biochem.* **2017**, *120*, 52–60. [CrossRef] [PubMed]
57. Ali, I.; Jan, M.; Wakeel, A.; Azizullah, A.; Liu, B.; Islam, F.; Ali, A.; Daud, M.K.; Liu, Y.; Gan, Y. Biochemical responses and ultrastructural changes in ethylene insensitive mutants of Arabidopsis thialiana subjected to bisphenol A exposure. *Ecotoxicol. Environ. Saf.* **2017**, *144*, 62–71. [CrossRef] [PubMed]
58. Mahmud, J.A.L.; Hasanuzzaman, M.; Nahar, K.; Rahman, A.; Hossain, M.S.; Fujita, M. gamma-aminobutyric acid (GABA) confers chromium stress tolerance in *Brassica juncea* L. by modulating the antioxidant defense and glyoxalase systems. *Ecotoxicology* **2017**, *26*, 675–690. [CrossRef] [PubMed]
59. Gonzalez, A.; Mar Gil-Diaz, M.; Pinilla, P.; Carmen Lobo, M. Impact of Cr and Zn on Growth, Biochemical and Physiological Parameters, and Metal Accumulation by Wheat and Barley Plants. *Water Air Soil Pollut.* **2017**, *228*, 419. [CrossRef]
60. Ahmad, R.; Ali, S.; Hannan, F.; Rizwan, M.; Iqbal, M.; Hassan, Z.; Akram, N.A.; Maqbool, S.; Abbas, F. Promotive role of 5-aminolevulinic acid on chromium-induced morphological, photosynthetic, and oxidative changes in cauliflower (*Brassica oleracea botrytis* L.). *Environ. Sci. Pollut. Res.* **2017**, *24*, 8814–8824. [CrossRef]
61. Zhu, X.; Hou, G.; Ru, G.; Zhang, L.; Wu, X.; Liu, G. Accumulation and antioxidant properties of chromium stress in *Pennisetum alopecuroides*. *J. Henan Agric. Univ.* **2017**, *51*, 330–334.
62. Yilmaz, S.H.; Kaplan, M.; Temizgul, R.; Yilmaz, S. Antioxidant enzyme response of sorghum plant upon exposure to Aluminum, Chromium and Lead heavy metals. *Turk. J. Biochem.* **2017**, *42*, 503–512. [CrossRef]
63. Kanwar, M.K.; Poonam, S.P.; Bhardwaj, R. Involvement of Asada-Halliwell Pathway During Phytoremediation of Chromium(VI) in *Brassica juncea* L. Plants. *Int. J. Phytoremediat.* **2015**, *17*, 1237–1243. [CrossRef]
64. Singh, M.; Kushwaha, B.K.; Singh, S.; Kumar, V.; Singh, V.P.; Prasad, S.M. Sulphur alters chromium(VI) toxicity in *Solarium melongena* seedlings: Role of sulphur assimilation and sulphur-containing antioxidants. *Plant Physiol. Biochem.* **2017**, *112*, 183–192. [CrossRef] [PubMed]
65. Anjum, S.A.; Ashraf, U.; Khan, I.; Tanveer, M.; Saleem, M.F.; Wang, L. Aluminum and Chromium Toxicity in Maize: Implications for Agronomic Attributes, Net Photosynthesis, Physio-Biochemical Oscillations, and Metal Accumulation in Different Plant Parts. *Water Air Soil Pollut.* **2016**, *227*, 326. [CrossRef]
66. Ding, H.; Zhu, X.; Liu, H.; Chen, Y.; Liang, J. Hexavalent chromium(Cr~(6+)) induced oxidative damage to maize (*Zea mays* L.) root tip cells. *J. Yangzhou Univ.* **2011**, *32*, 28–32.

67. Ding, H.; Wang, G.; Lou, L.; Lv, J. Physiological responses and tolerance of kenaf (*Hibiscus cannabinus* L.) exposed to chromium. *Ecotoxicol. Environ. Saf.* **2016**, *133*, 509–518. [CrossRef] [PubMed]
68. Huda, A.K.M.N.; Swaraz, A.M.; Abu Reza, M.; Haque, M.A.; Kabir, A.H. Remediation of Chromium Toxicity Through Exogenous Salicylic Acid in Rice (*Oryza sativa* L.). *Water Air Soil Pollut.* **2016**, *227*, 278. [CrossRef]
69. Cao, F.; Wang, N.; Zhang, M.; Dai, H.; Dawood, M.; Zhang, G.; Wu, F. Comparative study of alleviating effects of GSH, Se and Zn under combined contamination of cadmium and chromium in rice (*Oryza sativa*). *Biometals* **2013**, *26*, 297–308. [CrossRef] [PubMed]
70. Jabeen, N.; Abbas, Z.; Iqbal, M.; Rizwan, M.; Jabbar, A.; Farid, M.; Ali, S.; Ibrahim, M.; Abbas, F. Glycinebetaine mediates chromium tolerance in mung bean through lowering of Cr uptake and improved antioxidant system. *Arch. Agron. Soil Sci.* **2016**, *62*, 648–662. [CrossRef]
71. Zhang, H.; Yang, W.; Wang, Q.; Sun, J. The Sub-cellular Chromium(Cr~(6+))Distribution and Tolerance Mechanism to Chromium Stress in Different Tolerant *Brassica chinensis* L. Cultivars. *Acta Bot. Boreali-Occident. Sin.* **2016**, *36*, 954–963.
72. Shirong, Z.; Shuyi, L.; Xiaodong, D.; Fangbai, L.; Chuanping, L.; Xinrong, L.; Rongping, W. Silicon mediated the detoxification of Cr on pakchoi (*Brassica chinensis* L.) in Cr-contaminated soil. *J. Food Agric. Environ.* **2013**, *11*, 814–819.
73. Tian, B.; Zhang, Y.; Zhang, L.; Ma, X.; Jin, Z.; Liu, Z.; Liu, D.; Pei, Y. Effects of cadmium or chromium on growth and NADPH oxidase and antioxidant enzyme system of foxtail millet seedlings. *J. Agro-Environ. Sci.* **2016**, *35*, 240–246.
74. UdDin, I.; Bano, A.; Masood, S. Chromium toxicity tolerance of *Solanum nigrum* L. and *Parthenium hysterophorus* L. plants with reference to ion pattern, antioxidation activity and root exudation. *Ecotoxicol. Environ. Saf.* **2015**, *113*, 271–278. [CrossRef] [PubMed]
75. Chatterjee, J.; Kumar, P.; Sharma, P.N.; Tewari, R.K. Chromium toxicity induces oxidative stress in turnip. *Indian J. Plant Physiol.* **2015**, *20*, 220–226. [CrossRef]
76. Afshan, S.; Ali, S.; Bharwana, S.A.; Rizwan, M.; Farid, M.; Abbas, F.; Ibrahim, M.; Mehmood, M.A.; Abbasi, G.H. Citric acid enhances the phytoextraction of chromium, plant growth, and photosynthesis by alleviating the oxidative damages in *Brassica napus* L. *Environ. Sci. Pollut. Res.* **2015**, *22*, 11679–11689. [CrossRef] [PubMed]
77. Daud, M.K.; Mei, L.; Variath, M.T.; Ali, S.; Li, C.; Rafiq, M.T.; Zhu, S.J. Chromium(VI) Uptake and Tolerance Potential in Cotton Cultivars: Effect on Their Root Physiology, Ultramorphology, and Oxidative Metabolism. *Biomed Res. Int.* **2014**, *2014*. [CrossRef]
78. Islam, M.K.; Khanam, M.S.; Lee, S.Y.; Alam, I.; Huh, M.R. The interaction of arsenic (As) and chromium (Cr) influences growth and antioxidant status in tossa jute (*Corchorus olitorius*). *Plant Omics* **2014**, *7*, 499–509.
79. Yildiz, M.; Terzi, H.; Bingul, N. Protective role of hydrogen peroxide pretreatment on defense systems and BnMP1 gene expression in Cr(VI)-stressed canola seedlings. *Ecotoxicology* **2013**, *22*, 1303–1312. [CrossRef]
80. Sayantan, D. Shardendu. Amendment in phosphorus levels moderate the chromium toxicity in *Raphanus sativus* L. as assayed by antioxidant enzymes activities. *Ecotoxicol. Environ. Saf.* **2013**, *95*, 161–170. [CrossRef]
81. Yildiz, M.; Terzi, H.; Cenkci, S.; Yildiz, B. Chromium(VI)-Induced Alterations in 2-D Protein Profiles and Antioxidant Defence Systems of Barley Cultivars. *Hacet. J. Biol. Chem.* **2012**, *40*, 257–265.
82. Yu, X.-Z.; Lin, Y.-J.; Fan, W.-J.; Lu, M.-R. The role of exogenous proline in amelioration of lipid peroxidation in rice seedlings exposed to Cr(VI). *Int. Biodeterior. Biodegrad.* **2017**, *123*, 106–112. [CrossRef]
83. Smaoui-Jardak, M.; Kriaa, W.; Maalej, M.; Zouari, M.; Kamoun, L.; Trabelsi, W.; Ben Abdallah, F.; Elloumi, N. Effect of the phosphogypsum amendment of saline and agricultural soils on growth, productivity and antioxidant enzyme activities of tomato (*Solanum lycopersicum* L.). *Ecotoxicology* **2017**, *26*, 1089–1104. [CrossRef]
84. Zeng, F.; Qiu, B.; Wu, X.; Niu, S.; Wu, F.; Zhang, G. Glutathione-Mediated Alleviation of Chromium Toxicity in Rice Plants. *Biol. Trace Elem. Res.* **2012**, *148*, 255–263. [CrossRef] [PubMed]
85. Zeng, F.-R.; Zhao, F.-S.; Qiu, B.-Y.; Ouyang, Y.-N.; Wu, F.-B.; Zhang, G.-P. Alleviation of Chromium Toxicity by Silicon Addition in Rice Plants. *Agric. Sci. China* **2011**, *10*, 1188–1196. [CrossRef]
86. Silvina Aran, D.; Alfredo Harguinteguy, C.; Fernandez-Cirelli, A.; Luisa Pignata, M. Phytoextraction of Pb, Cr, Ni, and Zn using the aquatic plant *Limnobium laevigatum* and its potential use in the treatment of wastewater. *Environ. Sci. Pollut. Res.* **2017**, *24*, 18295–18308. [CrossRef] [PubMed]

87. Balal, R.M.; Shahid, M.A.; Vincent, C.; Zotarelli, L.; Liu, G.; Mattson, N.S.; Rathinasabapathi, B.; Martinez-Nicolas, J.J.; Garcia-Sanchez, F. Kinnow mandarin plants grafted on tetraploid rootstocks are more tolerant to Cr-toxicity than those grafted on its diploids one. *Environ. Exp. Bot.* **2017**, *140*, 8–18. [CrossRef]
88. Ashfaque, F.; Inam, A.; Inam, A.; Iqbal, S.; Sahay, S. Response of silicon on metal accumulation, photosynthetic inhibition and oxidative stress in chromium-induced mustard (*Brassica juncea* L.). *S. Afr. J. Bot.* **2017**, *111*, 153–160. [CrossRef]
89. Singh, D.; Agnihotri, A.; Seth, C.S. Interactive effects of EDTA and oxalic acid on chromium uptake, translocation and photosynthetic attributes in Indian mustard (*Brassica juncea* L. var. Varuna). *Curr. Sci.* **2017**, *112*, 2034–2042. [CrossRef]
90. Sinha, V.; Pakshirajan, K.; Manikandan, N.A.; Chaturvedi, R. Kinetics, biochemical and factorial analysis of chromium uptake in a multi-ion system by *Tradescantia pallida* (Rose) D. R. Hunt. *Int. J. Phytoremediat.* **2017**, *19*, 1007–1016. [CrossRef]
91. De Oliveira, L.M.; Gress, J.; De, J.; Rathinasabapathi, B.; Marchi, G.; Chen, Y.; Ma, L.Q. Sulfate and chromate increased each other's uptake and translocation in As-hyperaccumulator *Pteris vittata*. *Chemosphere* **2016**, *147*, 36–43. [CrossRef]
92. Jain, R.; Singh, S.P.; Singh, A.; Singh, S.; Tripathi, P.; Chandra, A.; Solomon, S. Study on physio-biochemical attributes and metallothionein gene expression affected by chromium(VI) in sugarcane (*Saccharum* spp. hybrid). *J. Environ. Biol.* **2016**, *37*, 375–382.
93. Terzi, H.; Yildiz, M. Interactive effects of sulfur and chromium on antioxidative defense systems and BnMP1 gene expression in canola (*Brassica napus* L.) cultivars differing in Cr(VI) tolerance. *Ecotoxicology* **2015**, *24*, 1171–1182. [CrossRef]
94. Terzi, H.; Yildiz, M. Variations in Chromium Tolerance and Accumulation among Canola (*Brassica napus* L.) Cultivars. *Bull. Environ. Contam. Toxicol.* **2014**, *93*, 113–119. [CrossRef] [PubMed]
95. Sinha, P.; Shukla, A.K.; Sharma, Y.K. Amelioration of Heavy-Metal Toxicity in Cauliflower by Application of Salicylic Acid. *Commun. Soil Sci. Plant Anal.* **2015**, *46*, 1309–1319. [CrossRef]
96. Prado, C.; Prado, F.E.; Pagano, E.; Rosa, M. Differential Effects of Cr(VI) on the Ultrastructure of Chloroplast and Plasma Membrane of Salvinia minima Growing in Summer and Winter. Relationships with Lipid Peroxidation, Electrolyte Leakage, Photosynthetic Pigments, and Carbohydrates. *Water Air Soil Pollut.* **2015**, *226*, 8. [CrossRef]
97. Sinha, V.; Pakshirajan, K.; Chaturvedi, R. Chromium(VI) Accumulation and Tolerance by *Tradescantia pallida*: Biochemical and Antioxidant Study. *Appl. Biochem. Biotechnol.* **2014**, *173*, 2297–2306. [CrossRef] [PubMed]
98. Liu, C.; Du, W.; Cai, H.; Jia, Z.; Dong, H. Trivalent chromium pretreatment alleviates the toxicity of oxidative damage in wheat plants exposed to hexavalent chromium. *Acta Physiol. Plant.* **2014**, *36*, 787–794. [CrossRef]
99. Sharmin, S.A.; Alam, I.; Kim, K.-H.; Kim, Y.-G.; Kim, P.J.; Bahk, J.D.; Lee, B.-H. Chromium-induced physiological and proteomic alterations in roots of *Miscanthus sinensis*. *Plant Sci.* **2012**, *187*, 113–126. [CrossRef]
100. Pesko, M.; Kral'ova, K.; Blasko, J. Phytotoxic Effects of trivalent Chromium on Rapeseed Plants. *Fresenius Environ. Bull.* **2012**, *21*, 761–768.
101. Thompson, C.M.; Fedorov, Y.; Brown, D.D.; Suh, M.; Proctor, D.M.; Kuriakose, L.; Haws, L.C.; Harris, M.A. Assessment of Cr(VI)-Induced Cytotoxicity and Genotoxicity Using High Content Analysis. *PLoS ONE* **2012**, *7*, e42720. [CrossRef]
102. Wakeman, T.P.; Yang, A.; Dalal, N.S.; Boohaker, R.J.; Zeng, Q.; Ding, Q.; Xu, B. DNA mismatch repair protein Mlh1 is required for tetravalent chromium intermediate-induced DNA damage. *Oncotarget* **2017**, *8*, 83975–83985. [CrossRef]
103. Chiu, A.; Shi, X.L.; Lee, W.K.P.; Hill, R.; Wakeman, T.P.; Katz, A.; Xu, B.; Dalal, N.S.; Robertson, J.D.; Chen, C.; et al. Review of Chromium (VI) Apoptosis, Cell-Cycle-Arrest, and Carcinogenesis. *J. Environ. Sci. Health Part C Environ. Carcinog. Ecotoxicol. Rev.* **2010**, *28*, 188–230. [CrossRef]
104. Chen, T.L.; LaCerte, C.; Wise, S.S.; Holmes, A.; Martino, J.; Wise, J.P., Jr.; Thompson, W.D.; Wise, J.P., Sr. Comparative cytotoxicity and genotoxicity of particulate and soluble hexavalent chromium in human and sperm whale (*Physeter macrocephalus*) skin cells. *Comp. Biochem. Physiol. C Toxicol. Pharmacol.* **2012**, *155*, 143–150. [CrossRef] [PubMed]

105. Fang, Z.; Zhao, M.; Zhen, H.; Chen, L.; Shi, P.; Huang, Z. Genotoxicity of Tri- and Hexavalent Chromium Compounds In Vivo and Their Modes of Action on DNA Damage In Vitro. *PLoS ONE* **2014**, *9*, e103194. [CrossRef] [PubMed]
106. Xia, W.; Hu, J.; Zhang, B.; Li, Y.; Wise, J.P., Sr.; Bassig, B.A.; Zhou, A.; Savitz, D.A.; Xiong, C.; Zhao, J.; et al. A case-control study of maternal exposure to chromium and infant low birth weight in China. *Chemosphere* **2016**, *144*, 1484–1489. [CrossRef] [PubMed]
107. Blasiak, J.; Kowalik, J. A comparison of the in vitro genotoxicity of tri- and hexavalent chromium. *Mutat. Res. Genet. Toxicol. Environ. Mutagenesis* **2000**, *469*, 135–145. [CrossRef]
108. Meng, X.; Fang, Z.; Wei, H.; Yang, Z.; Huang, Z. Genotoxicity investigation of tri-and hexavalent chromium using a yeast SUP4-o mutation assay. *Carcinog. Teratog. Mutagenesis* **2017**, *29*, 65–69.
109. Salnikow, K.; Zhitkovich, A. Genetic and epigenetic mechanisms in metal carcinogenesis and cocarcinogenesis: Nickel, arsenic, and chromium. *Chem. Res. Toxicol.* **2008**, *21*, 28–44. [CrossRef]
110. Alimba, C.G.; Dhillon, V.; Bakare, A.A.; Fenech, M. Genotoxicity and cytotoxicity of chromium, copper, manganese and lead, and their mixture in WIL2-NS human B lymphoblastoid cells is enhanced by folate depletion. *Mutat. Res. Genet. Toxicol. Environ. Mutagenesis* **2016**, *798*, 35–47. [CrossRef]
111. Kumari, V.; Yadav, A.; Haq, I.; Kumar, S.; Bharagava, R.N.; Singh, S.K.; Raj, A. Genotoxicity evaluation of tannery effluent treated with newly isolated hexavalent chromium reducing *Bacillus cereuss*. *J. Environ. Manag.* **2016**, *183*, 204–211. [CrossRef]
112. Bordeerat, N.K. Evaluation of genotoxicity in Welders exposed to hexavalent chromium. *Environ. Mol. Mutagenesis* **2017**, *58*, S65–S66.
113. Taju, G.; Majeed, S.A.; Nambi, K.S.N.; Hameed, A.S.S. Application of fish cell lines for evaluating the chromium induced cytotoxicity, genotoxicity and oxidative stress. *Chemosphere* **2017**, *184*, 1–12. [CrossRef]
114. Zhang, Y.; Zhang, Y.; Zhong, C.; Xiao, F. Cr(VI) induces premature senescence through ROS-mediated p53 pathway in L-02 hepatocytes. *Sci. Rep.* **2016**, *6*, 34578. [CrossRef] [PubMed]
115. Kim Linh, N.; Hoang Anh, N.; Richter, O.; Minh Thinh, P.; Van Phuoc, N. Ecophysiological responses of young mangrove species *Rhizophora apiculata* (Blume) to different chromium contaminated environments. *Sci. Total Environ.* **2017**, *574*, 369–380.
116. Suraweera, D.D.; Groom, T.; Taylor, P.W.J.; Jayasinghe, C.S.; Nicolas, M.E. Dynamics of flower, achene and trichome development governs the accumulation of pyrethrins in pyrethrum (*Tanacetum cinerariifolium*) under irrigated and dryland conditions. *Ind. Crop. Prod.* **2017**, *109*, 123–133. [CrossRef]
117. Vadde, B.V.L.; Challa, K.R.; Nath, U. The TCP4 transcription factor regulates trichome cell differentiation by directly activating *GLABROUS INFLORESCENCE STEMS* in *Arabidopsis thaliana*. *Plant J.* **2018**, *93*, 259–269. [CrossRef] [PubMed]
118. Speranza, A.; Ferri, P.; Battistelli, M.; Falcieri, E.; Crinelli, R.; Scoccianti, V. Both trivalent and hexavalent chromium strongly alter in vitro germination and ultrastructure of kiwifruit pollen. *Chemosphere* **2007**, *66*, 1165–1174. [CrossRef] [PubMed]
119. Mangabeira, P.A.; Ferreira, A.S.; de Almeida, A.-A.F.; Fernandes, V.F.; Lucena, E.; Souza, V.L.; dos Santos Junior, A.J.; Oliveira, A.H.; Grenier-Loustalot, M.F.; Barbier, F.; et al. Compartmentalization and ultrastructural alterations induced by chromium in aquatic macrophytes. *Biometals* **2011**, *24*, 1017–1026. [CrossRef]
120. Gill, R.A.; Ali, B.; Yang, S.; Tong, C.; Islam, F.; Gill, M.B.; Mwamba, T.M.; Ali, S.; Mao, B.; Liu, S.; et al. Reduced Glutathione Mediates Phone-Ultrastrcture, Kinome and Transportome in Chromium-Induced *Brassica napus* L. *Front. Plant Sci.* **2017**, *8*, 2037. [CrossRef]
121. Andosch, A.; Hoeftberger, M.; Luetz, C.; Luetz-Meindl, U. Subcellular Sequestration and Impact of Heavy Metals on the Ultrastructure and Physiology of the Multicellular Freshwater Alga *Desmidium swartzii*. *Int. J. Mol. Sci.* **2015**, *16*, 10389–10410, Erratum in **2015**, *16*, 20239.. [CrossRef]
122. Bukhari, S.A.H.; Zheng, W.; Xie, L.; Zhang, G.; Shang, S.; Wu, F. Cr-induced changes in leaf protein profile, ultrastructure and photosynthetic traits in the two contrasting tobacco genotypes. *Plant Growth Regul.* **2016**, *79*, 147–156. [CrossRef]
123. Bukhari, S.A.H.; Wang, R.; Wang, W.; Ahmed, I.M.; Zheng, W.; Cao, F. Genotype-dependent effect of exogenous 24-epibrassinolide on chromium-induced changes in ultrastructure and physicochemical traits in tobacco seedlings. *Environ. Sci. Pollut. Res.* **2016**, *23*, 18229–18238. [CrossRef]

124. El Fels, L.; Hafidi, M.; Silvestre, J.; Kallerhoff, J.; Merlina, G.; Pinelli, E. Efficiency of co-composting process to remove genotoxicity from sewage sludge contaminated with hexavalent chromium. *Ecol. Eng.* **2015**, *82*, 355–360.
125. Fargasova, A. Plants as models for chromium and nickel risk assessment. *Ecotoxicology* **2012**, *21*, 1476–1483. [CrossRef] [PubMed]
126. Chandra, S.; Chauhan, L.K.S.; Pande, P.N.; Gupta, S.K. Cytogenetic effects of leachates from tannery solid waste on the somatic cells of *Vicia faba*. *Environ. Toxicol.* **2004**, *19*, 129–133. [CrossRef] [PubMed]
127. Rodriguez, E.; Azevedo, R.; Fernandes, P.; Santos, C. Cr(VI) Induces DNA Damage, Cell Cycle Arrest and Polyploidization: A How Cytometric and Comet Assay Study in *Pisum sativum*. *Chem. Res. Toxicol.* **2011**, *24*, 1040–1047. [CrossRef]
128. Hemachandra, C.K.; Pathiratne, A. Assessing Toxicity of Copper, Cadmium and Chromium Levels Relevant to Discharge Limits of Industrial Effluents into Inland Surface Waters Using Common Onion, *Allium cepa* Bioassay. *Bull. Environ. Contam. Toxicol.* **2015**, *94*, 199–203. [CrossRef]
129. Qian, X.-W. Mutagenic effects of chromium trioxide on root tip cells of *Vicia faba*. *J. Zhejiang Univ. Sci.* **2004**, *5*, 1570–1576. [CrossRef]
130. Truta, E.; Mihai, C.; Gherghel, D.; Vochita, G. Assessment of the Cytogenetic Damage Induced by Chromium Short-Term Exposure in Root Tip Meristems of Barley Seedlings. *Water Air Soil Pollut.* **2014**, *225*, 1933. [CrossRef]
131. Miadokova, E.; Duhova, V.; Vlckova, V.; Sladkova, L.; Sucha, V.; Vlcek, D. Genetic risk assessment of acid waste water containing heavy metals. *Gen. Physiol. Biophys.* **1999**, *18*, 92–98.
132. Labra, M.; Grassi, F.; Imazio, S.; Di Fabio, T.; Citterio, S.; Sgorbati, S.; Agradi, E. Genetic and DNA-methylation changes induced by potassium dichromate in *Brassica napus* L. *Chemosphere* **2004**, *54*, 1049–1058. [CrossRef]
133. Labra, M.; Di Fabio, T.; Grassi, F.; Regondi, S.M.G.; Bracale, M.; Vannini, C.; Agradi, E. AFLP analysis as biomarker of exposure to organic and inorganic genotoxic substances in plants. *Chemosphere* **2003**, *52*, 1183–1188. [CrossRef]
134. Gill, R.A.; Hu, X.Q.; Ali, B.; Yang, C.; Shou, J.Y.; Wu, Y.Y.; Zhou, W.J. Genotypic variation of the responses to chromium toxicity in four oilseed rape cultivars. *Biol. Plant.* **2014**, *58*, 539–550. [CrossRef]
135. Qiu, B.; Zeng, F.; Cai, S.; Wu, X.; Haider, S.I.; Wu, F.; Zhang, G. Alleviation of chromium toxicity in rice seedlings by applying exogenous glutathione. *J. Plant Physiol.* **2013**, *170*, 772–779. [CrossRef] [PubMed]
136. Eleftheriou, E.P.; Adamakis, I.-D.S.; Melissa, P. Effects of hexavalent chromium on microtubule organization, ER distribution and callose deposition in root tip cells of *Allium cepa* L. *Protoplasma* **2012**, *249*, 401–416. [CrossRef] [PubMed]
137. Montoya-Palomino, W.; Javier Pena-Salamanea, E.; Andres Torres-Rodriguez, G. Ultraestructural changes induced by chromium(VI) in water hyacinth (*Eichhornia crassipes*) leaves. *Limnetica* **2015**, *34*, 85–94.
138. Maleci, L.; Buffa, G.; Wahsha, M.; Bini, C. Morphological changes induced by heavy metals in dandelion (*Taraxacum officinale* Web.) growing on mine soils. *J. Soils Sediments* **2014**, *14*, 731–743. [CrossRef]
139. Ali, S.; Farooq, M.A.; Yasmeen, T.; Hussain, S.; Arif, M.S.; Abbas, F.; Bharwana, S.A.; Zhang, G. The influence of silicon on barley growth, photosynthesis and ultra-structure under chromium stress. *Ecotoxicol. Environ. Saf.* **2013**, *89*, 66–72. [CrossRef]
140. Mangabeira, P.A.; de Almeida, A.A.F.; Souza, V.L.; dos Santos Junior, A.J.; Silva, D.C.; de Jesus, R.M. Ultrastructural damage in tomato plants exposed to chromium III. In Proceedings of the 16th International Conference on Heavy Metals in the Environment, Rome, Italy, 23–27 September 2012; Pirrone, N., Ed.; EDP Sciences: Ilhéus, Bahia, Brazil, 2013; Volume 1.
141. Hui, C.; Guo-Xin, S.H.I.; Qin-Song, X.U.; Wang, H.-X.; Yang, H.-Y.; Qiu-Hong, P.A.N. Toxic Effects of Cr~(6+) on Chlorophyll Fluorescence Parameters, Antioxidant Systems and Ultrastructure of *Potamogeton crispus*. *Bull. Bot. Res.* **2009**, *29*, 559–564.
142. Sruthi, P.; Shackira, A.M.; Puthur, J.T. Heavy metal detoxification mechanisms in halophytes: An overview. *Wetl. Ecol. Manag.* **2017**, *25*, 129–148. [CrossRef]
143. Yang, C.; Li, W.; Cao, J.; Meng, F.; Yu, Y.; Huang, J.; Jiang, L.; Liu, M.; Zhang, Z.; Chen, X.; et al. Activation of ethylene signaling pathways enhances disease resistance by regulating ROS and phytoalexin production in rice. *Plant J.* **2017**, *89*, 338–353. [CrossRef]

144. Farias, D.R.; Hurd, C.L.; Eriksen, R.S.; Simioni, C.; Schmidt, E.; Bouzon, Z.L.; Macleod, C.K. In situ assessment of *Ulva australis* as a monitoring and management tool for metal pollution. *J. Appl. Phycol.* **2017**, *29*, 2489–2502. [CrossRef]
145. Farias, D.R.; Schmidt, E.; Simioni, C.; Bouzon, Z.L.; Hurd, C.L.; Eriksen, R.S.; Macleod, C.K. Photosynthetic and ultrastructural responses of *Ulva australis* to Zn stress. *Micron* **2017**, *103*, 45–52. [CrossRef] [PubMed]
146. Liu, D.; Zou, J.; Wang, M.; Jiang, W. Hexavalent chromium uptake and its effects on mineral uptake, antioxidant defence system and photosynthesis in *Amaranthus viridis* L. *Bioresour. Technol.* **2008**, *99*, 2628–2636. [CrossRef]
147. Anjum, S.A.; Ashraf, U.; Khan, I.; Saleem, M.F.; Wang, L.C. Chromium toxicity induced alterations in growth, photosynthesis, gas exchange attributes and yield formation in maize. *Pak. J. Agric. Sci.* **2016**, *53*, 751–757.
148. Pandey, V.; Dixit, V.; Shyam, R. Chromium effect on ROS generation and detoxification in pea (*Pisum sativum*) leaf chloroplasts. *Protoplasma* **2009**, *236*, 85–95. [CrossRef] [PubMed]
149. Dixit, V.; Pandey, V.; Shyam, R. Chromium ions inactivate electron transport and enhance superoxide generation in vivo in pea (*Pisum sativum* L. cv. Azad) root mitochondria. *Plant Cell Environ.* **2002**, *25*, 687–693. [CrossRef]
150. Yewalkar, S.N.; Dhumal, K.N.; Sainis, J.K. Effect of chromate on photosynthesis in Cr(VI)-resistant Chlorella. *Photosynthetica* **2013**, *51*, 565–573. [CrossRef]
151. Cho, D.-W.; Song, H.; Schwartz, F.W.; Kim, B.; Jeon, B.-H. The role of magnetite nanoparticles in the reduction of nitrate in groundwater by zero-valent iron. *Chemosphere* **2015**, *125*, 41–49. [CrossRef]
152. El-Esawi, M.; Arthaut, L.-D.; Jourdan, N.; d'Harlingue, A.; Link, J.; Martino, C.F.; Ahmad, M. Blue-light induced biosynthesis of ROS contributes to the signaling mechanism of Arabidopsis cryptochrome. *Sci. Rep.* **2017**, *7*, 13875. [CrossRef]
153. Choudhary, K.K.; Agrawal, S.B. Assessment of Fatty Acid Profile and Seed Mineral Nutrients of Two Soybean (*Glycine max* L.) Cultivars under Elevated Ultraviolet-B: Role of ROS, Pigments and Antioxidants. *Photochem. Photobiol.* **2016**, *92*, 134–143. [CrossRef]
154. Dey, S.; Paul, A.K. Evaluation of chromate reductase activity in the cell-free culture filtrate of *Arthrobacter* sp. SUK 1201 isolated from chromite mine overburden. *Chemosphere* **2016**, *156*, 69–75. [CrossRef]
155. Gautam, M.; Singh, A.K.; Johri, R.M. Effect of chromium toxicity on growth, chlorophyll and some macronutrients of *Solanum lycopersicum* and *Solanum melongena*. *Indian J. Agric. Sci.* **2014**, *84*, 1115–1123.
156. Hammud, H.H.; Abbas, I.; Al-Khalili, D. Kinetics and thermodynamics of chromate and phosphate uptake by polypyrrole: Batch and column studies. *J. Incl. Phenom. Macrocycl. Chem.* **2015**, *82*, 395–405. [CrossRef]
157. Sheetal, K.R.; Singh, S.D.; Anand, A.; Prasad, S. Heavy metal accumulation and effects on growth, biomass and physiological processes in mustard. *Indian J. Plant Physiol.* **2016**, *21*, 219–223. [CrossRef]
158. Yasin, M.; Faisal, M. Comparative Analysis of Tannery-Effluent Contaminated Soil and Mixed Culture Bacterial Inoculation on *Helianthus annuus* L. Growth. *J. Chem. Soc. Pak.* **2012**, *34*, 1573–1577.
159. Li, S.; Huang, H.; Li, Z.; Li, Z.; He, Z.; Liang, H. Chromium removal capability and photosynthetic characteristics of *Cyperus alternifolius* and *Coix lacryma-jobi* L. in vertical flow constructed wetland treated with hexavalent chromium bearing domestic sewage. *Water Sci. Technol.* **2017**, *76*, 2203–2212. [CrossRef]
160. Yasin, M.; Faisal, M. Assessing the Phytotoxicity of Tannery Waste-Contaminated Soil on *Zea mays* (Lin) Growth. *Pol. J. Environ. Stud.* **2013**, *22*, 1871–1876.
161. Revathi, S.; Subhashree, V. Comparative Study of Hexavalent Chromium Induced Biochemical Changes With and Without EDTA in *Sesbania grandiflora* L. Pers. *J. Agric. Sci. Technol.* **2016**, *18*, 1289–1301.
162. Dias, M.C.; Moutinho-Pereira, J.; Correia, C.; Monteiro, C.; Araujo, M.; Brueggemann, W.; Santos, C. Physiological mechanisms to cope with Cr(VI) toxicity in lettuce: Can lettuce be used in Cr phytoremediation? *Environ. Sci. Pollut. Res.* **2016**, *23*, 15627–15637. [CrossRef]
163. Mathur, S.; Kalaji, H.M.; Jajoo, A. Investigation of deleterious effects of chromium phytotoxicity and photosynthesis in wheat plant. *Photosynthetica* **2016**, *54*, 185–192. [CrossRef]
164. Wang, B.; Xiao, J.; Feng, X.; Gan, L.; Tang, Y. Effects of Chromium stress on physiological and ecophysiological characteristics of male and female plants of *Humulus scandens*. *Acta Pratacult. Sin.* **2016**, *25*, 131–139.
165. Reale, L.; Ferranti, F.; Mantilacci, S.; Corboli, M.; Aversa, S.; Landucci, F.; Baldisserotto, C.; Ferroni, L.; Pancaldi, S.; Venanzoni, R. Cyto-histological and morpho-physiological responses of common duckweed (*Lemna minor* L.) to chromium. *Chemosphere* **2016**, *145*, 98–105. [CrossRef] [PubMed]

166. Sheetal, K.R.; Singh, S.; Prasad, S.; Mina, U.; Datta, S.P.; Anand, A. Physiological and biochemical responses of different vegetables to chromium. *Biochem. Cell. Arch.* **2015**, *15*, 421–425.
167. Da Conceicao Gomes, M.A.; Hauser-Davis, R.A.; Suzuki, M.S.; Vitoria, A.P. Plant chromium uptake and transport, physiological effects and recent advances in molecular investigations. *Ecotoxicol. Environ. Saf.* **2017**, *140*, 55–64. [CrossRef] [PubMed]
168. Vernay, P.; Gauthier-Moussard, C.; Hitmi, A. Interaction of bioaccumulation of heavy metal chromium with water relation, mineral nutrition and photosynthesis in developed leaves of *Lolium perenne* L. *Chemosphere* **2007**, *68*, 1563–1575. [CrossRef] [PubMed]
169. Dong, J.; Wu, F.; Huang, R.; Zang, G. A chromium-tolerant plant growing in Cr-contaminated land. *Int. J. Phytoremediation* **2007**, *9*, 167–179. [CrossRef]
170. Mallick, S.; Sinam, G.; Mishra, R.K.; Sinha, S. Interactive effects of Cr and Fe treatments on plants growth, nutrition and oxidative status in *Zea mays* L. *Ecotoxicol. Environ. Saf.* **2010**, *73*, 987–995. [CrossRef]
171. Xu, F.; Deng, J. Effects of Salicylic Acid on Germination of Soybean Seed under Chromium Stress. *Soybean Sci.* **2012**, *31*, 852–854.