

Journal of Applied and Natural Science

14(4), 1204 - 1224 (2022)

ISSN: 0974-9411 (Print), 2231-5209 (Online)

journals.ansfoundation.org

Review Article

A review on regulatory control of chromium stress in plants

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Article Info

https://doi.org/10.31018/ jans.v14i4.3824

Received: July 26, 2022 Revised: October 31, 2022 Accepted: November 8, 2022

How to Cite

Yadav, P. *et al.* (2022). A review on regulatory control of chromium stress in plants. *Journal of Applied and Natural Science*, 14 (4), 1204 - 1224. https://doi.org/10.31018/jans.v14i4.3824

Abstract

Chromium (Cr) is a non-biodegradable heavy metal that persists long in aquatic and terrestrial ecosystems and enters the food chain. It is cytotoxic even at low concentrations and reduces the yield of plants. Plants also have cellular mechanisms to manage the accumulation of metal ions inside the cell to diminish the possible injury from non-essential metal ions. This paper reviews current information on plant response to Cr, a key environmental pollutant. The harmful effects together with absorption, transfer, and aggregation of Cr are discussed. The roles of the cell wall, plasma membrane, and plant microbes as the primary hindrances for Cr ingression into the cell, along with sequestration and compartmentalization process, have also been discussed. Cr-generated oxidative injury is also regarded as the main deliberated effect of Cr toxicity. It interferes with NADPH oxidases (plasma membrane) and the electron transport chains, which develop electron leakage. Some genes related to Cr stress in plants get expressed, and suppression produces protective effects by activating the signal transduction pathways. The expression of genes like BnaCnng69940D and BnaC08g49360D is increased, which is involved in protein kinase activity, signal transduction, and oxidoreductase activity. The increased mRNA levels of Cr stress response proteins, including HSP90-1 and MT-1, have been reported in the *Brassica napus* plant. The stressed environment around the plants may stimulate the biosynthesis of phytochelatins and metal-binding proteins, which have a protective role in plant's growth and development.

Keywords: Abiotic stress, Chromium, Heavy metals, Oxidative stress, Phytochelatins

INTRODUCTION

In recent history, the total arable land area has diminished because of the population pressure and soil degradation by the industrial revolution and modern lifestyle. Lavish human activities have assisted the difficulties of atmospheric pollution by toxic metals (Singh et al., 2013; Shahid et al., 2017). Due to the quick expansion of factories and metropolitan regions, a broad range of pollutants like organic/inorganic compounds and heavy metals (HMs), etc., are regularly spreading in the environment (Ram et al., 2019) with eventual harmful impacts on biological entities (Sharma et al., 2019; Hashem et al., 2020; Saleem et al., 2020a). Among these heavy metals, chromium (Cr) is a wellknown pollutant and carcinogen that is fatal for plants and animals (Sharma et al., 2020). Effects of Cr depend upon plant species, valance state, amount, and

time of its exposure (Hose et al., 2016). It exists in variable oxidation numbers starting with Cr2- to Cr6+. Both forms (Cr3+) and (Cr6+) are prevalent and have more reliable oxidation numbers in the biosphere (Shahid et al., 2017; Singh and Prasad, 2019). The reactive oxygen species (ROS) generation, followed by oxidative stress, is the primary harmful effect of chromium in plants. Several investigations have suggested that Cr induces oxidative cellular damage directly via the Fenton reactions (Gomes et al., 2017; Yu et al., 2018; Patra et al., 2019) and indirectly by affecting the activities of the enzymes (Ahmad et al., 2020; Sharma et al., 2020; Wakeel et al., 2020). Phytotoxic effects due to overproduction of ROS under Cr stress have been documented in Brassica napus L. (Gill et al., 2015), Triticum aestivum L. (Ali et al., 2015), and Chenopodium quinoa Willd (Scoccianti et al., 2016). The occurrence of Cr³⁺ in a small fraction supports the metabolism of sugars and lipids. The Cr³⁺ form responded more toward expressed genes in roots than in shoots (Feng *et al.*, 2019). Cr stress also raised the levels of proteins in plants that are important for intracellular membrane-bound organelles, nitrile hydratase activity, cytoskeleton protein binding, and stress responses (Gill *et al.*, 2016). The crop plants absorb oxidized states of HMs (Cr, Pb, Cd, As, Hg, Ni), which lead to toxicity and reduction in nutrient content. So, there is a need for critical analysis of toxic HMs (Cr) and successfully developing efficient techniques for removing HMs from food chains.

Heavy metals' toxicity

HMs (heavy metals) are classified as essential metals (Co, Fe, Mn, Mo, Ni, Zn, Cu, Mg) used as micronutrients in the biological system and non-essential metals (Pb, Cd, As, Cr, Hg) having no role as nutrients, both types toxic even at very low concentrations (Maleki et al., 2017). Essential and non-essential HMs, when present in high concentrations, give rise to critical diseases in all living beings. The chief toxic HMs released from industries are copper, zinc, chromium, lead, nickel, arsenic, mercury, and cadmium (Mehdipour et al., 2015). These HMs are derived from the combustion of fuel, industrial effluents such as stain and fabric production, laminating debris, cycles and supplementary segments. welding and excavation operations, metal plating, waste matter treatment plants, chemical fertilizers, and garbage dumps (Zeng et al., 2017) and affect water and soil ecosystem. The uptake of HMs by plants depends on environmental factors such as pH of the soil and organic matter, metal relevance, water, air, and plant species (Shen et al., 2017). The solubility of HMs elevates under oxidizing environment (\pm) because of their ionic configuration, while in a reducing environment (†pH), their distribution declines due to less solubility (Lena and Rao, 1997). In plants, toxicity is associated with the decrease in photosynthesis, nutrient assimilation, root damage, and, ultimately, plant death (Ali et al., 2011; Gill et al., 2015; Zaheer et al., 2015). Different HMs have different sites of action within the plant due to differences in their solubility, transport, and chemical reactivity. HMs are highly reactive due to variable oxidation states and cause toxicity at the cellular and molecular levels. HMs bind firmly to oxygen, nitrogen, and sulfur atoms (Nieboer and Richardson, 1980) due to free enthalpy of the product and retard functions of necessary elements in biological- molecules, including pigments and enzymes (Ali et al., 2013) by binding with cysteine residues of enzymes, which inhibits soil enzyme activity or sulfhydryl groups of structural proteins (Hall, 2002). They also arrest functional groups of main cellular molecules (Hossain et al., 2012). HMs stress results in nutrient deficiency, oxidative stress, metabolic agitation, and genetic disorders in plants. A

higher concentration of HMs stimulates the formation of excess methylglyoxal, free radicals (O₂· and OH), and reactive oxygen species (Hossain *et al.*, 2012; Sytar *et al.*, 2013). So, to survive against these harmful metals, plants have developed intricate methods to regulate the absorption and aggregation of metals. There are different procedures of metal tolerance in plants, the general mechanism involved in different HMs tolerance is described in Fig. 1.

CHROMIUM TOXICITY IN HIGHER PLANTS

Chromium is a nonessential toxic HM possessing no role in plant metabolism (Hussain *et al.*, 2018). It is the 21st most common element in the earth's crust (Ertani et al., 2017). The agency for toxic substances and disease registry and the international agency for research on cancer (ATSDR and IARC) have declared it the first cancer-causing agent and positioned it as seventh out of twenty top dangerous substances (oh *et al.*, 2007; Brasili *et al.*, 2020). The source of chromium pollutants on earth is mainly anthropogenic activities like tanning, smelting, mining, textile dyes, pigments, ceramic glazes, refractory bricks, utilization of inorganic manures, insecticides, etc. (Fig. 2) (Tseng *et al.*, 2019; Sanjay *et al.*, 2020).

Both the Cr oxidation states (Cr3+ and Cr6+) show different chemical effects, toxicity, translocation, and climatic response (Choppala et al., 2018). Cr6+ is reported as more dangerous due to greater solubility, carcinogenicity, mobility, and oxidizer of cellular components resulting in low yield of plants (Ertani et al., 2017; Singh and Prasad, 2019). The transformation and absorption of Cr in plants are regulated by its oxidation number, concentration, soil pH, and plant species (Babula et al., 2008; Gomes et al., 2017). Gill et al. (2016) revealed that B. napus, cultivar ZS 758, had a powerful metabolism and was more resistant to Cr toxicity. The toxicity of Cr for crops in the nutrient solution is about 0.5-5.0 mg mL⁻¹, while for soil, 5-100 mg/g and 0.1 to 117 µg L⁻¹ in fresh water. Plants cannot uptake Cr directly from the soil (Singh et al., 2013), so its uptake occurs along the water and essential metal carriers such as Fe, S, and P

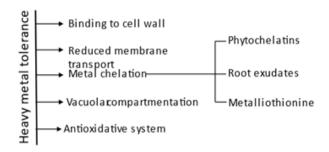


Fig. 1. General mechanism involved in different HMs tolerance (Kumar et al., 2016)

due to structural similarity (Farid et al., 2017; Shahid et al., 2017; Zhao et al., 2019). Cr stress causes Fe and N deficiency by inhibiting the plant's root Fe³⁺ reductase (Barton et al., 2000), nitrate reductase (Zou et al., 2009), and nitrogenase enzymes (Sessitsch et al., 2002). The symptoms of Cr injury in plants are limiting in plant growth or biomass (Danish et al., 2019), necrosis and chlorosis (Gupta et al., 2017), seed germination (Sultana et al., 2020), and wilting, etc. (Ahmad et al., 2020). However, such symptoms are not uniform, even in cultivars of the same plant. E.g., according to Gill et al. (2014), Zheda 622 was more sensitive to Cr than ZS 758, Zheda 619, and Zy 50 cultivars in B. napus. As chromium stress increases in plants, some changes in the shape and size of cellular organelles occur. In leaves of B. napus during Cr stress, an increase in size and quantity of starch grains, plastoglobuli, damaged thylakoid membranes, immature nucleoli, and mitochondria were observed, while roots showed enlarged vacuoles, damaged cell walls, and cell membranes, an increased number of mitochondria and size of the nucleolus as well as plasmolysis (Gill et al., 2014).

Cr toxicity has been manifested to cause decreased H⁺ ATPase function of cell membrane because of its binding capability with essential metal carrier channels (Sahid *et al.*, 2017). The Cr⁺⁶ form alters membrane function by oxidizing the membrane biomolecules, which triggers oxidative degradation of lipids (Shahid *et al.*, 2017; Sharma *et al.*, 2020) and disturbs chloroplast structure by degradation of enzyme - delta-aminolaevulinic acid dehydratase (Dey and Paul, 2016). A new Cr-responsive protein (CL2535.Contig1 All) was observed in *Brassica napus* during the Cr toxicity study (Gill *et al.*, 2016).

Chromium mobilization, uptake, and transport

The biological availability of metals depends on their solubility and binding capacities to soil particles (Cristaldi et al., 2017). Acidification of rhizosphere and root exudates such as malate, citrate, amino acids, etc., increase metal aggregation in plant roots (Kaur et al., 2018; Khanna et al., 2019). The uptake of Cr from the soil in plants depends upon plant species, types of root secretion, the surface area of the root (Ertani et al., 2017), soil pH, salinity, soil electrical conductivity (Islam et al., 2016), availability of soluble salts, soil redox potential, the quantity of organized material, temperature and the concentration of Cr and its oxidation state (Boechat et al., 2016; Gomes et al., 2017; Shen et al., 2017). Metal aggregation becomes low at high soil pH due to the complex formation with organic matter and oxides. Microorganisms also have prominent effects on metals because they secrete metabolites that bind with metals to enhance their translocation in the rhizosphere of plants (Chen et al., 2014). Cr is a non-essential toxic HM with no specified transporter for its absorption in plants (Singh et al., 2013). Its uptake occurs with water and essential elements. The plant roots can absorb both forms of Cr (Cr+3 and Cr +6). The uptake of Cr (III) is a passive process occurring at the cation inter-change spot of the cell wall without energy requirement (Shanker et al., 2005; Babula et al., 2008), while absorption of Cr (VI) occurs actively through plasma membrane carriers of essential elements such as sulfate (Singh et al., 2013; Shahid et al., 2017; Singh and Prasad, 2019). Cr also interferes with the uptake of Fe, S, N, K, Mg, Na, Ca, Zn, Mn, and P (Gomes et al., 2017; Zhao et al., 2019). Zaheer et al. (2019) reported that Cr toxicity causes decreased ac-

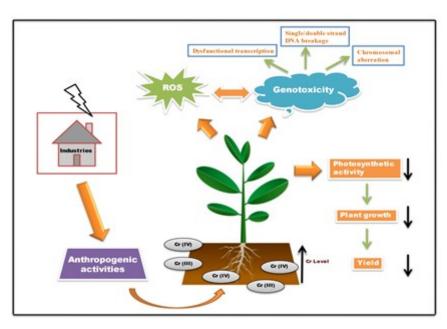


Fig. 2. Source of chromium and its entry into plants (Singh et al., 2013)

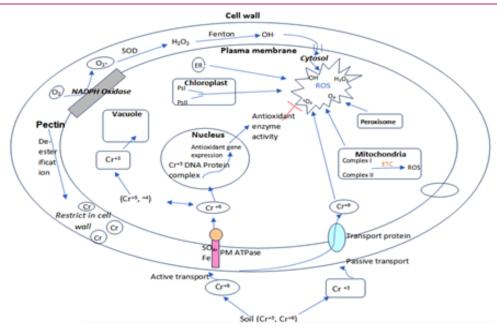


Fig. 3. Chromium uptake and its toxicity in plants (Shanker et al., 2005)

cumulation of Zn in all portions of *Spinacia oleracea* L. plant. The transformation ratio of Cr³⁺ and Cr⁶⁺ from roots to shoots is also different. Skeffington *et al.* (1976) noticed that extra Cr was transferred from roots to shoots when Cr⁶⁺ treatment was given instead of Cr³⁺. Cr can undergo an oxidoreduction reaction spontaneously in different earth circumstances (Shahid *et al.*, 2017). Wei *et al.* (2016) described that organic carbon matter reduces Cr (VI) to Cr (III). The chromium uptake mechanism and toxicity are shown below (Fig. 3).

After absorption by root hairs or binding to the cell wall, Cr is transported mostly through the plant xylem (Hayat et al., 2012). When Cr6+ moves across the endoderm via symplast, it is reduced to Cr3+ by root reductases and accumulates in root apoplast or vacuoles of root cortex cells (Shanker et al., 2005; Hayat et al., 2012), or it is transported through the xylem by symplastic system distributed in the cytoplasm of cortical cells (Mongkhonsin et al., 2011). After uptake into the root symplasm, further movement of metals into the xylem occurs through three stages: segregation of metals in root cells, simplistic transfer towards stele, and delivery within the xylem. Basically, the maximum Cr in plants is accumulated in the root system, followed by stems, leaves, and seeds (Tiwari et al., 2009). Ahmad et al. (2020) reported that Brassica oleracea L. germinated during Cr (VI) treatment demonstrated the highest aggregation of Cr in roots and least in flowers. The passage of metals in the xylem from the root to the stem mostly occurs along with transpiration, which creates a tension for the movement of water and solutes upwards (Taiz and Zeiger, 2002). In the leaves, metals are transferred along with membrane transport proteins.

Roots are the first plant organs to contact Cr, affecting them more than shoots (Zhao *et al.*, 2019). At low Cr⁶⁺ concentration, the root showed more injury because Cr⁶⁺ has significant potential to penetrate the plant-root system and cross the endodermis via symplast for reduction and retention in the root cortex cells (Shanker *et al.*, 2005). The apoplast of the root cortex is freely permeable for solutes, but further on, the endodermal layer of the cell wall serves as an obstacle for apoplastic diffusion.

Oxidative stress and ROS generation by chromium

Plants are immobile, so they are susceptible to various environmental stress like drought, HMs, temperature, salinity, etc. Stress conditions can interrupt plants' ROS equilibrium (Zaheer et al., 2019; Saleem et al., 2020c). The production of ROS such as superoxide free radicals (O2.), hydroxyl radicals (OH), hydroperoxyl radicals (HOO•), the paramagnetic singlet oxygen (¹O₂), nitrogen oxide radical (NO), hydrogen peroxide (H₂O₂), hypochlorous acid (HOCI) segments (Turkan et al., 2018) and cytotoxic compounds like methyl glyoxal (MG) is an unavoidable effect of metal toxicity in plants (Singh et al., 2016; Singh and Prasad, 2019). ROS result from metabolic pathways like photosynthesis and respiration and are produced in plant organelles such as chloroplast, mitochondria, peroxisomes, glyoxysome, and cytosol (Chen et al., 2017; Abbas et al., 2018). Cr directs excess ROS in plants by interfering with NADPH oxidases (plasma membrane) and the electron transport chains, which develop electrons leakage to an oxygen molecule (Singh and Prasad, 2019; Smirnoff and Arnaud, 2019). In plants, the concentration-dependent dual function of ROS is known. When

present at the basal level, they act as signalling molecules and manage the plant growth process (Mittler, 2017; Waszczak et al., 2018). The higher level of ROS triggers the destruction of macromolecules and a decline in plant growth (Qi et al., 2019). The basal level of ROS is attained during the non-stress condition by equilibrium and a complicated antioxidant enzymatic/ non-enzymatic support system (Shahid et al., 2014; Kushwaha et al., 2019). The vital antioxidant enzymes are superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), glutathione reductase (GR), glutathione peroxidase (GPX), single dehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione Stransferase (GST) (Kabir, 2016). Saleem et al. (2020d) and Mallhi et al. (2019) reported dual action of antioxidant enzymes in Hibiscus cannabinus L. and castor bean, respectively: minimal metal tension enhances the antioxidant enzyme activities, whereas elevated metal tension diminishes the action of antioxidant enzymes. During high-stress conditions, equilibrium is not maintained between the ROS formation and anti-oxidative systems, which causes oxidative stress and, finally, the destruction of the plant (Sharma et al., 2012; Xie et al., 2019). The response of antioxidant enzymes depends not only on the level of Cr supplied but also on plant species and their developmental phase. Pandey et al. (2005) observed that in *B. juncea* during Cr⁶⁺ treatment, SOD action diminished and APX action elevated in root and leaves parts of the plant (under 5 days of disclosure) but reduced later (15 days of disclosure). Catalase action remained unaffected in the roots but elevated in the leaves, while GR action was also elevated in both leaves and roots.

Although ROS has harmful effects on the plant system, sometimes it also acts as a signaling molecule.

Smirnoff and Arnaud (2019) reported that H₂O₂ act as a signaling molecule when present in a low amount and evoke signal transduction in plant tissues during metal stress. The H₂O₂ activates a cascade of signals (Van Breusegem et al., 2008) that create ROS surge within the cells, transferred and stored in various parts (Mittler et al., 2011). Yildiz et al. (2013) showed that in B. napus, H₂O₂ contributes to Cr tolerance by ameliorating antioxidant enzymes action, chlorophyll, thiol content, stimulation of metallothionein protein (BnMP1), and reduced oxidative degradation of lipids. The overview of oxidative stress generated through Cr toxicity is given in Fig. 4. Redox-active metals such as Cr, Cu, and Fe induce oxidative stress in plants through Haber-Weiss, and Fenton reactions, which significantly promote ROS and interrupt the equilibrium among prooxidant and antioxidant proportions. These metals have an unpaired electron in their orbitals, enabling them to accept or donate a single electron. This electron can be transferred to the ground state oxygen molecule and thus generate ROS (Houri et al., 2020). Chromium produced oxidative stress (Sharma et al., 2019; Kushwaha and Singh, 2020; Wakeel et al., 2020) via Haber-Weiss cycle and Fenton reactions like other heavy metals such as Cd and Pb, which reduce glutathione pool and increase prooxidant response. Different reports of the oxidative response to Cr stress revealed in higher plants are listed in Table 1.

Yildiz et al. (2013) studied the participation of H_2O_2 in the signalling process, due to which the expression level of antioxidant enzymes SOD, CAT, APX, and POD varied in *B. napus* plant under different Cr concentrations. Cr treatment increased lipid peroxidation in *Vigna radiata* (Gautam et al., 2020), *B. oleracea* (Ahmad et al., 2020), Maize (Anjum et al., 2017), and *H. annus* (Farid et al., 2020). SOD, APX, CAT, and GR

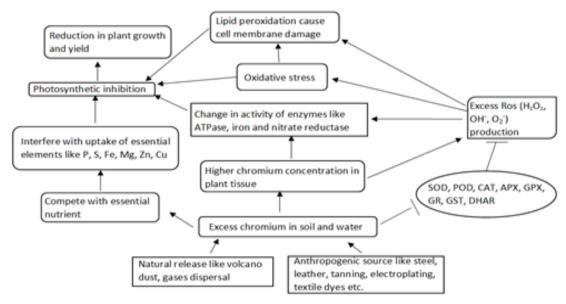


Fig. 4. Oxidative stress generated through Cr toxicity (Sharma et al., 2020)

activities vary according to Cr concentration and plant species (Yilmaz et al., 2017; Kushwaha and Singh, 2020). In B. napus and G. max, Cr increased glutathione content while activities of antioxidative enzyme SOD, APX, CAT, and GR increased or decreased according to Cr concentration and growth stage of the plant (Zaheer et al., 2020). In leaves and roots of H. annuus and B. oleracea, 10 mg/100µM Cr concentration increased the action of antioxidants CAT, SOD, APX, and POD, whereas enzymatic activities were suppressed at 20 mg/200 µM (Ahmad et al., 2020; Farid et al., 2020). Rai et al. (2004) and Gautam et al. (2020) reported that during Cr stress, protein content diminished while antioxidant enzymatic activities (SOD, GPX, and CAT), polyphenol content enhanced in Ocimum tenuiflorum and V. radiata plants, respectively. In T. aestivum, antioxidative enzyme activities (SOD, POD, CAT, and APX) in leaves and roots were decreased with increasing concentration (between 25 and 100 mg/kg) of Cr (Seleiman et al., 2020). Mallhi et al. (2020) reported that Cr stress generated oxidative injury in the leaves and roots of H. annuus plants due to the production of H₂O₂. During Cr treatment, the action of SOD and CAT increased in both roots and leaves, while GST activity was inhibited in P. sativum, S. Lycopersicon, and S. melongena (Kushwaha and Singh. 2020). Several experiments have been done under

various stresses that clearly show the potential role of aminolevulinic acid in combating oxidative stress. Gill et al. (2015) administered 5-aminolevulinic acid to find lessened oxidative stress in Brassica napus (ZS 758, Zheda 622) under Cr stress by promoting antioxidant enzyme activities (SOD, POD, CAT, APX, GR) and the expression of their associated genes. Gene's transcript levels were amplified by 77,76,177, 63 and 51 % in cultivar ZS 758 and 37, 25, 113, 47 and 22% in Zheda 622, respectively. The ALA is the ordinary ancestor of tetrapyrroles and helps in the growth regulation of plants. It has a role in photosynthesis and is well known for conserving plant development, cell turgidity, enhancing ALA content, and diminishing Cr concentration (Gill et al., 2015). Gill et al. (2016) demonstrated that plant hormone salicylic acid could increase tolerance in B. napus to Cr stress via enhancing the reactive oxygen scavenging by promoting enzymatic antioxidant activities, related gene expression, secondary metabolism, and cell structural alterations and transcript levels of particular stress-related proteins. Chromium and other related HMs cause significant damage to cellular organelles, mainly endomembrane, chloroplast, and mitochondria, as transport occurs across these membranes. Cr disrupts the organelles of plant cells by enhancing the size of starch grains and the number of plastoglobuli, causing damage to the chloroplast and

Table 1. Reports of the oxidative reaction to Cr stress revealed in higher plants

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Chromium concentration	Expo- sure time (days)	Plant species	Antioxidant enzymes modified	References
100 μΜ	21	Solanum lycopersi- cum L.	SOD, CAT, APX, GR, GST, GS, γ-GCS	Alamri <i>et al.</i> , (2020)
0, 25,50,100 mg/kg 5, 10, 20 mg/kg 0, 10, 100, 200 μM 30, 60, 90, 120, 150 μMol L ⁻¹	90 56 28	Basella alba L. Helianthus annuus L. B. oleracea L.	POD, SOD, CAT POD, SOD, CAT, APX SOD, CAT, POD	Zewail <i>et al.</i> , (2020) Farid <i>et al.</i> , (2020) Ahmad <i>et al.</i> , (2020)
	110	Zea mays L. SOD, POD, CAT, APX, GPX, GR SOD, CAT, POD, APX,		Anjum <i>et al.</i> , (2017)
0, 2, 8, 16 mg/ L	3	Oryza sativa L.	GR, GPX, MDHAR, DHAR	Fan <i>et al</i> ., (2020)
25 μΜ	7	S. lycopersicum L., Pisum sativum L. and Solanum melongena L.	SOD, CAT, GST	Kushwaha and Singh, (2020)
250 μΜ	7	Vigna radiata	POD, CAT, SOD, GR, APX, DHAR, PPO, GST and GPX	Gautam et al., (2020)
250 μΜ	17	Ricinus communis L.	POD, SOD, CAT, APX	Qureshi <i>et al</i> ., (2020)
0, 25, 50, 100 mg/L	80	T. aestivum L.	CAT, APX, SOD, POD	Seleiman <i>et al</i> ., (2020)
100 μg	21	S. lycopersicum L. and S. melongena L.	SOD, CAT, GST	Singh <i>et al.</i> , (2020)

SOD- Superoxide dismutase, CAT- Catalase, APX- Ascorbate peroxidase, POD- Peroxidase, GST- Glutathione S-transferase, GR-Glutathione reductase, PPO- Polyphenol oxidase, DHAR- Dehydro-ascorbate reductase, MDHAR- Mono dehydro-ascorbate reductase, GPX- Glutathione peroxidase, GS- Glutathione synthetase, γ -GCS- γ -Glutamyl cysteine synthetase, γ -Milligram, γ -Micromolar, γ -Microgram, L- Liter

Table 2. List of some Cr hyperaccumulator plants

Plant species	Metal	Family	Bioaccumulation	References
Zea mays L.	Cr	Poaceae	2538 mg/kg	Naseem <i>et al.</i> (2015)
Nymphaea spontanea	Cr	Nymphaeaceae	2,200 mg/kg	Choo <i>et al.</i> (2006)
Pteris vittate	Cr	Pteridaceae	5717 mg/kg	Wang <i>et al</i> . (2012)
Salvinia natans	Cr	Salviniaceae	5,200 mg/kg	Dhir et al. (2009)
Nopalea cochenillifera	Cr	Cactusaceae	25263 mg/kg	Adki <i>et al</i> . (2013)
Brassica napus	Cr	Brassicaceae	306.1 mg/Kg	Brunetti <i>et al</i> . (2011)
Prosopis juliflora	Cr	Fabaceae	372.13 mg/kg	Shukla <i>et al</i> . (2011)
Thlaspi caerulescens	Cr	Brassicaceae	3,400 mg/kg	Shahandeh and Hossner (2000)
Urtica dioica	Cr	Urticaceae	12-20 mg/Kg	Shams <i>et al.</i> (2010)
Gynura pseudochina	Cr	Asteraceae	1,611 mg/Kg	Mongkhonsin et al. (2011)
Baccharis sarothroides A. Gray	Cr	Asteraceae	162.6 mg/Kg	Haque <i>et al</i> . (2008)
Helianthus annuus L.	Cr	Asteraceae	1,356 mg/kg	Ranieri <i>et al.</i> (2013)
Salix babylonica L.	Cr	Salicaceae	1,278.96 mg/kg	Yu <i>et al</i> . (2008)
Brassica juncea	Cr	Brassicaceae	1,640 mg/kg	Diwan <i>et al.</i> (2010)
Allium griffithianum	Cr	Amaryllidaceae	568.33 mg/kg	Sajad <i>et al.</i> (2020)
Azolla pinnata	Cr	Salviniaceae	5000-15000 mg/kg	Arora <i>et al.</i> (2006)
Solanum viarum	Cr	Solanaceae	382 mg/kg	Afonso <i>et al.</i> (2019)
Origanum vulgare L.	Cr	Lamiaceae	1200 mg/kg	Levizou <i>et al</i> . (2018)
Vernonia cinerea (L.) Less.	Cr	Asteraceae	5500 mg/kg	Mohanty and Patra (2020)
Phragmites australis	Cr	Poaceae	4285 mg/kg	Calheiros et al. (2008)
Prosopis laevigata	Cr	Fabaceae	8090 mg/kg	Buendía-González <i>et al.</i> (2010)
Spartina argentinensis	Cr	Poaceae	15.1 mg/g	Redondo-Gómez et al. (2011)
Convolvulus arvensis L	Cr	Convolvulaceae	2800 mg /kg	Gardea-Torresdey <i>et al.</i> (2004)
Leersia hexandra	Cr	Poaceae	1844 mg/kg	Liu <i>et al.</i> (2011)

mitochondrion structures (Gill et al., 2016).

Chromium accumulation and detoxification

The accumulation of metal in plants depends upon its uptake capacity, intracellular binding sites, concentration, the affinity of the chelating agent, and translocation activities (Lopez Luna et al., 2009). Cr accumulates in the root by binding with the cell wall through functional groups like amino, phosphate, thiol, carboxyl, etc. (Eggs et al., 2012) and immobilization in vacuoles (Sinha et al., 2018) or root exudates (malic acid, amino acid) (Kaur et al., 2018; Khanna et al., 2019). Sobariu et al. (2017) described that Lepidium sativum accumulâtes Cr in the roots due to ion immobilization in vacuoles. Chromium accumulation in plants has effects on gene functions too. Gill et al. (2017) found that Cr stress increased the expressions of BnaA08g16610D, BnaCnng 19320D, and BnaA08g00390D genes in B. napus. These genes encoded proteins that bound nucleic acid and transition metal ions and protein kinase and phosphotransferase activities.

Plant microbes' interactions in Cr metabolism

Plant growth-promoting rhizobacteria (PGPR) are the plant integrated free-living, earth-born bacteria that se-

crete distinct metabolites such as organic acids, siderometal chelating (main agents), polysaccharide (EPS), hydrogen cyanide (HCN), biosurfactants, antibiotics and amplify the plant growth by minimizing the plant injury induced by living (microorganisms generated injury) and non-living (HM caused plant injury) components. These metabolic compounds can switch the mobility (chelation, precipitation, immobilization), the ionic position of metals including Cr, Fe, Hg, Se, and Mn (acidification, oxidation), and change the injurious dynamic configuration into a non-injurious static configuration (Ma et al., 2011). These increase the plants' phyto-remediation, phyto-stabilization, and phyto-volatilization capabilities (Ahemad, 2019). Microorganism inoculations can impart an alternative method of removing HMs from the soil. Karthik et al. (2017) revealed that inoculation by rhizobacteria Serratia (Srivastava and Thakur 2012) helped in the reduction and immobilization (decrease mobility and toxicity) of Cr (VI) by intricate methods such as ion-exchange, complexation, and coprecipitation. These rhizobacteria are established around the plant by the leakage of plant chemicals, amino acids, proteins, and antibiotics to cause a reduction of HMs toxicity. PGPR can be categorized, depending on their utility like biofertilizers (expand the soil-nutrient accessibility), Phyto-stimulators (trigger plant development by making plant hormones), rhizo-remediators (regulate the waste material proximity via metal dilution) and biopesticides (manage plant pathogen and infection by the emission of lysing agent and biochemical compounds) (Ahemad, 2019) and depends on inherent distinctiveness as root colonizer, assist plant growth, adjust, persist and challenge with other microbial foliage. PGPR stimulates plant growth in different ways, i.e., accelerates the soil-nutrient accessibility, triggers root development, cytokinesis along with expansion and metabolic counteraction, arrests HMs induced phytotoxicity, or enhances the induction of systemic resistance. They also prevent oxidative damage by producing different antioxidants and maintaining ROS proportion in plants (Karthik et al., 2016). The Cr stress in B. napus activated a wide range of metabolic pathways, including vitamin B₆, tryptophan, sulfur, nitrogen metabolism, zeatin biosynthesis, and linoleic acid production, proline, aspartate, and glutamate (Gill et al., 2016).

Cr modifies microbial diversity through different methods involving microbial biomass reduction, falling off particular microbial populations, and switching the microbial diversity layout. Inoculation of microbes in soil (e.g., arbuscular mycorrhiza and rhizospheric microbes) increases the hyper-accumulator plant remediation ability by translocating heavy metal from root to aerial parts (Rajkumar et al., 2010; Ma et al., 2011). Sheng et al. (2008) revealed that inoculation of Bacillus sp. elevated Cd uptake in plant tissue while P. aeruginosa boosted the uptake of Cr and Pb in maize plants (Braud et al., 2009). These microbes increase the bioremediation capacity of the plants and accelerate the tolerance limit of metal toxicity via nutrient recycling, conservation of earth layout, and managing infection. They have the capability to uptake the metal (Cr) by different methods, including adsorption, bioconversion, bio-sorption, bio-accumulation, biomineralization, precipitation, complexation, alkalization, bio volatilization, bio-leaching, and decomposition that assist the plants in mitigating their cytotoxicity (Karthik and Arulselvi, 2017). Moreover, Gill et al. (2016) discovered that Cr inhibits KEGG pathways in B. napus, including stilbenoid, diarlyheptanoid, gingerol production, limonene, and pentose degradation as well as glutathione metabolism in ZS 758, while ribosome and glucosinolate biosynthesis in Zheda-622. Rhizobium inoculations also increase the glutathione reductase action in P. sativum during Ni and Zn treatment (Wani et al., 2008). Anjana et al. (2007) reported that Nostoc calcicole and Chroococcus were effective Cr (VI) eliminators by biosorption. In certain microbes, bio-sorption and bioaccumulation impart resistance to Cr6+. Flores-Alvarez

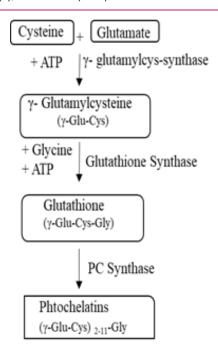


Fig. 5. Biosynthesis of PCs in plants (Sharma et al., 2016)

et al. (2012) showed that in Neurospora crassa, Cr6+ assembled in the vacuolar complex to increase its resistance. Different microbes like fungi, bacteria, algae, and actinomycetes reduce Cr6+ by various enzymatic and non-enzymatic methods (by vitamin C, H2S, cysteine, mercapto groups, and GSH) (Viti et al., 2014; Joutey et al., 2015). Some membrane enzymes of microbes also help reduce Cr (VI) (Joutey et al., 2015; Xia et al., 2018). For example: in Thermus scotoductus, dihydrolipoamide dehydrogenase acts as a Cr6+ reducer with the help of NADPH (electron donor). The overexpression of certain microbial genes can expand the Cr^{6+} consumption power of plants. Cytokinin β glucosidase genes of Agrobacterium tumefaciens overexpressed in Nicotiana lanfsdorffii while glutathione synthetase gene gshl of E. coli in B. juncea plant assimilated extra Cr (VI) as compared to wild counterparts (Del Bubba et al., 2013; Malandrino et al., 2017).

Cell wall and plasma membrane in Cr interaction

The cell wall is the first anatomical barrier protecting plants against biotic and abiotic stresses (Scheller and Ulvskov, 2010; Tucker and Koltunow, 2014). Environmental abiotic stresses modify the structure and composition of the cell wall (Berni *et al.*, 2019), and mainly the root system is affected due to direct contact with contaminated soil. The plant cell wall consists of polysaccharides (cellulose microfibrils, pectin, and hemicelluloses), proteins (Somerville *et al.* 2004), and phenolics which bind with HMs and store them in the cell wall (Krzeslowska, 2011; Vuletic *et al.*, 2014). The binding affinity of Cr ions depends on the number of functional groups (–COOH, –OH, and –SH) existing in the cell

wall (Pelloux et al., 2007). The cell wall structure also influences the translocation within the xylem. The first living structure called 'plasma membrane' is also affected by Cr toxicity due to the production of free radicals (ROS), which degrade the cellular components such as lipid peroxidation of unsaturated fatty acids (residues of phospholipids) oxidation and proteins (Schutzendubel and Polle, 2002). These damages change the structure, functions, and mobility of the membrane, which results in the imbalance of membrane-binding enzymes in the cell and disturb the cell metabolism process (Yadav, 2010). The plasma membrane also helps Cr tolerance by reducing their uptake or increasing metal efflux ions.

Chromium sequestration in plant cell

Plants have various methods at the cellular level, which are concerned with detoxification and help in tolerance to HMs stress (Hall, 2002). The accumulation of metal in plants depends upon its uptake capacity, intracellular binding sites, concentration, the affinity of the chelating agent, and translocation activities (Lopez Luna et al., 2009). The addition of chelating agents can amplify the absorption of Cr by the plants and trigger the metal absorption capability of the microbial population throughout the plant rhizosphere. Chelates enhance the metal tolerance and deposition hyperaccumulator plants, including Ricinus communis L. (Zhang et al., 2016). When chelating agents like ethylene diamine tetra acetic acid and citric acid are added to the earth, the solubility of metal increases because of the establishment of an aqueous dissolved metal network with the chelating agent. Organic chelates also ameliorate the availability of essential elements (Fe, S, P, Mg, Ca), which competes with Cr uptake (Bloem et al., 2017). Metallothioneins and phytochelatins (PCs) are two main classes of metal-binding proteins observed throughout the plant kingdom. Overall, the sequestration of Cr in organisms includes an attachment with cytosolic cysteine-rich MTs (Metallothionein's) polypeptides along with sequestration (Sacky et al., 2014). These peptides are enzymatically derived and synthesized when a cell is exposed to stress conditions. Their main role is to promote metal purification and equilibrium of vital micronutrients (Kneer and Zenk, 1992). PCs are small cysteine-rich, non-protein heavy-metal binding peptides, having a general structure (Glu-Cys)_n X, where X is Gly, γ -Ala, Ser or Glu (n = 2-11, based on living being) (Gupta et al., 2013; Shukla et al., 2013). Apart from the main PC families, different plant species have other groups of PCs like homo-phytochelatins (Glu-Cys)_n-Ala or iso-phytochelatins (Glu-Cys)_n-Glx). The chain length of PCs varies with plant species and metal type. Piechalak et al. (2002) reported in legumes that PCs with longer chains have a strong binding capacity to Pb as compared to those with shorter chains. The synthesis of PCs in plants takes place under different stresses like heat, salinity, UV-B, herbicides, and HMs (Cr, Cd, As, Pb, etc.) toxicity through enzymes such as PC synthase (Clemens, 2006; Emamverdian et al., 2015) by glutathione and its homologs act as substrates (Zagorchev et al., 2013). Cr bind with the enzyme γ-glutamylcysteinyl dipeptidyl transpeptidase (PC synthase) and activate it to assemble the transformation of GSH to PCs (Gharieb and Gadd, 2004). GSH is manufactured from its constituent amino acids in two steps, first, y -ECS (y-glutamylCys synthetase) joins Glu with Cys, and then GSH synthetase adds Gly to y -EC. The mechanism of biosynthesis of PCs in plants is detailed in Fig. 5. The synthesis of PCs occurs by reducing the GSH pool in roots, aerial parts (Rauser et al., 1991), and tissue cultures (Schneider and Bergmann, 1995). GSH, a thiol molecule, promotes the plant against metal stress (Cr, Cd, As, etc.) by activating signal transduction pathways. Gill et al. (2017) discovered that Cr stress, along with GSH treatment, enhances the expression of genes encoding protein kinases like BnaCnng69940D and BnaC08g49360D that were involved in protein kinase activity, signal transduction, and oxidoreductase activity. Some genes also govern the transport over the cell membrane. But most of the research proposed that PCs are initially synthesized in roots. The induction of PCs coupled with the antioxidant defense system in response to Cr stress suggested the combined role of PCs and antioxidants in conferring tolerance to accumulated Cr in B. juncea and, therefore, the plant's aptitude as a possible Cr remediator (Diwan et al., 2010). In V. radiata, there was lesser induction of PCs at high Cr concentration, which may be due to its transport to shooting or because PCs might have degraded due to excessive Cr accumulation (Harmens et al., 1993).

Yurekli and Kucukbay (2003) observed that in H. annuus during Cd stress, PCs extent in roots was greater than in leaves. Fidalgo et al. (2013) observed that in Solanum nigrum L., the productivity of PCs was increased in roots under copper stress which involved binding of excess Cu in the root and preventing its movement towards the shoot. Huda et al. (2017) observed that the accumulation of phytochelatin and the OsPCS1 (phytochelatin synthase) genes were highly stimulated by the combined treatment of Si and Cr compared to Cr-stressed plants. Similarly, Mukta et al. (2019) revealed that calcium-mediated inhibition of Cr translocation from root to shoot in rice seedlings, suggesting increased accumulation of phytochelatin binding Cr for vacuolar sequestration in roots. OsPCS1 (phytochelatin synthase), OsMT1 (metallothionein), and OsHMA3 (P-type ATPase 3) transcripts were considerably upregulated following SA supplementation under

Cr stress, indicating that these chelating agents may bind to Cr to increase its retention in roots (Huda et al., 2016). Heiss et al. (2003) signified that long-duration treatment of Cd in B. juncea resulted in greater aggregation of PCs in leaves than roots. In plants, PCs production, accumulation and movement depend upon the capacity of plant species to tolerate metal toxicity. Diwan et al. (2010) observed that at all doses of Cr treatment (50, 100, 150, and 200µM), PCs were considerably induced in the roots and shoots of both plants (B. juncea and Vigna radiata). Rabelo et al. (2018) showed glutathione as a substrate for metal complexing organic molecules (phytochelatins PC-SH). After attachment of metal with phytochelatins-SH, the metal system is transported by transporters such as Mg ATP-dependent carrier or ATP -binding cassette (ABC) transporter (Sytar et al., 2013) into vacuoles to convert toxic metal into nontoxic form (Song et al., 2014). Increased phytochelatins-SH during Cr treatment could be assessed as a compatible scheme of S. lycopersicum L. roots (Kushwaha et al., 2019). The artificial incorporation of PC genes in the transgenic plant (Nicotiana tabacum L.) increases their resistance to metal stress (Postrigan et al., 2012). This toxic metal sequestration procedure is considered as the main mechanism for plants to tolerate metal toxicitv. including that of Cr.

Like PCs, the MTs are naturally-occurring, intracellular cysteine-rich, low-molecular-weight cytoplasmic metalbinding proteins reported in some prokaryotes, fungi, invertebrates, mammals, and in plant systems (Du et al., 2012). They were first extracted from the equine kidney (Margoshes and Vallee, 1957). Plants cannot shun abiotic stress by re-motion; plants have developed a good system of acclimation methods to survive with alters in their surroundings. The signal transduction pathways are more prominently active for these responses with mRNA levels in plants. Gill et al. (2015) studied B. napus (ZS 758 and Zheda 622) under Cr stress. The mRNA level of stress response proteins, including HSP90-1 and MT-1, were marked up. The mRNA accumulation takes place when abiotic stress gets started in plants. Further, Gill et al. (2017) reported that in B. napus during Cr stress, three MT genes (BnaA04g26560D, BnaA02g28130D, and BnaA02g0 1980D) were responsible for transporting water across the cell membrane. Some angiospermic plants also encode the genes like MT genes known for transportation across the membranes of cells. The genes, namely BnaC01g29930D and BnaA07g14320D, were responsible for secondary active transmembrane transporter and protein transporter activities in B. napus under Cr stress (Gill et al., 2017). MT gene synthesis is affected by endogenous and exogenous factors like osmotic stress, drought, HMs, temperature, nutrient deficiency, the release of different hormones, tissue senescence, injuries, viral infections, etc. (Yang and Chu, 2011; Du

et al., 2012). MTs have been grouped into four types in plants depending on their Cys arrangement (Huang and Wang, 2009). Although MTs are expressed all over the plants, different classes of MTs have been found to be expressed in an organ-specific or development stage-specific manner. Kohler et al. (2004) and Yang and Chu (2011) reported that MT 1 is mainly expressed in roots, MT 2 in shoots, MT 3 in leaves or mature fruit, while MT 4 more in growing seeds. OsMT1b carries greater biomass in roots than in shoots during Cr chelation, but OsMT2c plays a bigger role in removing H₂O₂ build-up in shoots than in roots in Oryza sativa (Yu et al., 2019). These findings imply that varied Cr speciation in rice tissues caused inconsistent transcriptional alterations in OsMT genes, involved in distinct regulatory and response pathways during Cr detoxification, such as metal ion chelation and ROS scavenging. Agar et al. (2020) noticed that the response of MT genes to Cr stress differed amongst different tissues. MT genes (MT2-1 and MT4) were downregulated in the shoots but increased in the roots in response to Cr stress. MT2 -1 might be a useful gene resource in Cr remediation. ScMT2-1-3 overexpression in sugar cane cells in response to Cu stress shows that this gene is involved in Cu detoxification and storage (Guo et al., 2013). While Rice OsMT2b protein was discovered to exhibit ROS clearing capabilities (Wong et al., 2004). Each MT (1 to 4) is divided further and termed isoforms. Hassinen et al. (2011) observed that MT1a or MT2b is expressed in the phloem while MT2a and MT3 are in the mesophyll cells of young leaves or root tips. Memon et al. (2001) divided Arabidopsis MT4 into two classes, MT4a and MT4b. In Arabidopsis (Grennan, 2011), different MT isoforms MT1a, MT2a, MT2b, and MT3 are implicated in copper chelation, while MT4a and MT4b act as a zinc binder. In barely, MT3 maintains homeostasis of Zn and Cu, while MT4 was involved in Zn storage (Hegelund et al., 2012). MTs are synthesized through mRNA translation (Verkleij et al., 2003) and bind to different metals by establishing mercaptide bonds among the various Cys sublimates of the proteins and the metal (Blindauer and Leszczyszyn, 2010). Metal-MT complexes have low kinetic and high thermodynamic stability as a result, tight metal-binding occurs (Maret, 2000). MTs have been nominated as another method by which plants defend themselves from stress -generated oxidative injury (Hassinen et al., 2011; Ansarypour and Shahpiri, 2017). These have been reported to regulate cell growth, proliferation, immobilization, and DNA damage repair (Grennan, 2011), sequestration and detoxification of metal ions, or homeostasis of intracellular metal ions and their transport (Hossain et al., 2012; Guo et al., 2013), chelation of metal ions by MTs but their mechanism of action/transfer of metals-Metallothionine system from the cytosol to the vacuole is not known (Yang et al., 2011; Liu et al., 2015). The zinc contribution function of various metalloproteins is also observed (Cherian and Kang, 2006). A number of studies in plants reported the role of MTs in metal homeostasis. Metallothionein mRNA expression research revealed that higher Cr availability boosted MT gene expression. The upregulation of the MT gene due to high chromium levels in the growth medium may aid Saccharum spp. hybrid crop resistance to Cr toxicity (Jain et al., 2016). While there was no significant change in the expression level of two chelator genes, OsPCS1, and OsMT1, in roots and shoots of Oryza sativa L. (Pokkali and BRRI 51) during Cr stress (Kabir, 2016). Teixeira et al. (2013) showed that Cr (III) causes an elevation of MT2a-related transcripts in both roots and shoots and MT1- and MT2d-related transcripts only in roots, whereas Cr (VI) causes an elevation of MT2aand MT2d-related transcripts only in roots. The de novo accumulation of the MT2c-related transcripts in shoots suggests that these MTs are related to the Cr homeostasis in Solanum nigrum (Teixeira et al., 2013). Benatti et al. (2014) reported that MTs impaired variants assemble lesser copper in roots and shoots. Transgenic plants overexpressing MTs genes reduce ROS production and increase metal tolerance (Tomas et al., 2015). Xia et al. (2012) observed that the exhibition of E. haichowensis MT1 (EhMT1) in N. tabacum L. plants not only enhanced the intensity of transgenic *N. tabacum* L. to Cu toxicity but also diminished the production of H₂O₂ and ameliorate peroxidase activity (POD) in roots, accelerated tolerance of plants to reduce oxidative damage.

Cr hyperaccumulator plants

Depending on the metal sensitivity and metal storing capability, plants can be categorized into excluders (metal sensitive plants), indicators (insufficient metal transfer and its consumption), and accumulators (higher consumption and storing) (Khan et al., 2009). Plant species that can store higher levels of HMs without yield reduction are known as metal hyperaccumulators (Memon and Schroder, 2009). They are used in phytoextraction because of their high accumulation capability (Cristaldi et al., 2017). The higher aggregation of metal in plants involves the transfer of metals beyond the cell-membrane, xylem loading, and transformation (rapid as well as active translocation of the metal to the shoot via the xylem, which is upregulated by transpiration) (Rees et al., 2016), detoxification and sequestration of metal (amino acids, organic acids or metal-binding peptides). The plants can be categorized as metal hyperaccumulators when they persist in nutrients and do not exhibit any injuries even after storing the toxic metals. A hyperaccumulator plant can extract the metal at concentrations ten times higher than their concentrations in the soil. Also, hyperaccumulator plants have a shoot-to-root metal ratio >1 (Tangahu et al., 2011). About 721 hyperaccumulator plants (< 0.2% of entire flowering plants) are known. Hyperaccumulation depends on the metal, plant species, and soil physicochemical properties like hydrogen ion concentration, the extent of cation inter-change, litter, electroconductivity, etc. (Van der and Reeves, 2015). Cr hyperaccumulator plants may assemble greater than 1,000 mg Cr/kg dry weight of plant (leaves). These plants endure heavy metals stress through chelation (by appropriate connections with substances such as PCs, MTs, etc.), bioprocessing by reducing agents, and sequestration into the cytosol as well as in vacuoles. The metal uptake mainly depends on metal availability and the accumulator. The uptake, translocation, and accumulation of Cr in different plant parts tell the tolerance capability of the plant against Cr toxicity. Mainly species of the Brassicaceae family have been declared to assemble a significant amount of Cr. Some plants like Genipa americana (Barbosa et al., 2007), Allium griffithianum, Catharanthus roseus (Sajad et al., 2020), sunflower (Fozia et al., 2008; Farid et al., 2017), V. radiata (Jabeen et al., 2015), Pluchea indica (Sampanpanish et al., 2006), S. nigrum, B. napus (Afshan et al., 2015; Li et al., 2018), sweet basil (Chand et al., 2015) and Leersia. hexandra (You et al., 2014), etc., were found to be hyperaccumulators for Cr, while Ipomoea aquatica is a Cr (VI) tolerant plant with no toxicity signs up to 28 mg L⁻¹. H. annuus can assemble different heavy metals (HMs) like As (Imran et al., 2013), Cr (Fozia et al., 2008), Zn (Hao et al., 2012), Ni (Ahmad et al., 2011), Cd (Júnior et al., 2014), Cu (Lin et al., 2003) and Pb (Adesodun et al., 2010). P. oleracea is a Cr hyperaccumulator and tolerates high Cr (VI) concentration through different routes, either by the manufacturing of proline (retain osmotic stability) or by stimulating the antioxidant enzymes to prevent the oxidative stress of the heavy metals (Singh et al., 2013; Kale et al., 2015). Some hyperaccumulator plants are listed in Table 2. The assimilation of Cr by roots is promoted by organic compounds (available in the secretions of roots and make network with Cr) (Hayat et al., 2012) and stored in vacuoles of root cells (Babula et al., 2008). Bluskov et al. (2005) observed that in B. juncea, Cr formed a network with small molecular mass organic acids, which form Cr3+ (acetate) in roots and Cr3+ (oxalate) in leaves. The ability of Ocimum basilicum to condense harmful metals such as Cr, Cd, Cu, Pb, As, Zn, and Fe in their different parts, makes its use for the preparation of teas, spices, or raw materials consumption a potential health concern (Boechat et al., 2016).

Conclusion

Cr pollution increases continuously, which imposes a serious threat to the biosphere. Although plants have no special carrier for Cr uptake, they compete with other essential elements in the plant system and cause nutrient imbalance and leaf chlorosis. Cr can induce several toxic effects on plants, like low crop yield and nutrient starvation in vegetables and fruits. Higher Cr (III and IV) concentrations reduce plant growth, biomass, Chlorophyll biosynthesis, uptake of essential elements, antioxidant enzyme activities, and increase ROS in the plant system. The chlorosis, necrosis, and wilting are stimulated by Cr uptake in plants. Cr is seriously responsible for causing damage to DNA and lipid membranes. The Cr responsive proteins may get expressed from the functioning of MTs and HSPs genes. Various defence mechanisms implemented by plants like plant cell walls, plasma membrane, Cr sequestration, plant microbes, and chelation (PCs and MTs) are discussed herein.

Future prospectives

The newly expressed proteins study is important for abiotic stress research as Cr (VI) toxicity is fatal for plants. Therefore, it is necessary to recognize the possible mechanisms to diminish Cr uptake and lessen its harmful effects on the environment and ecosystem, mainly in plants. The mechanism inducing Cr toxicity at the proteomic and molecular levels still needs to be explored in detail.

ACKNOWLEDGEMENTS

The authors would like to extend their sincere thanks to University Grant Commission (UGC), New Delhi, for fellowship to Ms. Priyanka.

Conflict of interest

The authors declare that they have no conflict of interest.

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