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Functions and Toxicity of Chromium on Plants Physiological and Molecular Aspects: A Review

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ABSTRACT

Chromium exists in a variety of different oxidation states and is a polyvalent element; only trivalent chromium (III) and hexavalent chromium (VI) are found frequently in the natural environment. The biogeochemical procedures that regulate Cr (VI) mobilization, accumulation, bioavailability, toxicity in soils are discussed. Plants growing in chromium (VI) contaminated soils show reduced growth and development with lower agricultural production and quality. Furthermore, chromium (VI) exposure causes oxidative stress due to the production of free radicals that modifies plant morpho-physiological and biochemical processes at tissue and cellular levels. Nevertheless, plants may develop extensive cellular and physiological defensive mechanisms in response to Cr (VI) toxicity to ensure their survival. Chromium toxicity of (VI), plants avoid absorbing from either, soil or turn on the detoxifying mechanism, which involves producing antioxidants through enzymatic and non-enzymatic mechanisms for scavenging of reactive oxygen species. Chromium adversely affects the morphological and biochemical attributes of plants such as transport of nutrients, enzymatic activities, photosynthesis and overall maturation and development. Resistant of chromium varieties and mutation of targeted genes and can be selected to check the phytotoxicity and reduce the productivity of economically significant crops. There are very less number of plant species capable of hyper accumulating chromium in their shoot tissues. Mechanisms of detoxification role of organic ligands such as phytochelatins, methionine, glutathione, proteins, vitamins and amino acids are should be fully studies.

Keywords: Chromium phytotoxicity, environment, contamination, plant physiology and growth, remediation.

1. Introduction

Pushkar *et al.,* (2021) reported that heavy metal contamination has disastrous impacts on terrestrial as well as aquatic life, and significantly disrupted the natural ecosystem Zulfiqar *et al.,* (2022). The unplanned urban and industrial development that disregards the value of a healthy environment is the main cause of environmental pollution Dabir *et al.,* (2019); Wei *et al.,* (2022a). These actions have greatly increased the pollution from heavy metals that upsets the natural balance Posthuma *et al.,* (2019); Qianqian *et al.,* (2022). World Health Organization (WHO) reported that more than 1.7 million deaths because of exposure to harmful contaminants, such as heavy metals World Health Organization (WHO), (2017); Xu *et al.,* (2018). Increasing heavy metals pollution in the environment gradually increased the potential of human exposure to these heavy metals Zulfiqar *et al.,* (2019). Heavy metals may be harmful to living things due to their biodegradable properties Qianqian *et al.,* (2022). At different trophic levels, heavy metals frequently bio accumulate and move within the ecosystem Ushkar *et al.,* (2021). Degradation of heavy metals is a serious problem that requires immediate action,

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chromium is 17th the most plenteous element, and the valence state regulates its toxicity in plants. Chromium is widely used in a various industry, including the Cr plating, tanneries, mining, steel, and chemical industry Shahid *et al.,* (2017); Pushkar *et al.,* (2021). Chromium has become more prevalent as an environmental pollutant due to its increased industrial uses Pradhan *et al.,* (2019); Wei *et al.,* (2022a), and is a pervasive contaminant with significant environmental hazards, particularly for soil-plant ecosystem Ao *et al.,* (2022); Kapoor *et al.,* (2022). Trivalent and hexavalent of Chromium appears being the most persistent among the numerous chromium oxidation states (III to +VI) Chug *et al.,* (2016). Hexavalent chromium is known to be a dangerous metal relative to the trivalent due to its carcinogenic, mutagenic, and oxidizing properties Wei *et al.,* (2022a). Fig. (1)

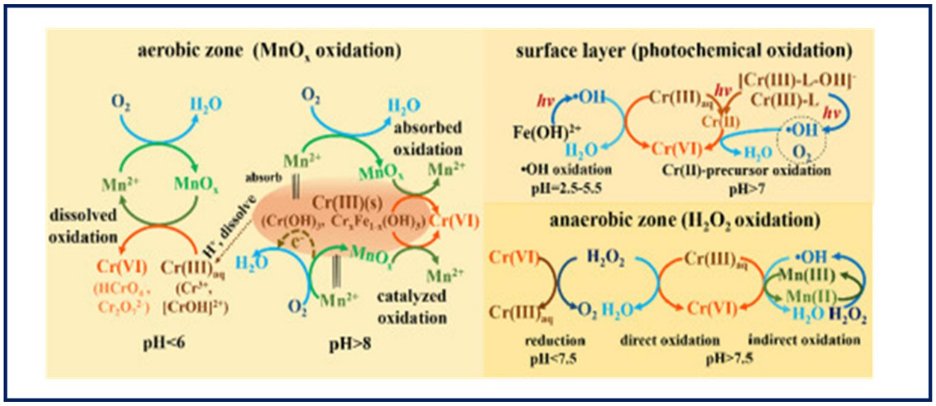


Fig. 1: Illustrates the formation of Cr (VI) via Cr (III) oxidation in soils and groundwater After: Liang *et al.,* (2021)

Liang *et al.* (2021) reported that hexavalent chromium (Cr (VI)) is a widespread, toxic contaminant in the environment. Owing to the increasingly strict requirements for green production and pollution emission, Cr (VI) generation via Cr (III) oxidation is gradually becoming the primary source of Cr (VI) in soils and groundwater instead of direct emissions. Herein, the formation of Cr (VI) by Cr (III) oxidation in soils and groundwater is systematically reviewed. The main oxidants of Cr (III) in soils are manganese oxides (Mn Ox), hydrogen peroxide (H_2O_2), and photochemical generated radicals, which respectively dominate in aerobic, anaerobic, and surface zones of soils. In aerobic zones, dissolved Cr (III) can be oxidized on the surface of Mn Ox under acidic conditions (pH < 6.0), while under alkaline conditions (pH = 8.0–9.4), Mn (II)-catalyzed oxidation plays a dominant role. In anaerobic zones, Mn (II) is the dominant species of Mn, thus H_2O_2, which is mainly produced by the serpentinization process, becomes the main oxidant involved in Cr (III) oxidation. In addition to direct oxidation, H_2O_2 can also indirectly oxidize Cr (III) during the catalysis of Mn (II) under alkaline conditions. The average soil concentration of chromium is about 40 mg. kg^{-1} Isak *et al.,* (2013). Chromium exhibits a wide range of potential states of oxidation, the Cr^{+3} state is vigorously persistent; the Cr^{+3} and Cr^{+6} forms are frequently seen in Cr groups, while the Cr^{+1}, Cr^{+4}, and Cr^{+5} states are uncommon. Chromium $FeCr_2O_4$ chromate, which contains about 70% of pure Cr_2O_3, is the main mineral possessing this element Lakshmi and Sundaramoorthy, (2010). Natural chromium exists in most soils as relatively inert forms of chromium (III) that must be liberated over time by acid discharge Chandra *et al.,* (2010). The manganese (Mn) oxides present in soils will oxidize chromium (III) into chromium (VI), but a minute proportion of chromium (III) in soils is typically found in oxidizable forms Mishra *et al.,* (2009). Within the soil, chromium is perfectly integrated, however effectively bound to organic materials on Fe and Mn oxides and hydroxides Balamurugan *et al.,* (2014).

In surface soils, •OH can be generated by the photolysis of Fe $(OH)^{2+}$, and it can further oxidize Cr (III) to Cr (VI). Moreover, photolysis of $[Cr(OH)n]^{3-n}$ can transform Cr(III) into Cr(II), which is more active and can be further oxidized into Cr(VI) by O^{-2}. In groundwater, both Mn Ox and H_2O_2 may oxidize Cr (III) in unconfined aquifers groundwater. In confined aquifers, H_2O_2 becomes the main oxidant for Cr (III) under alkaline conditions.

Compounds of Cr (VI) are thousand times more cytostatic and carcinogenic than chromium (III) Mamais *et al.,* (2016). Furthermore, as opposed to further forms, chromium (VI) is highly soluble and bioavailable, obtaining more consideration Xiao W. *et al.,* (2017). There is no known biological function of chromium in plants Srivastava *et al.,* (2021). Shahid *et al.,* (2017); Xiao *et al.,* (2021); Ao *et al.,* (2022),-reported that soil chemical properties, microbial activity, and soil moisture content, as well as the plant physiology, gradually influence the biogeochemical behavior of chromium in soil-plant systems. Plants lack specialized transporters and channels for absorbing chromium because it is a non-essential element for them Adhikari *et al.,* (2020). As a result, plants to accumulate chromium Anjum *et al.,* (2016a) use certain carriers of the necessary ions for plant metabolism, such as Fe for chromium (III) and phosphate and sulphate for chromium (VI). Fig.(2).

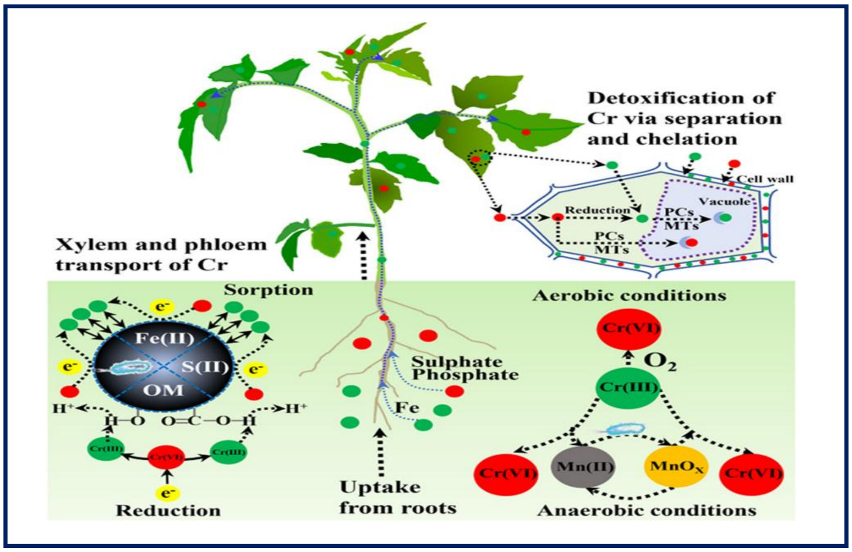


Fig. 2: Illustrates chromium biogeochemical behaviour in soil-plant systems and remediation. After: Ao *et al.,* (2022)

Ao *et al.,* (2022) stated that chromium (Cr) is a toxic heavy metal that is heavily discharged into the soil environment due to its widespread use and mining. High chromium levels may pose toxic hazards to plants, animals and humans, and thus have attracted global attention. Recently, much progress has been made in elucidating the mechanisms of chromium uptake, transport and accumulation in soil-plant systems, aiming to reduce the toxicity and ecological risk of chromium in soil. Accordingly, based on available data especially from the last five years (2017–2021) this review traces a plausible link among chromium sources, levels, chemical forms, and phytoavailability in soil; chromium accumulation and translocation in plants; and chromium phytotoxicity and detoxification in plants. Additionally, given the toxicity and hazard posed by chromium (VI) in soils and the application of reductant materials to reduce Cr (VI) to Cr (III) for the remediation of Cr (VI)-contaminated soils, the reduction and immobilization mechanisms by organic and inorganic reductants are summarized. Finally, some priority research challenges concerning the biogeochemical behaviour of chromium in soil-plant systems are highlighted, as well as the environmental impacts resulting from the application of reductive materials and potential research prospects.

The oxidative stress caused due to Cr toxicity may lead to reduce membrane stability due to the over-accumulation of reactive oxygen species (ROS) that may also damage the morpho-physiological attributes in the plants Eleftheriou *et al.,* (2015); Azeez *et al.,* (2021). Due to oxidative reactions such as mutilation of DNA and RNA, inhibition of enzymes, lipid peroxidation, and protein oxidation, ROS can induce cell death when produced in high concentrations Srivastava *et al.,* (2021). Cr toxicity Dotaniya *et al.,* (2014); Handa *et al.,* (2018a), and plant tissues exhibit chromosomal abnormalities as a result of Shahid *et al.,* (2017), reportedly suppress the functioning and regulation of many proteins.

ROS toxicity in different species is commonly regarded as oxidative stress, potentially causing a level of damage that led to intracellular and intercellular lethality. The O_2• −, •OH, H_2O_2 and $1O_2$

reactivity may vary across or within cells, due to the site of generation, and the nature of the biomolecules. Among them, O_2• − and $1O_2$ have longer half-lives ranging from 1–4 µs with a migration distance of 30 nm in mitochondria, chloroplast, and nuclei, conversely, H_2O_2 is closer to 1 ms with a migration distance of 1 µm reacting with DNA and sensitive cysteine (Cys) and methionine (Met) residues. Additionally, •OH's half-life is approximately 1 ns with a migration distance of 1 nm in the Fenton reaction Mittler, (2017). Furthermore, •OH's very short migration distance allows this ROS molecule to be extremely reactive with DNA, RNA, lipids, and proteins. The expression levels of ROS also vary across the subcellular organelles suggesting that the regulation of ROS is dynamic and that compartmentalization is utilized to reduce ROS lethality. ROS signaling can be mediated by mitochondrial nicotinamide adenine dinucleotide phosphate (NADPH) oxidases, specifically; the respiratory burst oxidase homologs (RBOHs) induce ROS production in the apoplast Suzuki *et al.,* (2011), Laurindo *et al.,* (2011) Fig. (3)

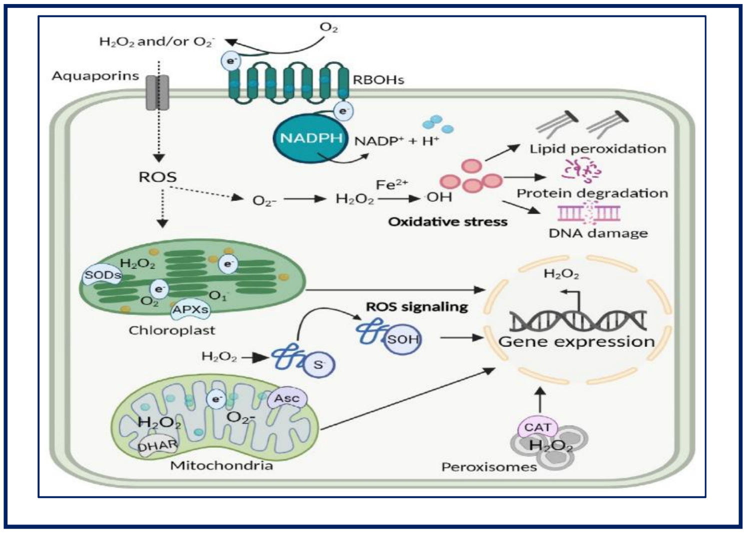


Fig. 3: The oxidative stress signaling in plant cell compartments. ROS, such as O2•─ and H_2O_2 are produced by NADPH oxidases specifically RBOHs at the apoplast, accumulating in chloroplast, mitochondria, peroxisomes, and nuclei. Accumulation of H_2O_2 in the presence of F^{2+} form hydroxyl radicals and initiates oxidative stress that results in distorting the structure of lipids, proteins, and DNA. Later, the integration of enzymes, such as SODs, APXs, DHAR, and CAT in cell organelles maintains ROS levels and gene expression. After: Adeel Riaz *et al.,* (2022)

The redox signaling complex largely consists of RBOHs, superoxide dismutases (SODs; different metal cofactors), catalases (CATs), peroxidase (PODs), glutathione peroxidase (GPXs), iron-dependent mechanisms and a network of thio- and glutaredoxins Mittler *et al.,* (2004), Sachdev *et al.,* (2021), Hasanuzzaman *et al.,* (2020). Knockout or knockdown of any of them results in modified redox signaling in plants Vanderauwera *et al.,* (2011).

In general, some physiological functions of plants are regulated via the interaction of ROS with Cys and Met residues of key proteins He *et al.,* (2018), Willems *et al.,* (2021). The oxidative posttranslational modifications (oxi PTM) oxidize the residues at physiological pH, thus altering the structure and functions of proteins He *et al.,* (2018), Willems *et al.,* (2021). Therefore, the passive ROS diffusion through aquaporins and the direct interaction occurring in chloroplasts and nuclei should be tightly controlled by antioxidant systems to neutralize ROS and oxidation to mitigate damage Mullineaux *et al.,* (2020), Tian *et al.,* (2016). For example, H_2O_2 profiling analyses showed that it catalyzes the biochemical reactions at lower concentration (e.g., average H_2O_2 concentration, 10 µM in cellular compartments especially peroxisomes and apoplast mediate normal cell division) but creates oxidative damage at higher concentrations in plants Cheeseman, (2006), Foyer and Noctor, (2016). The H_2O_2 scavenging is accomplished by coordinated activities of antioxidative enzymes Foyer and Noctor,

(2011) such as SODs, which processes $O_2{}^{\bullet-}$ to H_2O_2 and are ubiquitously expressed in apoplast, cytosol, peroxisomes, chloroplasts, mitochondria and nuclei Alscher *et al.,* (2002).

Chromium gradually affects various metabolic processes i.e., CO_2 fixations, electron transfer, photophosphorylation, and enzyme concentration, which directly impairs photosynthesis Anjum *et al.,* (2017); Sharma *et al.,* (2020); Ashraf *et al.,* (2022b). Taken to be critical indices that measure plant photosynthesis under chromium stress are photosynthetic rate, photosynthetic pigments, and photochemical efficiency Ma *et al.,* (2016). Chromium is a potent inhibitor of plant photosynthesis, according to numerous studies Shanker *et al.,* (2005); Shahzad *et al.,* (2016); Bashir *et al.,* (2020). According to Mathur, et al. (2014), chromium toxicity prevents CO_2 fixation, electron transfer, enzyme activity, and photophosphorylation in plants. The interaction of plant hormones and cellular redox is crucial for the process of photosynthesis under different abiotic stresses Mayzlish-Gati *et al.,* (2010); Kim *et al.,* (2012); Krumova *et al.,* (2013). Previously, it was evident that impaired photosynthetic light harvesting in Arabidopsis mutants has strong interaction between the control of excitation energy transfer and hormonal regulation Tikkanen *et al.,* (2014). The metabolism of phytohormone regulation network by ROS generation may intricate to complex hormonal crosstalk in response to stressful conditions. Strigolactones (SLs) play an important role in the regulation of genes associated with harvesting light. Synthetic SL compounds regulate several genes encoding LHC proteins, CAB proteins, and PSI and PSII components under stress conditions Mayzlish-Gati *et al.,* (2010). For example, in the Arabidopsis SL signaling mutant max2, the response to dehydration is down regulated because of the suppression of genes involved in photosynthesis, suggesting that the association between the mis-regulation of genes involved in photosynthesis reduced drought tolerance and sensitivity to the high-energy demands of photosynthesis in max2 plants Ha *et al.,* (2014). Gibberellins (GAs) regulates photosynthesis and promote seed germination and cell division Huerta *et al.,* (2008); Zhou *et al.,* (2011). In cucumber cotyledons, GA and kinetin influence the functional site of PSI and PSII reaction centers, thereby encouraging the development of the photosynthetic electron transport system Pedhadiya *et al.,* (1987). Similarly, in broad bean protoplasts, short-term GA-3 treatment increased the net photosynthetic rate and O_2 evolution Yuan and Xu, (2001). In transgenic *Brassica napus* plants, the photosynthetic capacity increased with the decrease in GA bioactivity Zhou *et al.,* (2011). Higher levels of endogenous GA remarkably up-regulate genes involved in photosynthesis and drought tolerance Huerta *et al.,* (2008). In wild-type and transgenic Arabidopsis plants, GA-3 treatment activated GA-responsive genes and enhanced tolerance to heat, salt and oxidative stresses Alonso-Ramirez *et al.,* (2009). However, further studies are required to exploit the relationship between photosynthesis and endogenous/exogenous GA-3 levels under various abiotic stresses. Brassinosteroids (BRs) play important roles in plant growth and development, abiotic stress responses and defense mechanism. BRs also influence the efficiency of PSII and photosynthetic CO_2 fixation in land plants Oh *et al.,* (2010); Choudhary *et al.,* (2012); Krumova *et al.,* (2013). Previous reports uncovered the relationship between BRs and photosynthesis related genes in several plant species Oh *et al.,* (2011); Bai *et al.,* (2012). In the Arabidopsis brassinosteroidinsensitive1 (bri1) mutant, genes involved in the regulation of photosynthesis were significantly down regulated, which reduced plant growth and photosynthetic activity Kim *et al.,* (2012). Moreover, further analysis revealed that Arabidopsis mutants with altered BR responses exhibit drastic changes in thylakoids, inhibition of O_2 evolution, reduction in PSII quantum yield and smaller PSII complex Krumova *et al.,* (2013). The BR-induced changes in the thylakoid structure and regulation of PSII during photosynthesis have also been described in other studies Dobrikova *et al.,* (2014); Rothová *et al.,* (2014). Although BR deficiency boosts the content of Chl and photosynthetic proteins in plants, changing the leaf color to dark green Komatsu *et al.,* (2010), exogenous BR treatment in pepper (*Capsicum annuum*) resulted in harmful effects on photosynthesis under drought stress by decreasing light use efficiency and non-photochemical quenching (NPQ) in PSII antennae Hu *et al.,* (2013). Based on the abovementioned studies, it can be concluded that intensive investigation should be practiced to describe the specific role of BRs in the PSII damage repair system and ameliorating changes in the thylakoid structure during the process of photosynthesis. The most widely studied hormone, abscisic acid (ABA), plays a dynamic role in response in plants during abiotic stresses. ABA directly regulates the PSII-associated O_2 evolution and granular chloroplast structure in plants Maslenkova *et al.,* (1989). Exogenous supply of ABA enhanced the amount of Chl, total carotenoids, and xanthophylls in leaves, and help in excessive excitation energy on PSII Barickman *et al.,* (2014). In barley seedlings, ABA treatment significantly increased the photosynthetic apparatus under heat stress, although heat shock reduced the damage to the initial chloroplast fluorescence Ivanov *et al.,* (1992). ABA treatment up-regulates the expression of LHCB gene family, which is mainly involved in the adaptation to abiotic stress Liu *et al.,* (2013). Additionally, down regulation of LHCB genes decreased ABA signaling, suggesting the involvement of ABA signaling in drought stress and ROS modulation Xu *et al.,* (2012). The inconsistency concerning the role of ABA in photosynthesis is possibly due to the dissimilar experimental system/methodology and the photosynthesis data obtained using different methods. Salicylic acid (SA), a phenolic compound, is extensively involved in the process of plant growth regulation, physiology and biochemical activities of cells as well as in the response to stress conditions Kunihiro *et al.,* (2011); Drzewiecka *et al.,* (2012), Li *et al.,* (2017). . Therefore, it is important to discover the role of SA related genes in photosynthesis during abiotic stresses. Investigation in *Phillyrea angustifolia* plants under drought stress showed increased assimilation of endogenous SA and significantly decreased Fv/Fm in leaves Munné-Bosch and Peñuelas, (2003). SA treatment improved the photosynthetic capacity of wheat plants Arfan *et al.,* (2007). Similarly, SA treated wheat leaves showed an improvement in Fv/Fm, photochemical activity of PSII, photosynthetic rate and electron transport, which reduced the damage caused by heat and high light intensity to the D1 protein and PSII Zhou *et al.,* (2011). Therefore, it can be established that SA pretreatment is associated with the chloroplastic heat shock proteins (HSPs), thereby upregulating the photosynthetic rate. In other crops such as barley, exogenous SA treatment facilitated the adaptation to salt stress and improved the cell membrane integrity El-Tayeb, (2005). In grapevine (*Vitis vinifera*) leaves, SA treatment under heat stress enhanced the PSII system parameters and net photosynthetic rate Wang *et al.,* (2010). To date, only a few studies have described the roles of methyl jasmonate (MeJA) and ethylene in photosynthesis, and the regulatory mechanisms that provide stability to PSI and PSII under abiotic stresses remain unclear. However, exogenous application of ethylene demonstrated its role in the regulation of tolerance to Ni- and Zn-induced heavy metal stress by improving photosynthetic efficiency Khan and Khan, (2014). Additionally, in sunflower, ethylene treatment increased the net photosynthetic rate and reduced the effects of excess Cu, thereby stabilizing the Fv/Fm ratio Ouzounidou and Ilias, (2005). Selenium (Se) guards the photosynthetic activity of *B. napus* seedlings under Cd stress, as high Cd-stressed plants may act as a trap free radicals stabilized by the starch matrix Filek *et al.,* (2010). Similarly, calcium (Ca) modification overturned the Cd stress-induced changes and increased the intercellular CO_2 concentration and NPQ as well as defied Cd accumulation in *B. napus* seedlings Wan *et al.,* (2011). In transgenic tobacco plants, cytokinin (CK) was shown to improve photosynthetic efficiency, cytochrome b6f (Cytb6f) complex formation, photosynthetic apparatus, and expression levels of genes associated with PSI and PSII as well as delay drought stress Rivero *et al.,* (2007) and (2010) Fig.(4).

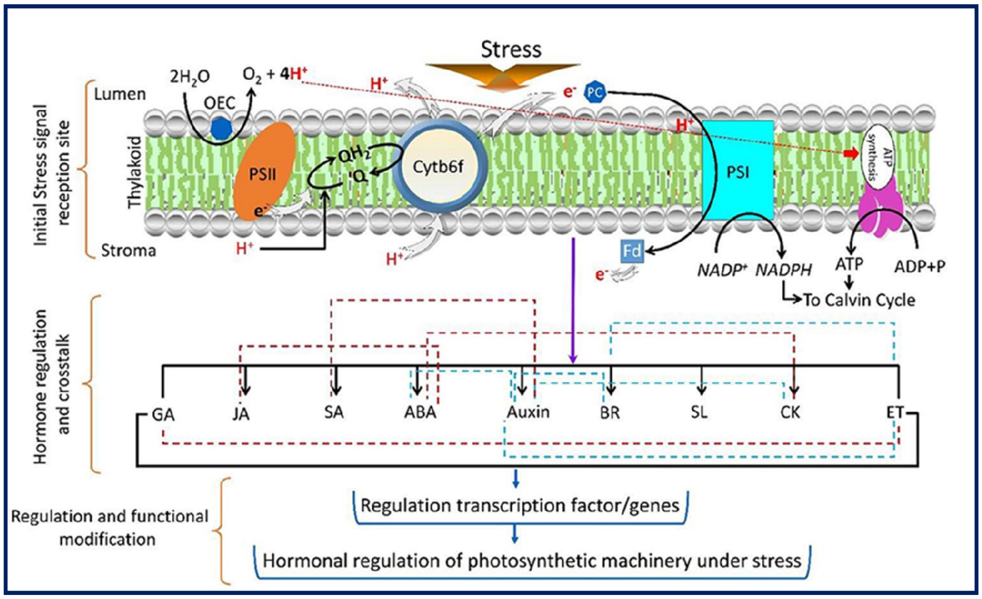


Fig. 4: Illustrates regulation of the complex phytohormone network under stress conditions. The imposition of stress on the photosystem reaction center induces the hormonal signal transduction. The red dotted lines indicate the regulation of two hormone inhibitions, and green lines indicate the co-regulation of two hormones. The regulation of gene transcription by different hormones shows the involvement of the photosynthetic machinery. After: Zulfiqar *et al.,* (2023)

The studies on phytohormones provide fundamental background information about their potential crosstalk under stress conditions, but gene regulation and plant response could be more easily explained after the mutational studies, which will further disclose the comprehensive approaches and specific roles of different plant hormones in photosynthesis under both normal and stress conditions. In addition to the analysis of individual phytohormones, some studies investigated the co-regulated hormonal responses to various stresses. For example, ABA and SLs together regulate carotenoid biosynthesis Barickman *et al.,* (2014) suggested that the potential crosstalk between ABA and SLs (carotenoid-derived hormones) plays a role in the light-harvesting pathways. Recently, it was found that BR dependent and GA-regulated transcriptome involved in cell wall formation and photosynthesis, the evidence indicates a strong association between various hormones and light harvesting pathways Attaran *et al.,* (2014); Cortleven *et al.,* (2014). Moreover, studies have reported that BRs modulate PSII efficiency and thylakoid architecture Oh *et al.,* (2011); Krumova *et al.,* (2013); Dobrikova *et al.,* (2014), which suggested that the coordinated crosstalk between BR and GA-signaling network regulates the adaptive response of plants to adverse environmental conditions. Additionally, the coordination and crosstalk among phytohormone signaling networks somehow established the adaptive responses of plants under unfavorable conditions Nishiyama *et al.,* (2011); Ha *et al.,* (2014). For example, abundance of ethylene during drought stress triggers leaf senescence and disturbs ABA-mediated regulation of photosynthesis in leaf expansion Bartoli *et al.,* (2013). This suggests that the relation between ethylene and ABA and their relative abundance control the response behavior of plants to drought stress. Further studies are required to measure the effect of co-regulated hormones and points of intersection, which alter the regulation of the photosynthetic machinery or its components and reduce photo inhibition in chloroplasts under stress conditions. Moreover, we propose that additional genes and their roles in chloroplast should be identified to improve photosynthesis under abiotic stress. This destroys the photosynthetic apparatus, specifically light-harvesting complex II, PSI, and PSII, and prevents the production of Calvin cycle enzymes (responsible for ATP production).Soil contamination with heavy metals such as cadmium (Cd), copper (Cu), zinc (Zn), nickel (Ni), cobalt (Co), chromium (Cr), lead (Pb), and arsenic (As) is generally caused by the application of phosphate-rich fertilizers, sewage sludge, industrial waste, wind-blown dust, incinerator emissions, traffic, volcanoes, and hard water practices Bagur *et al.,* (2009); Ghori *et al.,* (2019). Heavy metal pollution considerably inhibits plant growth by causing Chl degradation, DNA and protein damage as well as enzymatic inhibition Fig. (5). When coupled with other environmental stresses, heavy metal pollution causes more severe damage Srivastava *et al.,* (2012); Kumar *et al.,* (2019); Sharma *et al.,* (2020). Abiotic stresses like heavy metals induce excessive accumulation of ROS and cause oxidative stress in plants Li *et al.,* (2016). Interestingly, metallothioneins (MTs) have been proposed an alternative tool by which plants protect themselves from stress-induced oxidative damage Yu *et al.,* (2019). Hassinen *et al.,* (2011) reported the role of MTs in abiotic stress tolerance as ROS scavengers, though the mechanisms through which MTs mediate ROS homeostasis remain unclear Hassinen *et al.,* (2011).

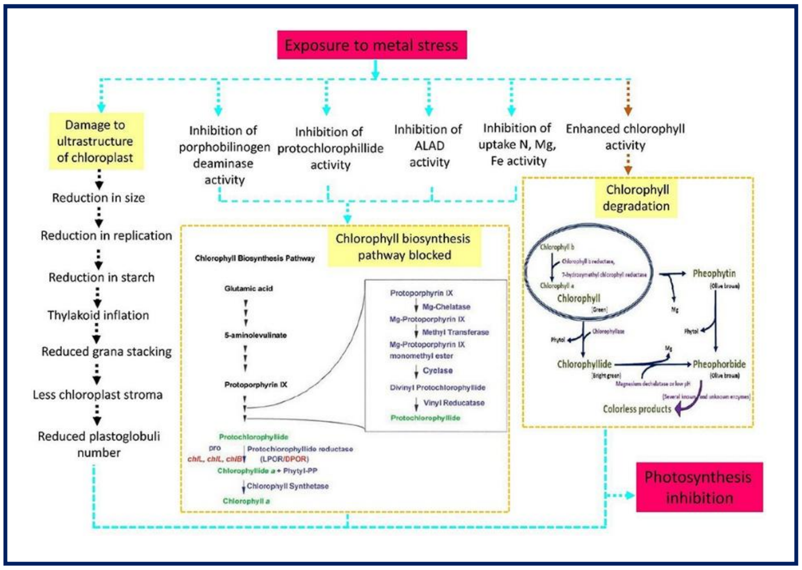


Fig. 5: Diagram showing the general and specific effects of heavy metals on plants. Heavy metals affect ROS production, inhibit ATP synthesis and damage DNA and proteins. The damage to DNA and proteins is shown separately. Free radicals damage DNA and cause membrane peroxidation when metal ions surround the site of tissue injury, causing ATP inhibition, and NADH depletion. After: Zulfiqar *et al.,* (2023)

Moreover, heavy metal stress considerably alters the biological, biochemical and metabolic processes of plants Anjum *et al.,* (2015) and (2016 a,b and c); Handa *et al.,* (2018); Shahzad *et al.,* (2018a); Khanna *et al.,* (2019); Kohli *et al.,* (2020), and alteration at the cellular and molecular levels causes severe damage, thus blocking the functional group and active site of enzymes, thereby disrupting membrane stability and transcriptional regulation Rascio and Navari-Izzo, (2011); Guo *et al.,* (2016) & (2017b). Metal ion toxicity causes DNA damage and/or impairs DNA repair mechanisms, disrupts membrane functional integrity, affects enzymatic activity, and perturbs protein function Tamás *et al.,* (2014), Fig.(6). LHCII (light harvesting complex II) is the basic pigment protein complex of PSII, which harvests light energy and converts it into chemical energy. This protein complex plays a protective role by dissipating excess light energy and efficiently channelize excitation energy Barros *et al.,* (2009). Cd stress affects the LHCII Parmar *et al.,* (2013). In rye (*Secale cereale*), Cd stress reduced the dissipation of excitation energy, indicating that Cd stress either altered the quenching center (QC) or interfered with energy transfer between proteins and pigments Janik *et al.,* (2010). Ahmed and Tajmir-Riahi, (1993) confirmed changes in LHCII by Pb, where imperfect assembly of its components triggered disintegration Ahmed and Tajmir-Riahi, (1993). Plants grown in metal contaminated soils exhibit leaf chlorosis due to the reduced chloroplast size Shahzad *et al.,* (2016), (2017). The ultra-structure of chloroplast is greatly affected by metal ions Fig. (6).

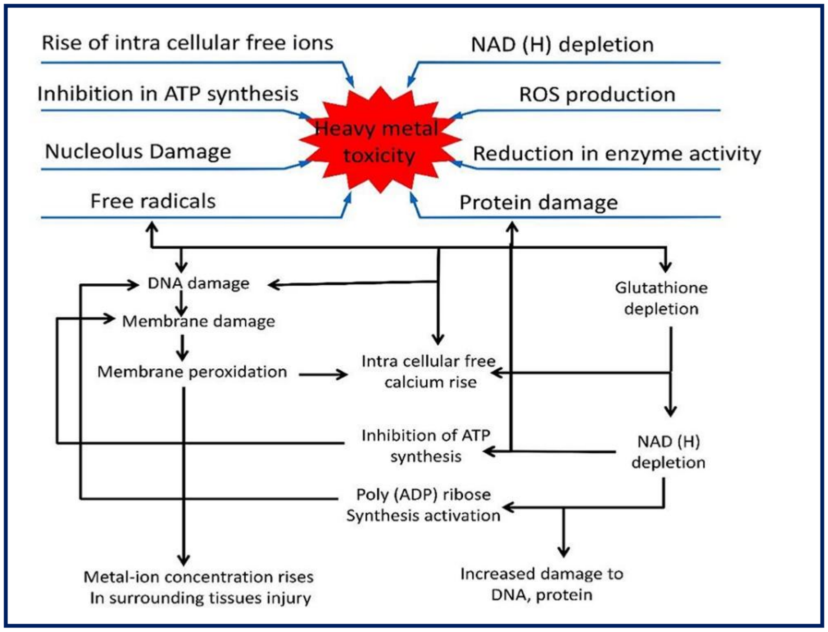


Fig. 6: Heavy metal stress damages the chloroplast structure and chlorophyll (Chl) biosynthesis and degradation processes during photosynthesis. Toxicity due to metal ions gradually affects enzymatic activity and inhibits Chl components and the uptake of essential elements, finally blocking the Chl biosynthesis pathway. The blue arrow depicts this process in a step-by-step manner. After: Zulfiqar *et al.,* (2023).

For example, Cd, a potent inhibitor of photosynthesis, alters the chloroplast shape, decreases chloroplast size, destroys Chl, reduces starch accumulation and expands the thylakoids Najeeb *et al.,* (2011); Parmar *et al.,* (2013); Kapoor *et al.,* (2019). Other metals such as Cr decrease the absorption of magnesium (Mg) and nitrogen (N), consequently reducing the Chl content Singh *et al.,* (2013). Pb toxicity accelerates Chl degradation by increasing the activity of chlorophyllase Drazkiewicz, (1994). High concentration of Ni affect the photosynthetic apparatus and inhibit the synthesis of pigments Soares *et al.,* (2016a) & (2019); Shahzad *et al.,* (2018a, b). Additionally, Ni stress alter the composition of lipid membrane and disturb the activity of chlorophyll molecule and Rubisco (ribulose-1,5-bisphosphate carboxylase oxygenase) Kohli *et al.,* (2020). Early studies established that the photosynthetic apparatus, Chl and carotenoid concentrations and plant growth were greatly decreased under Ni and UV-B combination stress. It is possible that Mg in Chl is replaced by Ni, which destroys Chl and damages thylakoid membranes in cabbage leaves and wheat shoots, respectively Molas, (2002); Gajewska *et al.,* (2006). Similarly, the combined effect of heavy metals and drought stress can cause deleterious effects on Chl content in red maple and effect the xylem structure and hydraulic conductivity De Silvam *et al.,* (2012). Transition metals (Cu, Zn, Mn, and Fe) play critical roles in physiological processes of all living organisms, such as Cu is essential for respiration, photosynthesis, cell wall integrity, ethylene perception, and ROS metabolism in plants Burkhead *et al.,* (2009). Excess amounts of transition metals leads of Chl degradation by Chl-degrading enzymes, thereby increasing the sensitivity of PSII to light Pätsikkä *et al.,* (2002). Cu, Hg, Ni, Zn, and aluminum (Al) metal ions interact with three extrinsic polypeptides, situated in the lumen of the thylakoid membrane, additionally, intrinsic proteins (inner antenna protein), are released from the PSII reaction center under Cu toxicity Sigfridsson *et al.,* (2004); Boisvert *et al.,* (2007). At optimum concentrations, Zn plays an important role in plant growth; however, excess Zn significantly reduces the synthesis of photosynthetic pigments and negatively affects photosynthesis Paunov *et al.,* (2018). Zn and Cd stresses exert a synergistic effect by increasing the oxidative stress and restoring the Chl content Cherif *et al.,* (2011). Therefore, we speculate that transition metals in combination may reduce or restore the damage caused to the photosynthetic machinery for a short period under specific conditions. Comparative analysis of Cd and Zn stresses in tobacco (*Nicotiana benthamiana*) leaves revealed that under Cd stress, key enzymes involved in Chl biosynthesis were significantly down-regulated, decreasing the Chl content, expression of PSII (donor, receptor and core side) proteins and photosynthesis Zhang *et al.,* (2020). Several studies have reported the harmful effects of Cd and Zn on photosynthesis, thylakoid membrane ultra-structure, photosynthetic pigments, Chl fluorescence, electron transport, light capture, dark respiration, stomatal conductance, and Calvin cycle enzymes Krupa, (1999); Vassilev *et al.,* (2011); Paunov *et al.,* (2018). Furthermore, both metals considerably reduce the activity of PSII and to some extent that of PSI as well as the rate of photosynthetic electron transport Krupa, (1999); Vassilev *et al.,* (2004).

Anjum *et al.,* (2016a) found that maize plants exposed to Cr stress had significantly lower the levels of net photosynthesis, chlorophyll contents, gas exchange capacity, transpiration rate, water use efficiency, and stomatal conductance. The degradation of photosynthetic pigments caused by exposure to the high concentration of chromium leads to reduction in light-harvesting capacity Handa *et al.,* (2018); Srivastava *et al.,* (2021). Net photosynthetic rate (Pn) and chlorophyll content in wheat (*Triticum aestivum*) were decreased as chromium exposure period gradually increased Srivastava *et al.,* (2021). Chromium prevents mitochondrial electron transport in higher plants, which increases the production of ROS and causes chloroplast modifications, pigment changes, and oxidative stress Sharma *et al.,* (2016 a, b). One of the crucial plant parts involved in photosynthesis is the leaf and total leaf area Srivastava *et al.,* (2021). In rice (*Oryza sativa*), the chromium (VI) toxicity reduced the number of leaves per plant by 50% while significantly affecting the overall leaf area and photosynthesis activity of plant Sundaramoorthy *et al.,* (2010). Under 3.4 mM chromium (VI) toxicity in nutritional media, smooth mesquite (*Prosopis laevigata*) was shown to have fewer leaves that significantly affect the chlorophyll content and photosynthesis activity of plant Srivastava *et al.,* (2021). Furthermore, it was shown that chromium toxicity significantly decreased the leaf's net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration, of sunflower with reductions of 36%, 71%, 57%, and 25%, respectively Sharma *et al.,* (2020). The first requirement for large plant yields is high plant biomass Srivastava *et al.,* (2021). Chromium is known to have negative impacts on several physiological and metabolic processes, which compromises plant production and yield equally Ali *et al.,* (2015). Various studies highlighted that Cr phytotoxicity results to minimize plant biomass and yield of melon (*Cucumis melo*) Akinci and Akinci, (2010), wheat (*Triticum aestivum*) Adrees *et al.,* (2015a), french bean (*Phaseolus vulgaris*) Sharma *et al.,* (2016), okra (*Hibiscus esculentus*) Amin *et al.,* (2013), turnip mustard (*Brassica campestris*) Qing, et al. (2015), Arabidopsis (*Arabidopsis thaliana*) Ding *et al.,* (2019), common duckweed (*Lemna minor*) Reale *et al.,* (2016), wheat (*Triticum aestivum*) (Ali *et al.,* 2015), barley (*Hordeum vulgare*) Ali *et al.,* (2013) maize (*Zea mays*) Anjum *et al.,* (2017), cotton (*Gossypium hirsutum*) Farooq *et al.,* (2016), makoi (*Solanum nigrum*) UdDin *et al.,* (2015). In plants, higher concentration of Chromium significantly affects various biochemical and morphological parameters i.e., minimized nutrient and water uptake, reduction in cell division, nutrients imbalance (translocation and uptake), the inefficiency of inorganic nutrient uptake by plant, higher oxidative stress, and ROS formation, oxidative stress damage to sensitive cell organelles such as chlorophyll, mitochondria, lipids, proteins, and reduction in photosynthesis activity that results to minimize the growth, biomass, yield of plant Shanker *et al.,* (2005); Shahid *et al.,* (2017); Ao *et al.,* (2022). At the cellular, molecular, organ, and plant levels, each of these elements, alone or in combination, have an impact on plant growth, development, and yield Shahid *et al.,* (2017). However, the type of plant and chemical speciation of chromium will determine which of these factors will be more severely impacted. The impact of Cr on plant development, however, differs depending on the variety of plants. In general, transgenic and hyperaccumulator plants have a lot of potential for chromium tolerance and selective accumulation Sarangi *et al.,* (2009).

Photosynthesis in chloroplasts is directly linked to cellular redox regulation in plants Dietz *et al.,* (2016). Chloroplast-associated $1O^{-2}$ is produced from chloroplast triplet state (3Chl) by interacting with O^{-2} molecules (ground state 3 O^{-2}), specifically in PSII under varying irradiance Foyer and Noctor, (2016), Fischer *et al.,* (2013) .Elevated $1O^{-2}$ levels in the PSII reaction center cause photo-inhibition resulting in oxidative damage Gollan *et al.,* (2015) and metabolic breakdown, leading to oxidation of the D1 protein, which specifically dephosphorylates the PSII reaction center Krieger-Liszkay *et al.,* (2008). The irreversible photo-inhibition drives the expression of $1O^{-2}$ related genes, which activate the antioxidative system, and ultimately induce resistance against high light (HL) and other stresses in plants Gollan *et al.,* (2015), Bobik and Burch-Smith,(2015) , Galvez-Valdivieso *et al.,* (2009) . Moreover, PSI oxidation is known as the Mehler reaction photo-reduction of $1O^{-2}$ Asada, (1999). This reaction is catalyzed by thylakoid and stromal-associated SODs, producing O2•− as the first product and then dismutase O_2•− to H_2O_2. H_2O_2 may cause oxidation to Calvin-Benson Cycle (CBC) components regulated by the thioredoxin system Michelet *et al.,* (2013), 2-Cys peroxiredoxin and ascorbate peroxidase (APX) Awad *et al.,* (2015). Further reduction of H_2O_2 to H_2O is catalyzed by the integration of APX, thiol related enzymes such as thioredoxin (TRX), peroxiredoxin (PRX) and NADPH. However, the enzymatic system is tightly regulated in cellular compartments where H_2O_2 retains the potential to move out of chloroplast and mitochondria interacting with transcription factors for retrograde signaling Bobik and Burch-Smith, (2015), Vogel *et al.,* (2014), Exposito-Rodriguez *et al.,* (2017), Zhao *et al.,*(2019), Zhao *et al.,* (2018), that regulate the gene expression in the nucleus. In Arabidopsis, the NAC domain containing protein 17 (ANAC017) interacts with enhanced H_2O_2 levels and modulates the gene expression Ng *et al.,* (2013). The ANAC017 activity is inhibited by radical-induced cell death 1 (RCD1), which mediates ROS-related retrograde signaling in mitochondria has also been anticipated Shapiguzov *et al.,* (2019). Examining the dynamics of chloroplast demonstrate that this organelle can actively sense environmental cues, regulating the nucleus-chloroplast communication and gene expression. Chloroplast associated ROS retrograde signaling is largely dependent on $1O^{-2}$, produced as a by-product of PSII reactions. The production of $1O^{-2}$ facilitates the chloroplast to nuclear communication, which ultimately modulates the gene expression, respond to stress, and programmed cell death op den Camp *et al.,* (2003). Taken together, these studies provide a mechanism for how PSII and PSI mediate redox reactions are the keys to balance photosynthesis.

Both PSII and PSI are sensitive to light intensities and other abiotic stresses. Redox homeostasis is disturbed when the rate of damage is higher than repair, causing photo inhibition Vass and Aro, (2008). The excessive energy under HL can be dissipated as heat via non-photochemical quenching (NPQ), which subsequently adjust the chloroplasts composition and metabolism. The presence of an antioxidant system in chloroplast helps in nucleus-chloroplast communication that drives the gene expression. In addition, peroxisomes accumulate H_2O_2 under photorespiration Foyer and Noctor, (2016), that is removed by peroxisome associated CATs Queval *et al.,* (2007). Recent findings indicate that antioxidants ascorbate (Asc) and glutathione (GSH) regulate gene expression under stresses. Devireddy *et al.,* (2021) Noctor *et al.,* (2014), suggesting their dynamic nature and high sensitivity to stress cues. In summary, the mechanisms are now well defined; reveal that moderate levels of ROS are essential for cell proliferation, photosynthesis mechanisms, and maintaining redox homeostasis at a basal level within chloroplasts. However, ROS signaling components are less studied in relation to the evolution of the key protein families from algae to plants.

Numerous techniques, including solvent extraction, adsorption, chemical reduction, bioremediation, and others, have been thoroughly investigated and evaluated, to remove hazardous form Cr (VI) to non-toxic Cr (III) form from polluted soil, water, and air Azeez *et al.,* (2021). Moreover, plants have evolved a variety of sophisticated adaptation methods, such as chelation by organic compounds followed by sequestration within vacuoles, to deal with high amounts of ROS produced under biotic and abiotic challenges Azeez *et al.,* (2021); Pushkar *et al.,* (2021) .

Harmanjit panel Kaur and Nandni Goyal, (2022) stated that ever-growing industrial development and urban sprawl has resulted in augmentation of heavy metals in the ecosystem, causing grave menace to all organisms, including plants. One of the chief outcomes of heavy metal stress in plants is the spurt of reactive oxygen species (ROS) viz. superoxide radical ($O_2^{\bullet -}$), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($OH^{\bullet}$). ROS are generated as natural metabolic byproducts and are essential for optimal performance of plants, but at elevated levels, they instigate oxidation of numerous cellular biomolecules leading to irrevocable metabolic disorder and eventually cell death. To detoxify various types of ROS, plants are stocked with an intricate grid of biochemical adaptive strategies (antioxidant system). Broadly divided into two categories, **(a)** which eliminate oxygen radicals and their products (enzymatic), such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), etc. **(b)** which quench ROS without themselves transforming to harmful radicals (nonenzymatic) like glutathione, ascorbate, phenolics, etc Fig.(7). Additionally, plants produce certain redox buffering compounds, for instance, phytochelatins (PCs), metallothioneins (MTs), proline and organic acids that form complexes with metals and assist in vacuolar compartmentalization. Chronological and contemporaneous action of all these antioxidant mechanisms constitutes the cell's antioxidative power that regulates redox state within certain limits.

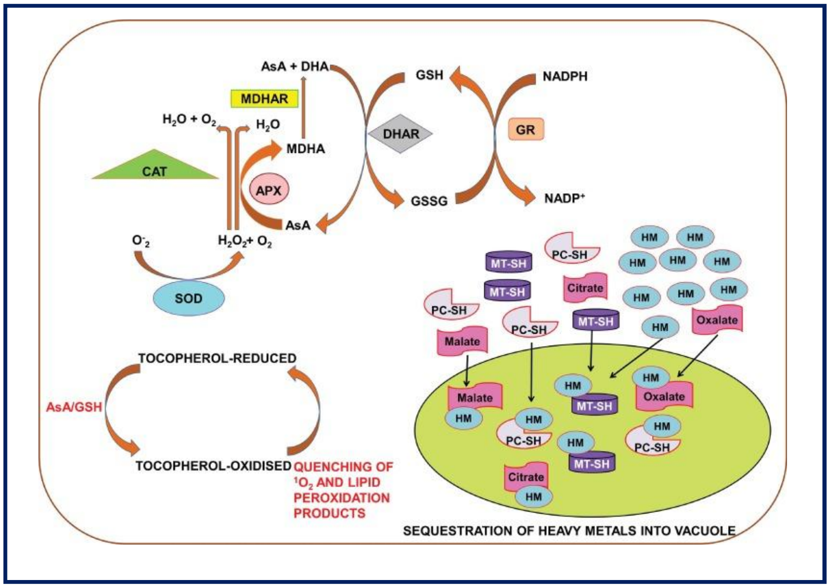


Fig. 7: Illustrates the biochemical adaptations in plants under heavy metal stress. After: Harmanjit panel Kaur Nandni Goyal, (2022)

To combat the elevated amounts of chromium -mediated ROS, plants also have a secondary mechanism for generating antioxidant enzymes Srivastava *et al.,* (2021); Ao, *et al.,* (2022). Understanding the biogeochemistry of chromium in soil-plant environments and the effects that high levels of chromium will have on the ecosystem is crucial. Chromium toxicity on agricultural productivity, lipid peroxidation, ROS production, and potential remediation procedures have been described in a number of previous research Shanker *et al.,* (2005); Shahid *et al.,* (2017); Azeez *et al.,* (2021); Srivastava *et al.,* (2021); Ao *et al.,* (2022).The toxic effects of chromium on key metabolic functions of plants leading to growth and yield impairment are reported.

1- Uptake and translocation of chromium mechanism

Roots of plant secrete various organic acids that acts as ligands and can change insoluble metals present in the soil into soluble forms. Hexavalent Cr is actively taken up by the plasma membrane by involving phosphate and sulfate transporters, Fig (8) Munees Ahemad, (2014) reported that chromium pollution is increasing because continuing industrialization. Of various oxidation states, Cr^{6+} is very toxic due to its carcinogenic and mutagenic nature. It also has deleterious effects on different microorganisms as well as on plants. Many species of bacteria thriving in the Cr^{6+} contaminated environments have evolved novel strategies to cope with Cr^{6+} toxicity. Generally, decreased uptake or exclusion of Cr^{6+} compounds through the membranes, biosorption, and the upregulation of genes associated with oxidative stress response are some of the resistance mechanisms in bacterial cells to overcome the Cr^{6+} stress. In addition, bacterial Cr^{6+} reduction into Cr^{3+} is also a mechanism of specific significance as it transforms toxic and mobile chromium derivatives into reduced species that are innocuous and immobile. Ecologically, the bacterial trait of reductive immobilization of Cr^{6+} derivatives is of great advantage in bioremediation. The present review is an effort to underline the bacterial resistance and reducing mechanisms to Cr^{6+} compounds with recent development in order to garner a broad perspective. Whereas trivalent chromium enters via cation exchange, sites present in plant's cell wall Zaheer *et al.,* (2022).

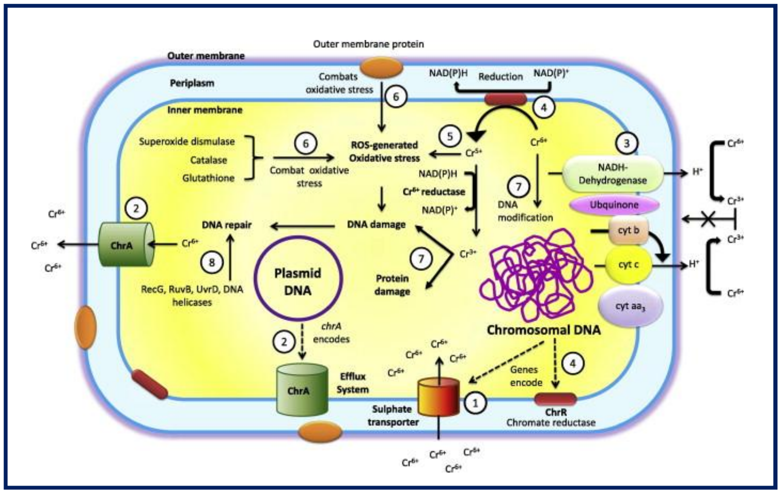


Fig. 8: Illustrates schematic depiction of chromium resistance and toxicology in bacterial cell: (1) chromate due to the structural similarity with sulfate enters the bacterial cell through sulfate transporter encoded by the chromosomal DNA. (2) Plasmid DNA encoded efflux systems are used to expel the intracellular chromates outside the bacterial cell to resist the chromate toxicity. (3) Aerobic Cr^{6+} reduction into Cr^{3+} involves soluble reductase which requires NAD(P)H as an electron donor while anaerobic Cr^{6+} reduction occurs in the electron transport pathway by cytochrome b (cyt b) or cytochrome c (cyt c) along the respiratory chains in the inner membrane; Cr^{3+} cannot pass the bacterial cell membranes due to the insolubility of Cr^{3+} derivatives. (4) Membrane-embedded chromate reductase which is encoded by the chromosomal DNA, reduces Cr^{6+} anaerobically in the presence of electron donors. (5) Cr^{5+} produced during the redox cycle of Cr6+ produces oxidative stress by the production of reactive oxygen species (ROS). (6) To combat the ROS generated oxidative stress, protective metabolic enzymes superoxide dismutase, catalase and glutathione are secreted. Some outer membrane proteins are also involved to counter the oxidative stress. (7) Cr^{6+} and principally Cr^{3+} not only negatively affects DNA replication and RNA transcription by damaging DNA but also alters gene expression. In addition, Cr^{3+} also damages proteins by impairing their functions. (8) DNA repair system is activated in order to repair the damaged DNA. After: Munees Ahemad, (2014)

Chromium dispensation and translocation in plants depend on oxidation state of Cr ions, its amount in the nutrient medium and species of plants Datta *et al.,* (2011), and the chromium content in roots is hundred times higher as compared to shoots Ertani *et al.,* (2017); GracePavithra *et al.,* (2019). Sinha *et al.,* (2018) reported that chromium valence state is one of the main factors affecting Cr transport inside the plant cell Banks *et al.,* (2006). Very few studies have been conducted to illustrate Cr uptake pathway in plants, Since Cr is a nonessential element, and plants lack any specific mechanism or transporters for its uptake. It has been reported that for its entry inside the plant cell, reduction of Cr (VI) to less harmful Cr (III) takes place on plant root surface. Plant cell constituents such as NAD(P)H, glutathione, several pentoses, FADH2, ascorbic acid, cyanocobalamin, cytochrome P-450, and the mitochondrial respiratory chain are involved in the reduction process Cheung and GU, (2007). In contrast, some authors have suggested that Cr (III) forms water insoluble compounds in non-acidic aqueous solutions and, therefore, become impermeable to bio membranes. Some research studies have further demonstrated that Cr (VI) uptake in plants occurs without undergoing reduction. Cr (VI) compounds structurally resembles SO_4^{-2} ions, and enters the cell through carriers of essential anions such as sulphate and phosphate transporters which are essential plant nutrients that easily cross the plant cell membranes (Fig. 9).

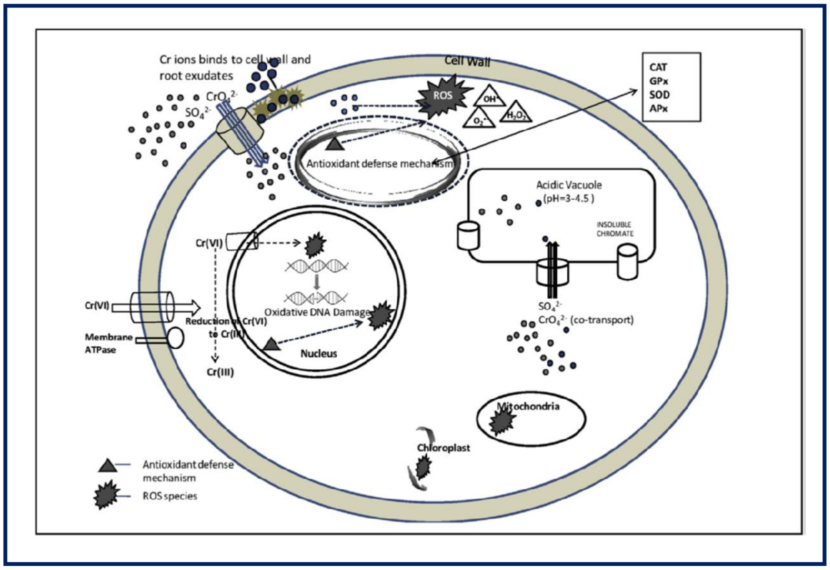


Fig. 9: Illustrates chromium uptake, transport and antioxidant defence mechanism adopted by plant cells. After: Sinha *et al.,* (2018)

Chromate transport across biological membranes is thus reported to be an active process Schiavon *et al.,* (2012); Marieschi *et al.,* (2015). Thus, it can be concluded that Cr active or passive transportation pathway depends on its oxidation state. For instance, Cr (III) uptake occurs through simple and passive diffusion through cation exchange sites of plant cell wall. In contrast, sulphate carriers present in plants transport Cr (VI) actively. Following uptake, Cr (VI) is reduced to Cr (III) in plant roots. The involvement of sulphate transporters in Cr (VI) uptake is evident from recent studies carried out on the inhibition of sulphate transport and assimilatory pathway using transgenic, enzymatic and metabolic inhibitors Schiavon *et al.,* (2012). Following uptake and inside the cell cytoplasm, Cr (VI) detoxification pathway follows reduction of Cr (VI) to Cr (III) via intermediate formation of the unstable Cr (V) and Cr (IV) states which leads to ROS generation Gupta and Ballal, (2015). Contrary to this, no differences in the uptake of either Cr (III) or Cr (VI) were observed in *Phaseolus vulgari* Nath *et al.,* (2009) and *Triticum aestivum L.* Subrahmanyam, (2008). It has been shown that addition of multidentate chelating agents like EDTA and vermicompost enhance the Cr bioavailability and thus increases the uptake of Cr by the plants Jean *et al.,* (2008). This is ascertained by the fact that chelating agents possess functional groups capable of Cr absorption and conversion. Supplementation of the contaminated soil with vermicompost was reported to further enhance the plant biomass growth, thus favouring the plant bioaccumulation potential as found in sorghum

Plants restrict metals and metalloids accumulation in the less susceptible organelles to prevent its degradation at level of cells Masciarelli *et al.,* (2017). The presence of electron-dense particles in the cell wall is a defense strategy of cells for heavy metal toxicity. Deposition of electron-dense particles in between cell wall and cell membrane, vacuoles, plastids, between endoplasmic reticulum cisternae and cytosol of seedlings of *arabidopsis* have been reported due to hexavalent chromium exposure GracePavithra *et al.,* (2019). The accumulation of chromium in root cells vacuoles might be due to the sequestration of chromium as a defensive process. The transport of Chromium from roots to the leaves of plants was not observed as hexavalent is converted to trivalent Cr in cells of plants and it binds with cell wall, which inhibits its transfer in different plant tissues Jobby *et al.,* (2018). Chromium uptake by the plant organs mainly depends upon the Cr level in the soil, plant species and growth medium GracePavithra *et al.,* (2019)

Bishehkolaei *et al.,* (2011), reported that *Ocimum basilicum L.* seedlings were exposed to different concentrations of Cr (0-8 mg L^{-1} of Cr^{3+}) in order to evaluate the cellular localization of chromium, plant accumulating capacity, and potential cellular defense mechanisms against Cr stress. Dried plant tissues (roots and shoots) were exposed to X-ray microanalysis for element determination (including Cr, Cu, Zn, Co, Ni, and Mo). Results showed that the highest amount of Cr had accumulated in the roots of the plants treated with 8 mg L-1 of Cr^{3+}, while less Cr was transported to the shoots Fig. (10). TEM micrographs of *Ocimum basilicum* root cortex cells exposed to 4, 6, and 8 mg L^{-1} of Cr^{3+} revealed dense granular metal deposits in the periplasmic zone along the cell walls; such deposits were not observed in leaf mesophyll cells. Root cortical cells of the control seedlings grown in the absence of Cr^{3+} exposures were void of such granular metal deposits. While Cr was the predominant element, lower amounts of Cu, Zn, Co, Ni, and Mo were also detected in the chromium bearing deposits analyzed by X-ray microanalysis. Formation of Cr bearing deposits in the root cells of *Ocimum basilicum* may have the effect of maintaining relatively low cytoplasmic concentration of the element and possibly reduce the toxic effects of chromium on cellular metabolism as a detoxification mechanism.

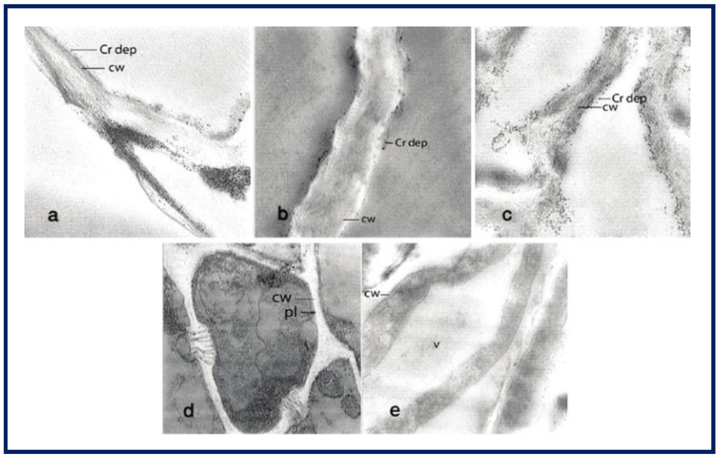


Fig. 10: TEM micrographs of *Ocimum basilicum* root cortical cells treated with a: 4 mg L-1 Cr^{3+}, b: 6 mg L-1 Cr^{3+}, c: 8 mg L-1 Cr^{3+} showing chromium bearing granular deposits along the innermost layer of cell wall, d: untreated showing some cytoplasmic organelles with no metal deposits, e: 2 mg L-1 Cr^{3+} showing no chromium bearing deposits in cytoplasm and along the cell wall. CW: cell wall; v: vacuole; Pl: plasmalemma; Cr dep: chromium bearing deposits. After: Bishehkolaei *et al.,* (2011).

Madhu and Sadagopan, (2020) reported that Cr (III) is passively transported to the aboveground part of the plant; while Cr (IV) is actively transported to the plant parts Ahmad *et al.,* (2019). It was also reported that Cr (IV) is not easily transported to the plant parts due to the subsequent assimilation pathways and its interference with some essential nutrients, which may affect its transportation to the aboveground plant parts Dube *et al.,* (2003). Furthermore, Cr (IV) has a high soil-plant transfer index and is also affected by metabolic inhibitors, which make it difficult to be up taken by the plants Kimbrough *et al.,* (1999); Ali *et al.,* (2018). Chromium is the slightest moveable metal among all different heavy metals Tripathi *et al.,* (2012); Eleftheriou *et al.,* (2015) and UdDin *et al.,* (2015). Moreover, amount of chromium in the roots is found to be 100 times more than that present in the aboveground parts of the plants Jun *et al.,* (2009). The trend of chromium uptake/absorption in various plant parts (roots > shoots) has been previously observed in *Brassica napus* Zaheer *et al.,*(2020), *Arabidopsis thaliana* Eleftheriou *et al.,* (2015), *Helianthus annuus* Farid *et al.,* (2018) and *Typha angustifolia* Bah *et al.,* (2011). Previous studies reported that accumulation of large amount of chromium in the vacuoles of plant root cells Liu *et al.,* (2009). Due to the formation of some chemicals inside the plant tissues, the transportation of chromium from the roots to the aboveground parts is limited Gardea-Torresdey *et al.,* (2005). Another possible reason behind this mechanism is the formation of Cr (III) in plant cells Shahid *et al.,* (2017). Heavy metals such as Cu Saleem *et al.,* (2020), Pb Madhu and Sadagopan, (2020), and Zn Murakami and Ae, (2009) have the ability to penetrate into the plant tissues and could be transported to the aboveground plant parts through the vascular bundle channels. The group of gene family involved in these mechanisms may include NRAMP, HMA and CDF Nagajyoti *et al.,* (2010). These gene families are helpful in metal transport/accumulation and help in the tolerance of the plants to stress conditions. More studies are should needed to supported the functional role of these gene families in various plant species. Cr (IV) usually needs active mechanisms to be transported into the aboveground plant parts. For the transportation of chromium to the aboveground plant parts, Cr usually uses the channels of Fe and S for its proper translocation into the plant tissues Kumar *et al.,* (2016).

2- Impacts of chromium toxicity in plants

Chromium is a noxious element that adversely affects the metabolic processes in plants and reduces the growth and productivity of crops Pradhan *et al.,* (2017); Ugwu and Agunwamba, (2020). Chromium induced phytotoxicity is because of free radicals production which enhances degradation of biomolecules present in cells of plants Ertani *et al.,* (2017); Ranieri *et al.,* (2020). Moreover , treatment of chromium showed cytotoxic, genotoxic impacts and hormonal imbalance which checks germination and development of plants and reduce dry matter production Chebeir *et al.,* (2016); Jobby *et al.,* (2018). Excessive deposition of chromium in plant tissues showed adverse effects by modulation in cell division and cell cycle, water and minerals imbalance, alters enzymatic activities, nitrogen assimilation, and degradation of chlorophyll, reduction in growth, free radicals generation and derangement of antioxidant defense system Masciarelli *et al.,* (2017); Ugwu and Agunwamba, (2020). The toxic level of chromium can incite physical, chemical and molecular alterations in plants and its long-term retention in soil can reduce crop yield and grain quality Shahid *et al.,* (2017).

Sajad *et al.,* (2023) stated that Different heavy metal; stressors very often confront plants that adversely impair their growth and productivity. Chromium is one of the most prevalent toxic trace metals found in agricultural soils because of anthropogenic activities, lack of efficient treatment, and unregulated disposal. It has a huge detrimental impact on the physiological, biochemical, and molecular traits of crops, in addition to being carcinogenic to humans Fig. (11).

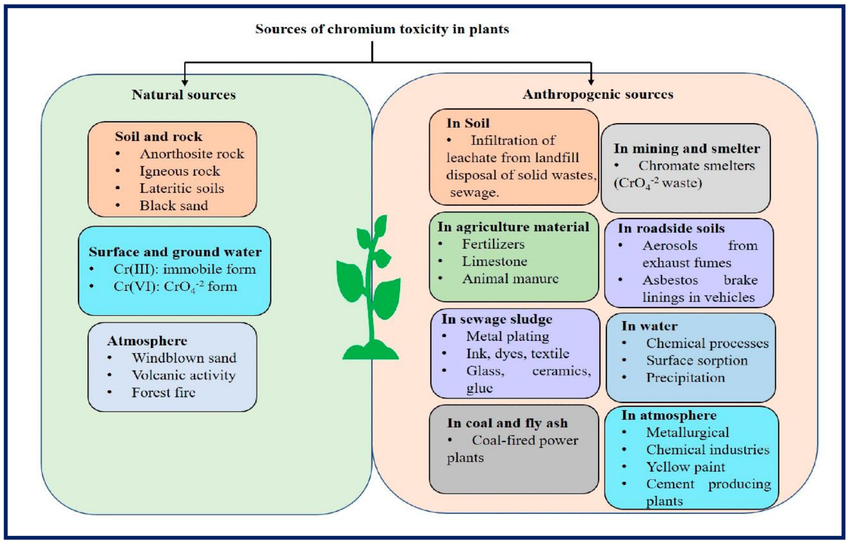


Fig. 11: Represents sources of Cr contamination in agricultural soils and other environments. In this figure, we have highlighted both natural and anthropogenic sources of Cr in agricultural soils. After: Sajad *et al.,* (2023)

Chromium in soil exists in different forms, including Cr (III) “trivalent” and Cr (VI), but the most pervasive and severely hazardous form to the biota is Cr (VI). Despite extensive research on the effects of chromium stress, the exact molecular mechanisms of chromium sensing, uptake, translocation, phytotoxicity, transcript processing, translation, post-translational protein modifications, as well as plant defensive responses are still largely unknown. Even though plants lack a chromium transporter system, it is efficiently accumulated and transported by other essential ion transporter. This review, we discussed chromium toxicity in plants, signaling perception, and transduction. Further, we highlight various mitigation processes for chromium toxicity in plants, such as microbial, chemical, and nano-based priming. We also discuss the biotechnological advancements in mitigating chromium toxicity in plants using plant and microbiome engineering approaches. Additionally, we also highlighted the role of molecular breeding in mitigating chromium toxicity in sustainable agriculture. Finally, some conclusions are drawn along with potential directions for future research in order to better comprehend Cr signaling pathways and its mitigation in sustainable agriculture.

Thirty-two plant species in which 94% species showed significant reduction in stem growth when exposed to 1000 mg kg^{-1} hexavalent chromium Junaid *et al.,* (2016). Accumulation of chromium was recorded in the roots, stems, leaves and seeds of wheat plants, indicating that this element is moving from down to up da Conceicao Gomes *et al.,* (2017). Chromium interferes with several metabolic processes, resulting in impaired photosynthesis, inhibited plant growth, stunted development and plant death Gill *et al.,* (2015); Kalve *et al.,* (2011); Kumar *et al.,* (2016); Maqbool *et al.,* (2018); UdDin *et al.,* (2015) and Zaheer *et al.,* (2020). Chromium may enhance plant development at low concentrations and hinder plant growth at higher concentrations, according to some research, even though there is no concrete proof to substantiate its positive participation in plant metabolism Ao *et al.,* (2022) Fig. (12). Zulfiqar *et al.,* (2023) reported that chromium has a significant impact on root growth and development in addition to seed germination Shahid *et al.,* (2017). The roots, which are a major organ for nutrient uptake and are consequently linked to chromium uptake, act as a major source of chromium toxicity in plants Srivastava *et al.,* (2021). A considerable reduction in root length of sour orange (*Citrus aurantium*) seedlings was discovered while conducting an experiment in a greenhouse experiment, under doses of 200 mg/kg chromium (III), Shiyab, (2019). In water lettuce (*Pistia stratiotes*), chromium promotes root length, width, and laminal length at low concentrations (0.25 mg L-1) when compared to controls, but at higher concentrations (2.5 mg L-1), the root length was observed to be reduced Kakkalameli *et al.,* (2018).

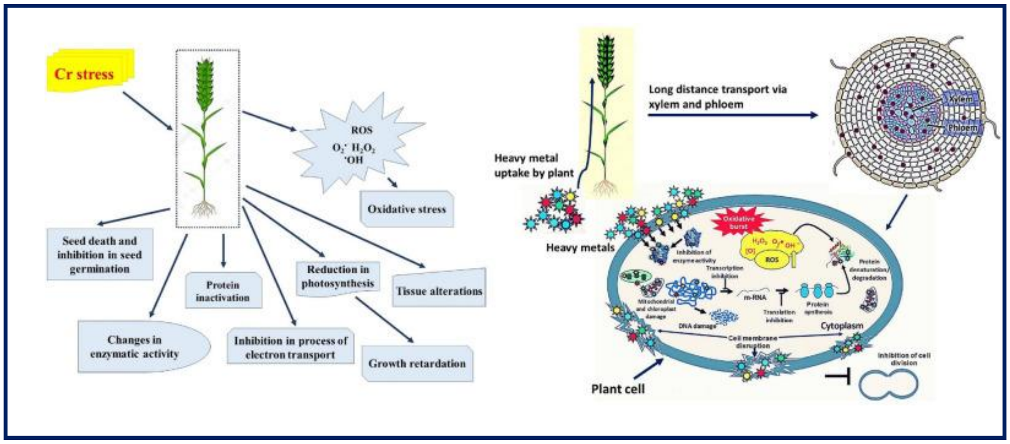


Fig. 12: Illustrates schematic representation from the sequestration of chromium (Cr) into a plant cell to the plant's death, through a series of events. Cr toxicity decelerates photosynthesis by preventing seedling establishment and root growth, which in turn slows down essential nutrient and water uptake. Moreover, toxicity of Cr alters photosynthetic pigments content in plant leaves, and these alterations typically result in chlorosis and necrosis of the leaves. In addition, to decreasing membrane integrity, high Cr stress also causes the loss of osmolytes and cell turgor pressure, which causes stomatal closure impacting overall osmoregulation. Additionally, Cr toxicity disrupts the equilibrium between the generation of reactive oxygen species (ROS) and the antioxidant defense system, which causes ROS to build up and cause oxidative damage to cellular organelles. DNA damage, protein and lipid synthesis, lipid peroxidation, enzyme activity, and impaired cell division are all affected by the formation of ROS, which ultimately leads to plants death Shanker *et al.,* (2005); Rizvi *et al.,* (2020) and After Zulfiqar *et al.,* (2023)

Similarly, it was observed that chromium toxicity minimized the shoot length of oats (*Avena sativa*) by 41% as compared to control Shanker *et al.,* (2005). The growth of lateral roots and the quantity of secondary roots are further effects of chromium Mallick *et al.,* (2010); Srivastava *et al.,* (2021). Root cell division may have decreased because of the chromium -induced reduction in root length. Chromium (VI) prevents plants from absorbing nutrients and water, which shortens roots and reduces cell division Shahid *et al.,* (2017). Treatment with chromium (VI) in maize (*Zea mays*) resulted in shorter and fewer root hairs, as well as a brownish color Mallick *et al.,* (2010). Even various studies claimed that the cell cycle extended when exposed to Cr toxicity Sundaramoorthy *et al.,* (2010). According to Zou *et al.,* (2006), green amaranth (*Amaranthus viridis*) root tip cells had their mitotic index reduced because of exposure to chromium. Another growth metric that is frequently impacted by chromium exposure is plant stem growth Ding *et al.,* (2019). The shoot length of sunflower (*Helianthus annus*) was observed to decrease when chromium (VI) content increased Fozia *et al.,* (2008). Similarly, when the soil's chromium (III) concentration was raised in sour orange (*Citrus aurantium*) the shoot length decreased by 90.4% at 200 mg kg^{-1} of chromium Shiyab, (2019). After being exposed to 600 mg kg-1 chromium (III), tea (*Camellia sinensis*) developed a short stem that grew slowly Tang *et al.,* (2012). According to Lukina *et al.,* (2016), chromium (VI) toxicity (1000 mg kg^{-1}) in 32 species had a negative impact on 94% of the species' stem growth. The chromium-reduced root growth and development, which results in decreased water and nutrient transfer to the aboveground plant components, may be the cause of the decreased stem growth and height Srivastava *et al.,* (2021) Fig. (13).

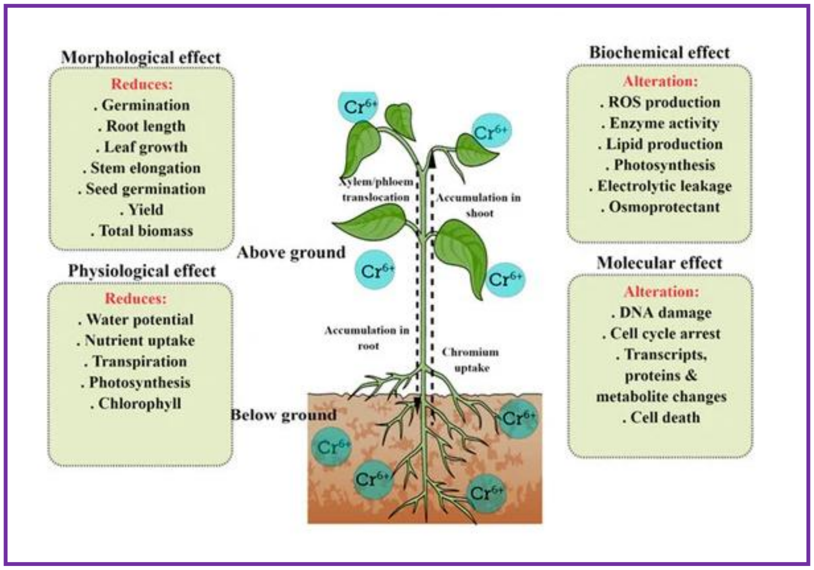


Fig. 13: Effect of Cr toxicity (in the form of Cr^{6+} or $CrO_4{}^{2-}$) on various morphological, Physiological and biochemical traits in plants. After: Aly *et al.,* (2023)

Additionally, increased chromium transport to shoot tissues may directly interact with delicate plant tissues (leaves) and functions (photosynthesis), affecting shoot cellular metabolism and resulting in a shorter plant Sharma *et al.,* (2020).

In plants, higher concentration of chromium significantly affects various biochemical and morphological parameters i.e., reducing seed germination, plant biomass, photosynthetic efficiency, root damage, and eventually causes plant mortality Zayed and Terry, (2003); Zaheer *et al.,* (2015). Excess amounts of Cr can cause stunted growth of the plant Faisal and Husnain, (2005a). Essential nutrients and Cr interaction can disturb the uptake pattern of various essential nutrients (Ca^{2+} and Mg^{2+}) in the plant because of the interaction of Cr with soil Zupančič*et al.,* (2004).

Kazi Md. Kamrul Huda, (2013), reported that food security is in danger under the continuous growing threat of various stresses that leads to a reduction in crop yields. Calcium plays a very important role in many signal transduction pathways including stress signalling. Different extracellular stimuli trigger increases in cytosolic calcium, which is detrimental to plants. To cope with such stresses, plants need to develop efficient efflux mechanisms to maintain ionic homeostasis. The Ca^{2+} - ATPases are members of the P-type ATPase superfamily, which perform many fundamental processes in organisms by actively transporting ions across cellular membranes. In recent years, many studies have revealed that, as well as efflux mechanisms, Ca^{2+} - ATPases also play critical roles in sensing calcium fluctuations and relaying downstream signals by activating definitive targets, thus, modulating corresponding metabolic pathways. As calcium-activated calmodulin (CaM) is reported to play vital roles in stress tolerance, the presence of a unique CaM-binding site in type IIB (Ca^{2+} - ATPases) indicates their potential role in biotic as well as abiotic stress tolerance. The key roles of (Ca^{2+} - ATPases) in transport systems and stress signalling in cellular homeostasis are addressed in this review. A complete understanding of plant defence mechanisms under stress will allow bioengineering of improved crop plants, which will be crucial for food security currently observed worldwide in the context of global climate changes. Overall, this article covers classification, evolution, structural aspects of Ca^{2+} - ATPases, and their emerging roles in plant stress signalling. They also stated that a submicromolar Ca^{2+} concentration triggers activation of Ca^{2+} - ATPases, which are therefore, known as high-affinity pumps Møller *et al.,* (2010). Ca^{2+} transport is closely linked to ATP hydrolysis and if the membranous region of the Ca^{2+} - ATPases fails to bind, Ca^{2+} hydrolysis will not occur Morth *et al.,* (2011). Fig. (14) shows a schematic diagram of Ca^{2+} transporters involved calcium sequestration in plant cells and their subcellular localization. The environmental stress causes an increase in cytosolic Ca^{2+} that activates Ca^{2+} - ATPases due to binding of Ca^{2+} to their transporter sites Bose *et al.,* (2011). After Ca^{2+} binding, IIB Ca^{2+} - ATPases proceeds to ATP hydrolysis directly because it contains only a single membranous Ca^{2+}-binding site Brini and Carafoli, (2009).

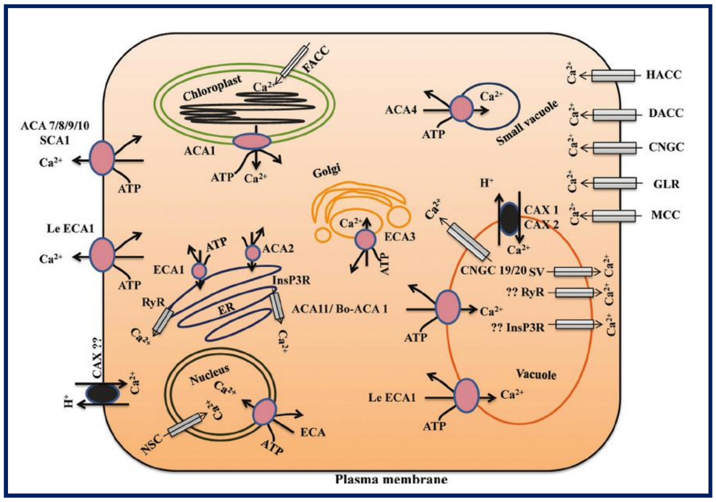


Fig. 14: Schematic diagram of Ca^{2+} transporters involved in calcium sequestration in plant cells and their subcellular localization. All P-type Ca^{2+}-ATPases have low affinity but high capacity Ca^{2+} efflux across membranes. ECA1 is present in the endoplasmic reticulum (ER) and ECA3 in the Golgi. Le-ECA1 is in the tonoplast and plasma membrane, while Ca^{2+}-ATPase is in the nuclear envelope (not characterized at the molecular level). Plant IIB calcium pumps represent: ACA1 in the chloroplast; ACA2 in the ER; ACA4 in the small vacuole; Bo-ACA1 and ACA11 in the vacuole; and ACA7/8/9/10 and Gm-SCA1 in the plasma membranes. Apart from these, many of the plant IIB calcium pumps are also present in different membranes . CAX, calcium exchanger; CNGC, cyclic nucleotide gated channel; DACC, depolarization activated cation channel; FACC, fast-activating cation channel; GLR, glutamate receptor-like channel; ACC, hyperpolarization activated cation channel; InsP3R, inositol 1,4,5-trisphosphate receptor-like channel; MCC, mechanosensitive cation channel; NSC, non-selective cation channel; RyR, cyclic ADP-ribose (cADPR)-activator ryanodine receptor-like channel; SV, slow-activating vacuolar channel. After: Kazi Md. Kamrul Huda, (2013)

Moreover, agricultural soils with high levels of chromium contamination adversely affect the crop yield Kanwal *et al.,* (2014), Adrees *et al.,* (2015a) throughout the growth cycle, plants are sensitive to chromium toxicity, and detailed information about the toxic effect of chromium on morpho-physiological and biochemical parameters and toxicity mechanisms Fig. (15)

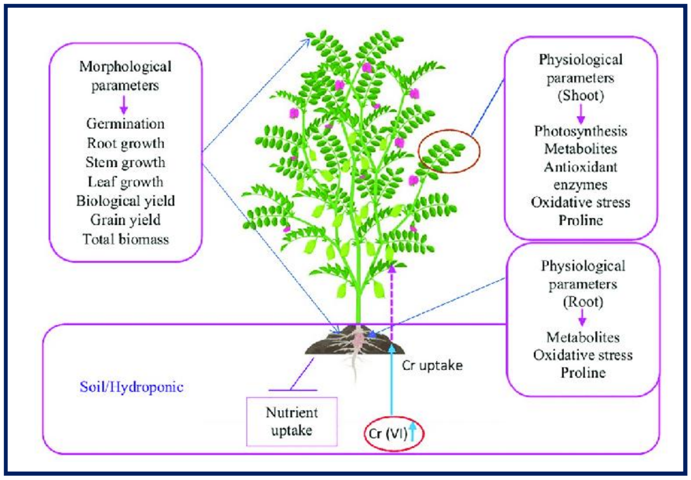


Fig. 15: Illustrates a schematic outlining of mechanism of chromium (Cr) toxicity in soil and the potential deleterious effects of Cr pollution on morphological and physiological aspects of chickpea plants. After: Singh *et al.,* (2020)

3-1 Germination and growth of seedling

Considering seed germination is the first physiological activity that chromium affects, a seed's capacity to germinate in a medium containing chromium would be an indication of how tolerable it is to this metal Shanker *et al.,* (2005); Rath and Das, (2021). Rath and Das, (2021) stated that *(Vigna mungo L.)* Hepper commonly known as blackgram is an important legume crop with good quality dietary proteins and vitamins. Low production of blackgram in the chromium rich soil of Odisha is a serious concern against its demand. Chromium (VI) was tested on *V. mungo* var. B3-8-8 at 100, 150, 200, 250 and 300 lM concentrations on growth, anti-oxidative enzymes and chromium content at 15, 30 and 45 d of treatments Fig. (16). Seed germination and growth decreased with increase dose and duration. Chromium uptake induced oxidative burst with significant increase of osmolytes was observed in cell at lower doses but failed to adjust homeostasis at higher dose. Increase of GPX and SOD and decrease of CAT was observed as dose dependent. Increased protein content was detected in \200 lM chromium concentration whereas; significant decrease of protein was noted thereafter. Down regulation of proteins (29.2 kDa and 32.6 kDa) was observed at 250 lM of Cr. Total chromium uptake was greater in root than in shoot that might be due to poor translocation of heavy metal or detoxification. Thus, blackgram was able to maintain homeostasis at lower concentrations of chromium by activating the cascade of enzymes following cellular detoxification mechanism. They also reported that increased exposure to chromium brought a remarkable reduction in germination and growth in blackgram (*Vigna mungo* var. B3-8-8). The roots were more severely affected with a marked decrease in their lengths as compared to shoot. The reduction in the total chlorophyll carbohydrates, proteins and reducing sugars contents confirm that Cr adversely affects the concerned plant. On the contrary, an increase in the concentrations of carotenoids might be compensated with the decrease of Chl b reducing PSII activity. A substantial increase in free amino acids, proline and total polyphenols in higher concentration (i.e. 250 and 300 lM) indicate that chromium induces severe oxidative stress in blackgram that is managed by up-regulation of secondary metabolites for maintaining the cellular equilibrium. The increase in the levels of the antioxidative enzymes also indicated that they have a very appreciable role in scavenging mechanisms that plants opted during stressful conditions. The accumulation levels of Cr indicate that blackgram var. B3-8-8 can accumulate moderate amount of Cr in root and translocate insignificant amount to shoot, thus can be recommended for growing safely in surrounding areas of chromium mine with Cr-contaminated sites.

Symptoms of chromium phytotoxicity comprise the early development of seedling or impediment of seed germination, suppressed root growth, and leaf chlorosis. Chromium prominently reduced the seed germination of different plants such as vegetables cauliflower (*Brassica oleracea* L.), citrullus (*Citrullus vulgaris*), and crops, wheat (*Triticum aestivum L.*), barley (*Hordeum vulgare L.*), and maize (*Zea mays L.*) Shahid *et al.,* (2017); Ao *et al.,* (2022). It was noted that higher toxicity of Cr in soil reduced the germination rate of jungle rice (*Echinochloa colona*), bush bean (*Phaseolus vulgaris*), alfalfa (*Medicago sativa*), and sugarcane (*Saccharum officinarum*) by 25%, 48%, 23%, and 57%, respectively as compared with control Shanker *et al.,* (2005).

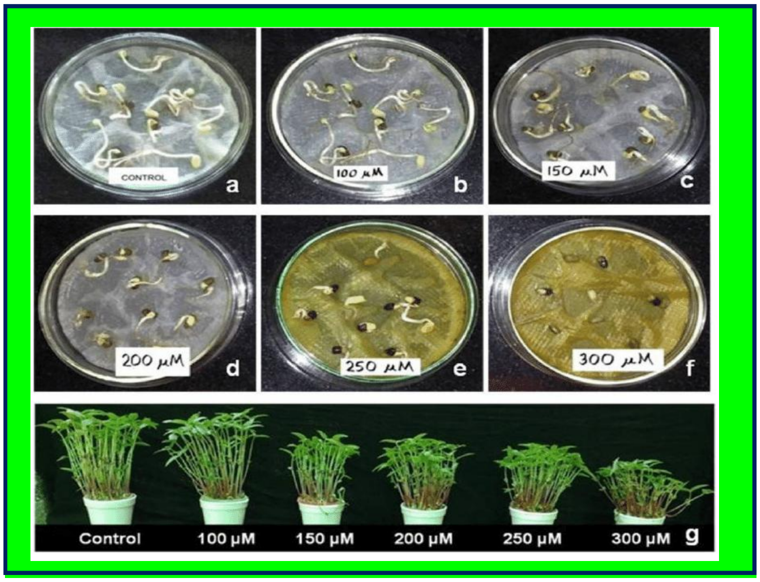


Fig. 16: Illustrates Seed germination of *V. mungo* var. B3-8-8 in different concentration of chromium in petridish (a-f). Seedling growth of *V. mungo* var. B3-8-8 plants in different concentrations of Cr in hydroponic culture (g). After: Rath and Das, (2021)

According to several investigations, with an increase in Cr concentration in the external medium i.e., soil/nutrients solution, the DNA content of bean seedlings gradually improved and as a result, the DNA content followed a trajectory that was the opposite of the radical expansion DalCorso, (2012). Higher concentrations of chromium significantly minimized the bean roots by interfering the cell division process in roots Zeid, (2001); Singh *et al.,* (2013). During seed germination, accumulated reserve materials like proteins and starch are hydrolyzed to produce precursors like sugars and amino acids for the development of embryo axis as well as substrates for different metabolic processes Ao *et al.,* (2022). Ma *et al.,* (2017) stated that during germination of barley *(Hordeum vulgare L.)* seeds, important morphological and physiological changes take place, including development of organs and tissues and activation of metabolic pathways Fig. (17). Germination and dormancy of seeds are regulated by abscisic acid, gibberellins, reactive oxygen species (ROS), reactive nitrogen species (RNS) and several other factors. Activities of ascorbate glutathione cycle enzymes, responsible for scavenging ROS, strongly increase. Catalase and superoxide dismutase activities, also scavenging ROS, decrease at the onset of seed germination and then increase. With the increase in aerobic metabolism after radicle protrusion, the activities of the fermentation enzymes lactate and alcohol dehydrogenase decline rapidly. The RNS-scavenging activity of S-nitrosoglutathione reductase decreases in the course of seed germination, in concert with elevation of nitric oxide production and protein nitrosylation. This activity supports the role of RNS in regulating seed germination. Transcription of various genes at different phases of seed germination exhibits phase-specific changes. During imbibition, genes involved in cell wall metabolism are highly expressed; in the middle phase of seed germination before radicle protrusion, genes involved in amino acid synthesis, protein synthesis, and transport and nucleic acid synthesis are upregulated significantly, and after radicle protrusion, genes involved in photosynthetic metabolism are induced. In summary, signal transduction and metabolic regulation of seed germination involve diverse reactions and complex regulation at different levels of metabolic organization.

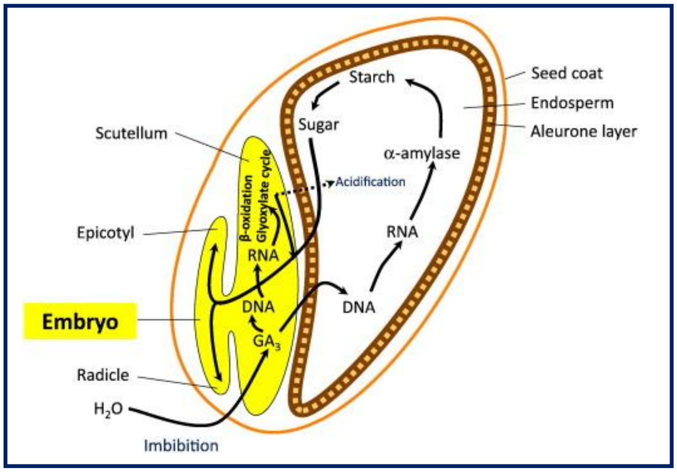


Fig. 17: Illustrates the metabolic processes occurring in embryo and endosperm during barley seed germination. After: Ma *et al.,* (2017)

When the chromium content gradually increased, the activity of the a- and b-amylases of the developing seeds decreased, which may be responsible for the inhibition of seed germination Oliveira, (2012). Seed germination of black gram (*Vigna mungo*) was reduced to 50.70% with the presence of Cr (VI) contents (300 μM) in nutrient solution Rath and Das, (2021). Singh and Sharma, (2017) observed that 42.60 and 53.53%, respectively decreased chickpea (*Cicer arietinum*) and green bean (*Phaseolus aureus*) seed germination, when chromium was present at higher concentrations (100 mg/L). More than 90% of the 45 tomatoes (*Solanum lycopersicum*) genotypes displayed reduced and delayed germination within 14 days under 78 mg/L Cr (VI) stress, according to a recent study by Hafiz and Ma, (2021). Higher ROS production from Cr treatment may have facilitated the breakdown of stored nutrients in seeds cotyledon, which ultimately leads to changing the characteristics of cell membranes, hence results in reduced seedling germination Shafiq *et al.,* (2008); Shah *et al.,* (2010). The significant reduction in seedling length under chromium stress might be due to the reduced water potential and secondary stress-causing obstructed nutrient absorption John *et al.,* (2009). Because there are fewer meristematic cells in root tips than in cotyledons and shoot apex, Cr treatment also results in diminished seedling growth, particularly of roots Rath and Das, (2021). The hydrolytic enzymes' activity is impacted by chromium stress, depriving the radical and plumule of seed and ultimately slowing seedling growth Stambulska *et al.,* (2018). According to Sundaramoorthy *et al.,* (2009), hexavalent chromium concentration even results in chromosomal abnormalities in the roots of seedling, which stimulate c-mitosis and result in extremely reduced root growth. The amylase activity of seeds under chromium stress may be inhibited, which would lead to a reduction in the transfer of carbohydrates to the germ Stambulska *et al.,* (2018). Additionally, treatment of chromium gradually stimulates protease activity, which results in a lower rate of seed germination or possibly seed death Khan *et al.,* (2020); Ao *et al.,* (2022).

Legumes are able to uptake chromium from soil and show various negative impacts like reduction in germination of seeds, biomass of seedlings and overall crop productivity. However, the extent of the damage varies with the crop species and the relative concentration of chromium. Besides its effects on seed emergence, chromium may also cause stunted bud growth, reduced radical length and shortening of coleoptiles Adhikari *et al.,* (2020); El-Demerdash *et al.,* (2019). Chromium toxicity can inhibit seed germination Kumar *et al.,* (2016); Sinha *et al.,* (2018), and its deleterious effects are more pronounced on the subsequent growth of emerging Scoccianti *et al.,* (2006), Beta seedlings Ali *et al.,* (2015); Yu *et al.,* (2018). Wheat seeds germination and seedling growth are gradually inhibited by Cr (VI) toxicity Danish *et al.,* (2019). Sharma *et al.,* (2016) reported that 0.5 mM chromium could inhibit 90% of seed germination in Phaseolus vilgairs. This might be due to the lesser nutrient and water transport. Jun *et al.,* (2009) reported that *Lablab purpureus* responded differently under varying levels of chromium toxicity (0, 0.1, 0.2, 0.4, 0.8, 1.6, and 3.2 mM) whereby the coleoptile growth and root elongation were reducing with increasing chromium concentration.

Abdul Wakeel and Ming Xu, (2020) reported that chromium (Cr) is considered as one of the chronic pollutants that cause damage to all living forms, including plants. Various industries release an excessive amount of Cr into the environment. The increasing accumulation of Cr in agricultural land causes a significant decrease in the yield and quality of economically important crops. The Cr-induced biochemical, molecule, cytotoxic, genotoxic, and hormonal impairments cause the inhibition of plant growth and development. In the current study, we reviewed Cr morpho-phytotoxicity related scientific reports published from 2009 to 2019. We mainly focused on the Cr-induced inhibition of seed germination and total biomass production. Furthermore, Cr-mediated reduction in the root, branches, and leave growth and development were separately discussed. The Cr uptake mechanism and interference with the macro and micronutrient uptake were also discussed and visualized via a functional model. Moreover, a comprehensive functional model has been presented for the Cr release from the industries, its accumulation in the agricultural land, and ultimate morpho-phytotoxicity. It is concluded that Cr-reduces plant growth and development via its excess accumulation in the plant different parts and/or disruption of nutrient uptake Figs. (18 and 19). The forms of chromium revealed differently effects on various crops. Lopez-Luna *et al.,* (2009) reported that the tannery sludge was less toxic than Cr III and Cr VI, and A. sativa germination was less affected as compared to *T. astivum* and sorghum. Seed coat prevents the excess penetration of Cr^{2+} into the seed, however once the seed gets germinated, there is no barrier to protect the subsequent seedling from toxic ions, making Cr^{2+} becomes more toxic for seedling growth Coetzee *et al.,* (2018); Ranieri and Gikas, (2014).

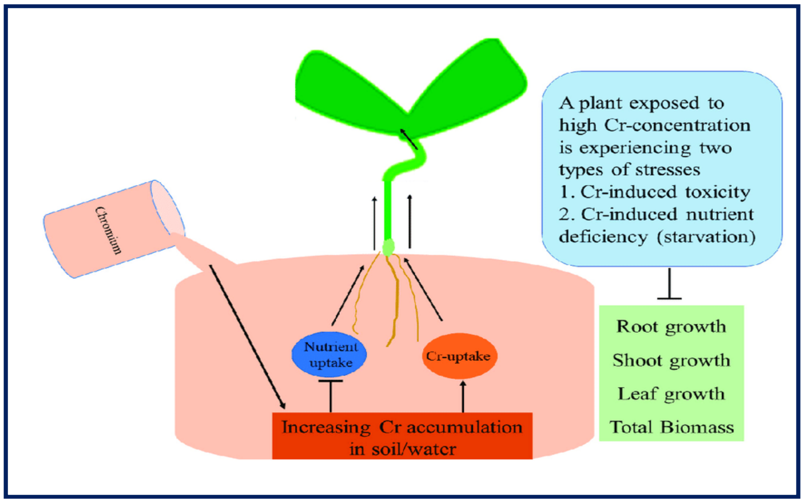


Fig. 18: Illustrates a functional model for the release, accumulation, and toxicity in plants. Cr is released from/through the industrial processes and anthropogenic activities in the soil. The model also visualizes the uptake of Cr by the plant roots, translocation to the shoots. The Cr-induced morphological, physiological, biochemical, molecular, hormonal, and Ultrastructural changes in plants are also summarized in the model. After: Abdul Wakeel and Ming Xu, (2020)

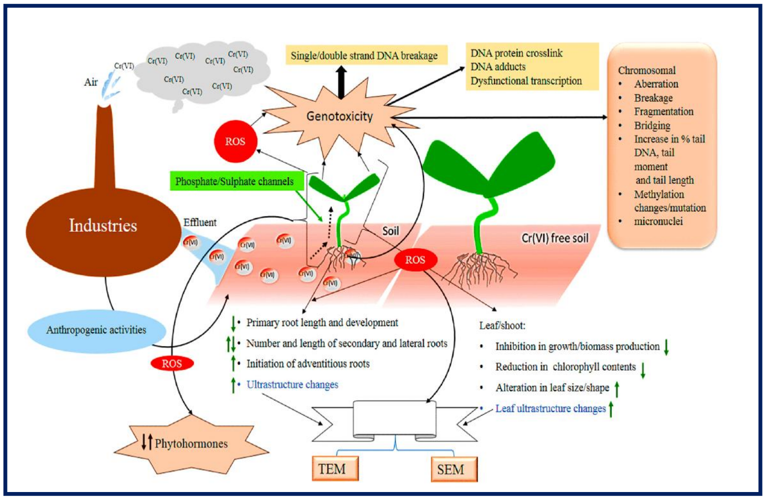


Fig. 19: Illustrates functional model for the Cr-induced nutrient uptake inhibition and plant growth retardation. Increasing concentration of Cr in soil/water compete with the nutrients uptake that is leading in the increasing Cr accumulation in plant and reduction of nutrients. in the presence of high Cr concentration plant faces two stress simultaneously: 1. High Cr accumulation-mediated phytotoxicity. 2. Nutrient deficiency-mediated metabolic abnormality. After: Abdul Wakeel and Ming Xu, (2020).

3-2 Interaction of chromium with other elements

Chromium have a significant impact on the metabolism of minerals and causes phytotoxicity in soil-plant systems due to alteration of soil nutritional composition and controlling plant nutrient absorption, distribution, and transport Chen *et al.,* (2018). Chromium can alter the mineral nutrition of plants in a complex way because of its structural resemblance to some critical elements Ding *et al.,* (2019). Several researchers have focused most of their emphasis on how chromium affects the absorption and accumulation of other inorganic nutrients. Plants to absorb chromium Ao *et al.,* (2022) use different processes. Both forms, Cr (III) and Cr (VI), have the potential to obstruct the uptake of several other ionically related ions, including Fe and S. Researchers Ding *et al.,* (2019), Askari *et al.,* (2021), Ashraf *et al.,* (2022a) they reported that Cr (III) and Cr (VI) interfere with macronutrient elements (Ca, K, Mg, N, P, and S) and trace elements (Cu, Fe, Mn, Si, and Zn). Sharma *et al.,* (2020) reported that heavy metal stress affects nutrient uptake in plants by interacting with other essential minerals Fig. (20). Chromium restricts the uptake of nutrients in soil by forming insoluble compounds Chignon *et al.,* (2019). Nutrient uptake is thereby inhibited by the metal toxicity especially, when the concentration of the metal exceeds its permissible limits Osu *et al.,* (2012). For instance, excessive Cr had been observed to reduce the uptake of essential minerals like iron (Fe), magnesium (Mg), phosphorus (P) and calcium (Ca) by masking the sorption sites and forming insoluble complexes Kabata-Pendias and Szteke (2015), Osu *et al.,* (2012) . However, Cr transport to different parts of *Citrullus* plants had increased leading to enhancement in the concentrations of manganese (Mn) and P, and reduction in sulphur (S), copper (Cu), zinc (Zn) and iron (Fe) contents in the leaves, suggesting that Cr disturbs the nutrient balance Dube *et al.,* (2003) . Turner and Rust, (1971) also suggested the similar effects of Cr on the uptake of various nutrients under Cr toxicity. A gradual decrease in the uptake of micronutrients like Zn, Cu, Fe, Mn and macronutrients like potassium (K), P and nitrogen (N) had been noticed in the paddy plants (Oryza sativa L.) under excessive Cr exposure Sundaramoorthy *et al.,* (2010) . This reduced nutrient uptake may occur due to decline in the root growth and impairment of the root penetration under Cr toxicity, or may be due to the decrease in essential element translocation because of the displacement of nutrients from the physiologically important binding sites Shahzad *et al.,* (2018), Mengel and Kirkby, (1987).

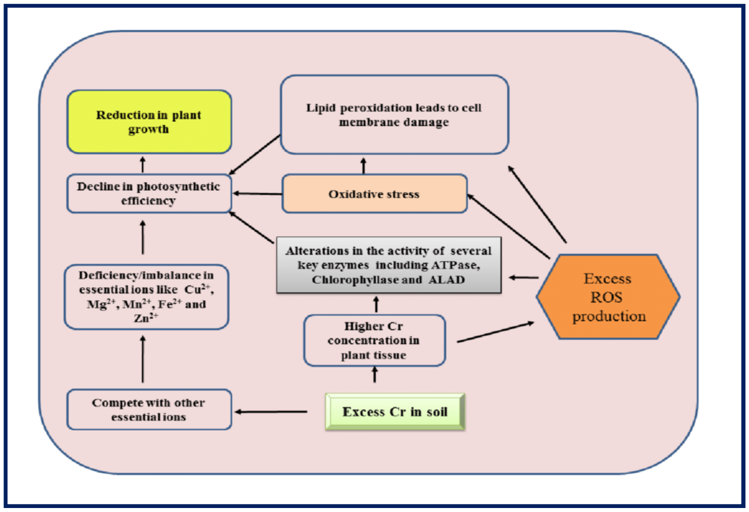


Fig. 20: Illustrates Consequences of oxidative stress generated under chromium toxicity.After: Sharma *et al.,* (2020)

The competitive uptake, even though the methods and pathways by which plants absorb Cr (III) and Cr (VI) differ complex barriers caused by chromium prevent plants from absorbing essential minerals. The existence of chromium and critical nutrients in soil and plant cells may be the cause of their antagonistic interactions and competitive absorption Shahid *et al.,* (2017). Recent studies by De-Oliveira *et al.,* (2016); Chen *et al.,* (2018) reported that excessive chromium toxicity minimizes adsorption sites and forms insoluble/low-bioavailable compounds in rhizosphere soil, that prevents the accumulation of nutrients such as Ca, Cu, Fe, Mg, P, S, and Zn . Sundaramoorthy *et al.,* (2010) noticed that the absorption of N, P, and K in paddy irrigation soil reduced with increasing the concentration of Cr (VI).

The translocation of secondary nutrients under chromium toxicity differs from crop to another. Chromium toxicity severely decreases Ca content in perenne leaves, resulting in declined oxidation of water and electron flow at the photosynthesis process because Ca is a necessary cofactor for O_2 evolution and has a role in water oxidation Vander Meulen *et al.,* (2004). Levels of Cl and Na were enhanced at 0.5 mM and 0.1 mM of chromium, whereas both levels of chromium reduced Ca and Mg levels in *Solanum nigrum* and *Parthenium hysterophorus*. Gardea-Torresdey *et al.,* (2004). The interaction of chromium with Ca and Mg varies based on the growing media. Turner and Rust, (1971) observed that in soybean, the total contents of Ca and Mg in the water culture were reduced with increasing chromium level above 0.1 ppm in roots tissues, whereas under soil conditions, the contents of Ca and Mg increased as chromium might interfere with plants ability to uptake these elements. Vajpayee *et al.,* (2000) discovered that chromium VI could dispatch Mg from the enzymes active sites, resulting in inhibition of chlorophyll formation. Moreover, Ca content in tomato roots was reduced with increasing chromium although the Ca content in top plant parts was not influenced by chromium toxicity Han *et al.,* (2004). Chromium is structurally similar to sulphate Dube *et al.,* (2003); Ulhassan *et al.,* (2019). The interaction between chromium and S is antagonistic. The consumption of S in plants has been documented to be reduced due to increase chromium concentration Sullivan *et al.,* (2000); Burton *et al.,* (2008). The translocation of S from plant roots to shoots was also reduced, resulting in higher S contents in root cells as compared to floral parts Sullivan *et al.,* (2000); Dube *et al.,* (2003). Moreover, sulphate content in growth medium minimizes chromium (VI) uptake by plant Oliveira, (2012).

Increasing the concentration of chromium reduce nutrients as well as the intake of vital elements. The high level of chromium (VI) could alter the normal absorption of Mn, Cu and Zn, which can lead to a nutrient deficiency and slow plant development Dube *et al.,* (2003); Ulhassan *et al.,* (2019). Chromium enhanced the Mn uptake but reduced the levels of Fe, Cu, Zn, and S in watermelon leaves Chen *et al.,* (2017). Moreover, the application of Cr at 0.4 mM increased Zn concentration in stem and root cells but decreased Zn in middle leaves Zaheer *et al.,* 2019). Cr stress also reduced the translocation of P, S and Zn from plant root to leaves Chatterjee and Chatterjee, (2000). However, the translocation of Mn, Cu and B was less affected. Zn-lysine foliar application also reduced Cr hazards and protected the plants via improving oxidative defense mechanisms Afzal *et al.,* (2018). Cu and Zn were reduced in the root and shoot of chamomile plants Kováčik *et al.,* (2013). Chromium (VI) interrupted the mineral nutrition by interfering with the uptake and translocation of Fe, Ca, and Mg in *Lolium perenne* Vernay *et al.,* (2007). Toxicity of chromium (VI) is responsible for the depletion and unavailability of Fe in leaves of radish and spinach Sehrish *et al.,* (2019); Tiwari *et al.,* (2013), thus, leading to Fe deficiency Chatterjee and Chatterjee, (2000). Moreover, Cr stress induced Mn deficiency in *Vigna Radiata* and Brassica oleracea Karuppanapandian *et al.,* (2006). On the other hand, in higher plants, chromium (VI) increased the Mn uptake and translocation in the younger leaves of *Lolium perenne* and *Citrullus Vulgaris* Dube *et al.,* (2003); Ducic and Polle, (2005). A negative correlation of chromium with Fe, Zn and Cu was also recorded Barcelo *et al.,* (1985). Fe acts as a signal that can be interpreted through the plant root and induces molecular mechanisms. Furthermore, could possibly alter cells division and differentiation through the action of certain transcription factors López-Bucio *et al.,* (2014). Furthermore, the presence of Fe in growth media can directly reduce Chromium (VI) translocation by plant Handa *et al.,* (2017).

Previous studies also reported synergistic relations between chromium and some essential nutrients such as Cu, Mg and Mn Vernay *et al.,* (2007); Wei-Dong *et al.,* (2007). In the aerial parts of *Citrullus,* the excess of chromium was also inhibited by the absorption of Cu, whereas Cu concentration was higher in leaves than in roots. Adding Chromium to the nutrient solution resulted in reduced Cu level in leaves and increased level in stems and roots Dube *et al.,* (2003). Hence, under chromium toxicity, a tough completion is present between chromium and essential nutrients required for plant growth and yield production. Zeng *et al.,* (2011) also indicated that Chromium stress limits the movement, accumulation of major, and microelements in rice crop.

Nutrient uptake and biomass of plants affected largely under chromium stress. In fact, chromium interferes with uptake of essential nutrients in a complex manner. Both chromium (III) and (VI) have been found to interfere with the uptake of macronutrients like N, P, K, and Mg Turner and Rust, (1971); Sela *et al.,* (1989); Biddappa and Bopaiah, (1989); Moral *et al.,* (1995); Davies *et al.,* (2002). Chromium (III) gradually decreased the uptake of essential mineral elements Moreira *et al.,* (2005) and reduced the Ca levels in cells Marschner, (1999). Chromium (III) at 100 μM decreased N, P, and K levels and enhanced Al, Fe, and Zn concentrations in H. annuus Davies *et al.,* (2002). Liu *et al.,* (2008) demonstrated that chromium (VI) reduced the uptake of Cu, Fe, and Zn in *A. viridis*. Exposure to Cr (VI) led to increased accumulation of P and Zn and decline of S and Cu in *Citrullus vulgaris* Dube *et al.,* (2003). As regards the effect of chromium (VI) on Mn uptake, there have been conflicting reports. Chromium (VI) enhanced Mn uptake in *C. vulgaris* Dube *et al.,* (2003) and *L. perenne* Vernay *et al.,* (2007) and decreased Mn uptake in *B. oleracea* Chatterjee and Chatterjee, (2000) and *A. viridis* (Liu et al. 2008). Ahmad *et al.,* (2011) stated that application of Chromium (VI) (50–500 mg. kg^{-1} soil) decreased the contents of N, P, and K in *O. sativa* leaves. Chatterjee and Chatterjee, (2000) stated that chromium (VI) is competitive with Fe for binding sites and with P for surface root site. Chromium (VI) interferes with the absorption of Fe, thereby decreasing Fe accumulation required for the biosynthesis of chlorophyll and heme, and reduced the activities of heme enzymes in *S. oleracea* suggesting interference in iron metabolism Gopal *et al.,* (2009). Turner and Rust, (1971) opined that reduced biomass in *G. max* upon chromium (VI) exposure is due to direct interference of chromium in P metabolism and restricted incorporation of S in certain essential amino acids. Sundaramoorthy *et al.,* (2010) demonstrated that reduction in total dry weight of root and shoot of *O. sativa* in response to chromium (VI) toxicity was primarily due to reduced water uptake and enlarged root cells. However, Han *et al.,* (2004) reported that 57 % high shoot dry mass in *B. juncea* under 500 μM chromium to impaired metabolic processes that restrict the utilization of stored compounds in the cotyledon required for plant growth and development. Chromium's (VI; 2 μM) inhibit uptake of K^+ and H^+ in Z. mays roots, suggesting an interference with transport activities of plasma membrane Zaccheo *et al.,* (1985). Chromium (5–20 mg. l^{-1}) has been found to decrease the uptake of K, P, Mg, and Cu in roots and Ca, Fe, and Cu in the leaves of S. kali; however, the effect varied with Cr speciation. Gardea-Torresday *et al.,* (2005) reported that absorption of macro and microelements was; lower particularly under chromium (III) than chromium (VI). Redondo-Go´mez et al. (2011) stated that Chromium (III) at concentration of 1.5 mg. g^{-1} caused a reduction in the uptake of essential nutrients in cordgrass, *Spartina argentinensis*. Barcelo´ and Poschenrieder (1997) stated that chromium (VI) uptake occur through sulfate carriers (membrane transporter) in cells of higher plants. Kleiman and Cogliatti (1997) found an increase in Cr (VI) influx in sulfate deprived *T. aestivum* plants, thereby indicating the role of sulfate in chromium transport. Furthermore, decreasing in sulfate uptake and repression of sulfate transporter (BjST1) under chromium (VI) stress in roots of B. juncea suggesting sulfate carriers are involved in chromium transport. Lindblom et al. (2006) reported that accumulation of chromium (VI) gradually is greater in *B. juncea* with enhancing sulfate transporter (SHST1). Kim et al. (2006) reported that overexpression of MSN1, a putative yeast transcriptional activator, regulates chromium (VI) uptake and chromium (VI) tolerance in transgenic tobacco (*Nicotiana tabacum*).

Rana *et al.,* (2020) stated that phosphorus is the second most important nutrient after nitrogen; it has a key role in several metabolic processes in plants. Chromium (VI) is structurally similar to phosphorus. Ma *et al.,* (2020); Zhu *et al.,* (2016) reported that phosphorus deficiency caused by the interferes of chromium with the uptake, translocation and/or accumulation. In watermelons, the reduced level of chromium increased the uptake of phosphorus in order to compete with other metals such as Zn and Fe Dube *et al.,* (2003). James and Bartlett, (1984), reported that there is a competition between chromium (VI) and phosphorus to enter into plant cells. Kumar *et al.,* (2016), Pradhan *et al.,* (2017), stated that high concentration of chromium resulted in reducing plant growth and phosphorus concentration in plant leaf tissues. Several cases, phosphorus concentration was reduced in roots and increased in younger leaves at 0.2 mM chromium, but it decreased beyond this level in *Citrullus* Dube *et al.,* (2003). López-Bucio *et al.,* (2014) noticed that high chromium concentration antagonistically affected root growth and induced the expression of genes responsive to Pi scarcity. Turner and Rust, (1971) stated that chromium and potassium (K) interaction is also antagonistic like other macronutrients, application of where 0.1 ppm of chromium was able to decrease potassium (K) in shoots of soybean plants . Sundaramoorthy et al. (2010) reported in flooded rice, plants decreased potassium (K) uptake was noticed with increasing chromium (VI) level.

Under chromium toxicity, the translocation of secondary nutrients were differs from crop to another. Chromium toxicity severely decreases Ca content in perenne leaves, resulting in declined oxidation of water and electron flow at the photosynthesis process because Ca is a necessary cofactor for O_2 evolution and has a role in water oxidation Vander Meulen *et al.,* (2004). Gardea-Torresdey *et al.,* (2004) stated that Cl and Na were enhanced the concentration of chromium at 0.5 mM and 0.1 mM whereas, reduced both Ca and Mg levels in *Solanum nigrum* and *Parthenium hysterophorus*. The interaction of chromium with Ca and Mg varies and depend on the growing media. Turner and Rust (1971) observed that in soybean, the total contents of Ca and Mg in the water culture reduced with increasing chromium level above 0.1 ppm in roots tissues, whereas under soil conditions, the contents of Ca and Mg increased as chromium might interfere with plants ability to uptake these elements. Vajpayee et al. (2000) observed that chromium (VI) could dispatch Mg from the enzymes active sites, resulting in inhibition of chlorophyll formation. Moreover, Ca content in tomato roots was reduced with increasing chromium although the Ca content in top plant parts was not influenced by chromium toxicity Han *et al.,* (2004). Chromium is structurally similar to sulphate Dube *et al.,* (2003), Ulhassan *et al.,* (2019). The interaction between chromium and sulphate is antagonistic. The consumption of sulphate in plants was reduced due to chromium increased ,Sullivan *et al.,* (2000) and Burton *et al.,* (2008). The translocation of sulphate from plant roots to shoots was reduced, resulting in higher sulphate contents in root cells as compared to green parts Sullivan *et al.,* (2000), Dube *et al.,* (2003). Moreover, sulphate content in growth medium minimizes chromium (VI) uptake by plant Oliveira, (2012).

Gopal *et al.,* (2009) stated that toxicity of chromium; reduce Fe content in leaf tissue, indicating that chromium (VI) involvement in Fe supply, leading to instability in Fe metabolism instability. Under chromium stress the nutrients uptake decreased as a result of decreasing root development and restriction the penetration. Furthermore, the reduction in translocation of essential elements Shahzad *et al.,* (2018), Sharma *et al.,* (2020). The competition binding of chromium (VI) to common carriers may decrease the absorption of several nutrients. The suppression of plasma membrane H+ ATPase could be a possible explanation for the lower absorption of many of these elements under chromium stressed Shanker *et al.,* (2005). Kitagawa *et al.,* (2015) stated that increasing chromium that buildup in the plant cell wall might harm the plasmodesmata, which serve as crucial channels for the transport of mineral nutrients, resulting in an imbalance in their metabolism. Additionally, studies have reported the negative impacts of chromium toxicity on other biochemical aspects in plants. For example, chromium (VI) caused an inhibition of ethylene biosynthesis from endogenous 1-aminocyclopropane-1- carboxylic acid (ACC) in *P. vulgaris* Poschenrieder *et al.,* (1993). The inhibitory effect was not due to chromium -caused membrane disintegration, but was due to chromium (VI)-induced metabolic alterations that could be either inhibition of ACC synthase activity or diversion of metabolic steps prior to ACC catalyzed reactions Poschenrieder *et al.,* (1993). Chromium (VI) (at 20 and 200 μM) found to inactivate electron transport chain in mitochondria isolated from root cells of *P. sativum* Dixit *et al.,* (2002). A significant inactivation was noticed in NADH: cytochrome c oxidoreductase and succinate: cytochrome c oxidoreductase activities and cytochrome oxidase was the most susceptible Dixit *et al.,* (2002). Chromium (VI; 150-mg. l^{-1}) caused a decrease in IAA and IBA content in roots and shoots, and an increase in seeds of T. aestivum Zhang *et al.,* (2009). Chromium (VI) increased NADPH-dependent superoxide production and the activity of NADPH oxidase and decreased the activity of NADH ferricyanide oxido-reductase in P. sativum root plasma membrane vesicles, thereby suggesting interference of Cr (VI) with plasma membrane functionality Pandey *et al.,* (2009). Of late, the presence of Cr (1,346 mg.kg^{-1}soil) in metallurgical landfill soil has been found to alter the leaf fatty acid composition in Lactuca serriola Le Gue´dard *et al.,* (2012). Chromium (VI) also interferes with the activity of plasma membrane H+-ATPase Shanker *et al.,* (2005a) and Na^+/ K^+-dependent ATPase Pauls *et al.,* (1980) whereas, chromium (III) has been found to interfere with Ca^{2+}-dependent ATPase Serpersu *et al.,* (1982).

3-3 Plant water relations

Barcelo´ *et al.,* (1986) stated that there is a relation between chromium (VI) and soil water depending on type of leaves. At growth retarding concentrations, ψs and ψw were decreased and ψp was increased in primary leaves. However, at non-inhibitory concentrations, ψw and ψp were increased and ψs decreased, while an opposite effect was observed in trifoliate leaves. Gopal *et al.,* (2009) demonstrated the Cr (VI) reduces the physiological availability of water as indicated by a decrease in leaf water potential and increase in diffusive resistance in S. oleracea leaves, thereby suggesting development of water stress. Waseem *et al.,* (2014) reported that detrimental consequences of chromium concentrations could not be precisely predicted in soil and surface water. Plant roots always serve the primary purposes of absorbing inorganic and organic nutrients, and water, protecting and anchoring the plant body to the ground, storing nutrients, and promoting vegetative reproduction Rucinska-Sobkowiak, (2016).

Shanker *et al.,* (2005), Burkhead *et al.,* (2009), stated that roots contain higher chromium concentrations as compared to shoots and is the first points of contact with harmful metals like chromium - ions. Accumulation of chromium ions in tissues may influence soil water absorption and tends to lower the water content in plant roots Kumar *et al.,* (2016). Ahmed *et al.,* (2016) stated that direct involvement of chromium - ions with the guard cells or the early effects of chromium buildup on plant parts are what induce stomata to close. Chow *et al.,* (2018) stated that chromium's effects on water supply in soils, root development, reduced water absorption, and other harmful effects are distinct from its influence on the connection between plants and soil water. The osmotic ability of soil solution in Cr-enriched soils may be less than that of root cell sap Vernay *et al.,* (2007). In these circumstances, osmotic pressure, and soil solution will significantly restrict plant water absorption levels Vernay *et al.,* (2007), Rucinska-Sobkowiak, (2016). Kumar *et al.,* (2016), Levitt, (1972) reported that as chromium concentration hits the 10^{-3} M threshold level, osmotic pressure is thought to exist. Adjustments to endogenous factors, such as root structure and morphology, are more likely to influence plant water absorption indirectly. After being exposed to chromium, green amaranth (*Amaranthus viridis*) showed a substantial decrease in total root area Sampanpanish *et al.,* (2006). Shanker *et al.,* (2005), Chow *et al.,* (2018) stated that reducing root hair surface, primary root elongation, increased root dieback, and poor secondary development is abnormalities in chromium - stressed plants that affected how water and plants interacted in the soil. Vazques *et al.,* (1987) reported that in epidermal and cortical cells of bush bean plants unveiled to chromium, there was impaired turgor and plasmolysis. According to Gopal et al. (2009), chromium (VI) inhibits the physiological water supply, as evidenced by a drop in leaf water capability and elevation in diffusional stiffness in spinach leaves, implying that they are growing under water stress. Ertani *et al.,* (2017) stated that chromium -induced structural changes reduce plant ability to acquire water in the soil and cause insufficient root-soil interaction. A broad range of water-related changes is brought about by chromium exposure throughout the entire plant. Srivastava *et al.,* (2021) stated that reduced water absorption and restriction of short-distance water transport in the apoplast and symplast pathways are effects of chromium toxicity in roots. Additionally, the apoplasts resistance to water flow is increased by the thickening of the cell wall brought on by chromium - ions or other incrusting substances within cell walls Bhalerao and Sharma, (2015). Ullah *et al.,* (2019a) reported that the inhibition of aquaporin functions and variations in protein expression is most likely to blame for the impaired water transport through the membrane. Such changes affect the flow of water via the vascular system and reduce root sap exudation Chen *et al.,* (2010). Long-distance water transfer is reluctant, which causes a reduction in leaf water and, as a result, a water deficit in leaves Shahid *et al.,* (2017).

Gorgues *et al.,* (2022) reported that plants face a constantly changing environment, requiring fine-tuning of their growth and development. Plants have therefore developed numerous mechanisms to cope with environmental stress conditions. One striking example is root response to water deficit. Upon drought (which causes osmotic stress to cells), plants can among other responses alter locally their root system architecture (hydropatterning) or orientate their root growth to optimize water uptake (hydrotropism). They can also modify their hydraulic properties, metabolism and development coordinately at the whole root and plant levels. Upstream of these developmental and physiological changes, plant roots must perceive and transduce signals for water availability. They also stated that much progress has been made in deciphering the mechanisms for sensing and signaling water deficit. Te identification of several sensing molecules exemplify the central role of osmosensing in plant. Nevertheless, how these molecules interconnect remains mostly unexplored. They might act in parallel pathway reflecting the diversity of osmotic signal that cells have to face. Alternatively, they could share some redundancy in the perception machinery or in triggering the downstream signaling. Unfortunately, our current knowledge remains too fragmented to assess the proper kinetic of events. Interestingly, most of the molecular actors described so far are localized to the plasma membrane, as it is suspected to be the ideal place for water sensing. Nevertheless, we realize that changes in cell volume or turgor could be perceived in subcellular compartments or structures deprived of membranes. Liquid-liquid phase separation (LLPS) is a process where two liquids can be separated into non-miscible phases depending on concentration and which can be modulated by physico chemical alterations of the system Cuevas-Velazquez and Dinneny (2018); Korkmazhan et al. (2021). Liquid-liquid phase separation (*LLPS*) can happen at many cell locations including contacts with a membrane but also in the cytoplasm or nucleoplasm, where it was originally discovered (Nucleolus, Cajal bodies, nuclear speckles). In animal cells, processing bodies (PBs) containing mRNA-decapping enzyme 1A (DCP1A) are examples of subcellular compartments that are deprived of membranes and rapidly phase separate under hyperosmotic stress while dissolving back upon isotonic rescue Jalihal et al. (2020). Tese PBs sequestrate pre-mRNA cleavage factors from actively transcribing genome loci Jalihal et al. (2020). Tis example provides a mechanical framework for gene regulation under hyperosmotic stimulation. Similarly, the apoptosis signal-regulating kinase 3 (ASK3) is inhibited by phase separation under hyperosmotic stress Watanabe et al. (2021). In plants, phase separation can be associated to many processes like regulation of fowering time, temperature sensing, and auxin or SA signaling, Fang et al. (2019); Powers et al. (2019); Zavaliev et al. (2020); Jung et al. (2020). Regarding water sensing, FLOE1, a prion like structured protein, undergoes phase separation in vitro and during seed imbibition Dorone et al. (2021). Te biophysical state of FLOE1 modulates its biological activity in suppressing seed germination under unfavorable environments. Moreover, it was found that natural variation in the coding sequence of FLOE1 is associated with adaptive germination strategies in natural populations Dorone et al. (2021). Tese fndings on significance of LLPS in biology open new avenues to re-investigate the molecular mechanisms of plant osmotic sensing. Like for osmotic perception, a large and ever increasing number of molecules have been proposed to act in local and long distance signaling of water availability. Strikingly enough, most of these signaling molecules and their corresponding receptors are likely to possess more functions than those that were originally assigned, revealing a complex array of interactions and interplays. Moreover, these molecular mechanisms have been identified in a limited number of model plants cultivated under highly controlled and often artificial growth conditions. In contrast, responses at the whole plant level have been mostly investigated in crops or understudied species. This is particularly striking for PRD where researches were conducted in crops/trees grown in a wide range of stresses (localization intensity, duration). Thus, it is difficult to integrate all available information to build a systemic signal network for plant response to heterogeneous water distribution. Furthermore, many of the signal molecules and mechanisms identified under homogeneous water deficit condition have not been or very partially investigated under heterogeneous water distribution. Accordingly, little is known about the nature, the temporality and the function of sensing, local, and systemic responses to heterogeneous water availability. We believe that studying rapid and long-term responses to local water deficit in model species and under controlled conditions should lead to breakthroughs in the identification of the molecules and of their interactions that trigger plant acclimation responses. Identifying the main actors that trigger, prime or coordinate plant responses to water availability will provide first step toward improving the efficiency and coordination of these responses. In the long term, these studies will allow identifying novel breeding targets to enhance crop tolerance to drought and develop new varieties that are well adapted to water saving irrigation strategies Fig. 21, 22 and 23). Events that enhance plants' capacity to retain water include a quick fall in root vacuolization, osmotic ability, and alternation in the tissues of stems and leaves Srivastava *et al.,* (2021) and Ao *et al.,* (2022).

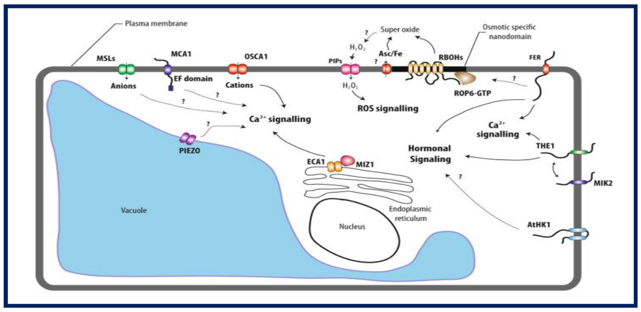


Fig. 21: Illustrates nature of the osmotic signal and suspected sensing mechanisms. A Drawing of the relation between osmotic, water fuxes and cellular volume regulation. A reduced (hypotonic) or increased (hypertonic) external osmolarity results in an influx or efux of water, respectively. Depending on cell wall elasticity, these fuxes lead to changes in cellular volume. B Relative variations of cell turgor and volume in response to an increase of external osmolarity. In the absence of cellular osmoregulation, the turgor tends to decrease linearly with increasing osmolarity. In contrast, the cellular volume is expected to decrease in a two-phase mode, a quasi-linear mode as long as turgor is maintained in the cell, followed by a hyperbolic decay when turgor is absent. C Based on the literature 3 classes of perception mechanism can sense the osmotic signal. Osmotic signal may be perceived at the membrane from either a local osmotic imbalance (e.g. AtHK1) or a change in membrane tension (e.g. MSL) or from a perturbation of cell wall integrity (e.g. Cr RLK). After: Gorgues *et al.,* (2022)

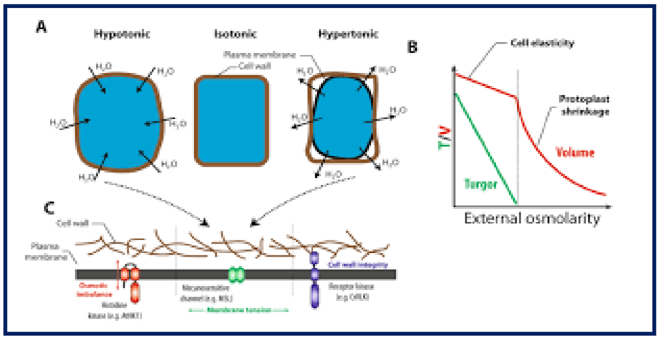


Fig. 22: Summary of currently known osmotic perception mechanisms in plants. Changes in membrane tension induced by osmolarity imbalance can be perceived by membrane mechanosensors such as OSCA1, MSLs, MCA1, PIEZO, ECA1/MIZ1. By transporting cations or anions, these sensors initiate cell calcium signaling by yet unknown mechanisms. Receptor-like kinases belonging to the CrRLK family (e.g. FER, THE) perceive the cell wall status and their activation eventually leads to cell wall reinforcement. Whereas their exact role as osmotic sensors has yet to be established, these receptors definitely fine tune signaling of hormones such as ABA, auxin and jasmonate that are known to regulate plant development and physiological acclimation to osmotic stress. At the cell membrane, a partial integration of signals can be observed. For instance, LRR kinase MIK2, a receptor for phytocytokines

that controls plant immunity, genetically interacts with THE, pointing to a link between osmotic and pathogen signaling. By similarity to the yeast system, the AtHK1 two component histidine kinase may also participate in osmotic signaling by modulating ABA signaling. In addition to hormones and calcium signaling, Reactive Oxygen Species (ROS) are also participating in early cell responses to osmotic stimuli. Cellular accumulation of ROS is dependent on NADPH oxidases (RBOHD and F) and iron reduction processes. Upon cell stimulation, ROP6 forms nanodomains together with the superoxide-producing enzyme RBOHD/F. Therefore, superoxide can be dismutate to hydrogen peroxide (H_2O_2) by apoplastic SOD (Superoxide dismutase). H_2O_2 transport through the cell membrane is in turn facilitated by aquaporins. After: Gorgues *et al.,* (2022)

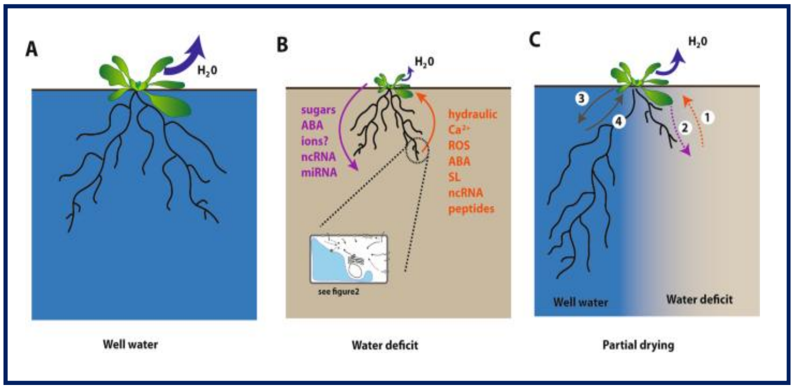


Fig. 23: Long-distance and developmental response to homogeneous or local water deficit. Roots and moves through xylem vessels to the leaves absorb a Soil water where it is eliminated via transpiration (blue arrow). B When plants experience water shortage, they first dramatically reduce transpiration and modify root and shoot growth according to water availability. Roots, which perceive locally the osmotic stress as described , activate long-distance signaling (orange arrow) conveyed by hydraulic signals or a wide range of molecules, including calcium (Ca^{2+}), Reactive oxygen species (ROS), phytohormones (Abscisic acid (ABA), Strigolactones (SL), etc), non-coding RNA (ncRNA) and peptides. In return, water deficit induces a shoot-to-root signaling (violet arrow) that relies on a set of molecules including sugars, ABA, ncRNA and micro RNA (miRNA). C When plants encounter a local water deficit also named partial root zone drying (PRD) in agronomy, the transpiration rate is reduced but not as severely as under a uniform water deficit. Therefore, shoot development can be maintained or has a limited reduction depending on the intensity and duration of the local water deficit or on the plant developmental stage. Root growth in the drying part is strongly repressed whereas it is maintained or stimulated in the wet part through a compensatory growth stimulation. It was proposed that, during PRD, roots are sensing the local low water potential in the drying soil resulting in a reduction in cell turgor, then transmitting the signal to the shoot (arrow 1). In return, a shoot-to-root signal (arrow 2) represses root growth. Since root development and water uptake are stimulated in the well-watered part, the existence of both a shoot-to-root and a root-to-shoot signaling can be hypothesized (arrows 3 and 4). Besides ABA, the nature of other putative signals remains totally unknown. After: Gorgues *et al.,* (2022)

3-4 Effects of chromium on cell division and root maturity

Chromium reflected delay in cell division, elongation and maturation of roots. The high concentration of chromium inhibits root growth, while the lower levels of Cr (20–40 µM) stimulate it, as recorded for Arabidopsis seedlings López- Bucio *et al.,* (2014). Martinez and Gil (2015) reported that concentration of chromium at 100 µM severely inhibited root growth due to the reduction of cell division and the primordial formation. Reduction of root growth under toxicity of Cr (VI) was mainly due to the inhibition of root cell elongation and reductions in tissue uptake of water and nutrients Chebeir *et al.,* (2016), Jobby *et al.,* (2018). López-Bucio *et al.,* (2022) stated chromium, particularly the oxyanion chromate Cr (VI) behaves as a toxic environmental pollutant that strongly damages plants due to oxidative stress, disruption of nutrient uptake, photosynthesis and metabolism, and ultimately, represses growth and development Fig. (24). However, mild chromium (VI) concentrations promote growth, induce adventitious root formation, reinforce the root cap, and produce twin roots from single root meristems under conditions that compromise cell viability, indicating its important role as a driver for root organogenesis. In recent years, considerable advance has been made towards deciphering the molecular mechanisms for root sensing of chromate, including the identification of regulatory proteins such as SOLITARY ROOT and MEDIATOR 18 that orchestrate the multilevel dynamics of the oxyanion. Chromium (VI) decreases the expression of several glutamate receptors, whereas amino acids such as glutamate, cysteine and proline confer protection to plants from hexavalent chromium stress. The crosstalk between plant hormones, including auxin, ethylene, and jasmonic acid enables tissues to balance growth and defense under chromium (VI)-induced oxidative damage, which may be useful to better adapt crops to biotic and abiotic challenges. The highly contrasting responses of plants manifested at the transcriptional and translational levels depend on the concentration of chromate in the media, and fit well with the concept of hormesis, an adaptive mechanism that primes plants for resistance to environmental challenges, toxins or pollutants. Major portion of chromium retains in plant root cell wall, representing 83.2% as previously reported (Liu *et al.,* 2009). Chromium toxicity mainly impairs the primary growth of the emerging seedlings of *Triticum asstivum* and *Arabidopsis thaliana* López-Bucio *et al.,* (2014); Rellán-Álvarez *et al.,* (2006).

Moreover, chromium accumulation was observed in the root cells of various crops, including rice Hussain *et al.,* (2018), barley Ali *et al.,* (2011), *Vicia faba* Khadra *et al.,* 2019), wheat Zhang *et al.,* (2010) and *Brassica napus* Zaheer *et al.,* (2020). Sundaramoorthy *et al.,* (2010) reported that Cr (VI) irregulates the cell cycle and cell division process, causing inhibition of the root. Sharmin *et al.,* (2022) stated that the possible mechanisms that might be activated by the *M. sinensis* cell in detoxification during Cr stress using proteomic approach. *c* is a heavy metal tolerant species Stewart *et al.,* (2009), Ezaki *et al.,* (2008).

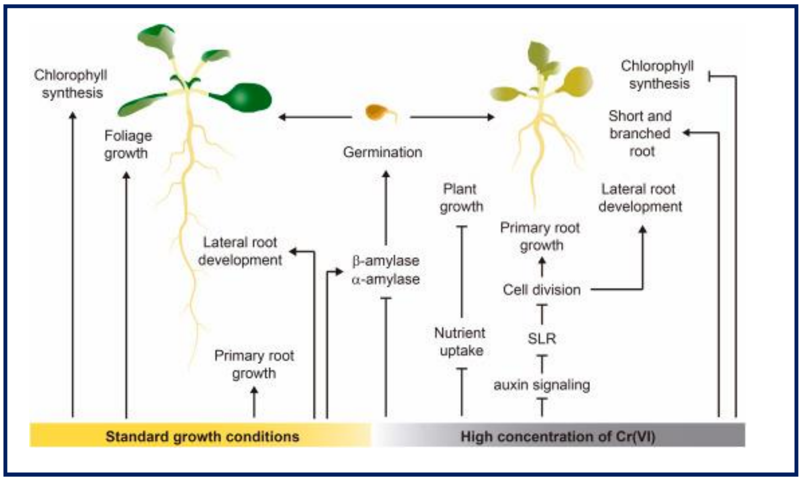


Fig. 24: Chromium in plant growth and developments: Toxicity, tolerance and hormesis After: López-Bucio *et al.,* (2022).

However, a preliminary study was necessary to define the concentrations of Cr that induce cellular response without leading to immediate cell death. A short exposure to low concentration of Cr (50–300 µM) did not exhibit any sign of growth reduction (Supplementary Fig. 25 A). In low level of Cr, *Miscanthus* plants continued to grow for several weeks. MDA content in roots were almost similar to non-treated plants (Supplementary Fig. 25 B), suggesting a short exposure to low level Cr cause negligible oxidative damage. However, growth suppression was observed starting from 500 µM of Cr with the highest inhibition occur-ring at 1000 µ M. Under control condition, new roots were being developed, while their formation was suppressed over 500 µM. At 1000 µM, new root formation was severely affected. These observations suggested that *M. sinensis* is relatively tolerant to Cr like maize. Arduini *et al.,* (2006) reported that low concentration of Cr have positive effect on root growth of *Miscanthus*. Thus, based on the growth pattern and earlier reports, 500–750 µM could be considered moderate to toxic, while 1000 µM or higher concentrations are acutely toxic. Labra *et al.,* (2006) also carried out a proteomic analysis of maize seedling subjected to 340 and 1019 µM Cr based on growth suppression. A short exposure to moderate to acute toxic Cr may reveal the proteins involved in altered metabolic homeostasis. When *M. sinensis* seedlings were subjected to 500–1000 µM of Cr for 3 days, a considerable reduction in root growth was observed in parallel with the doses of Cr in the medium. The decreases in root growth following Cr treatment were characterized by reductions in root lengths and dry weight with increasing Cr concentrations (Fig. 25A and B). Chromium accumulation in *M. sinensis* roots increased with increasing concentrations of potassium dichromate added to the solution (Fig. 25 C). After 3 days of exposure to 1000 µM, the root tissue accumulated 1308 mg kg−1 on a dry weight basis. No Cr accumulation could be detected in the control plants.

To investigate whether growth inhibition was associated with oxidative stress, the amount of H_2O_2 and malondialdehyde (MDA) were examined. As shown in Fig. 26, H_2O_2 accumulation was much higher in Cr-treated root samples compared to the control. Although physiological concentrations of ROS have important func-tions in stress signaling, excess amount can cause oxidative stress, leading to cell death, if they are not detoxified. Membrane lipids are the main cellular targets that are susceptible to damage, and lipid peroxidation is believed to be a free radical-mediated process Thompson and Thorpe, (1987).

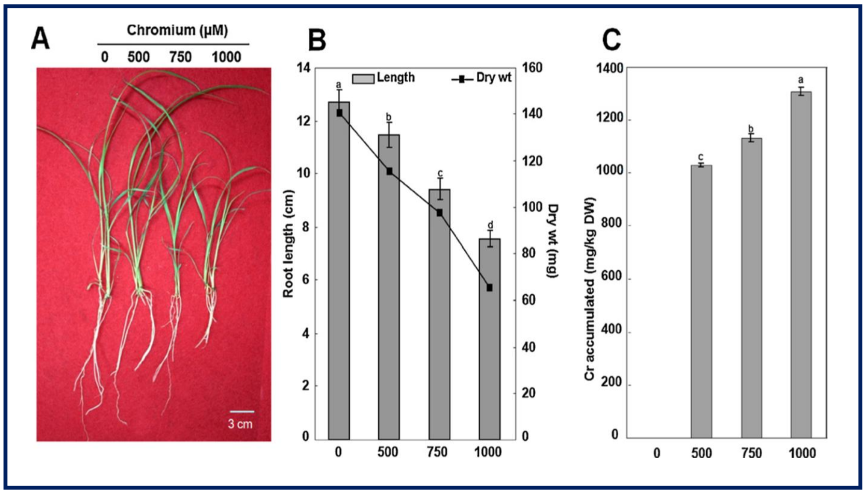


Fig. 25: Illustrates effect of Cr treatment on morphology (A), root growth (B) and Cr content (C) in M. sinensis roots after treated with indicated concentrations of $K_2Cr_2O_7$ for 3 days in hydroponics in a Hoagland medium. Dry weights were calculated from pooled root samples of 12 plants. The root length and Cr amounts represent the mean values and SE. Different letters above the bars indicate statistically significant differences ($p < 0.05$). After: Sharmin *et al.,* (2022)

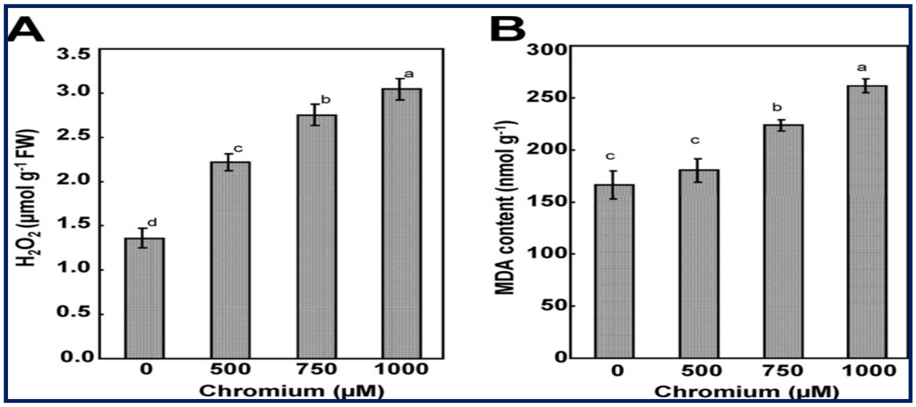


Fig. 26: Physiological responses of *M. sinensis* roots subjected to treatment. H_2O_2 (A) and MDA (B) concentration in control and Cr-treated roots. The data represent the mean values and SE of three

independent experiments. Different letters above the bars indicate statistically significant differences ($p < 0.05$). After: Sharmin *et al.,* (2022)

Thus, we estimated lipid peroxidation in roots by the thiobarbituric acid (TBA) method, in which the quantified TBA-reactive substance was malondialdehyde, a product of lipid peroxidation. MDA concentrations were increased markedly in 750 and 1000 µM of Cr, indicating increased lipid peroxidation. The occurrence of lipid peroxidation induced by Cr was further validated by a histochemical assay, using Schiff's reagent. As shown in Fig. 27 A, an intense coloration was detected by Schiff's stain with increasing concentra-tions of Cr. By contrast, control roots had very small stain. Together with the quantitative estimation, the histochemical detection pro-vides additional advantages for localizing TBA-reactive products in situ in roots with high sensitivity Yamamoto *et al.,* (2001). These results suggested that like other heavy metals, Cr toxicity also generated ROS, which resulted in oxidative stress in the *Miscanthus* roots. Increased lipid peroxidation induced by heavy metals such as aluminum Sperotto *et al.,* (2008) lead Yamamoto *et al.,* (2001), Verma and Dubey (2003) and arsenic toxicity Ahsan *et al.,* (2008) have been reported in various plants. Evans blue staining indicated that cell death occurred earlier and more robustly with increasing Cr concentrations (Fig. 27 B). These results are consistent with those from the lipid peroxidation assay, indicating that *Miscanthus* suffers from Cr-induced oxidative stress at high concentrations. Cr (VI)-mediated •OH radical generation in cells has been reported, Panda (2007). Taken together, these results indicated that plants exposed to Cr treatment generate ROS, which resulted oxidative stress and cell death in roots.

Therefore, chromium is more toxic for the growth of plant roots and its sequestration in root vacuoles may happen due to its precipitation as insoluble salts or due to its immobilization with sugar, celluloses and hemicellulos Akinci and Akinci (2010); Chebeir *et al.,* (2016); Danish *et al.,* (2019); Mohanty and Patra (2011); Riaz *et al.,* (2019). Like other plant parts, shoot growth is sensitive to chromium toxicity.

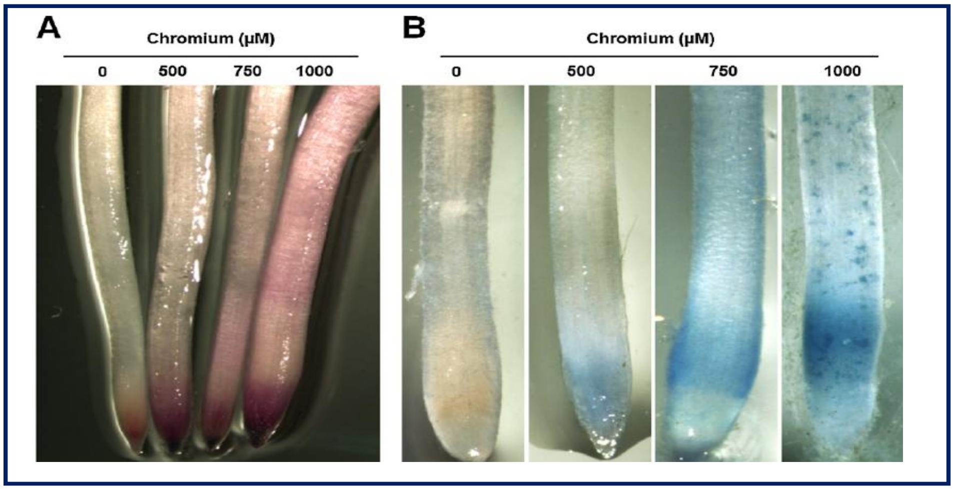


Fig. 27: Illustrates histochemical localization of lipid peroxidation and loss of plasma membrane integrity. (A) Differentially stained *M. sinensis* roots by Schiff's reagent under different concentrations of Cr. A more intense pink color indicates more TBA-reactive products. (B) Loss of plasma membrane integrity detected by Evan is blue staining. Higher concentration of Cr accumulates more frequent and intense pigmentation because of greater damage compared to control. After: Sharmin *et al.,* (2022)

Decreasing in shoot growth and height can be due to the Cr-reduced root growth and development, resulting in decreased water and nutrient translocation to the above ground plant parts. Moreover, increasing concentration of chromium transport to shoot tissues can directly interact with sensitive plant tissues (leaves) and processes (photosynthesis), which affect cellular metabolism of shoots thereby, reducing plant height Ali *et al.,* (2018); Zaheer *et al.,* (2020). The pathway for Cr (VI) movement form root to shoot is an active mechanism and using essential nutrient transporters Ranieri *et al.,* (2020). Chromium concentration predominantly is low in stem as compared to root Medda and Mondal, (2017). Toxic effects of chromium on the plant shoot growth were recorded in various plant species Nath *et al.,* (2005); Maqbool *et al.,* (2018); Nafees *et al.,* (2018). Gill et al. (2015) reported that reduction of shoot growth could be due to the Ultrastructural changes in plant organs. Different levels of chromium showed variable effects on plant shoot in different crops. For instance, the shoot growth of maize and wheat was stimulated at 0.5 ppm and 0.25 ppm of Cr (III), respectively, but it was inhibited at 5 ppm and strongly restricted at 50 ppm for both crops Ali *et al.,* (2015); Datta *et al.,* (2011). Similar results were also observed in corn James and Bartlett (1984), who reported that 10 mmol of Cr caused a stunted plant shoot growth as compared to control. The reduction in shoot elongation and biomass accumulation might also be due to the restricted root growth, which results in reduced transport of water and nutrients to the above ground plant parts. Moreover, Cr transport to the aerial plant parts has direct impacts on the cellular metabolism of shoots may lead to the reduction of shoot elongation Liu *et al.,* (2009); Ahmad *et al.,* (2019).

3-5 Chromium affects Plant leaf

Chromium can indirectly affect the foliar plant parts and is responsible for reducing the photosynthetic pigments and protein contents in plant leaves Li *et al.,* (2018); Patra *et al.,* (2019). Nikolaou *et al.,* (2022). Chromium toxicity is considered within the most severe and dangerous nutritional disorders and it can often be observed in crops grown in industrial areas. In a pot hydroponic experiment, own-rooted Merlot and Cabernet Franc grapevine cultivars or cultivars grafted onto 1103P and 101-14 Mgt rootstocks were exposed to 120 µM Cr (VI). Leaf interveinal chlorosis appeared after forty-five days of treatment. Overall leaf chlorosis and brown root coloration after sixty days was reported. A significant effect on the majority of the measured parameters due to the Cr (VI) treatment was observed. Chromium stress increased the total Cr concentrations in all parts of the vines, i.e., leaves, shoots, roots, and trunks. When comparing between the studied plant sections, the roots presented the highest Cr concentrations, ranging from 396 to 868 mg kg−1 d.w. and then, in descending order, the Cr concentrations ranged from 41 to 102 mg kg−1 d. w. in the trunks, from 2.0 to 3.3 mg kg−1 d. w. in the leaves, and from 1.9 to 3.0 mg kg−1 d. w. in the shoots. Between the assessed rootstocks, 1103P was identified to be a better excluder of Cr concentration in the roots and other aerial parts of the vines. Additionally, chromium toxicity negatively affected the concentrations and compartmentalization of the most important nutrients. Leaf chlorophyll (Chl) concentration decreased down to approximately 53% after sixty days of Cr stress. Chromium toxicity significantly reduced the stem water potential (SWP), net CO_2 assimilation rate (A), stomatal conductance (gs), and PSII maximum quantum yield in all the cases of grafted or own-rooted vines. At chromium stress increased the leaf total phenolic content from 46.14% in Merlot vines to 75.91% in Cabernet Franc vines Fig. (28), they also reported that Grapevines after exposure to 120 µM Cr (VI) for sixty days exhibited toxicity symptoms in terms of stunted root and shoot growth, leaf chlorosis (Fig. (28), and discoloration of the roots Fig. (29).

Fig. 28: Illustrates chromium (VI)-induced leaf chlorosis (left: first appearance in young leaves 45 days after the beginning of Cr (VI) treatment; right: overall leaf chlorosis 60 days after the beginning of Cr(VI) treatment). After: Nikolaou *et al.,* (2022).

Fig. 29: Root browning sixty days after the beginning of chromium (VI) treatment (Left: chromium (VI) treatment; right: control). After: Nikolaou *et al.,* (2022)

Afshan *et al.,* (2015) reported that 100 and 500 µM of Cr could decrease the content of chlorophyl in *B. napus*. Vajpayee et al. (2000) reported that Cr stress treatment above 1 µM inhibited the activities of ALAD and NR, enhanced ALA levels, and reduced chlorophyll and protein contents in *Nymphaea alba*.

Moreover, radish crop showed marginal chlorosis, which would be able to spread to the upper parts after 5 days of exposure to Cr at 0.30 and 0.40 mM of $K_2Cr_2O_7$ Tiwari *et al.,* (2013). The presence of Cr (VI) seriously affected the plant leaves, turning them to become yellow and wilted due to the loss of petioles turgor. The number and size of leaves was also reduced Kimbrough *et al.,* (1999). The chlorosis of leaves under Cr stress may be due to the decreased concentrations of N, P, K and Fe in leaves tissues Kassaye *et al.,* (2017); Medda and Mondal, (2017); Shanker *et al.,* (2005). The photosynthetic rate and stomatal conductance rate observed were minimized due to Cr stress in barley Ali *et al.,* (2011). Cr is also deformed the ultrastructure of chloroplast, causing deleterious effects on biochemical activities and reduction in the photosynthetic pigment content in plant leaves Afshan *et al.,* (2015); Ali *et al.,* (2011); Zaheer *et al.,* (2020).

3-6 Influence of chromium on yield production

Several researchers, Ali *et al.,* (2018); Kumar *et al.,* (2016); Zeng *et al.,* (2011) reported that plant biomass is the first prerequisite for high yield production, chromium always induce noxious effects to several physiological and biochemical processes, consequently, plant yield and productivity are equally compromised. Saud *et al.,* (2022) reported that heavy metals-induced soil pollution has increased due to the widespread usage of chromium (Cr) in chemical industries. The release of Cr into the environment has reached its peak causing hazardous environmental pollution. Heavy metal-induced soil pollution is one of the most important abiotic stress acting the dynamic stages of plant growth and development. In severe cases, it can kill the plants and their derivatives and thereby, pose a potential threat to human food safety. The chromium ion effects on plants varies and depends upon its severity range. It mainly influences the numerous regular activities of the plant's life cycle, by hindering the germination of plant seeds, inhibiting the growth of hypocotyl and epicotyl parts of the plants, as well as damaging the chloroplast cell structures Fig. (30). In this review article, we tried to summarize the possible effects of chromium-induced stress on plant growth, developmental physiology, biochemistry, and molecular regulation and provided the important theoretical basis for selecting remedial plants in chromium-induced contaminated soils, breeding of low toxicity tolerant varieties, and analyzing the mechanism of plant resistance mechanisms in response to heavy metal stress**.**

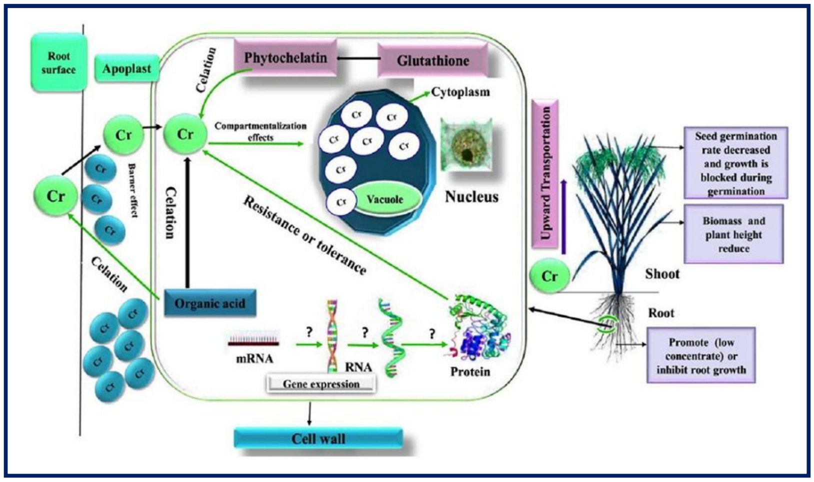


Fig. 30: Illustrates diagram of the influence of heavy metal chromium on plant growth, physiology, and Molecular regulation. After: Shanker *et al.,* (2005) and Saud *et al.,* (2022).

Rai *et al.,* (2004), stated that in O. tenuiflorum, chromium toxicity at concentration 100 mM significantly decreased the plant biomass as compared to the control. Moreover, lower concentration (20 and 40 µM Cr), gradually enhanced the shoot fresh weight as compared to control, however increasing the concentration of chromium (80–140 µM Cr) reduced the biomass production of *Arabidopsis thaliana* López-Bucio *et al.,* (2014). Similarly, plant root and shoot were decreased at chromium concentrations of 0.5 mM. Datta *et al.,* (2011); Ali *et al.,* (2015) observed that biomass and seed yield were also reduced 75%–80% at 0.1 mM Cr. The seed yield of *Triticum aestivum* and *Cucumis sativus* were also reduced by 70% at 0.2 mM Cr (VI). Ali *et al.,* (2015) reported that the morphological parameters of wheat plants, such as root growth, number of tillers per plant and grain length, were significantly reduced with increasing chromium concentration. Chromium toxicity may influence the total biomass and yield as a consequence of poor production and partitioning of assimilates Luna *et al.,* (2009); Chebeir *et al.,* (2016); Hussain *et al.,* (2018); Lopez- Nafees *et al.,* (2018). Chromium-induced decrease in plant development, growth and yield due to several factors: such as, reducing both water and nutrient uptake. Decreasing in cell division and rate, imbalance in nutrient uptake and translocation, inefficiency of plants for selective inorganic nutrient uptake. Enhancing the production of reactive radicles and the resulting oxidative stress, causing, oxidative damage to sensitive plant tissues such as mitochondria, pigment contents, DNA, RNA, lipids etc. Chen *et al.,* (2017); Maqbool *et al.,* (2018).

3-7 Influences of chromium on anatomical and structural changes

3-7-1 Anatomical changes

Studies have been conducted to investigate the effect of chromium on structural and ultra-structural alterations in various organs of plants. Chromium (VI) reduced the number of palisade and spongy parenchyma cells in leaves, induced clotted depositions in the vascular bundles of stems and roots, and enhanced the number of vacuoles and electron dense materials along the walls of xylem and phloem elements in B. juncea Han et al. (2004).

Han etal (2004) stated that Indian mustard grown in chromium (III) - and chromium (VI)-treated soils showed cellular structural changes in leaves compared to the control group. Compared to that in control soil Fig. (31a), a decrease in number of palisade and spongy parenchyma cells in plants grown in chromium (VI)-treated soils (500 mg kg^{-1} Cr addition) Fig. (31b) was observed in the SEM micrographs. The changes in cellular structure are confirmed with light micrographs obtained at regular intervals during the process of metal treatment (data not shown). The changes in internal structure of the leaves were not significant between plants in both the control soil and chromium -contaminated soils at lower concentrations and between plants in the control soil and chromium (III)-treated soils (data not shown).

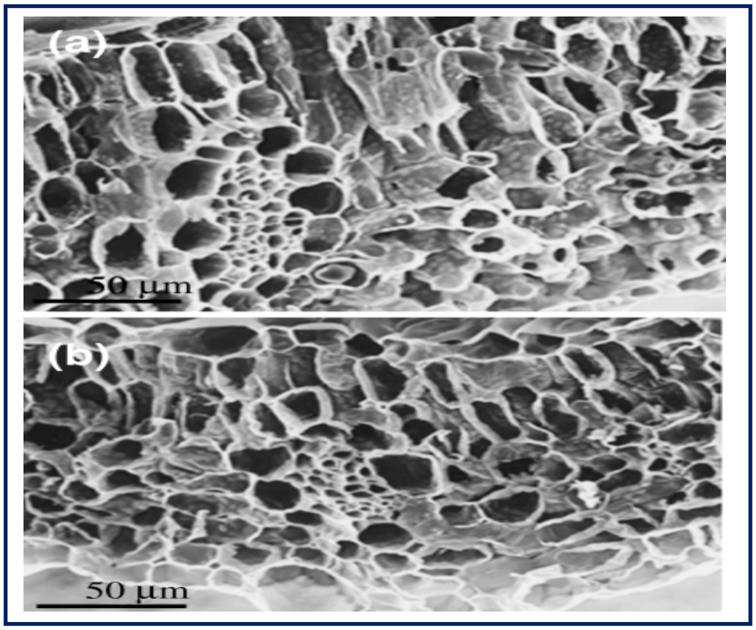


Fig. 31: Illustrates scanning electron micrographs showing transverse sections of leaves of Indian mustard (*Brassica juncea*) grown in a control soil (a) and a Cr(VI)-treated soil with Cr addition of 500 mg. kg^{-1} (b). After: Han *et al.,* (2004).

Further, compared to control group Fig. (32 a), the thickly stained areas surrounding the vascular bundles in stems of Indian mustard in chromium (VI)-treated soils Fig. (32 b) was observed in LM micrographs. SEM Fig. (32 c, d,e) micrographs of roots of Indian mustard in chromium (VI)-treated Fig. (32 d) and chromium (III) - treated Fig. (32 e) soils showed reduced cell size and clotted depositions Fig. (32 d) compared to the control Fig. (32 c) group. These vascular depositions are more prominent in roots of plants in chromium (VI)-treated soils compared to the control and chromium (III)-treated soils Fig. (32 c, e). TEM micrographs of stems from plants in chromium (III)-treated soils Fig. (32 g) and chromium (VI)-treated soils Fig. (32 h) indicated increased number of vacuoles and electron dense material along the walls of the xylem and phloem vessels. Stems of plants in chromium (III) treated soils with 2000 mg. kg^{-1} Cr addition showed less electron dense depositions along the cell walls Fig. (32 g) compared to those in chromium (VI)-treated soils Fig. (32 h). The roots from plants in chromium (III)-treated soils Fig. (32 f) showed an increase in size of vacuoles and electron dense depositions all along the cell walls.

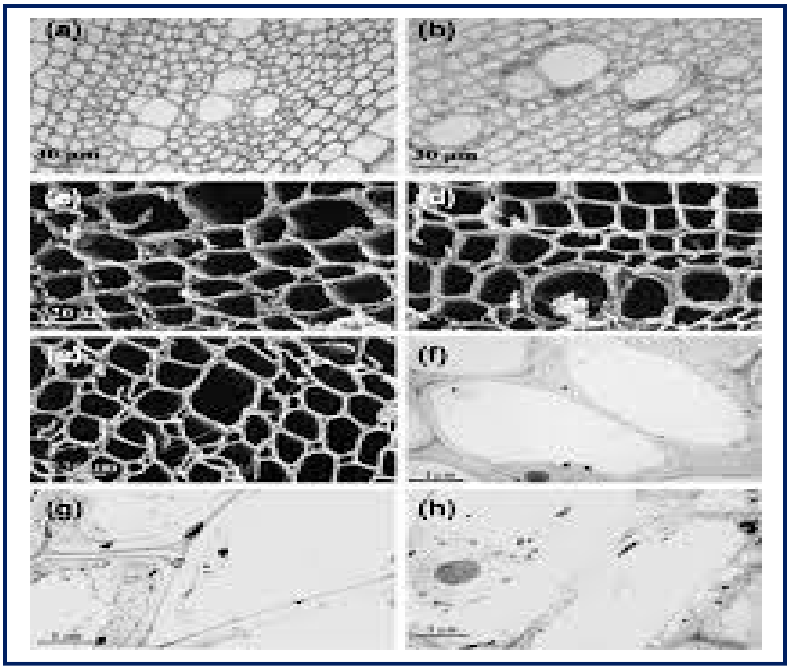


Fig. 32: Illustrates Light microscopy (LM; a, b), scanning electron micrographs (SEM; c, d, e) .Transmission electron micrographs (TEM; f, g, h) showing transverse sections of stems and roots of Indian mustard (*Brassica juncea*) grown in control, Cr(III)- and Cr(VI)-treated soils (with 2000 and 500 mg. kg^{-1} of Cr additions for Cr(III) and Cr(VI), respectively). LM micrographs of stems of Indian mustard grown in control (a) and Cr(VI)-treated soils (b), SEM micrographs of roots of Indian mustard grown in control (c), Cr(VI)-treated (d) and Cr(III)-treated (e) soils, and TEM micrographs of roots of Indian mustard in Cr(III)-treated soil (f) and stems of Indian mustard grown in Cr(III)-treated (g) and Cr(VI)-treated (h) soils. After: Han *et al.,* (2004).

Plants in both chromium (III) and (VI)-treated soils at higher concentrations showed a decrease in the number of palisade and spongy parenchyma cells compared to control plants. The decrease in the number of parenchyma cells may be the result of slower growth rate of plants due to metal accumulation in the plant shoot system. More structural changes in the stems and roots of plants on chromium (VI)-treated soils compared to chromium (III)-treated soils and the control group may be attributed to the difference in chromium toxicity from chromium (III) - and chromium (VI)-contaminated soils, and to increased accumulation of chromium from chromium (VI)-treated soils compared to chromium (III)-treated soils. Although chromium (VI) was suggested to be immediately reduced in the roots after plant uptake Skeffington *et al.,* (1976); Cary *et al.,* (1977); Marschner, (1995); Lytle *et al.,* (1998); Zayed *et al.,* (1998), faster uptake of chromium from initially chromium (VI)-treated soil Skeffington *et al.,* (1976); McGrath, (1982) led to higher accumulation of chromium in both leaves, stems and roots of Indian mustard than in those grown in chromium (III)-treated soil Fig. (33), resulting in higher phytotoxicity of chromium in chromium (VI)-treated soil.

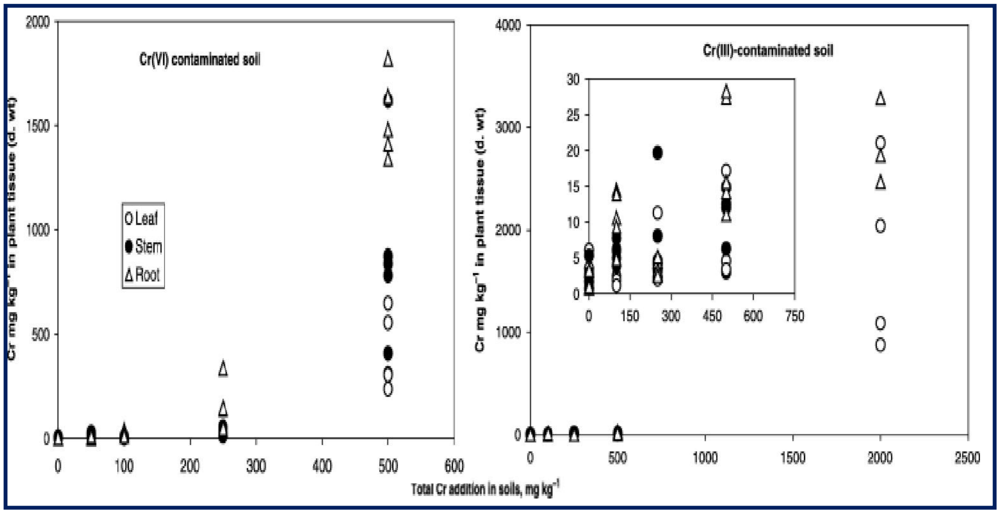


Fig. 33: Chromium (Cr) concentrations in leaves, stems and roots of Indian mustard (*Brassica juncea*) grown on Cr (III) - and Cr (VI)-contaminated soils. After: Han *et al.,* (2004).

Chromium from both chromium treated soils caused significant changes in the roots compared to the control group. The depositions in roots Fig. (32 d) may be simple chromium salts or large organic molecules such as proteins and carbohydrates and complexed with chromium. Vazquez et al. (1987) reported that treated bush beans grown in hydroponic solution containing chromium (VI) had much smaller cells and more reduced intercellular spaces than controls. In leaves of chromium -treated plants, the cells showed a great central nucleus, small vacuoles, and were less mature than cells in control plants. Poor differentiation between pallisade and lacunar parenchyma cells was found in leaves of chromium -treated plants. Our observation confirms the finding on changes of leaf structures of plants due to chromium (VI) by Vazquez et al. (1987). The leaf surface showed an increase of trichomes. Most of the elliptically shaped, sunken stomata and poorly differentiated stomata were present in treated plants. If chromium concentrations in cells exceed the storage capacity of vacuoles, chromium may affect the cytoplasm, producing condensed and irregular structure and damage membranes, especially tonoplast (Vazquez *et al.,* 1987). In summary, bioavailability of chromium in contaminated soils is relatively low, and Indian mustard plants only accumulate threshold values, Indian mustard plants are able to accumulate a significant amount of chromium in both shoots and roots, despite severe phytotoxic symptoms.

Chromium (III, VI) has been reported to cause complete destruction of cortical tissue in roots of *T. aestivum* seedlings Hasnain and Sabri, (1997). Bianchi *et al.,* (1998) reported that exposure to chromium (VI) (20 and 40 mg. l^{-1}) induced structural alterations in roots of *Mentha aquatica*. These include browning of roots with black tips, absence of statolytes on root cap, disorganization of cells in central cylinder, heavy thickening of tangential walls and development of lateral roots in the root hair zone Bianchi *et al.,* (1998). Leaves in chromium (VI)-treated *M. aquatica* plants showed a loss of tissue organization, change in shape of palisade layer cells, increase in intercellular spaces and reduction in mesophyll layer, and decrease in chloroplast and starch granule development Bianchi *et al.,* (1998). Under chromium (VI) stress, reduction in wax deposition and wide opening of stomata with enlarged subsidiary cells were observed in leaves of *Phyllanthus amarus* Rai and Malhotra, (2008). Chromium (500 mg kg^{-1} chromium [VI] and 1,000 mg. kg^{-1} chromium [III]) has been found to decrease the number of palisade and spongy parenchyma cells in fronds of *P. vittata* Su *et al.,* (2005).

3-7-2 Ultrastructural deformation of root and shoot

Scanning micrograph of control root and shoot clearly revealed that proper arrangement of xylem and phloem. However, gradual increase of chromium concentration leads to deformation of both organelles (Fig. 34).

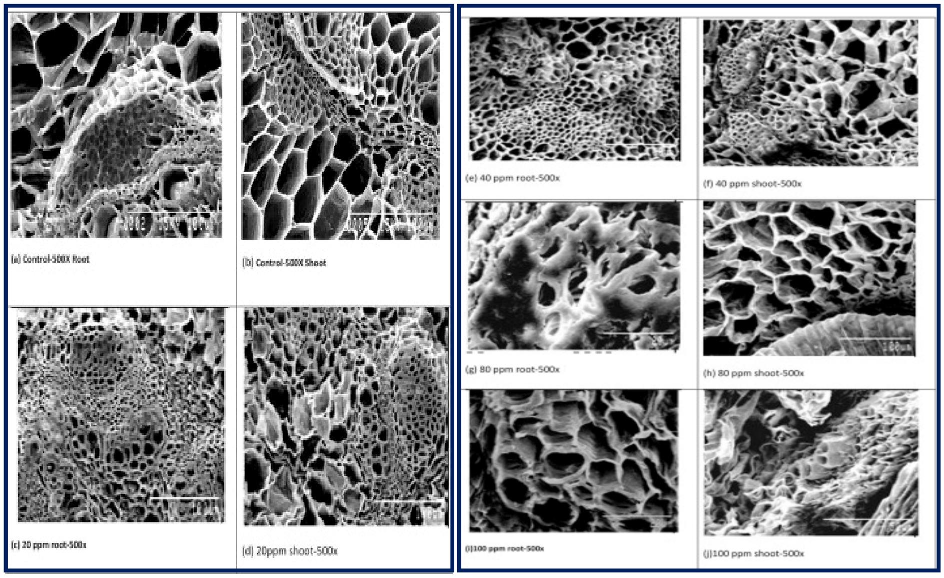


Fig. 34: Illustrates Ultrastructural deformation of C. arietinum under different concentration of chromium (VI) stress. After: Shreya Medda and Naba Kumar Mondal, (2017)

Shreya Medda, Naba Kumar Mondal, (2017) reported that chromium (Cr) is a potent heavy metal that pollutes both soil and aquatic body. Therefore, it should be considered as a hazardous element. Chromium can exists in various from in the environment, among them most stable from of chromium is chromium (VI). The present study demonstrate the adverse impacts of hexavalent chromium on *Cicer arietinum*, development and growth morphology, including elongation of coleoptile, number of metabolic responses related to growth and ultra-structural deformation of root and shoot. Exogenous application of chromium (VI) from 20 ppm to 100 ppm progressively inhibited seed germination and coleoptile growth and dramatically damaged root aperture (xylem and phloem) even at the lowest dose. Results also revealed that the maximum reduction of germination was recorded at 80 mg/L chromium (VI) solution during 72 h of incubation. However, at 80 mg/L of chromium (VI) solution, coleoptile growth reduces to 30% with respect to control. The chlorophyll ('a' and 'b' and total chlorophyll) level significantly declined by chromium treatment. On the other hand, SEM picture clearly indicate the distinct structural change of xylem and phloem with increasing the concentration of hexavalent chromium from 20 ppm to 100 ppm.

From the SEM picture Fig. (34), it is clear that distinct feature of xylem and phloem are gradually distorted with increasing the concentration from 20 mg/L to 100 mg/L. However, most severe condition was recorded from 80 mg/L. On the other hand, shoot organelles showed much lower severity and complete destruction of organelles was observed at 100 mg/L. Almost similar deformation recorded for root structure also. Some results almost similar those were reported by Mondal *et al.,* (2013), Mondal *et al.,* (2015) for their earlier work on mercury and cadmium. However, shoot showed deformation at 40 mg/L chromium, but root at 20 mg/L. These damaged perhaps due to ROS production. At higher concentration, ROS generation is enhanced and it cause oxidative damage at cellular level Shanker *et al.,* (2005). Moreover, at lower dose, root showed more damaged than shoot. This is perhaps due to chromium (VI) cross the endodermis via symplast than chromium (VI) probably readily reduced to chromium (V) which retained in the root cortex cells under lower concentration Shanker *et al.,* (2005). However, another study, Shanker *et al.,* (2004) demonstrated that an accumulation in roots of the plants could be the damage of root and shoot part by chromium toxicity may result from the displacement of other cations, including Ca^{+2}þ, from binding sites in the plasma membranes and cell walls, leading to cell malfunction Scoccianti *et al.,* (2006). Root elongation data suggest concomitant reduction of root growth with increases of concentration. Root growth drastically affected by chromium toxicity in plant Suseela *et al.,* (2002). This could be due to chromium toxicity that inhibit the root cell division/root elongation or to the extension of cell cycle in the roots Shanker *et al.,* (2005). On the other hand, root growth/24 h. Results revealed that at lower concentration, root growth/24 h is impressive. However, with increasing concentration root growth gradually decrease. On the other hand, correlation study between root length and coleoptiles length showed that significant positive reduction of both root length and coleoptiles growth at 8 mg/L chromium salt solution. Therefore, Ultrastructural deformation clearly revealed that root is more severally affected than shoot. This is perhaps due to poor translocation of chromium from root to shoot and most of the metals are sequestered in the root vacuoles Shanker *et al.,* (2004).

Chromium (III, VI) has been reported to alter structures of chloroplast and nuclei and membrane ultrastructure in plants Bassi et al. (1990); Mangabeira et al. (2011). Electron microscopic studies have demonstrated that chromium (VI) exposure damage membrane systems of thylakoids, chloroplast envelope, plasmalemma, tonoplast, and mitochondria in *Spirodela polyrhiza* Appenroth et al. (2003). chromium (VI; 1 mg. l^{-1}) induced disorganization of plastids with poorly developed lamellar system and widely spaced thylakoid having fewer grana, retraction of plasma membrane, thickening of tracheids, irregular nuclei, and heavily packed starch grains in *L. cristatum* Garg et al. (1994). In *S. polyrhiza*, exposure to chromium (VI) (at 100 µM for 2 days or 500 µM for 1 day) caused an accumulation of starch grains in chloroplast Appenroth et al. (2003). However, increase in chromium (VI) concentration (to 1,000 µM for 1 day) or extending the period of exposure (100 µM for 4 days) reversed the effect resulting in disappearance of starch grains and appearance of plastoglobuli Appenroth et al. (2003). chromium (III, VI) has also been reported to cause chromatin condensation, swelling of mitochondria, cytoplasmic vacuolization, and perturbed arrangement of endoplasmic reticulum cisternae in pollen grains of kiwi (*A. deliciosa* var. deliciosa), and chromium (III) was more toxic than chromium (VI) Speranza et al. (2009). Panda (2007) demonstrated that exposure of chromium (VI) at 100 µM for 48 h caused distortion in the cell ultrastructure including increased vacuolization, detachment of the cell wall from the plasma membrane, and appearance of dense lysosomes like organelles. Mangabeira et al. (2011) found alterations in the shape of the chloroplasts and nuclei in Alternanthera philoxeroides and Borreria scabiosoides under chromium (III) stress. Chromium (VI) has been found to interfere with microtubule organization, perturb morphology and distribution of endoplasmic reticulum, and induce heavy callose deposition (as cellular defense reaction) in root tip cells of *A. cepa* Eleftheriou et al. (2012).

3-8 Influence of chromium oxidative stress

Trace metal stress plants by oxidizing them either directly or indirectly by producing reactive oxygen species (ROS) Qianqian *et al.,* (2022). Chromium toxicity causes oxidative damage in plants through overproduction of ROS such as O^{2-}, H_2O_2, and OH^- Shahid *et al.,* (2017); Basit *et al.,* (2022). The process of reducing chromium (VI) to lower oxidation states is the root cause of chromium toxicity, where only ROS are produced Shanker *et al.,* (2005); Shahzad *et al.,* (2018). Wakeel et al. (2020) reported that when chromium (VI) is radical reduced, the unstable intermediates i.e., chromium (IV) and chromium (V), which contribute to the generation of ROS, are created. Various plant organelles, such as mitochondria, peroxisomes, and chloroplasts, create these ROS as byproducts of diverse metabolic activities Srivastava *et al.,* (2021) Fig. (35).

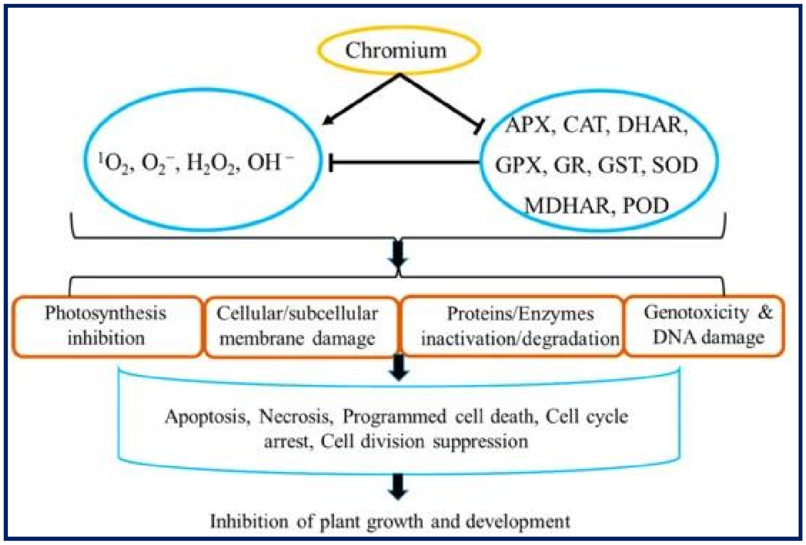


Fig. 35: Chromium (VI)-induced ROS mediated alteration in plants: Cr(VI)-induces ROS accumulation by suppressing enzymatic antioxidant system, which damages cellular and subcellular membranes; induces Ultrastructural changes in cell organelles such as mitochondria, plastids, and thylakoids; inhibits 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 (O2−), 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. After: Wakeel *et al.,* (2020)

The primary causes of ROS generation in plant organelles i.e., mitochondria and chloroplasts are the inhibition of CO_2 fixation and excessive decrease of the electron transport chain Ao *et al.,* (2022). Furthermore, the production of ROS is caused by the leakage of electrons from O_2 caused by electron transport activity in mitochondria, peroxisomes, and chloroplasts Anjum *et al.,* (2016b). Chromium toxicity in plants tends to share electrons; sulfhydryl groups in proteins establish covalent interactions with redox-inactive minerals Anjum *et al.,* (2017). Numerous studies showing a dramatic escalation in ROS Sharma *et al.,* (2019) with an increase in malondialdehyde (MDA) content with chromium toxicity Adrees *et al.,* (2015b).

Plants under normal circumstances play a pivotal part as signaling pathways molecules and mediators of responses to cellular metabolic disturbance, environmental stimuli, pathogen infection, various developmental stimuli, and a variety of biological and physiological responses when appropriate concentrations of ROS are present Waszczak *et al.,* (2018). However, the overproduction of ROS in plants results in disruption of cell homeostasis, cell membrane or protein fragmentation, DNA strand breaks, deactivation and degradation of genetic material, and harm to photosynthetic pigments Srivastava *et al.,* (2021); Ao *et al.,* (2022). Similar findings Ullah et al. (2019b), reported that increased ROS generation in plants with chromium toxicity results in oxidative damage, inflicting damage to DNA, lipids, pigments, and proteins, and stimulating the lipid peroxidation functions. These effects inhibit plant growth by preventing cell division or inducing cell death, which lowers biomass production Wakeel *et al.,* (2020). According to Shahid et al. (2014), the duration of exposure, chromium content, plant species, stage of development, level of stress, and particular organs all affect how hazardous Cr-induced ROS are for plants. Several researchers Kamal *et al.,* (2022); Rehman *et al.,* (2020); Saleem *et al.,* (2020) stated that plants are often exposed to stress, as they have no choice to escape from unfavorable environmental conditions. Under chromium exposure, plants suffer through morphological biochemical alterations because of the imbalance between the production and removal of free radicals also known as an oxidative burst Ali *et al.,* (2011); Sallah-Ud-Din *et al.,* (2017); Zaheer *et al.,* (2020). Free radicals are generated in different organelles such as chloroplast, peroxisome and mitochondria as a byproduct of different biochemical processes. Chromium disrupts enzyme active sites by attaching with functional groups and changes enzymatic activities. Hence, cations disruption from binding sites of enzyme disturbs equilibrium of cells and generates free radicals Irshad *et al.,* (2021); Saleem *et al.,* (2021). Chromium stress exhibits enhanced ROS production and damage in biological membrane Tripathi *et al.,* (2012), by disruption in DNA and membrane lipids. Chromium mediated reduction in essential amino acids showed significant decrease in nitrogen and protein contents Danish *et al.,* (2019); Maqbool *et al.,* (2018). Chromium deactivates plant defense mechanisms and increases the formation of ROS observed in wheat Adrees *et al.,* (2015). Various studies revealed that higher concentration of chromium is responsible for induced MDA Ali *et al.,* (2011). Zaheer *et al.,* (2019). Panda and Choudhury, (2005) found that lipid peroxidation and MDA content increased with the increase of chromium (1, 10, and 100 mM) in wheat plant. In maize, chromium stress (30, 60, 90, 120, and 150 µmol L^{-1}) initiated the generation of lipid peroxidation in the form of (MDA), H_2O_2 and thiobarbituric acid reactive substances Adhikari *et al.,* (2020) ; Nafees *et al.,* (2018). Eleftheriou *et al.,* (2015) stated that chromium VI specifically damaged the roots of Arabidopsis thaliana. Oxidative species gradually formed in roots through the exposure to 100 µM of $K_2Cr_2O_7$, toxification of chromium inducing oxidative stress in the plant cell as well as the actions of antioxidant activities.

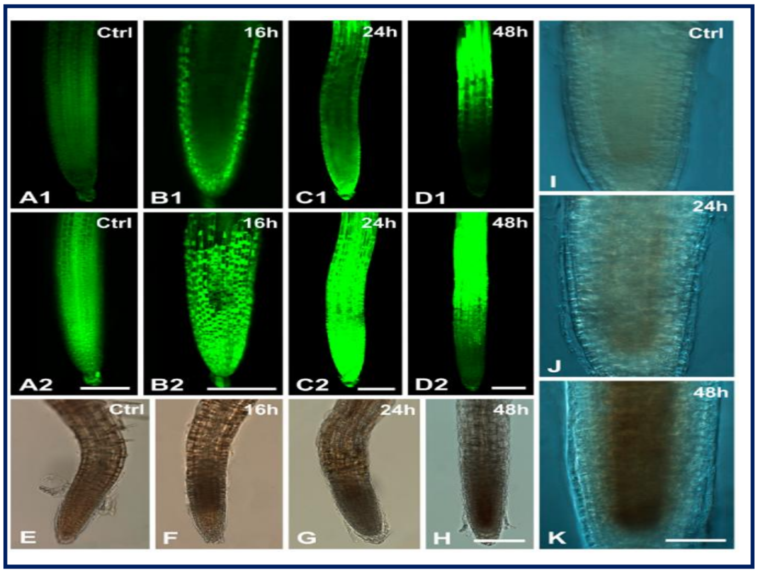


Fig. 36: Visualization of H_2O_2 concentration and peroxidase activity in root tips of A. thaliana. (A–D) 2,7-dichlorofluorescein diacetate (DCF-DA) staining of control (A) and variously Cr(VI)-treated roots (B–D) at single median CLSM sections (designated as 1) and maximum projections of serial CLSM sections (designated as 2). Note the intensification of the fluorescent signal after a 16 and 24 h effect, primarily localized in the undifferentiated root zone, indicative of increasing H_2O_2 accumulation; (E–K) Detection of peroxidase activity in Cr (VI)-treated roots by pyrogallol staining in bright field at low magnifications of whole mounts (E–H) and higher magnifications of centrally focused images under differential interference contrast optics (I–K); An increasing peroxidase activity occurs in a time-of-exposure dependent manner (E–H), localized mainly in the internal root tissues (I–K). Scale bars: (A–H): 100 µm; (I–K): 50 µm. After: Eleftheriou *et al.,* (2015)

3-9 Antioxidant enzymes defense system

Ahmad *et al.,* (2019); Bah *et al.,* (2011); Tripathi *et al.,* (2012); UdDin *et al.,* (2015) illustrated that plants with an effective antioxidant system are able to control high concentration of chromium. The nonenzymatic antioxidants are composed of less molecular weight compounds like carotenoids, ascorbic and phenolic acids, flavonoids, glutathione etc. that function as redox buffer and affect plant growth and maturation by alteration in various cellular processes. Chromium stress stimulate the potentially three forms of metabolic changes in plants. **(A)** Modification in the synthesis of organic pigments facilitates the growth and development of plants (e.g., anthocyanin, and chlorophyll Shanker *et al.,* (2005); Shahid *et al.,* (2017). **(B)** Enhanced the synthesis of metabolites (e.g., ascorbic acid, and glutathione) as a direct reaction to chromium stress that will affect the plants Srivastava *et al.,* (2021) and (**C**) Modifications in the metabolic-pool to channelize the synthesis of new biochemically associated metabolites that will confer tolerance or resistance to Cr stress (e.g., histidine and phytochelatins) Shanker *et al.,* (2005); Ao *et al.,* (2022) Fig.(37).

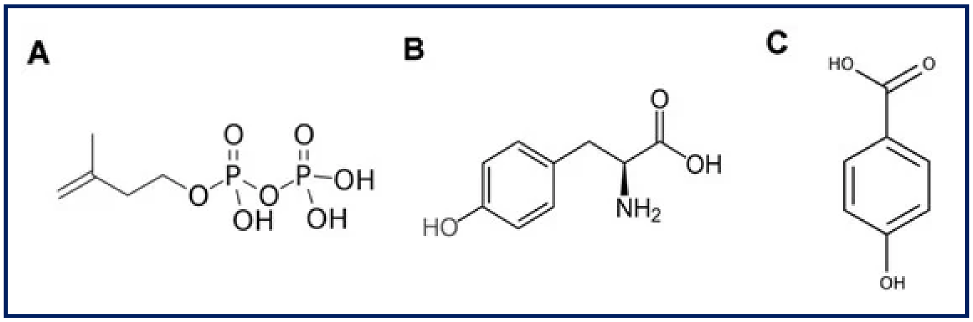


Fig. 37: Illustrates the chemical structures of the main precursors in isoprenoid synthesis. (**A**) Isopentenyl Diphosphate; (**B**) L-tyrosine; (**C**) 4-hydroxybenzoic acid. After: Rudenko *et al.,* (2023)

Rudenko *et al.,* (2023), reported that Plants are exposed to a variety of abiotic and biotic stresses leading to increased formation of reactive oxygen species (ROS) in plant cells. ROS are capable of oxidizing proteins, pigments, lipids, nucleic acids, and other cell molecules, disrupting their functional activity. During the process of evolution, numerous antioxidant systems were formed in plants, including antioxidant enzymes and low molecular weight non-enzymatic antioxidants. Antioxidant systems perform neutralization of ROS and therefore prevent oxidative damage of cell components. In the present review, we focus on the biosynthesis of non-enzymatic antioxidants in higher plants cells such as ascorbic acid (vitamin C), glutathione, flavonoids, isoprenoid, carotenoids, tocopherol (vitamin E), ubiquinone, and plastoquinone. Their functioning and their reactivity with respect to individual ROS will be described. This review is also devoted to the modern genetic engineering methods, which are widely used to change the quantitative and qualitative content of the non-enzymatic antioxidants in cultivated plants. These methods allow various plant lines with given properties to be obtained in a rather short time.

Plants cannot escape environmental pressures such as metal pollution, these challenges have driven the evolution of numerous mechanisms to efficiently detect, react, and ultimately adapt to these pressures. Likewise, plants also use multidimensional defense responses against Cr toxicity via complexation by organic ligands, vacuolar compartmentalization, and activation of the antioxidative system. These defense responses are modulated or regulated by an intricate signaling cascade that takes place in different cellular components. Although a plethora of studies have highlighted how Cr induces the oxidative stress that leads to an array of detrimental effects on its cellular system, the exact molecular mechanisms of Cr translocation, accumulation, phytotoxicity, and plant defensive responses are still largely unknown. For plants to adapt to biotic and abiotic stressors, signal perception, transduction, and post-translational regulation are crucial. The initial perception of stressors involves different sensors, such as cell wall receptors and ion channels, as well as signaling molecules, including calcium, ROS, hormones, protein kinases, and transcriptional factors, that play key roles in downstream signaling cascades. The roles of the above signaling players have been well addressed during biotic and many abiotic stressors. However, their roles in heavy metal stress, including Cr, are largely known. The molecular dynamics of Cr signaling from the exterior (cell wall) and interior (plasma membrane and cytosol) are not fully understood and many knowledge gaps are remaining.

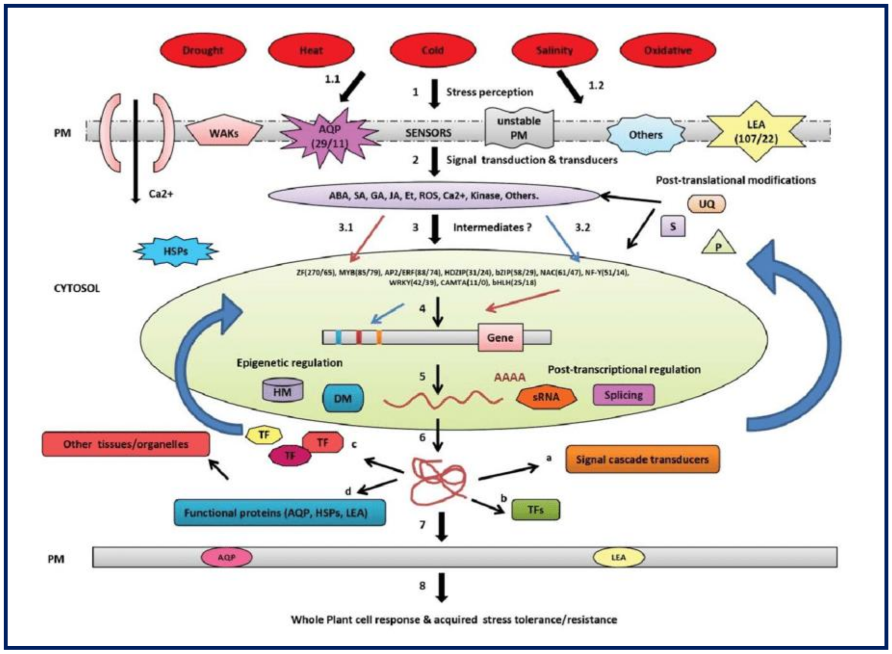


Fig. 38: Schematic presentation of abiotic stress induced changes in plant cell showing role of functional and regulatory proteins. 1. Abiotic (single/multiple) stress signals are perceived by sensors (opening of Ca^{2+} channels, membrane instability, wall associated kinase (WAK e.g. RLK; receptor like kinase, HK; histidine kinase, COLD1; cold responsive, OSCA1; reduced hyperosmolalityinduced calcium increase 1), others (TRP (transient receptor potential channel proteins, G-protein coupled receptors, RBOHD; ROS producing enzyme, Calmodulin binding receptors, CNGCs; cyclic nucleotide-gated channels, GLRs; glutamate receptor-like channels) (Zhu, 2016). 1.1 & 1.2 Functional proteins (AQP, LEA, HSP) become active in PM, Cytosol and other cellular organelles. 2. The stress signals are transduced by various transducers and plant hormones. 3. Various intermediates (unknown) transmit the signal to nucleus. 3.1 Red arrow indicates hormone dependent regulation. 3.2 Blue arrow indicates hormone independent regulation. 4. Single (blue arrow) or couple of Transcription factors (red arrow) bind to =>1 cis-elements of SRG (stress responsive gene). 5. The resulted mRNA undergoes post-transcriptional regulation (sRNA; small RNA, alternative splicing, poly-A tail) and epigenetic regulation (HM; histone methylation, DM; DNA methylation). 6. mRNA is translated into protein (a: involved in signal cascade where post-translational modify cations occurs; UQ; ubiquitination, S; sumoylation and P; phosphorylation. b & c: as TF; transcription factors go back to nucleus. d: functional proteins that are directly involved in stress tolerance mechanism). 7. AQP and LEA synthesized goes to PM for instant reaction to stress stimuli. 8. Such downstream complex pathways and proteins cascades results in stress resistance/tolerance plant. After: Monica Jamla and Sunil Archak, (2019)

Monica Jamla and Sunil Archak (2019) reported that Abiotic stress, a complex phenomenon, has been established as a major factor affecting quality and quantity of crop production. Plants have evolved mechanisms to survive abiotic stress conditions and a set of protein families have been identified that work at cellular level to make plants tolerant. Modern genetic engineering and synthetic biology techniques are capable of deploying specific genes to develop crop varieties tolerant to abiotic stress factors. This and the availability of patent protection on the genetic sequences and protocols can make gene banks redundant unless gene banks equip themselves with genomic resources of priority and niche crop species. Here, we review the status of knowledge in 13 protein families, miRNAs and epigenetic regulation known to be involved in plant abiotic response pathways among nine major crops. A comparative analysis is presented of sequence depositions in public databases, research papers and patent protection sought in the area of abiotic stress response pathway in plants.

However, with the advent of multiomics, a few studies have recently reported transcriptional, translational, and metabolic reprogramming in various plant systems after Cr exposure, thus providing novel insight into Cr perception and signal transduction. For example, in rice plants, Cr (VI) triggered ROS and Ca^{2+} production followed by activation of NADPH oxidase and calcium-dependent protein kinase, all of which are critical for downstream signaling cascades Trinh *et al.,* (2014). There is mounting evidence that calcium and ROS signaling systems interact reciprocally, with important ramifications for optimizing cellular signaling networks. They also identified many transcriptional factors involved in Cr signaling cascades, such as WRKY and AP2/ERF TF genes, which added to the notion of their role in defense against metal stress. Similarly, many phosphate kinase genes (PP2C-A, PP2C-D, and PP2C-F) were identified in response to Cr (VI) stress, which further provided evidence that these might be involved in regulating various signaling cascades during Cr stress. Earlier gene expression profiling of rice plants under Cr stress revealed the inactivation of gibberellic acid-related pathways and stimulation of ethylene (ET), abscisic acid (ABA)-, and jasmonate-mediated signaling cascades. This provided novel insight into the role of different hormones during Cr stress Trinh *et al.,* (2014). Another study reported that transcriptome profiling of rice plants after Cr (VI) exposure showed a distinct gene expression profile. For example, genes involved in membrane transport and signal transduction, xenobiotics, amino acid metabolism, and biosynthesis of secondary metabolites were upregulated, whereas genes related to cell growth and energy metabolism were downregulated. Huang *et al.,* (2014) found that Cr (VI) induced an array of genes related to ROS, calcium, MAPKs, and CDPK-like kinases, all of which are key players in perception and signal transduction pathways. Similarly, various miRNA were identified in tobacco plants that were distinctly regulated during Cr (VI) stress Bukhari *et al.,* (2015). On the other hand, a proteomic perspective has also been used to identify differential proteins during Cr stress. For example, 64 proteins were successfully identified in rice seedlings that were related to several cellular processes, viz., cell wall synthesis, electron transport, primary metabolism, energy production, and detoxification Zeng *et al.,* (2012). In the last 10 years, a number of studies have been published on the effects of HMs on the metabolome of both model plants and cultivated cultivars. Similarly, a metabolomics study of rice plants after Cr exposure showed a significant accumulation of proline and ornithine, which could be involved in the defense response of rice plants against oxidative stress during Cr exposure Dubey *et al.,* (2010). These studies further highlight the importance of omics tools in identifying various key players in Cr signal perception and transduction. However, the integration of multiomics along with gene knock out studies is further required to determine the roles of different genes or other key signaling players in Cr signaling that will provide novel insight for the development of Cr-tolerant crop cultivars. In this review, based on the available data, we have presented a model describing Cr signaling in plants, as shown in Figure 3. We also highlight some of the important players in the initial and downstream signaling cascades that might be involved in Cr signal perception and transduction. However, studies that are more comprehensive are required to fully understand the molecular dynamics of Cr signaling in plants, such as the roles of cell wall sensors, plasma membrane channels, and intracellular signaling cascades in different compartments after Cr exposure. Cr perception. Following Cr sensing, an ROS burst and calcium waves will occur, which can be sensed by different sensors, such as kinases or calcineurin B-like protein (CBL)-CBL interacting protein kinase (CIPK) and calmodulin (CaMs)/calmodulin-like proteins (CMLs), which can lead to significant transcriptional and translational reprogramming in several intracellular compartments, as depicted in the figure. The Cr (VI) transporter in this instance is a sulphate or phosphate transporter, which could ease its entry into the root cells. We also highlight the roles of various molecules, including hormones, nitric oxide (NO), hydrogen sulfide (H_2S), and antioxidants, in Cr-mediated signaling.

Initially at germination stage, toxicity of chromium significantly reduced the activity of gibberellin (GA), enhanced the activity of abscisic acid (ABA) which lead to seed imbibition, and reduced germination rate Seneviratne *et al.,* (2019). Similarly, according to Yan *et al.,* (2014) hydrolyzing enzymes secreted by the aleurone layer of seeds are crucial for seed germination. By releasing food reserves from the endosperm, enzymes i.e., acid phosphatases (ACPs), a-amylases, and proteases promote effective seedling establishment and growth (see section 5.1). Acid phosphatase, a-amylase, and alkaline phosphatase activity were decreased in the endosperm of cereals i.e., wheat, oat, barley, and maize seeds when chromium was present Seneviratne *et al.,* (2019). In addition, the enzymes involved in the assimilation of important nutrient nitrogen i.e., nitrogenase, nitrate reductase, nitrite reductase, glutamine synthetase, glutamate synthase, glutamate dehydrogenase were significantly reduced with the contamination of chromium in plants Sangwan *et al.,* (2014). Deficiency of nutrients in plants due to chromium toxicity results into degradation of various amines, alkaloids, pigments, vitamins, coenzymes, nucleic acids, and nucleotides as nutrients are structural component of these organelles Shanker *et al.,* (2005); Sangwan *et al.,* (2014). Similarly, the activities of enzymes involved in photosynthesis NADP-malic enzyme (NADP-ME), pyruvate, phosphate dikinase (PPDK), and Phosphoenolpyruvate carboxylase (PEPC), plant respiration i.e., a-ketoglutarate dehydrogenase and isocitrate dehydrogenase, and gene transcription i.e., RNA polymerase are significantly reduced in various plants due to phytotoxicity of chromium.

The level of antioxidant activities against the toxic concentration of ROS depends upon the ROS type and its generation Parveen *et al.,* (2020); Saleem *et al.,* (2020); Alatawi *et al.,* (2022); Ali *et al.,* (2022); Ashraf *et al.,* (2022); Dominic *et al.,* (2022). Various antioxidant compounds work in coordination with each other to decrease the toxic effect of ROS. In higher plants, the activities of antioxidants can increase or decrease against the chromium toxicity in the soil Ali *et al.,* (2022); Ali *et al.,* (2022); Zaheer *et al.,* (2020). Zaheer et al. (2019) indicated that the addition of different levels of wastewater (0%, 33%, 66%, and 100%) in the natural soil induced the oxidative damage in the roots and leaves of in *Spinacia oleracea*. They also revealed that the severe chromium toxicity in soil caused a significant ($p < 0.05$) decrease in the activities of various antioxidants. On the other hand, chromium toxicity in the soil significantly enhanced the activities of various antioxidants in the roots and leaves of *Spinacia oleracea* plants Adhikari *et al.,* (2020); Ali *et al.,* (2011); Liu *et al.,* (2008).

3-10 Effects of chromium on photosynthesis.

Several researchers among them Rehman *et al.,* (2019); Saleem *et al.,* (2020); Saleem *et al.,* (2019); Ulhassan *et al.,* (2019) reported that excessive chromium has negatively affects on photosynthesis by affecting enzymes of Calvin cycle, thylakoid membrane and photosynthetic electron transport. The presence of chromium showed reduction in pigment biosynthesis, inhibition in net photosynthetic rate, stomatal conductance, electron transport chain, fixation of carbon dioxide, photosynthetic phosphorylation, plastids structure and negatively affects light/dark reactions Chen *et al.,* (2017); Hussain *et al.,* (2018) Fig.(39).

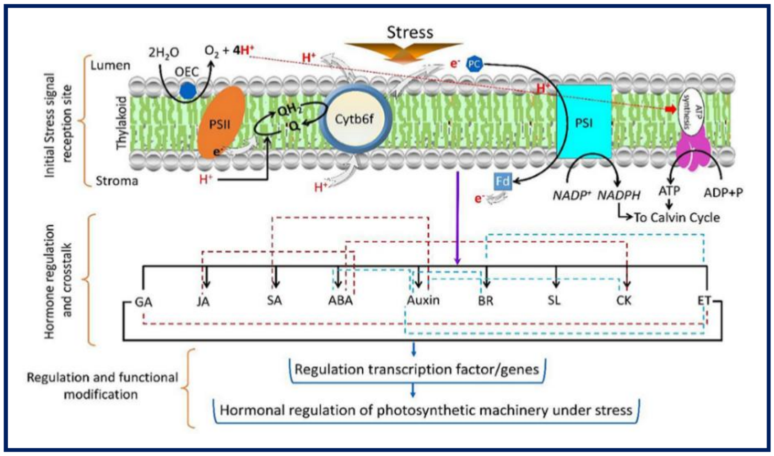


Fig. 39: Regulation of the complex phytohormone network under stress conditions. The imposition of stress on the photosystem reaction center induces the hormonal signal transduction. The red dotted lines indicate the regulation of two hormone inhibitions, and green lines indicate the co-regulation of two hormones. The egulation of gene transcription by different hormones shows the involvement of the photosynthetic machinery. After: Muhammad *et al.,* (2021)

Muhammad *et al.,* (2021) stated that photosynthesis sustains plant life on earth and is indispensable for plant growth and development. Factors such as unfavorable environmental conditions, stress regulatory networks, and plant biochemical processes limits the photosynthetic efficiency of plants and thereby threaten food security worldwide. Although numerous physiological approaches have been used to assess the performance of key photosynthetic components and their stress responses, though, these approaches are not extensive enough and do not favor strategic improvement of photosynthesis under abiotic stresses. The decline in photosynthetic capacity of plants due to these stresses is directly associated with reduction in yield. Therefore, a detailed information of the plant responses and better understanding of the photosynthetic machinery could help in developing new crop plants with higher yield even under stressed environments. Interestingly, cracking of signaling and metabolic pathways, identification of some key regulatory elements, characterization of potential genes, and phytohormone responses to abiotic factors have advanced our knowledge related to photosynthesis.

However, our understanding of dynamic modulation of photosynthesis under dramatically fluctuating natural environments remains limited. Here, we provide a detailed overview of the research conducted on photosynthesis to date, and highlight the abiotic stress factors (heat, salinity, drought, high light, and heavy metal) that limit the performance of the photosynthetic machinery. Further, we reviewed the role of transcription factor genes and various enzymes involved in the process of photosynthesis under abiotic stresses. Finally, we discussed the recent progress in the field of biodegradable compounds, such as chitosan and humic acid, and the effect of melatonin (bio-stimulant) on photosynthetic activity. Based on our gathered researched data set, the logical concept of photosynthetic regulation under abiotic stresses along with improvement strategies will expand and surely accelerate the development of stress tolerance mechanisms, wider adaptability, higher survival rate, and yield potential of plant species.

Chromium toxicity induces negative impacts on plant development UdDin *et al.,* (2015), antioxidant compounds Liu *et al.,* (2008), stomatal conductance Maqbool *et al.,* (2018) and water use efficiency Hussain *et al.,* (2018) Fig.(40).

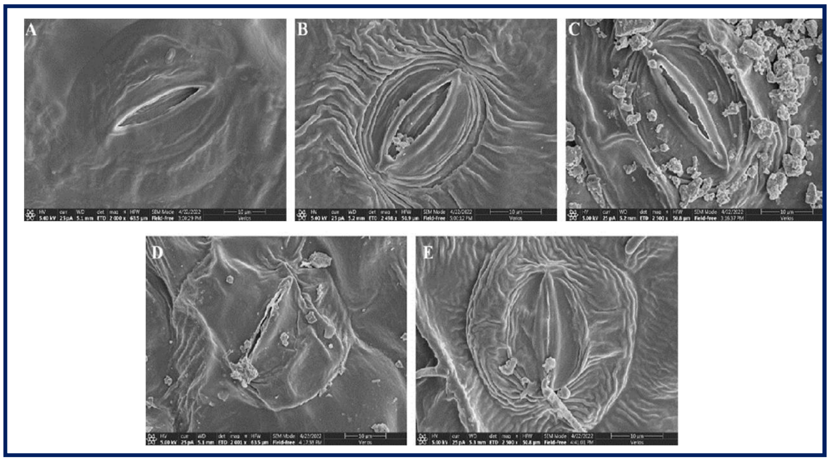


Fig. 40: Impact of Cr on the stomatal traits in the leaves of sweet potato. (**A**) Ck, (**B**) 25 µM, (**C**) 50 µM, (**D**) 100 µM, and (**E**) 200 µM. Scale bar is 10 µm and magnification is (**A**) 2000×, (**B**) 2498×, (**C**) 2500×, (**D**) 2001×, and (**E**) 2500×. After: Kumar et al.0, (2022)

Kumar *et al.,* (2022) reported that sweet potato was hydroponically grown, and treatments of 0, 25, 50, 100, and 200 µM Cr were applied for seven days. This study exhibited that a low level of Cr treatment (25 µM) enhanced the growth, biomass, photosynthesis, osmolytes, antioxidants, and enzyme activities. However, significant deleterious effects in growth, biomass, photosynthetic attributes, antioxidants, and enzymes were observed at higher levels of Cr treatment. The remarkable reduction in plant growth traits was associated with the over-accumulation of H_2O_2 and MDA contents (410% and 577%, respectively) under the highest rate of Cr (200 µM). Under 200 µM Cr, the uptake in the roots were 27.4 mg kg−1 DW, while in shoots were 11 mg kg−1 DW with the highest translocation rate from root to shoot was 0.40. The results showed that the higher accumulation of Cr negatively correlated with the phenotypic and physiological parameters. It may be proposed that Cr toxicity causes oxidative damage as sustained by augmented lipid peroxidation, reactive oxygen species, and reduced photosynthetic rate, chlorophyll, and stomatal traits. The chloroplastic ultrastructure was damaged, and more apparent damage and size reduction were observed at higher Cr levels. Furthermore, aggregated Cr concentration positively correlates with the increase of osmolytes and superoxide dismutase (SOD) activity in the leaves of sweet potato. Moreover, improved osmolytes and SOD do not help protect sweet potato against high Cr stress. Overall, these findings will improve the understanding of the defense mechanisms of sweet potato to Cr stress.

Previous studies reported that the toxic level of chromium in the soil reduced photosynthetic pigments in the leaves of *Brassica Rapa* Ali *et al.,* (2018), Triticum *aestivum* Subrahmanyam (2008) and *Brassica napus* Zaheer *et al.,* (2020). The toxic level of chromium in the soil may also cause ultrastructure alterations in the chloroplast and other membrane bounded organelles which in turn result in the reduction of photosynthetic pigments Rai *et al.,* (2004); Zaheer *et al.,* (2019). Under chromium stress, such these alterations were observed in *Brassica napus* (Afshan *et al.,* (2015), *Lolium perenne* Vernay *et al.,* (2007), *Amaranthus viridis* Liu *et al.,* (2008) and *Pisum sativum* Bishnoi *et al.,* (1993).

Kumar *et al.,* (2016); Ertani *et al.,* (2017), reported that chromium toxicity in the soil also affects light and dark reactions via inducing alterations in the thylakoid membrane. Under concentration of chromium toxicity in the soil, excess of electrons is generated during the photochemical processes that are not used in the carbon fixation cycle. Furthermore, the toxic levels of chromium cause redox changes in Cu and Fe heme group, which is the main factor of photosynthesis reduction in plants Masciarelli *et al.,* (2017); Shahid *et al.,* (2017) Fig.(41). Ugwu and Agunwamba (2020), illustrated that chromium stress-induced, decrease in photosynthesis in plants may due to the overproduction of ROS in the soil through oxidation reduction mechanisms which ultimately leads to induction of oxidative stress and reduction of plant growth, biomass and yield Farid *et al.,* (2019); Vernay *et al.,* (2007).

Sharma *et al.,* (2020) reported that numerous metal transporter gene families including CDF (cation diffusion facilitator), HMA (heavy metal ATPase), ATP binding cassette (ABC) superfamily and ZIP (ZRT, IRT-like protein) have been identified for different metals like Pb, Cd, Zn and As Shahid *et al.,* (2017) , Assuncao *et al.,* (2010) Kim *et al.,* (2007) . However, the role of transporter families in the translocation of Cr in plants is still unclear. The translocation of Cr (VI) to shoots is an active process that involves phosphate and sulfate transporters Shahid *et al.,* (2017) . Hence, iron (Fe) and sulfur (S) channels in the roots that lead to the competition might mediate the translocation of Cr between metals e.g., Fe and Cr Shahid *et al.,* (2017), Zayed et a.,l (1998) . Cary *et al.,* (1977) had reported Cr uptake and translocation to the aerial shoots in Fe hyperaccumulators Brassica rapa and Spinacia oleracea signifying that Cr may be transported through Fe channels. However, the presence of Fe in the growth media reduced Cr translocation to the shoots Mallick *et al.,* (2010), which could be due to the competition of carrier channels or due to the precipitation of Fe with Cr.

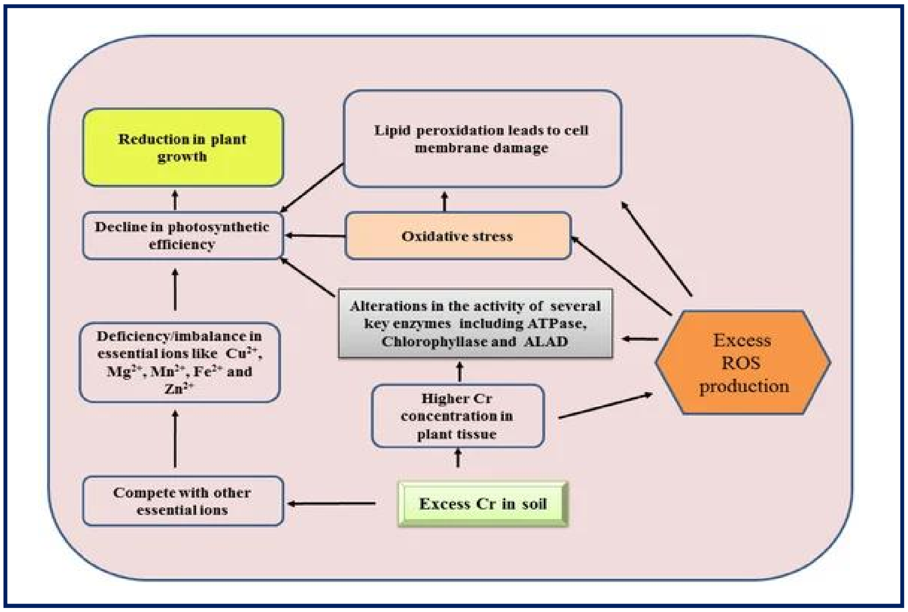


Fig. 41: Consequences of oxidative stress generated under chromium toxicity. After: Sharma *et al.,* (2020)

3-11 Effects of chromium toxicity on plant nutrients.

Chromium having a close structural resemblance to many of the essential elements can influence the mineral nutrient status in plants Ali *et al.,* (2018), Dube *et al.,* (2003) Fig. (42).

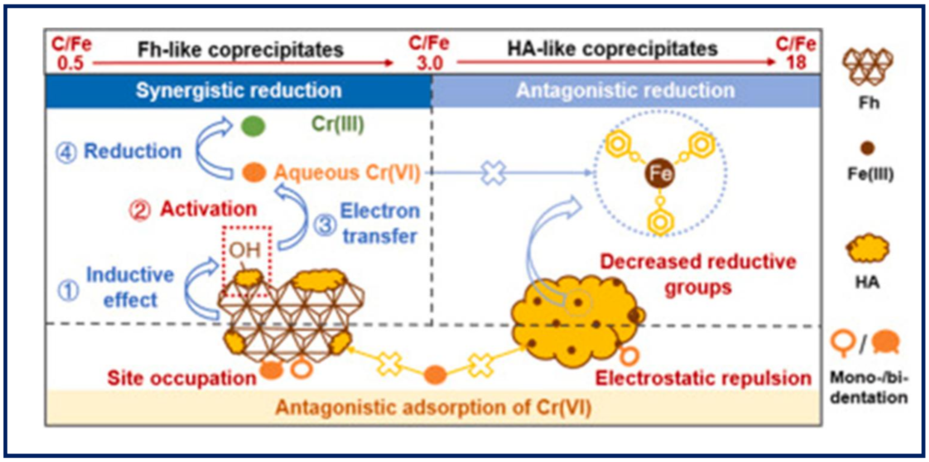


Fig. 42: Illustrated Synergistic/antagonistic effects and mechanisms of Cr (VI) adsorption and reduction by Fe (III)-HA coprecipitates. After: Wang *et al.,* (2021)

Wang *et al.,* (2021) reported that widespread Fe(III)-humic acid (HA) coprecipitates (FHCs) have substantial impacts on the adsorption and reduction of Cr(VI) in soils and sediments, but whether this process is equal to the sum of their individual components remains unknown. In this study, ferrihydrite (Fh)- and HA-like FHCs (C/Fe<3 and C/Fe>3, respectively) were synthesized by controlling the initial C/Fe ratios (0.5–18) to explore the potential synergistic/antagonistic effects during the adsorption and reduction of Cr(VI). According to the results, antagonistic effects on Cr(VI) adsorption (5%−80%) were observed on Fh- and HA-like FHCs, where the antagonistic intensity increased with increasing HA proportions, respectively caused by the more serious occupation of adsorption sites and the stronger electrostatic repulsion to Cr(VI). Notably, significant synergistic reduction effects (5%−650%) occurred on Fh-like FHCs were found to be achieved by the activation of low-molecular HA (0.1–0.3 kDa) with primary/secondary hydroxylic groups, which might be induced by the inductive effect of Fh on complexed HA molecules according to density-functional theory (DFT) calculation. While slight antagonistic reduction effects (2%−45%) by HA-like FHCs were attributed to the decreasing accessibility of Cr(VI) to reductive phenolic groups, which might be blocked within FHC particles or complexed with Fe(III) ions through cation bridges.

Chromium is a nonessential element; thus, plant has no specific mechanism for its uptake Gardea-Torresdey *et al.,* (2004); Tiwari *et al.,* (2013). Having a similar structure with sulfur phosphorus and iron, chromium may interfere with the uptake, translocation, and accumulation of these nutrients Dube *et al.,* (2003); Ulhassan *et al.,* (2019); Zaheer *et al.,* (2020) Fig.(43).

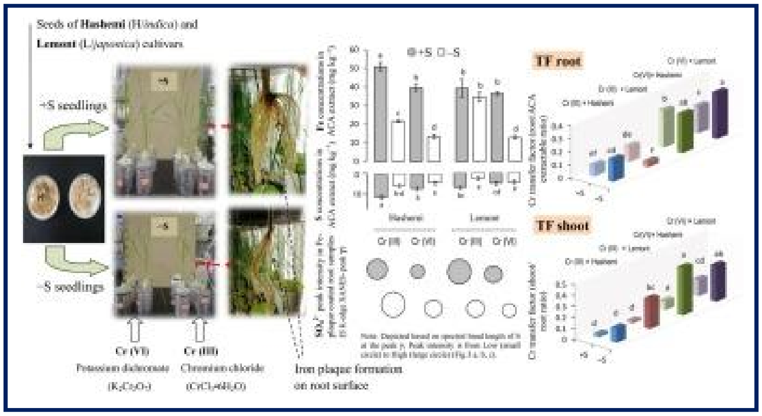


Fig. 43: Impact of sulfur addition and rhizoplane iron plaque on chromium uptake by rice (*Oryza sativa* L.) Seedlings in solution culture. After: Panel Peiman Zandi *et al.,* (2020)

Panel Peiman Zandi *et al.,* (2020) reported that heavy metal uptake is confined by other elements, namely iron (Fe) and sulfur (S). There are yet no reports on the contribution of S supply to the attenuation of chromium (Cr) uptake when different species of Cr are employed. The bioaccumulation of Cr in two cultivars of rice seedlings subjected to 1.0 mg L^{-1} Cr (III and VI) stress under S deprived or non-deprived conditions were examined in a hydroponic experiment. Sulfur nutrition promoted the root and shoot growth of rice cultivars under Cr stress. For both + S/ − S seedlings, the concentration of both Cr species followed the sequence ACA (ascorbic citrate acetic) extract > root > shoot, with less Cr accumulated in shoots of + S seedlings to that of − S seedlings. The concentrations of Cr and Fe in ACA extracts were significantly. Compared to + S treatment, Cr and Fe contents in iron plaque without S treatment were markedly reduced, especially for Cr (VI). Cr content in roots and shoots was indicated to be at par between cultivars; however, it significantly differed for S and Cr treatments. The Cr translocation between different parts of plaque-harboring seedlings was more pronounced in Cr (VI) treatment relative to Cr (III) treatment. Increased immobilization of Cr in iron plaque of + S seedlings and its subsequent reduction in aerial tissues may likely shed some light on the barrier function of iron plaques in the uptake of both Cr species by rice seedlings.

It easily interrupts the uptake of the essential elements required for the plant life cycle Sundaramoorthy *et al.,* (2010). Generally, the nutrients availability also depends on root structure and element concentration in medium Chandrasekhar and Ray, (2017); González-Pérez *et al.,* (2004). Tiwari et al. (2013) reported that chromium affects the plant metabolism via interfering with the essential nutrients or via activating enzymes at the functional sites.

3- Effects of chromium on nitrogen fixation and uptakes

Nitrogen is an essential macroelement that is a constituent of biomolecules such as nucleic acids, purines, pyrimidines, porphyrins, and co-enzymes and plays a significant role in growth, development, and produce of plants. The most readily available form of N to plants is nitrate (NO^{3-}). Nitrate reductase (NR) is a key enzyme involved in the assimilation of NO^{3-} to ammonium (NH^{4+}) as it catalyzes the reduction of NO^{3-} to NO^{2-} (nitrite), which is further converted to NH^{4+} by nitrite reductase (NiR) (Raghuram and Sopory, 1995). Sessitsch *et al.,* (2002), Janczarek *et al.,* (2014) reported that nitrogen is an essential element for plant growth and development. Major component of chlorophylls, amino acids, nucleotides, nucleic acids, coenzymes, vitamins, amines, and other plant constituents Fig.(44).

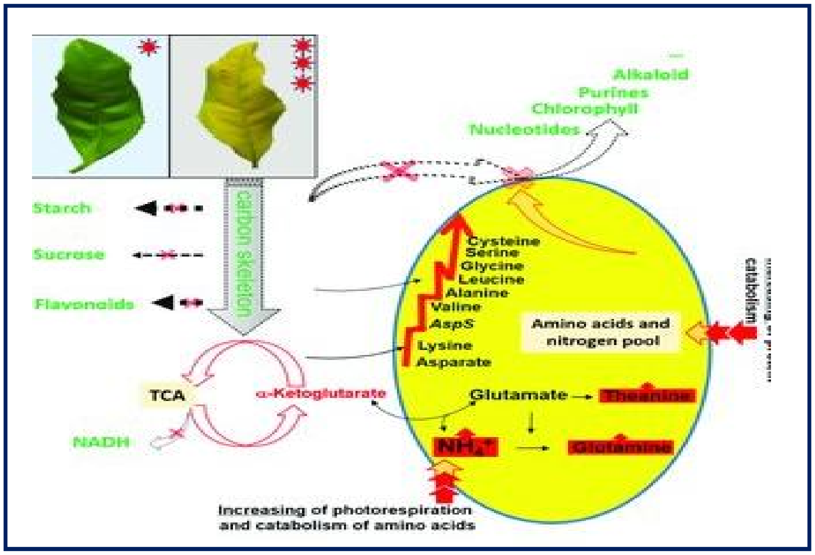


Fig. 44: Schematic presentation of amino acid metabolism as affected by the chlorotic mutation.

To be provided with nitrogen for their needs, plants absorb nitrogen in the forms of nitrate (NO^3 $^-$) and ammonium (NH^{4+}) from soil but cannot use free nitrogen gas (N_2) from the atmosphere.

The conversion of atmospheric nitrogen into ammonia is provided by many chemical processes, and biological nitrogen fixation is the most important among them Menendez *et al.,* (2017), Janczarek *et al.,* (2014). Biological nitrogen fixation is carried out with a large group of soil free-living, associative, or symbiotic prokaryotes called collectively diazotrophs Sessitsch *et al.,* (2002), Mus *et al.,* (2016), Volkogon (2000). They include the nodule bacteria from families Rhizobiaceae, Phyllobacteriaceae, Bradyrhizobiaceae, and Hyphomicrobiaceae. Menendez *et al.,* (2017), Mus *et al.,* (2016) stated that these bacteria are able to establish symbiosis with plants from Fabaceae family and accumulate atmospheric nitrogen to cover more than 60% of plant needs in nitrogen. The formation and functioning of legume-rhizobial symbiosis is a complex process with a few coordinated stages, which are regulated by signals from both nodule bacteria and the host plant. The stages include **(a)** pre infection, **(b)** infection with nodule formation, and **(c)** functioning of the mature nodule and its death Mus *et al.,* (2016), Volkogon (2000). The symbiotic interaction is initiated, when nodule bacteria infect root hair of the host plant. Chemotaxis of soil nodule bacteria to root exudates plays an important role in the initiation of symbiosis Mus *et al.,* (2016), Yost *et al.,* (2003). Both rhizobia and host plants exhibit a strong specificity. To identify rhizobia as benefit partners, the host plants secrete specific compounds, which are recognized by the homologous (compatible) bacteria. The main compounds of the root exudates are carbohydrates, organic acids, amino acids, and phenols Bais *et al.,* (2006). Root exudates attract and induce attachment of compatible rhizobia to walls of the root hair cells Halbleib and Ludden, (2000). Subsequently, rhizobia adhere to and colonize the root surface. Rhizobia are attached to root hairs by the specific surface polysaccharides, which interact with lectin receptors on root hair cell walls Mus *et al.,* (2016), Halbleib and Ludden, (2000), Skorupska *et al.,* (2006). After attachment, the bacteria interact with certain flavonoids, which are produced by root legumes. Plant flavonoids trigger the expression of bacterial nodulation genes (nod-genes), which control the formation of nodules in plant roots Halbleib, and Ludden, (2000), Ribeiro *et al.,* (2015), Foreman *et al.,* (2010). The products of nod-genes are involved in synthesis and export of specific lipochitooligosaccharides called Nod factors. Bacterial nod factors serve as signaling molecules that initiate nodule formation in root cortex Gourion *et al.,* (2015), Rinaudi and Gonzalez, (2009) Fig. (45). previously it has been assumed that binding plant lectins to bacterial surface polysaccharides plays a key role in the specificity between rhizobia and their legume hosts. In accordance with recent data, the host specificity of legume plants is presumably determined by the Nod factors and to a lesser extent by surface polysaccharides of the nodule bacteria Downie (2010). In addition to nod factors, rhizobial surface polysaccharides, such as exopolysaccharides, lipopolysaccharides, capsular polysaccharides, and cyclic glucans, are also important for development of root nodules and modulation of host specificity. In particular, binding of plant lectins to bacterial polysaccharides can influence adhesion of bacteria to root hairs in pea plants: the mutant *R. leguminosarum* strain, defective in synthesis of surface glucomannan, had an impaired ability to attach to root hairs Williams *et al.,* (2008). Recently, exopolysaccharides receptor has been identified in Lotus japonicus that controls rhizobial infection and distinguishes between compatible and incompatible exopolysaccharides Kawaharada *et al.,* (2015). In general, the formation of a nodule requires the reprogramming of differentiated root cells to form a primordium, which a nodule can develop from. The bacteria enter the developing nodule via formation of infection threads. Regulation and stages of root nodule formation have been comprehensively reviewed previously Baryla *et al.,* (2001), Schultze and sKondorosi, (1998), Geurts and Bisseling, (2002).

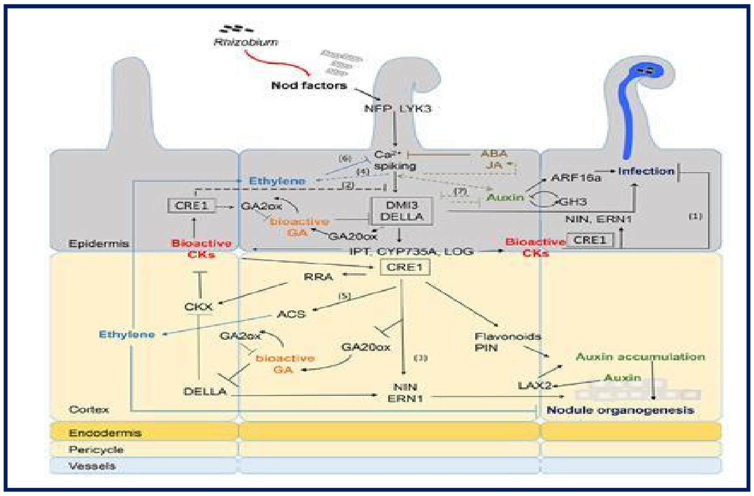


Fig. 45: Recapitulative spatio-temporal scheme of the interactions between NF signaling and downstream hormonal pathways. Rhizobia produce NFs that are perceived in root hairs (RHs) through LysM-RLK receptors such as NFP and LYK3. NF perception leads to calcium spiking and activation of DMI3 that acts upstream of the CK receptor MtCRE1. The signaling cascade involving DMI3 and CRE1 is likely involved in both epidermal and cortical signaling (black boxes). NF treatment triggers early CK biosynthesis gene (IPT/CYP735A/LOG) expression and CK accumulation in M. truncatula roots downstream of DMI3 but independently of CRE1 signaling (van Zeijl *et al.,* 2015b). Although tissue specificity of this CK production was not determined, evidence from L. japonicus and M. truncatula suggests that epidermal CK accumulation is a negative regulator of RH infection (1) and NF signaling (2) (Held *et al.,* 2014; Jardinaud *et al.,* 2016). In contrast, cortical CK is a positive regulator of nodule organogenesis (3) (Gonzalez-Rizzo *et al.,* 2006; Murray *et al.,* 2007; Reid *et al.,* 2017). Bioactive CKs are perceived by CRE1 and induce expression of NIN and ERN1 (Ariel *et al.,* 2012), which are positive regulators of both infection and nodule organogenesis (Andriankaja *et al.,* 2007; Marsh *et al.,* 2007). This induction might be partly through regulation of DELLA activities. GA is a negative regulator of DELLA protein stability. Bioactive GA pools are likely present in both epidermis and cortex early after NF treatment (Fonouni-Farde *et al.,* 2016; Jardinaud *et al.,* 2016; Herrbach *et al.,* 2017). DELLAs play a positive regulatory role on symbiotic gene expression such as ERN1 and they negatively regulate CK degradation (Fonouni-Farde *et al.,* 2016, 2017; Jin *et al.,* 2016). In contrast, CK positively regulate GA inactivation enzymes and down-regulate expression of the GA20ox activation enzyme (Fonouni-Farde *et al.,* 2018), suggesting a negative feedback of CK on GA active pools. NF signaling induces ethylene production, both independently of the LHK1/CRE1 CK pathway (4) (Reid *et al.,* 2018) and downstream of CK perception (5) (van Zeijl *et al.,* 2015b). Ethylene reduces CK production in M. truncatula roots, possibly through negative feedback on NF signaling (6) (van Zeijl *et al.,* 2015b). Ethylene negatively regulates NF-induced calcium spiking, RH infection, and nodule organogenesis (Heidstra *et al.,* 1997; Penmetsa *et al.,* 2008). Regulation of auxin biosynthetic and conjugation enzyme (GH3) genes occurs in NF treated RHs and upon S. meliloti inoculation in an NF-dependent manner (Breakspear *et al.,* 2014; Larrainzar *et al.,* 2015; Jardinaud *et al.,* 2016; Herrbach *et al.,* 2017). Reciprocal positive and negative feedback regulatory loops between some auxin and NF

regulated genes (7) was shown by comparing the combined effect of auxin and NFs to either treatment alone (Herrbach *et al.,* 2017). Downstream of CK perception, control of auxin transport in the cortex seems regulated by differential expression of PIN genes (Plet *et al.,* 2011) or accumulation of flavonoid compounds. MtLAX2 that is induced upon S. meliloti infection in vasculature and early nodule primordia, and which is required for nodule organogenesis (Roy *et al.,* 2017) also mediates auxin accumulation. In parallel, epidermal auxin signaling controls infection thread (IT) formation, at least partly through ARF16a (Breakspear *et al.,* 2014). Exogenous application of high concentrations (µM range) of ABA or JA inhibits NF-induced calcium spiking (Sun *et al.,* 2006; Ding *et al.,* 2008) but this inhibition is so far not supported by any transcriptomic data. Plain bars represent negative and plain arrows positive regulations. Dashed lines are hypothetical relationships, and solid lines have evidence from the literature. Different hormones are highlighted by different colors. CK, cytokinins; GA, gibberellins; ABA, abscisic acid; JA, jasmonic acid; NF, Nod factors. Bacteria entrapped in curled root hair and IT are shown in blue. After: Buhian and Bensmihen, (2018).

The nodule formation is completed when nodule bacteria are transformed in nitrogen-fixing bacteroids Karunakaran *et al.,* (2009), Mergaert *et al.,* (2006). The formed nodules may be either determinate or indeterminate depending on the host. Determinate nodules have a short-lived meristem, and they grow by plant cell expansion and division, resulting in nodules progressing through well-defined developmental stages. Legumes, which formed determinate nodules, include *Lotus sp., Phaseolus sp*., and *Glycine max*. In contrast, indeterminate nodules have a persistent meristem and infection is continuous. New nodule cells are subsequently infected by rhizobia residing in the nodule. *Medicago sp., Vicia sp., Trifolium sp.,* and *P. sativum* are typical legumes with indeterminate nodules Muszynski *et al.,* (2016). In nodules, bacteroids are provided with microaerobic environment required for expression of enzymes of the nitrogenase complex. A plant-produced oxygen-binding protein, called leghemoglobin Baryla *et al.,* (2001), controls oxygen supply to bacteroids. Nitrogenase complex located on internal membranes of bacteroids is responsible for ATP-dependent reduction of free nitrogen to ammonia Halbleib and Ludden, (2000), Hoffman *et al.,* (2009). Further, ammonia interacts with intracellular keto acids (α- ketoglutaric, pyruvic, or oxalic acids) in dehydrogenase and transaminase-catalyzed reactions forming respective amino acids, such as glutamine, alanine, or asparagine White *et al.,* (2009). In the form of free ammonia, amino acids or amides, nitrogen-containing substances are transported from nodules to the roots, and then to the aboveground parts of plants Munoz *et al.,* (2001). Biological nitrogen fixation is closely connected with photosynthesis, since the latter provides assimilates and energy resources to nodule bacteria, and the bacteria, in turn, provide photosynthetic apparatus of plants with nitrogen compounds White etal (2009) Voisin *et al.,* (2003).The intensity of photosynthesis and ammonium inclusion in the plant metabolism depends on content and functional activity of chloroplasts, the structural elements of the photosynthetic apparatus Wu *et al.,* (2007). At the same time, products of bacterial nitrogen fixation substantially affect the intensity of photosynthesis and transport of photo assimilates from plants to nodules Sehnke *et al.,* (2001).Thus, this is a real symbiosis providing mutual benefits for both partners, plants and bacteria

Chromium (VI) stress concentration of protein nitrogen decreased thereby, suggesting its interference with N uptake and assimilation Sharma et al. (1995) Fig. (46).

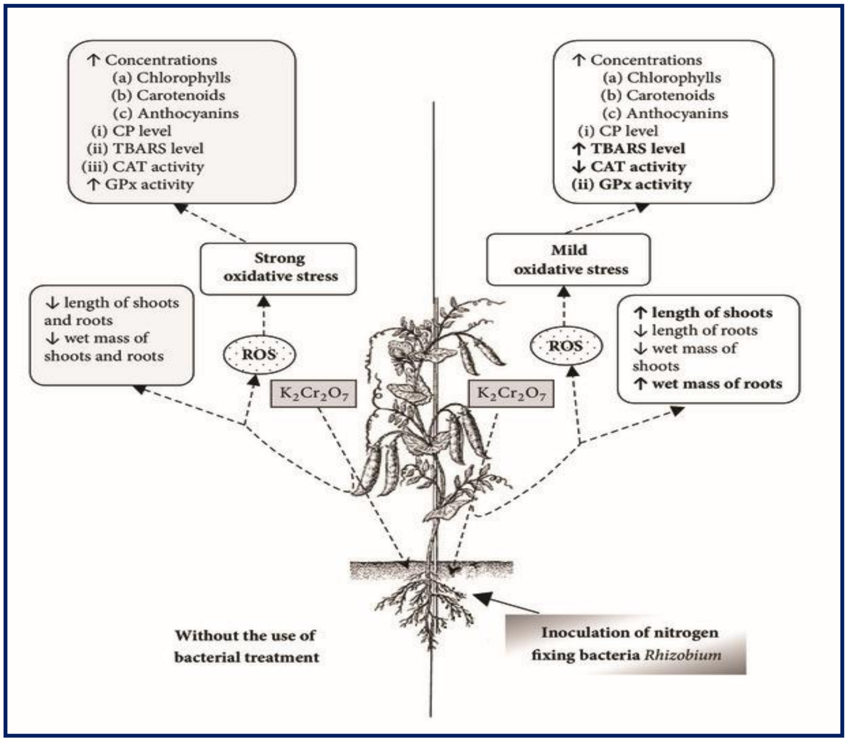


Fig. 46: Effects of Cr (IV) exposure alone and in combination with nodule rhizobacteria on selected growth parameters and ROS homeostasis in *P. sativum* plants. Arrows ↑ and ↓ indicate the increase and decrease in the parameter, respectively. After: Stambulska *et al.,* (2018)

Stambulska *et al.,* (2018) stated that the ability of nodule bacteria to form a symbiosis with legume plants depends on many environment factors, such as temperature, humidity, aeration, pH medium, soil structure, and presence of labile nitrogen forms, phosphorus, potassium, and magnesium in the soil. Heavy metals, including Cr, inhibit the activity of nitrogenase in nodules leading to decreased intensity of nitrogen fixation Sessitsch *et al.,* (2002) Mechanisms of chromium toxicity to nodules are not well studied, but one may suggest they include oxidative stress development and protein modification. Since nitrogenase is very sensitive to oxidation, chromium treatment can lead to inactivation of the enzyme and impair functioning of nodules. Several studies have reported that nitrogen-fixing bacteria can diminish the toxicity of heavy metals on host plants Johnston *et al.,* (2001) Taghavi *et al.,* (2014), Kong *et al.,* (2015). Accordingly, the nodule bacteria are exposed more to heavy metals than the host plant. Resistance of the bacteria to heavy metals is both species- and strain-specifc Kong *et al.,* (2015). One can suppose that if bacteria have powerful defense mechanisms against heavy metal toxicity, the protective effect of these bacteria on the host plant will be more pronounced. Like other bacteria, protective mechanisms of rhizobia against chromium toxicity apparently include direct and indirect reduction of chromium (Cr^{6+} to Cr^{3+}), metal binding with further isolation or elimination, and upregulation of antioxidant defense Cervantes *et al.,* (2001). In the case of exposure to Cu, the rhizobial symbiosis with *Sinorhizobium meliloti* CCNWSX0020 also upregulated expression of genes encoding components of antioxidant defense in both, plants and bacteria. The results indicated that the rhizobial symbiosis with *S. meliloti* CCNWSX0020 not only enhanced plant growth and metal uptake, but also improved the responses of plant antioxidant defense to Cu excess Kong *et al.,* (2015). Regarding Cr influence, we have recently found that inoculation with highly effective nitrogen-fixing bacteria decreased the toxic effects of chromium (IV) on *P. sativum*. Te protective Efects included improvement of the length of shoots and mass of the plant roots and enhanced levels of chlorophylls, carotenoids, and anthocyanins compared with the effects of chromium on pea plants without inoculation Fig. (46) Stambulska, (2017). In addition, treatment with potassium dichromate did not affect level of oxidized proteins but increased levels of lipid peroxidation products and decreased catalase activity in plants preinoculated with nitrogen-fixing rhizobia, but not in no inoculated pea plants Stambulska, (2017). Despite increased levels of lipid peroxidation products, pea plants grew better when treated with chromium in the presence of nodule bacteria if compared with the plants treated only with chromium. We suppose that nodule bacteria are able to decrease chromium toxicity to pea plants and their protective effects could be connected rather with modulation of synthesis of plant pigments than with involvement of enzymatic antioxidant defense. Since carotenoids and anthocyanins have antioxidant properties, they might be involved in minimization of negative effects from oxidative stress induced by chromium. It is possible that accumulation of chromium in root nodules decreased chromium transport to other plant parts allowing the latter to develop protective mechanisms that are more effective. Previous studies have demonstrated that Cr (VI) interferes with the nitrogen metabolism in plants Joshi *et al.,* (2003); Dubey and Rai, (1987); Kumar and Joshi, (2008); Gangwar and Singh, (2011). Wyszkowski and Radziemska, (2010) reported that accumulation of NO^{3-}– N was lesser in *H. vulgare* plants growing in Cr (VI)-contaminated soil. Joshi *et al.,* (2003) demonstrated that Cr(VI; 2–6 ppm) decreased the activity of NR and NiR in leaves, and nitrogenase activity in nodules, and the activities of glutamine synthetase (GS), glutamate dehydrogenase (GDH), glutamate synthase (GOGAT), and urease increased in leaves, roots, and nodules of guar (*C. tetragonoloba*).

Ulhassan *et al.,* (2019); Zaheer *et al.,* (2020), reported that both form of (NH_4^+) and (NO_3^-) ions may affect the uptake and translocation of chromium. Chromium (VI) at lower concentrations is able to fix atmospheric N by assisting the formation of nodules. However, at higher concentration of chromium , the potential of the developed nodules to fix N could be impaired, as previously recorded in Pea Bishnoi *et al.,* (1993); Handa *et al.,* (2017). Both forms of Cr (VI) and Cr (III) could limit the availability of N, reduce chlorophyll content, and disturb photosynthesis and respiration process in plants Ali *et al.,* (2013). Chromium (VI) severely affects the activity of photosystem I as compared to photosystem II Bishnoi *et al.,* (1993). Protein deficiency in plant leaves, due to lack of N, was observed in rice and wheat under chromium toxicity Nagajyoti *et al.,* (2010). The interaction between inorganic N and heavy metals such as chromium is also influenced by the specific plant species and its growth stage Ashraf *et al.,* (2017). Sulfur intake in plants decrease due to increasing chromium in plants Wuana and Okieimen, (2011). Nitrogen availability is also influenced by the source of nitrogen. Calcium, nitrates for instance, is able to reduce the accumulation of chromium in plants as compared to the ammoniacal form Ali *et al.,* (2013).

4- Effects of chromium on phosphorus and potassium uptakes

Rana *et al.,* (2020) stated that phosphorus is the second most important nutrient after nitrogen; it has a key role in several metabolic processes in plants. Chromium (VI) is structurally similar to phosphorus. Therefore, interferes of chromium with the uptake, translocation and/or accumulation of phosphorus, causing phosphorus deficiency (Ma *et al.,* 2020; Zhu *et al.,* 2016). In watermelons, the reduced level of chromium increased the uptake of phosphorus in order to compete with other metals such as Zn and Fe Dube *et al.,* (2003). Sharma *et al.,* (2020) reported that heavy metal stress affects nutrient uptake in plants by interacting with other essential minerals. Chromium restricts the uptake of nutrients in soil by forming insoluble compounds Chigonum *et al.,* (2019). Nutrient uptake is thereby, inhibited by the metal toxicity especially, when the concentration of the metal exceeds its permissible limits Osu *et al.,* (2016) . For instance, excessive Cr had been observed to reduce the uptake of essential minerals like iron (Fe), magnesium (Mg), phosphorus (P) and calcium (Ca) by masking the sorption sites and forming insoluble complexes Kabata-Pendias and Szteke, (2015), Osu *et al.,* (2016) . However, Cr transport to different parts of *Citrullus* plants had increased leading to enhancement in the concentrations of manganese (Mn) and P, and reduction in sulphur (S), copper (Cu), zinc (Zn) and iron (Fe) contents in the leaves, suggesting that Cr disturbs the nutrient balance Dube *et al.,* (2003) . Turner and Rust, (1971) also suggested the similar effects of Cr on the uptake of various nutrients under Cr toxicity. A gradual decrease in the uptake of micronutrients like Zn, Cu, Fe, Mn and macronutrients like potassium (K), P and nitrogen (N) had been noticed in the paddy plants *(Oryza sativa L.)* under excessive Cr exposure Sundaramoorthy *et al.,* (2010) . This reduced nutrient uptake may occur due to decline in the root growth and impairment of the root penetration under Cr toxicity, or may be due to the decrease in essential element translocation because of the displacement of nutrients from the physiologically important binding sites Shahzad *et al.,* (2018), Mengel and Kirkby, (1987).

It has been reported that there is a competition between chromium (VI) and phosphorus to enter into plant cells James and Bartlett, (1984). High concentration of chromium result in reduced plant growth and phosphorus concentration in plant leaf tissues.

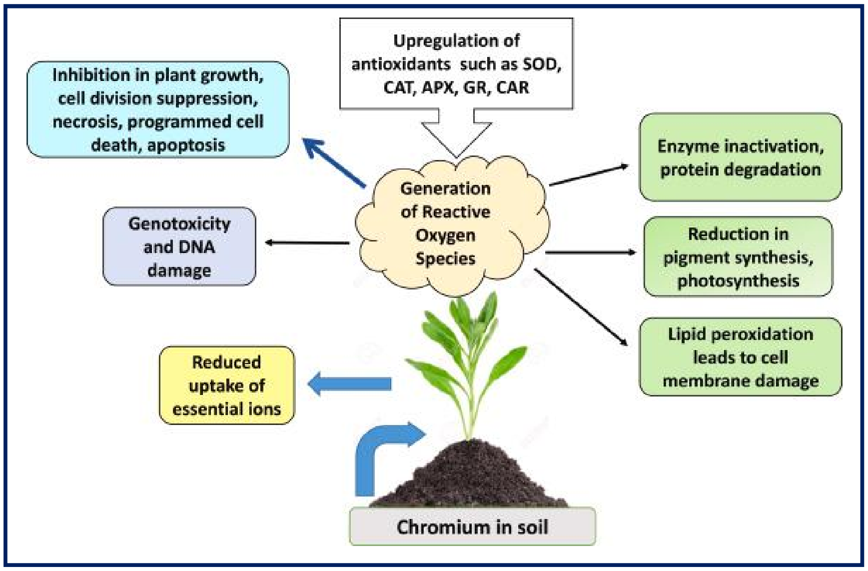


Fig. 47: Illustrates chromium concentration result in reduced plant growth and phosphorus concentration in plant leaf

Likewise, the leaf area is reduced and the light-dependent reactions are hindered Kumar *et al.,* (2016), Pradhan *et al.,* (2017). In several cases, phosphorus concentration was reduced in roots and increased in younger leaves at 0.2 mM chromium, but it decreased beyond this level in *Citrullus* Dube *et al.,* (2003). High chromium concentration antagonistically affected root growth and induced the expression of genes responsive to Pi scarcity López-Bucio *et al.,* (2014).Chromium and potassium (K) interaction is also antagonistic like other macronutrients, where 0.1 ppm of chromium was able to decrease K level in soybean shoots Turner and Rust, (1971). Sundaramoorthy et al. (2010) reported a decreased uptake of K with increasing s (VI) level in flooded rice plants.

6- Genetic mechanisms to control Cr toxicity in plants,

A significant problem is avoiding and reducing the harmful effects of heavy metals contamination in soil Zeeshan *et al.,* (2021). Genetic engineering can significantly improve a plant's ability to transform, translocate, and lessen the adverse impacts of heavy metals Raza *et al.,* (2021). Omic tools have gained a lot of interest recently for their use in plant development and programs to mitigate agricultural production challenges, especially, to mitigate heavy metal stress Khan *et al.,* (2021). To identify target genes, proteins, and metabolites linked to chromium detoxification and stress tolerance responses in plants, genomics, proteomics, and metabolomics have become effective methods Chaudhary *et al.,* (2019). It is possible to modify the chromium stress responsive genes, proteins, and metabolites to either increase plant tolerance to chromium stress or decrease chromium accumulation Thakur *et al.,* (2019). Tools for genetic engineering that are particularly effective at changing the genes involved in the acquisition, transport, and accumulation of chromium inside the plant are necessary for this type of manipulation Khan *et al.,* (2021). The main goal of genetic engineering is the creation of tolerant varieties using either a transgenic approach or genome editing Raza *et al.,* (2021). Anwar and Kim, (2020) reported that through genome editing active participation in the control of plant metabolism, essential genes important for increased metal tolerance have been developed into transgenics, which provide insights into how to understand and improve the tolerance capacity of plants. A successful method for creating resistant cultivars is to transfer candidate genes from plants with a high tendency for HM hyper-accumulation (Rahman *et al.,* 2022). The best way to reduce metal toxicity within cellular locations is to use transgenic plants with altered efficiencies for metal transport into vacuoles Khan *et al.,* (2021). Heavy metals (HM) transporter genes are thought to be potential candidates for genetic engineering to improve metal tolerance in plants Zhang *et al.,* (2018). OsMTP1 in cultivated tobacco *(Nicotiana tabacum)* and PgIREG1 in Arabidopsis are two examples of metal transporter genes that have been genetically modified Merlot *et al.,* (2014); Das *et al.,* (2016) Fig. (48). Other metal transporter genes include those that encode metal chelators, metallothioneins (MTs) Peng *et al.,* (2017), and genes associated with antioxidant machinery Peng *et al.,* (2017); Raza *et al.,* (2021).

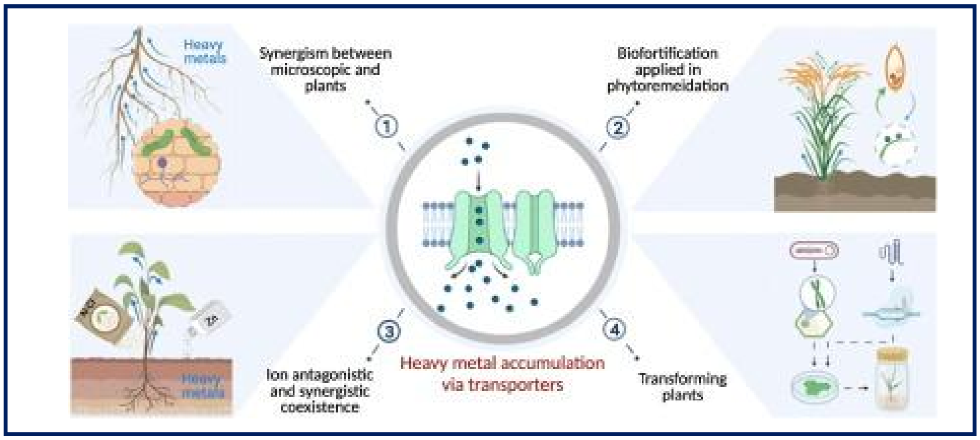


Fig. 48: Illustrates heavy metal transporters functional mechanisms regulation and application in phytoremediation. After: Yang *et al.,* (2021)

Yang *et al.,* (2021) stated that heavy metal pollution in soil is a global problem with serious impacts on human health and ecological security. Phytoextraction in phytoremediation, in which plants uptake and transport heavy metals (HMs) to the tissues of aerial parts, is the most environmentally friendly method to reduce the total amount of HMs in soil and has wide application prospects. However, the molecular mechanism of phytoextraction is still under investigation. The uptake, translocation, and retention of HMs in plants are mainly mediated by a variety of transporter proteins. A better understanding of the accumulation strategy of HMs via transporters in plants is a prerequisite for the improvement of phytoextraction. In this review, the biochemical structure and functions of HM transporter families in plants are systematically summarized, with emphasis on their roles in phytoremediation. The accumulation mechanism and regulatory pathways related to hormones, regulators, and reactive oxygen species (ROS) of HMs concerning these transporters are described in detail. Scientific efforts and practices for phytoremediation carried out in recent years suggest that creation of hyperaccumulators by transgenic or gene editing techniques targeted to these transporters and their regulators is the ultimate powerful path for the phytoremediation of HM contaminated soils. The use of transgenic techniques to increase resistance to metal oxidation has also been documented. Transgenic hyperaccumulators may be created by manipulating the antioxidant system to maintain redox equilibrium to avoid the destruction of biomolecules such as DNA, proteins, and lipids and to maintain the structural and functional stability of cellular structures of plant under chromium stress Du *et al.,* (2019). Transgenic plants that overexpress antioxidant genes for SOD, CAT, and APX with reduced ROS generation under chromium stress have been created to prevent metal toxicity induced oxidative stress Gao *et al.,* (2016) Fig. (49).

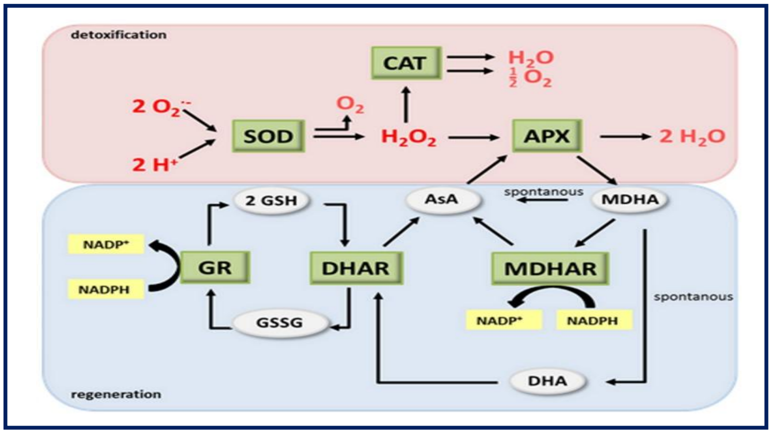


Fig. 49: Illustrates the antioxidant system. (modified after Buchanan *et al.,* 2002). AsA, ascorbate; DHA, dehydroascorbate; SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; MDHA, monodehydroascorbate; MDHAR, MDHA reductase; DHAR, DHA reductase; GR, glutathione reductase; GSH glutathione; GSSG, glutathione disulphide. After: Groß *et al.,* (2013)

Additionally, enhanced antioxidant systems in transgenic lines are associated with higher growth performance in terms of photosynthesis, mineral uptake, maintenance of redox homeostasis, and enzyme activity Khan *et al.,* (2021). Although transgenic lines reated for over-expression traits do not always show the expected benefits, they can nevertheless have positive consequences by influencing the alternative tolerance mechanisms. The phytochelatins (PCs), which contain hazardous metal ions and are enzymatically generated from GSH, amino acids, organic acids, or MTs, are another crucial area for improving the chromium stress tolerance in plants Yadav, (2020). It should be noted that only MTs have coding genes, but the production of other compounds (such as GSH, amino acids, and organic acids) is controlled by the actions of the enzymes involved. Better physiological and transformed plants Khan *et al.,* (2021), display biochemical characteristics, including membrane function and antioxidant activity. According to Ai *et al.,* (2018), overexpression of MYB1 from grown radish improved PC and anthocyanin synthesis, giving transgenic Petunia higher resistance against several metal toxicities, including chromium Fig. (50).

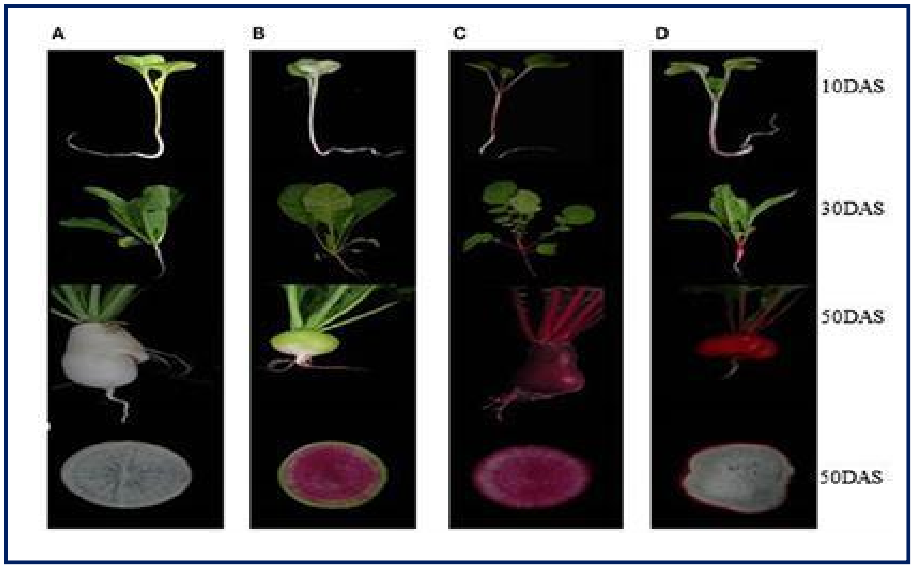


Fig. 50: Illustrates four different colored radish genotypes at different developmental stages. (A) “NAU-XBC”, (B) “NAU-XLM”, (C) “NAU-YZH”, (D) “NAU-YH”. After: Muleke *et al.,* (2017)

Muleke *et al.,* (2017) Anthocyanins are natural pigments that have important functions in plant growth and development. Radish taproots are rich in anthocyanins that confer different taproot colors and are potentially beneficial to human health. The crop differentially accumulates anthocyanin during various stages of growth, yet molecular mechanisms underlying this differential anthocyanin accumulation remains unknown. In the present study, transcriptome analysis was used to concisely identify putative genes involved in anthocyanin biosynthesis in radish. Spatial-temporal transcript expressions were then profiled in four-color variant radish cultivars. From the total transcript sequences obtained through illumina sequencing, 102 assembled unigenes, and 20 candidate genes were identified to be involved in anthocyanin biosynthesis. Fifteen genomic sequences were isolated and sequenced from radish taproot. The length of these sequences was between 900 and 1,579 bp, and the unigene coverage to all of the corresponding cloned sequences was more than 93%. Gene structure analysis revealed that RsF3′H is intronless and anthocyanin biosynthesis genes (ABGs) bear asymmetrical exons, except RsSAM. Anthocyanin accumulation showed a gradual increase in the leaf of the red radish and the taproot of colored cultivars during development, with a rapid increase at 30 days after sowing (DAS), and the highest content at maturity. Spatial-temporal transcriptional analysis of 14 genes revealed detectable expressions of 12 ABGs in various tissues at different growth levels. The investigation of anthocyanin accumulation and gene expression in four color variant radish cultivars, at different stages of development, indicated that total anthocyanin correlated with transcript levels of ABGs, particularly RsUFGT, RsF3H, RsANS, RsCHS3 and RsF3′H1. Our results suggest that these candidate genes play key roles in phenotypic and spatial-temporal anthocyanin accumulation in radish through coordinated regulation and the major control point in anthocyanin biosynthesis in radish is RsUFGT. The present findings lend invaluable insights into anthocyanin biosynthesis and may facilitate genetic manipulation for enhanced anthocyanin content in radish. They also reported that four advanced inbred radish lines “NAU-YH”, “NAU-XLM”, “NAU-XBC”, and “NAU-YZH” were used. The cultivars exhibit red skin-white flesh, green skin-pink-purple flesh, white skin white flesh and red skin-red flesh, respectively Fig. (50) . Seeds were selected and surface sterilized before being germinated on moist filter paper in darkness for 3 days. They were then transplanted into plastic pots containing 1:1 mixture of sterilized soil and peat substrate, and cultured in the greenhouse. The growth conditions included a 14 h light/10 h darkness photoperiod with an average temperature of 18◦C. The inability of radish cortex cells to undergo division and expansion results in splitting, an occurrence that is vital for the initiation of taproot thickening. The development of cortex splitting is an important signal of the initiation of taproot thickening growth in radish due to the inability of the cortex cells to undergo division and expansion Wang *et al.,* (2013). Cortex splitting has been found to begin at around 12 days after sowing (DAS), thus 10 DAS is the pre-cortex splitting, while the peak of root cortex splitting is at 30 DAS. The maximum taproot thickening is achieved at 50 DAS. Subsamples of leaf and taproot issues were collected at 10 DAS (pre-cortex splitting stage), 30 DAS (cortex splitting stage) and 50 DAS (taproot thickening stage). At maturity stage, prior to experiments, radishes were briefly, manually peeled to separate the skin and the flesh, which were then cut into small cubes. Samples in three biological replicates were separated into different batches for anthocyanin and total RNA extraction. Samples for anthocyanin were used immediately, while those for RNA extraction were frozen in liquid nitrogen and stored at −80◦C until use.

Improved growth and stomatal density were seen in MYB1 over-expressing lines mainly due to the maintenance of relative water content (RWC), chlorophyll, and antioxidant activity. Transgenic aimed at creating cultivars with improved metal tolerance will have a considerable impact on crop production in the future Ai *et al.,* (2018). The engineering of transcription factors (TFs) that control the synthesis of important metabolic chemicals also has an impact on the Chromium stress tolerance in addition to the previously described essential regulators of metal tolerance. Many transcription factors (TF) gene families play a vital role in the ability of HMs to withstand stress, including R2R3-type MYB, ZAT6, Zinc-Finger type, bZIP, GeBP-LIKE 4 (GPL4), and NAC Khan *et al.,* (2021); Raza *et al.,* (2021). It was noted that transgenic rice that overexpresses OsMYB-R1 has a noticeable increase in lateral roots, which was assumed to be related to improved tolerance to chromium Tiwari *et al.,* (2020). Further supporting the role of lateral roots in chromium tolerance is the correlation between the increase in lateral roots and a corresponding increase in auxin accumulation in transgenic lines as compared to wild type plants Fig.(51). Along with that, it was also thought that the OsMYB-R1 over-expressing lines had significantly higher antioxidant activity and proline accumulation, which were likely mediated by salicylic acid (SA) signaling and contributed to the transgenic rice's ability to tolerate chromium Tiwari *et al.,* (2020).

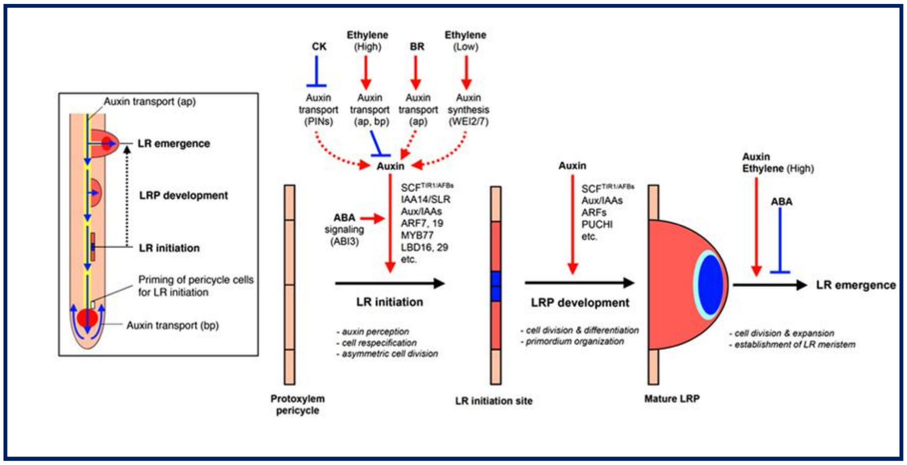


Fig. 51: Hormonal and genetic control of lateral root formation in Arabidopsis. LR formation is a three-stage process consisting of LR initiation, LRP development, and LR emergence. LR initiation is positively regulated by auxin but negatively regulated by CK and high concentrations of ethylene [high concentrations of exogenous 1-aminocyclopropane-1-carboxylic acid (ACC)]. The polar auxin transport with a balance of influx and efflux in both acropetal and basipetal directions is necessary for LR initiation and setting up auxin gradient to organize LR primordium (LRP; blue color in LR initiation site and primordium). CK inhibits auxin maxima by altering the expression of PINs, thereby inhibiting auxin gradient for LR initiation. High concentrations of ethylene or exogenous ACC, an ethylene precursor, inhibited LR initiation by enhancing acropetal (ap) and basipetal (bp) auxin transport. BR promotes LR initiation by increasing acropetal (ap) auxin transport. Low concentrations of ethylene (low concentrations of exogenous ACC) promote LR initiation by increasing Trp-dependent auxin synthesis mediated by WEI2 and WEI7. Normal ABA signaling mediated by ABI3 is necessary for proper auxin responsiveness for LR initiation. Auxin also promotes LR primordium development but CK inhibits LR primordium development and affects auxin maxima by altering the expression of PINs. ABA inhibits LR emergence whereas auxin and ethylene (via high concentrations of exogenous ACC) promotes LR emergence (modified from Fukaki and Tasaka, 2009). After: Jung and Susan, (2013).

Jung and Susan, (2013). Root system architecture (RSA) the spatial configuration of a root system is an important developmental and agronomic trait, with implications for overall plant architecture, growth rate and yield, abiotic stress resistance, nutrient uptake, and developmental plasticity in response to environmental changes. Intrinsic, hormone-mediated pathways, intersecting with pathways that perceive and respond to external, environmental signals, modulate Root architecture. The recent development of several non-invasive 2D and 3D root imaging systems has enhanced our ability to accurately observe and quantify architectural traits on complex whole-root systems. Coupled with the powerful markerbased genotyping and sequencing platforms currently available, these root phenotyping technologies lend themselves to large-scale genome-wide association studies, and can speed the identification and characterization of the genes and pathways involved in root system development. This capability provides the foundation for examining the contribution of root architectural traits to the performance of crop varieties in diverse environments. This review focuses on our current understanding of the genes and pathways involved in determining RSA in response to both intrinsic and extrinsic (environmental) response pathways, and provides a brief overview of the latest root system phenotyping technologies and their potential impact on elucidating the genetic control of root development in plants. As a result, TFs are essential molecular regulators that help plants tolerate chromium stress and lessen the negative effects of exposure to metals, which supports plant growth and development. However, the identification and functional confirmation of several additional TFs from diverse TF families, many of which are still mostly unknown, could, therefore, be helpful in creating enhanced plant types with high HM tolerance.

7- Mitigation of Chromium Toxicity in Agriculture Lands

Chromium contaminants in several ecosystems have dramatically increased due to growing urbanization and industry, which has become a serious concern across the globe. Chromium contamination on plants and human health, it is critically important to look into quick, efficient and cost effective approaches to remove chromium from the soil and other environmental locations. In addition, chromium poses a potential risk because it is not degradable and will remain in the soil for years. We systematically discuss copious mitigation approaches against chromium toxicity in sustainable agriculture. The role of chemical priming in mitigating chromium toxicity such as hormones, NO, H_2S, polyamines, compatible solutes, ions, etc.~~)~~are reported . Mitigating heavy metals toxicity in plants is shown in Fig. (52).

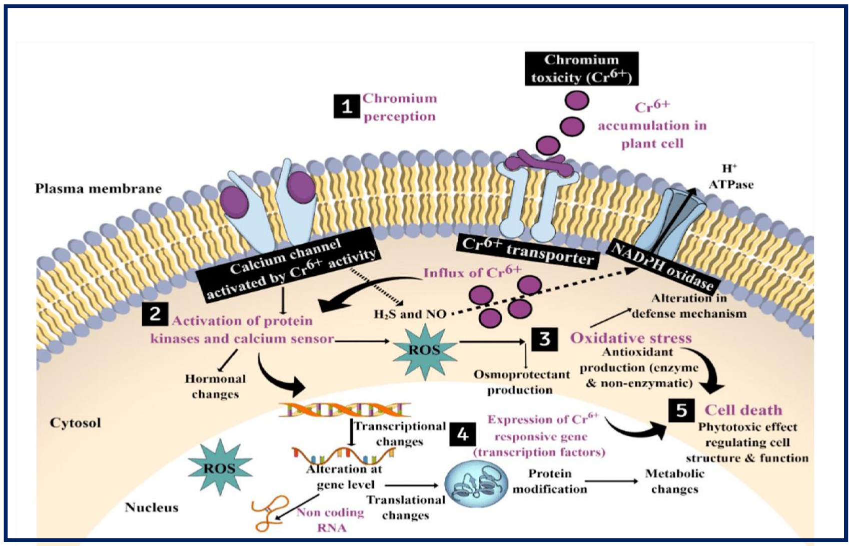
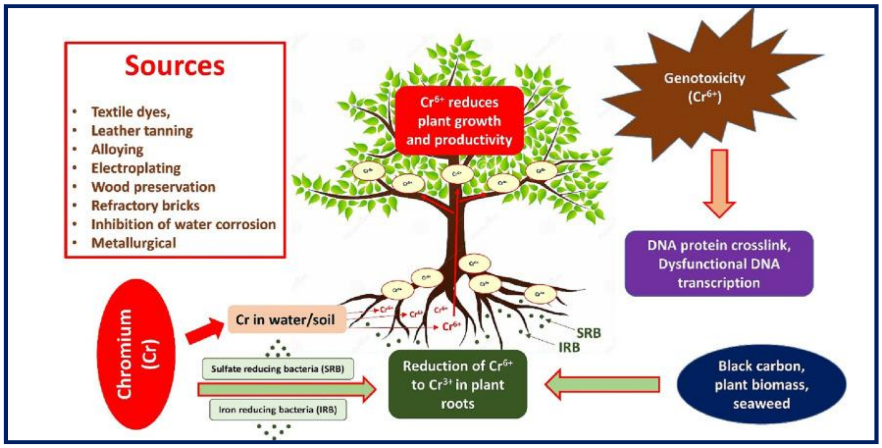


Fig. 52: A hypothetical model showing Cr perception and signal transduction in plants. Plants have different types of sensors, such as receptor-like kinases and channels, which can take part in early Cr perception. Following Cr sensing, an ROS burst and calcium waves will occur, which can be sensed by different sensors, such as kinases or calcineurin B-like protein (CBL)-CBL interacting protein kinase (CIPK) and calmodulin (CaMs)/calmodulin-like proteins (CMLs), which can lead to significant transcriptional and translational reprogramming in several intracellular compartments, as depicted in the figure. The Cr (Vi) transporter in this instance is a sulphate or phosphate transporter, which could ease its entry into the root cells. We also highlight the roles of various molecules, including hormones, nitric oxide (NO), hydrogen sulfide (H2S), and antioxidants, in Cr-mediated signaling. After: Ali *et al.,* (2023)

Also the role of nanoparticle, which has become one of the major frontiers against heavy metals toxicity in sustainable agriculture.

7-1. Minimization of Chromium Toxicity Through Chemical Treatments

Tian and Lei, (2007), Paredes *et al.,* (2009) reported that chemical treatments is one of the best approaches to intensify the tolerance of both cultivated and non-cultivated plant species hostile to a wide range of stress factors. However, to date, very few reports have backed this commitment in connection to its role in the stress tolerance of plants against abiotic stress factors. Shanker *et al.,* (2005) stated that the chromium produced because of metallurgical processes and effluent discharges used in the tanning and preservation of wood is extremely toxic to plants Fig, (53).



Fig, 53: Illustrates source impact factors affecting chromium uptake by plants and mechanisms behind phytoremediation of chromium-contaminated soils. After: Sadeeq Ullah *et al.,* (2023)

Becquerel *et al.,* (2003) reported that chromium exists in different stable forms such as trivalent chromium (III) and hexavalent chromium (VI) species, with the latter being most stable and toxic to plant metabolism and growth. The toxicity of chromium leads to the production of ROS, such as hydroxyl radicals (•OH), hydrogen peroxide (H_2O_2), and superoxide anions (O2•), which lead to several serious complications in plants, including lipid peroxidation and inhibition of enzyme activities, growth retardation, degradation of photosynthetic pigments, and chromosomal aberrations. Hence, to minimize the detrimental effects of chromium in plants, scientists have devised diverse strategies, such as chelation, detoxification, and subcellular compartmentalization of chromium, using both biological as well as chemical methods. Bamagoos *et al.,* (2022), Cheng *et al.,* (2022) stated that several reports have suggested that chromium toxicity can be alleviated by exogenous application of ABA, glutathione, Cys and sulfur, and melatonin Fig. (54). Yang *et al.,* (2023) stated that melatonin, a pleiotropic regulatory molecule, is involved in the defense against heavy metal stress. Using a combined transcriptomic and physiological approach to investigate the underlying mechanism of melatonin in mitigating chromium (Cr) toxicity in *Zea mays L*. Maize plants were treated with either melatonin (10, 25, 50 and 100 µM) or water and exposed to 100 µM $K_2Cr_2O_7$ for seven days. Melatonin treatment significantly decreased the chromium content in leaves. However, the chromium content in the roots was not affected by melatonin. Analyses of RNA sequencing, enzyme activities, and metabolite contents showed that melatonin affected cell wall polysaccharide biosynthesis, glutathione (GSH) metabolism, and redox homeostasis. During chromium stress, melatonin treatment increased cell wall polysaccharide contents, thereby, retaining more chromium in the cell wall. Meanwhile, melatonin improved the GSH and phytochelatin contents to chelate chromium, and the chelated complexes were then transported to the vacuoles for sequestration. Furthermore, melatonin mitigated chromium -induced oxidative stress by enhancing the capacity of enzymatic and non-enzymatic antioxidants. Moreover, melatonin biosynthesis-defective mutants exhibited decreased chromium stress resistance, which was related to lower pectin, hemicellulose 1, and hemicellulose 2 than wild-type plants. These results suggest that melatonin alleviates chromium toxicity in maize by promoting chromium sequestration, re-establishing redox homeostasis, and inhibiting chromium transport from the root to the shoot. They also reported that modulation of melatonin content in *Arabidopsis* confers enhanced chromium Stress Tolerance to further confirm the positive role of melatonin in regulating the heavy metal binding ability of the cell wall; a melatonin biosynthesis-defective snat mutant was employed. Under chromium stress, exogenous melatonin-treated wild-type (WT) plants grew better and displayed a higher level of endogenous melatonin, while the snat mutants grew worse and showed a lower level of endogenous melatonin in comparison to non-treated WT plants (Fig. 54 A,B). Melatonin-treated WT plants displayed higher root length, while the snat mutants showed lower root lengths than non-treated WT plants (Fig. 54 C). Moreover, melatonin-treated WT plants displayed higher levels of pectin, HC1, HC2, and PME, while the snat mutants showed lower levels of pectin, HC1, HC2, and PME in comparison to non-treated WT plants (Fig. 54 D–G). Melatonin and chromium induced changes in gene transcripts involved in melatonin biosynthesis in maize roots and leaves (A). The effect of melatonin on endogenous melatonin content in maize under chromium stress (B). Different letters in one measure (roots or leaves) denote significant differences at $p < 0.05$. Data are shown as mean ± SE (n = 3). 2.8. Modulation of Melatonin Content in *Arabidopsis* confers enhanced chromium Stress Tolerance to further confirm the positive role of melatonin in regulating the heavy metal binding ability of the cell wall; a melatonin biosynthesis-defective snat mutant was employed. Under chromium stress, exogenous melatonin-treated wild-type (WT) plants grew better and displayed a higher level of endogenous melatonin, while the snat mutants grew worse and showed a lower level of endogenous melatonin in comparison to non-treated WT plants (Fig. 54 A,B). Melatonin-treated WT plants displayed higher root length, while the snat mutants showed lower root lengths than non-treated WT plants (Fig. 54 C). Moreover, melatonin-treated WT plants displayed higher levels of pectin, HC1, HC2, and PME, while the snat mutants showed lower levels of pectin, HC1, HC2, and PME in comparison to non-treated WT.

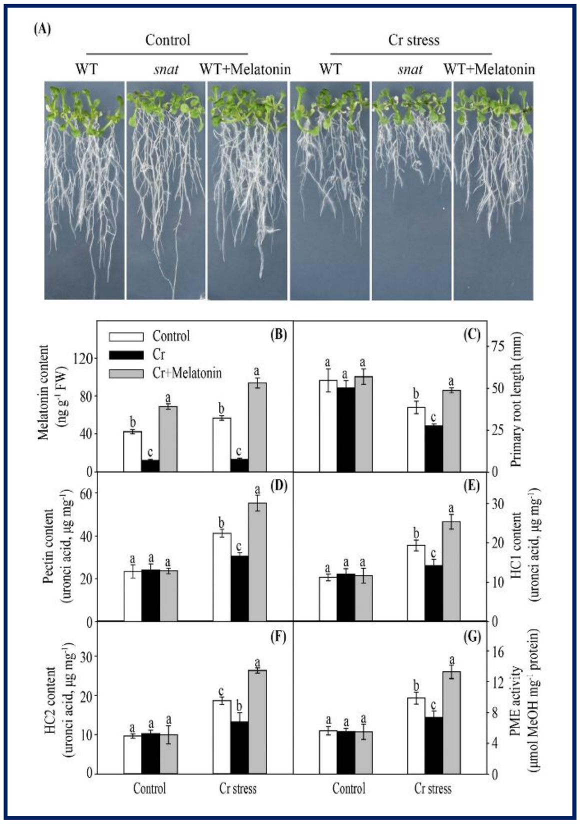


Fig. 54: Illustrates Phenotypes of *Arabidopsis* after Cr stress treatment (A). The modulation of melatonin affects endogenous melatonin content (B), root growth (C), uronic acid contents of cell wall polysaccharides ((**D**), Pectin; (**E**), hemicellulose 1; (**F**), hemicellulose 2), and pectin methyl esterase (PME) activity (**G**) in *Arabidopsis* roots under Cr stress. Different letters in one measure (control or chromium stress) denote significant differences at $p < 0.05$. Data are shown as mean ± SE (***n*** = 3). After Yang *et al.,* (2023)

Huang *et al.,* (2011) stated that metallothioneins (MTs) have emerged as important ligands to chelate and detoxify heavy metal ions such as Chromium in plants way back. Chen *et al.,* (2010) reported that under salinity and drought stress, genes such as metallothionein protein (BnMP1) and metallothioneinlike (LSC54) for MT were upregulated in B. napus, proving a lead role of MTs in stress tolerance. Xu *et al.,* (2008), Hu *et al.,* (2009) suggested that exogenous application of H_2S led to enhanced expression of MT genes in plants, thus providing a platform for chemical priming of plants to overcome chromium toxicity. For instance, Mustafa *et al.,* (2009) reported that exogenous application of H_2S helped to overcome the toxic effects of chromium (VI) in *B. napus* by enhancing the activity of antioxidant enzymes, decreasing lipid peroxidation, and increasing the thiol and chlorophyll content Fig.(55).

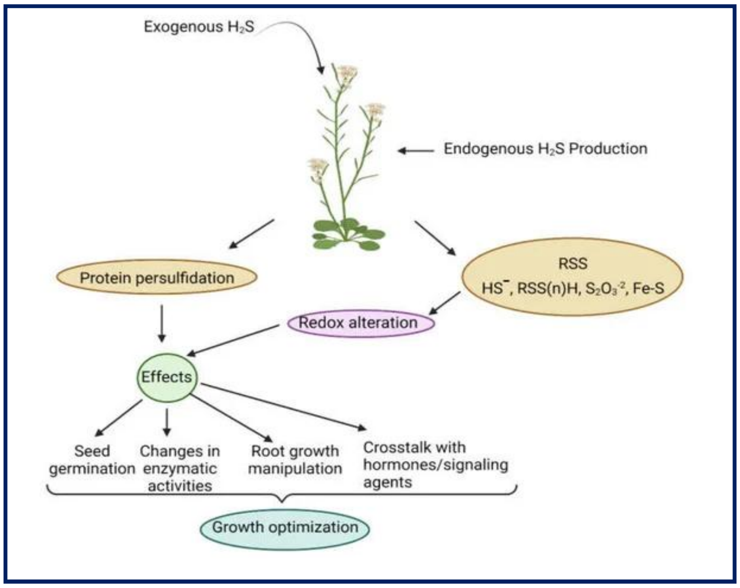


Fig. 55: Overview of hydrogen sulfide (H_2S) production and the regulation of several physiological, metabolic, and morphological processes by H_2S to optimize growth in plants. After: Khan *et al.,* (2022)

Similarly, it was reported that exogenous application of 5-amenolevulinic acid (ALA) enhanced the growth and metabolism of plants and decreased the concentration of chromium in B. napus under chromium toxicity Fig (56). Kaya *et al.,* (2023) reported that chromium [Cr (VI)] pollution is a major environmental risk, reducing crop yields. 5- Aminolevunic acid (5-ALA) considerably improves plant abiotic stress tolerance by inducing hydrogen peroxide (H_2O_2) and nitric oxide (NO) signalling. They noticed that chromium alone decreased plant biomass and photosynthetic pigments, but increased oxidative stress markers, i.e., H_2O_2 and lipid peroxidation (as MDA equivalent). Electrolyte leakage (EL), nitric oxide (NO), nitrate reductase (NR), phytochelatins (PCs), glutathione (GSH), and enzymatic and non-enzymatic antioxidants were also increased. However foliar application with 5-ALA before chromium treatment gradually improved plant growth and photosynthetic pigments, whereas both H_2O_2 , MDA content, and Electrolyte leakage (EL) were diminished, in additional enhancements of enzymatic and non-enzymatic antioxidants, NR activity, and NO synthesis. In chromium -treated tomato seedlings, 5-ALA enhanced GSH and PCs, which modulated chromium sequestration to make it nontoxic. 5-ALA-induced chromium tolerance was further enhanced by sodium nitroprusside (SNP), a nitric oxide (NO) donor. When sodium tungstate (ST), a NR inhibitor, was supplied together with 5-ALA to chromium -treated plants, it eliminated the beneficial effects of 5-ALA by decreasing NR activity and nitric oxide (NO) synthesis, while the addition of SNP inverted the adverse effects of ST. We concluded that NR-generated NO mediates the mechanism by which 5-ALA induced chromium tolerance in tomato seedlings. Thus, NR and nitric oxide (NO) are twin players, reducing chromium toxicity in tomato plants via antioxidant signalling cascades. Nitric oxide (NO) was found to trigger spermine in order to reduce the accumulation of Cr in rice plants in addition to its role in increasing carbon assimilation and reducing ROS-mediated damage Basit *et al.,* (2022) Fig. (57). Moreover, it was reported that taurine aided in the protection against lipid peroxidation in membranes and ROS scavenging to promote plant growth Hao *et al.,* (2004). This amino acid was reported to enhance the growth of wheat plants by reducing the oxidative damage under chromium toxicity stress Ahmad *et al.,* (2020). These results also showed that taurine triggered an increase in the concentrations of nutrients and secondary metabolites (phenolics and flavonoids) to alleviate chromium toxicity.

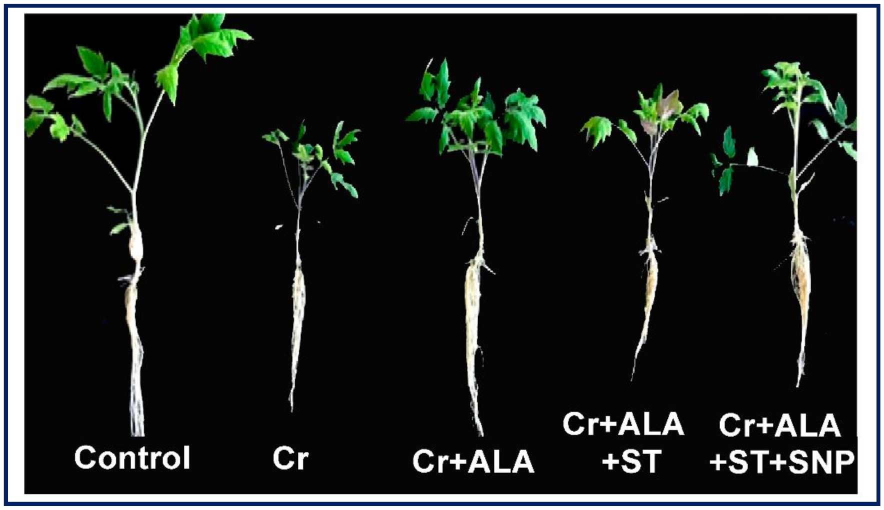


Fig. 56: The effects of chromium (Cr) alone, or combined with 5-aminolevulinic acid (5-ALA), sodium tungstate (ST), and sodium nitroprusside (SNP) on tomato seedlings. Chromium was applied for 14 days on 13-day-old tomato seedlings pre-treated with 5-ALA for 3 days. Photographs were taken at the end of the experiments with both control seedlings and treatments being 27 days old. After Kaya *et al.,* (2023).

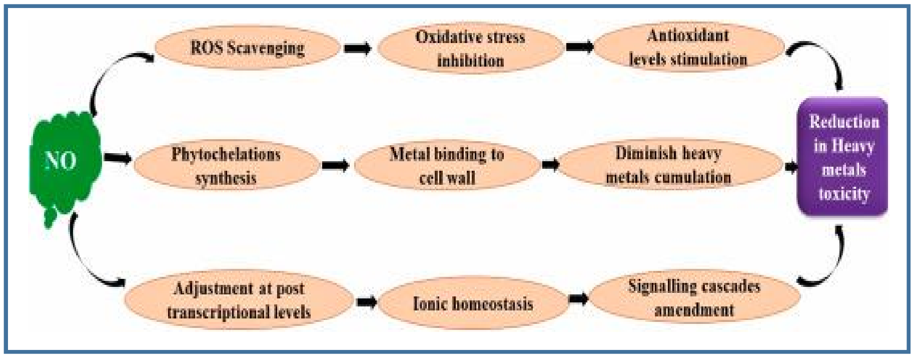


Fig. 57: Illustrates nitric oxide mediated alleviation of abiotic challenges in plants. After: Praveen, (2022)

Praveen, (2022) reported that agriculture and ecosystem are negatively influenced by the abiotic stresses, creating solemn pressures on plants, as they are sessile in nature leading to excessive losses in economy. For maintenance of sustainable agriculture and to fulfil the cumulative call of food for rapidly growing population worldwide, it becomes crucial to protect the crop plants from climate fluctuations. Plants fight back against these challenges by generation of redox molecules comprising reactive oxygen species (ROS) and reactive nitrogen species (RNS) and cause modulation at cellular, physiological and molecular levels. Nitric oxide (NO) deliver tolerance to several biotic and abiotic stresses in plants by acting as signalling molecule or free radicals. It is also intricate in several developmental processes in plants using different mechanisms. Supplementation of exogenous NO reduce toxicity of abiotic stresses and provide resistance. They summarize the research studies (five years) depicting the functional role of NO in alleviation of abiotic stresses such as drought, cold, heat, heavy metals and flooding. Moreover, by investigating studies found that among heavy metals works associated with Hg, Pb, and Cr is limited comparatively. Additionally, role of NO in abiotic stress resistance such as cold, freezing and heat stress less/poorly investigated. Consequently, further emphasis should be diverted towards how NO can facilitate protection against these stresses. In recent studies mostly beneficial role of NO against abiotic challenges have been elucidated by observing physiological/biochemical parameters but relatively inadequate research done at the transcripts level or gene regulation subsequently researchers should include it in future. Lastly, brief outline and an evaluative discussion on the present information and future prospective provided. Altogether, these inclusive experimental agendas could facilitate in future to produce climate tolerant plants. This will help to confront the constant fluctuations in the environment and to reduce the challenges in way of agriculture productivity and global food demands.

Ahmad *et al.,* (2020) reported that taurine administration improved the accumulation of proline to enhance tolerance to boron (B) and chromium and aided in the regulation of metabolic activities. Another chemical, H_2S, was found to play a profound role in enhancing tolerance to chromium, aluminum, boron, and copper toxicity in addition to its role in drought stress tolerance Zhang *et al.,* (2008), (2009), Wen *et al.,* (2022). Similarly, chromium toxicity was circumvented in barley by exogenous supplementation of H_2S through its effect on enhancing growth via the upregulation of photosynthetic machinery Wang *et al.,* (2020). The supplementation of H_2S was found to trigger the generation of chromium Cr^{6+}-binding peptides such as metallothioneins and phytochelatins to compartmentalize chromium Cr^{6+} to insensitive regions in *Arabidopsis* Wen *et al.,* (2022). Recently, it was reported that the exogenous application of glutathione decreased the translocation, absorption, and chelation of chromium in soybean, hence improving plant biomass by adjusting the soluble proline and phenol content Chandrasekaran, and Shahidi, (2011). These compounds are reported to aid in the removal of ROS under stress conditions Barrameda-Medina *et al.,* (2014). In addition, the accumulation and detoxification of chromium helped to enhance the plant's physiological activities upon administration of exogenous glutathione under Cr toxicity Gill *et al.,* (2015). The mechanism behind the alleviation of Cr toxicity lies in the formation of Cr–GSH complexes due to the presence of the thiol group (-SH), hence reducing free Cr in plants Fang *et al.,* (2020).

Moreover, glutathione was reported to neutralize the ROS generated by chromium toxicity via the formation of the ascorbate–glutathione cycle (ASA–GSH cycle) Nakamura *et al.,* (2020) Fig.(58) .

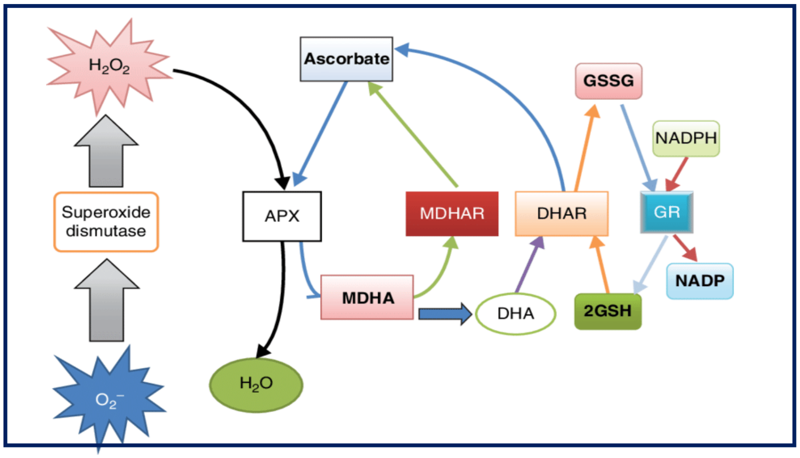


Fig. 58: Illustrates the ascorbate-glutathione (AsA-GSH) cycle is often regarded as the redox-regulating hub of the cell. Here, hydrogen peroxide produced on detoxification of superoxide radical by superoxide dismutase (SOD) is immediately scavenged by ascorbate peroxidase (APX) to produce a water molecule. During this reduction, AsA acts as the reducing equivalent and itself is oxidized into monodehydroascorbate (MDHA). MDHA can be recycled back to AsA by the action of MDHA reductase (MDHAR). The reducing equivalent in this reaction is NADPH, which is oxidized by MDHAR into NADP (not shown in figure). Usually, MDHA produces dehydroascorbate (DHA) which also gets recycled to form ascorbate catalyzed by DHA reductase (DHAR). For recycling of DHA to AsA, DHAR utilizes the cellular reducing equivalent, that is, reduced glutathione (GSH), and oxidizes it to oxidized glutathione (GSSG). GSH is regenerated from GSSG by the catalytic reaction of glutathione reductase (GR) via the oxidation of NADPH to NADP. Thus, the AsA-GSH cycle regulates

the GSH:GSSG ratio in the cell to scavenge the ROS and minimize widespread oxidative damage. After: Aditya Banerjee and Arya deep Roy Choudhury, (2017)

In conclusion, scientists validated the role of glutathione in considerably maintaining the chlorophyll content of plant leaves by decreasing chromium toxicity in plants Adrees *et al.,* (2015), Askari *et al.,* (2021). Previous studies have reported that exogenous foliar administration of mannitol (M) to wheat plants enhanced the tolerance to chromium toxicity by decreasing Cr uptake and translocation, increasing the activity of antioxidant enzymes, and enhancing the concentration of photosynthetic pigments in plants Asif *et al.,* (2019). Menadione sodium bisulfite (MSB) is another chemical used in priming plants to circumvent chromium toxicity due to its redox properties augmenting the plant's physiological properties. MSB has been reported to reduce the levels of chromium in the aerial parts of plants, enhance the antioxidant systems, and decrease oxidative damage in plants Mir *et al.,* (2022). Moreover, H_2S reportedly alleviated chromium toxicity in barley to mediate chromium tolerance Ali *et al.,* (2013). All of these reports strongly suggest that chemical priming may aid in alleviating Cr toxicity in crop plants and is a leading approach to enhance the yield and productivity of crops in the future. Phytohormones such as auxins (IAA), brassinosteroids (BRs), ABA, cytokinins (CK), gibberellins (GA), jasmonic acid (JA), and salicylic acid (SA) are another series of biomolecules that have been employed to enhance the tolerance of crop plants against a wide range of biotic as well as abiotic stressors, including Chromium, to maintain proper metabolism and physiology Mumtaz *et al.,* (2022), Choudhary *et al.,* (2012). For instance, Mumtaz *et al.,* (2022) reported that 24-epibrassinolide induced commendable enhancement in the growth, physiology, and upregulation of defense systems in pepper plants under Chromium (VI) stress. Chromium stress was also mitigated by the application of the polyamine brassinosteroid to maintain phytochemical and physiological attributes in Raphanus sativus L. Gangwar *et al.,* (2011). Additionally, it was reported that a reduction in oxidative stress was observed in Pisum sativum L. upon administration of indole acetic acid (IAA) on seedlings under chromium stress conditions Husain *et al.,* (2022). The alleviation of Chromium (VI) stress was accomplished by the application of ET and H_2S in black bean and mung bean crop plants Kamran *et al.,* (2021). In this study, it was observed that H_2S impaired ET signaling to reduce the negative effects of chromium stress. JA is another plant hormone found to prime the alleviation of chromium stress by decreasing chromium uptake, thus enhancing the regulation of glyoxalase and the oxidative defense system in choysum *(Brassica parachinensis L.)* Jan *et al.,* (2018). Similarly, JA application in *P. sativum L.* seedlings was found to be associated with the regulation of other hormones and increased the uptake of mineral ions such as calcium (Ca^{2+}), which was linked to detoxification under chromium toxicity conditions Khan *et al.,* (2015) . SA is a critical phytohormone useful for the induction of defense mechanisms against a wide range of abiotic stress factors Sharma *et al.,* (2020), Yang *et al.,* (2021) . This hormone ameliorates chromium toxicity by regulating ion homeostasis, the ultrastructure of cells, and the modulation of the antioxidant defense system Pereira *et al.,* (2021). This brief account of phytohormones displays considerable evidence of their role in alleviating chromium toxicity in plants. Hence, it must be concluded that phytohormones can be substantially employed as a possible strategy to circumvent the toxic effects of chromium in plants.

7.2. Nano-Priming As Pilot Strategy to Alleviate Chromium

Toxicity in Plants Currently nanotechnology is at the forefront of attaining sustainable development of the agricultural sector through its diverse tools, such as nanosensors, nanopesticides, and nanofertilizers Grillo *et al.,* (2021), Singh *et al.,* (2021). Evidently, nanoparticles have been employed to positively regulate the development and growth of plants and withstand the challenges of stress factors Saleh *et al.,* (2021), Saleh *et al.,* (2021). A large number of reports have validated the role of nanoparticles in priming seeds for speedy germination, thus leading to improved growth and tolerance to stressors and obtaining higher yield and growth Ye *et al.,* (2020), . Khalaki *et al.,* (2019). For instance, the germination of Festuca ovina under drought stress was stimulated by the nanopriming approach using silver nanoparticles at concentrations ranging from 25% to 75% El-Badri *et al.,* (2021). Similarly, zinc oxide nanoparticle (ZnONP)-based priming was utilized to enhance the resilience of rapeseed *(B. napus L.),* thereby, enhancing germination under salinity stress conditions Ismail, *et al.,* (2018). Moreover, silver nanoparticles (AgNPs, 1 mg/L) were utilized as priming agents to enhance seed germination in wheat and help to reverse the effects of salt stress in wheat plants Yousefi *et al.,*

(2017) . Increased germination rates and decreased germination times were reported in hopbush *(Dodonaea viscosa L.)* seeds when supplemented with multi-walled carbon nanotubes (MWCNTs) Sharma, *et al.,* (2022). Seed priming is another approach to enhance the stress tolerance in plants by allowing partial hydration with chemicals to amplify the different metabolic processes El-Badri *et al.,* (2021). Nano priming of seeds by zinc oxide significantly enhanced seed germination El-Badri *et al.,* (2021). On the other hand, use of AgNPs with fenugreek (*Trigonella foenum-graecum*) seeds helped to promote seed germination. It was reported that indole acetic acid (IAA) and silicon nanoparticles (SiNPs) in combination and alone primed rice seedlings to enhance tolerance to Cr toxicity Ahmad *et al.,* (2022). In combination with Staphylococcus aureus, ZnONPs were shown to mediate the alleviation of Cr toxicity in wheat plants, thus, enhancing the defense system, growth, and physiology Jasim *et al.,* (2017) Fig.(59). Similarly, the application of ZnONPs enhanced the activities of CAT, APX, SOD, and POD in mustard plants under Cr toxicity conditions Sharma, *et al.,* (2022), Jasim *et al.,* (2017).

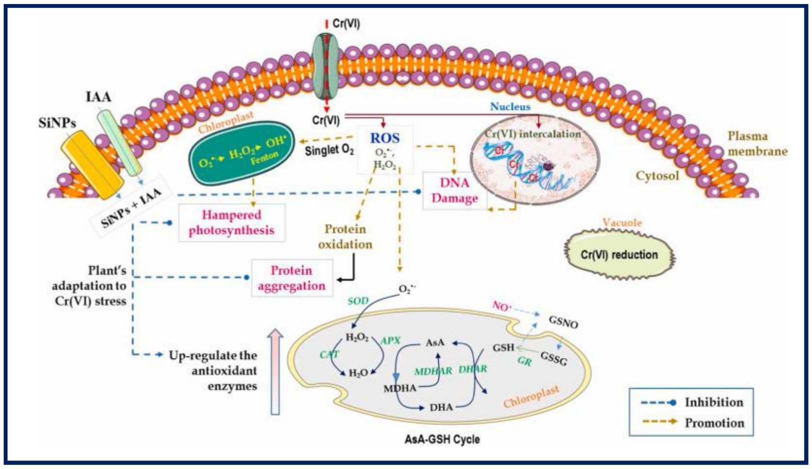


Fig. 59: Illustrates synergistic action of silicon nanoparticles and indole acetic acid in alleviation of chromium (Cr^{VI}) toxicity in *Oryza sativa* seedlings, After: Sharma *et al.,* (2022)

7.3 Genetic mechanisms to control Cr toxicity in plants

A significant problem is avoiding and reducing the harmful effects of heavy metals contamination in soil Zeeshan *et al.,* (2021). Genetic engineering can significantly improve a plant's ability to transform, translocate, and lessen the adverse impacts of heavy metals Raza *et al.,* (2021). Omic tools have gained a lot of interest recently for their use in plant development and programs to mitigate agricultural production challenges, specially, to mitigate heavy metal stress Khan *et al.,* (2021).

Raza *et al.,* (2022) stated that Plant responses to toxic metals/metalloids toxicity rely on the regulation of molecular factors. Therefore, an integrated omics approach has been extensively used to comprehend the plant's biological interactions and molecular mechanisms against toxic metals/metalloids toxicity. Regardless of the incredible advancements in genomics, it is essential to evaluate other omics tools for wide-ranging knowledge at the molecular level Fig. (60). Scientific investigations and existing information derived by omics tools target signaling pathways, key molecular regulators, and integrated mechanisms to enhance tolerance toward toxic metals/metalloids toxicity for crop improvement. Genomics includes characterization, data sequencing, structural organization, genetic alignments, interactions, and functions of a whole organism (plant) Gilliham *et al.,* (2017). Genomics is interrelated to the terms like transcriptomics, metabolomics, trans genomics, epigenetics, and phenomics. These approaches, associated with high throughput (HTP) technologies, have made significant advancements in plant genomics research and have enabled the improvement of multiple important crop plants Varshney *et al.,* (2020) and (2021a). Genomics can help to identify genes, enzymes, or other molecular factors involved in stimulating toxic metals/metalloids stress. Genomics-based findings and online genomic data sets provide a way forward to open new windows for multi-omics technologies and genome editing tools.

To identify target genes, proteins, and metabolites linked to Cr detoxification and stress tolerance responses in plants, genomics, proteomics, and metabolomics have become effective methods Chaudhary *et al.,* (2019). It is possible to modify the Cr stress responsive genes, proteins, and metabolites to either increase plant tolerance to Cr stress or decrease Cr accumulation Thakur *et al.,* (2019). Tools for genetic engineering that are particularly effective at changing the genes involved in the acquisition, transport, and accumulation of Cr inside the plant are necessary for this type of manipulation Khan *et al.,* (2021). The main goal of genetic engineering is the creation of tolerant varieties using either a transgenic approach or genome editing Raza *et al.,* (2021).

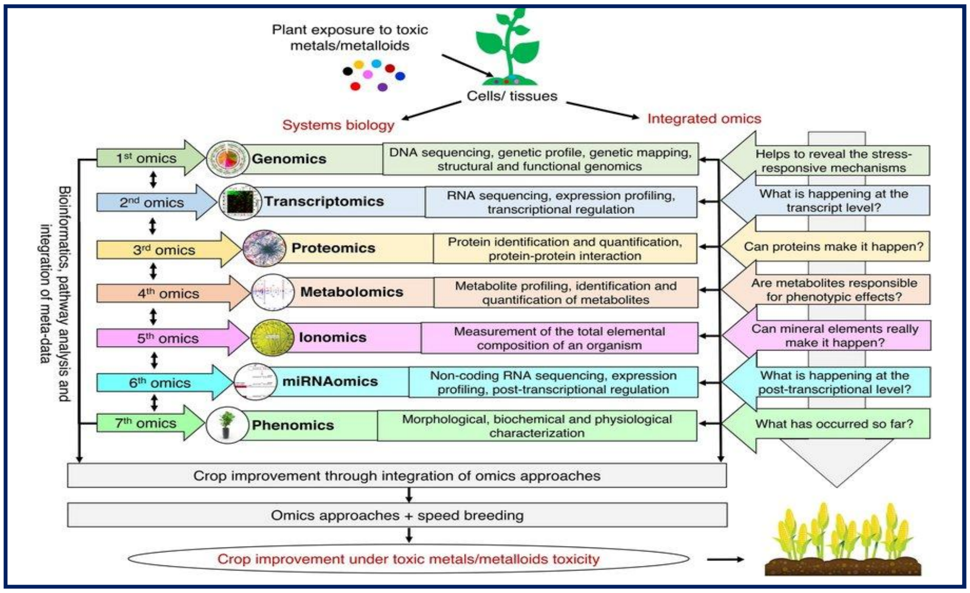


Fig. 60: Integrated omics approach for developing toxic metals/metalloids tolerant plants. The use of multi-omics approach can help to reveal stress-responsive mechanisms at the genomic level, understand what is happening at the transcript and proteome level, provide clues about the interaction of metabolites with the phenotype, understand the role of different mineral elements, and unravel phenotypic changes in plants in response to toxic metals/metalloids toxicity. Integrating state-of-the-art omics approaches with speed breeding will help to meet the challenge of feeding a burgeoning human population. After: Raza *et al.,* (2022)

Anwar and Kim, (2020) reported that through genome editing active participation in the control of plant metabolism, essential genes important for increased metal tolerance have been developed into transgenics, which provide insights into how to understand and improve the tolerance capacity of plants. A successful method for creating resistant cultivars is to transfer candidate genes from plants with a high tendency for HM hyper-accumulation Rahman *et al.,* (2022). The best way to reduce metal toxicity within cellular locations is to use transgenic plants with altered efficiencies for metal transport into vacuoles Khan *et al.,* (2021). Heavy metals (HM) transporter genes are thought to be potential candidates for genetic engineering to improve metal tolerance in plants Zhang *et al.,* (2018). OsMTP1 in cultivated tobacco (*Nicotiana tabacum*) and PgIREG1 in *Arabidopsis* are two examples of metal transporter genes that have been genetically modified Merlot *et al.,* (2014); Das *et al.,* (2016). Other metal transporter genes include those that encode metal chelators, metallothioneins (MTs) Peng *et al.,* (2017), and genes associated with antioxidant machinery Peng *et al.,* (2017); Raza *et al.,* (2021). The use of transgenic techniques to increase resistance to metal oxidation has also been documented. Transgenic hyperaccumulators may be created by manipulating the antioxidant system to maintain redox equilibrium to avoid the destruction of biomolecules such as DNA, proteins, and lipids and to maintain the structural and functional stability of cellular structures of plant under Cr stress Du *et al.,* (2019). Transgenic plants that overexpress antioxidant genes for SOD, CAT, and APX with reduced ROS generation under Cr stress have been created to prevent metal toxicity induced oxidative stress

Gao *et al.,* (2016). Additionally, enhanced antioxidant systems in transgenic lines are associated with higher growth performance in terms of photosynthesis, mineral uptake, maintenance of redox homeostasis, and enzyme activity Khan *et al.,* (2021) Fig. (61). Sachdev *et al.,* (2021) reported that the accumulation of non-essential metals showed toxicity in plants via ROS generation. However, the unrestricted uptake of essential nutrients also induced ROS production Saleem *et al.,* (2020). Heavy metals such as iron (Fe), chromium (Cr), and Cu are major redox-active metals that impose oxidative stress in plants owing to their high concentrations in soil Schutzendubel *et al.,* (2002). Heavy metal stress triggers ROS production mediated through ETC of chloroplast, mitochondria, apoplast, and peroxisome Pandey et al., (2009), Trinh *et al.,* (2014).

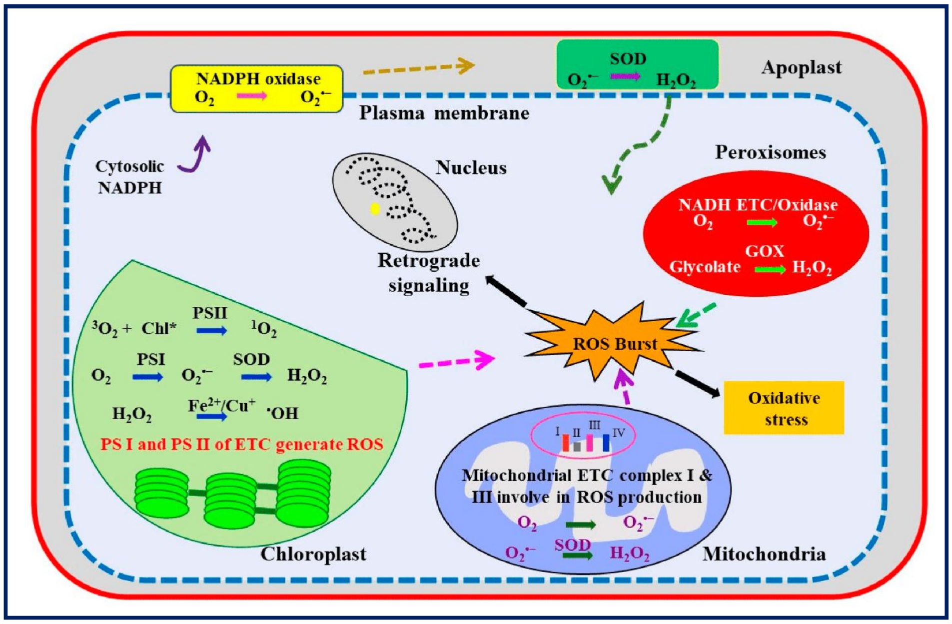


Fig. 61: Abiotic stresses induced the production of ROS in different plant cell organelles that either initiate signaling (retrograde) or cause oxidative stress. In chloroplast singlet oxygen ($^1O_2$), superoxide radical (O2 •–), hydrogen peroxide (H_2O_2), and hydroxyl radical (•OH) are produced by an excited chlorophyll (Chl*), via the electron transport chain (ETC) at PS I and II (Mahler's reaction), dismutation of O2 •– by superoxide dismutase (SOD) and via the Fenton reaction catalyzed by reduced iron (Fe^{2+}) and copper (Cu^{+}), respectively. At peroxisomes, photorespiration (glycolate), enzymes, and NADH (nicotinamide adenine dinucleotide) dependent small ETC induce the production of O2 •– and H_2O_2 . Mitochondrial ETC participates in the generation of O2 •– which on dismutation by SOD produces H_2O_2 . Cytosolic NADPH induces conversion of O2 into O2 •– by the action of NADPH oxidase of the plasma membrane which further dis-mutates into H_2O_2 in the apoplast by SOD. ROS produced in different cell organelles under the duress of abiotic stresses mediate signaling pathways at a low/moderate concentration or induce oxidative stress at a high concentration. After: Sachdev *et al.,* (2021)

Cadmium (Cd) is a non-essential metal that causes toxicity in plants. Cd supersedes Cu or Fe ions in antioxidant metalloenzymes with their impeded activities, indirectly inducing ROS production, impairing respiratory ETC, and interfering with the redox status in cells Shin *et al.,* (2005). Despite being an essential micronutrient, the excess accumulation of Fe also initiates the production of ROS in plants through a series of reactions Becanne *et al.,* (1998) and causes damage to the lipid membrane and chlorophyll Hajiboland, (2012). The reduced form of Fe oxidizes to produce H_2O_2 and O_2 •– . In turn, H_2O_2 oxidizes the reduced Fe compounds to generate highly toxic •OH Hajiboland, (2012). This auto-oxidation of redox-active metals such as Fe and Cu consequently results in ROS formation, mediated by the Fenton-type reaction Schutzendubel *et al.,* (2002). Homologous to heavy metals, xenobiotic compounds such as pesticides also trigger ROS production leading to oxidative stress

Sharma *et al.,* (2019). Out of the total pesticides applied, only 1% reaches the target, the remaining very large proportion accumulates in soil and non-target living organisms Sachdev and Singh, (2018). Pesticides retard plant growth, abridge photosynthetic efficiency, induce molecular alterations, increase ROS production, and modify the antioxidant status Sharma *et al.,* (2019), Yuzbasıoglu and Dalyan, (2019). The degradation of chlorophyll with an increase in H_2O_2 and MDA level has been reported in tomato leaves treated with thiram Yuzbasıoglu and Dalyan, (2019). In another study, imidacloprid declines the chlorophyll content in *B. juncea* seedlings. The reduction in chlorophyll is attributed to an enhanced expression of gene CHLASE encoding chlorophyllase enzyme that catalyzes chlorophyll degradation Sharma *et al.,* (2019). Moreover, insecticides enhance the RBOH transcript level and ROS accumulation.

Although transgenic lines reated for over-expression traits do not always show the expected benefits, they can nevertheless have positive consequences by influencing the alternative tolerance mechanisms. The phytochelatins (PCs), which contain hazardous metal ions and are enzymatically generated from GSH, amino acids, organic acids, or MTs, are another crucial area for improving the Cr stress tolerance in plants Yadav, (2020).

It should be noted that only MTs have coding genes, but the production of other compounds (such as GSH, amino acids, and organic acids) is controlled by the actions of the enzymes involved. Better physiological and transformed plants Khan *et al.,* (2021), display biochemical characteristics, including membrane function and antioxidant activity. According to Ai et al. (2021), overexpression of MYB1 from grown radish improved PC and anthocyanin synthesis, giving transgenic *Petunia* higher resistance against several metal toxicities, including Cr. Improved growth and stomatal density were seen in MYB1 over-expressing lines mainly due to the maintenance of relative water content (RWC), chlorophyll, and antioxidant activity. Therefore, it can be concluded that transgenic research aimed at creating cultivars with improved metal tolerance will have a considerable impact on crop production in the future Ai *et al.,* (2021) Fig.(61).

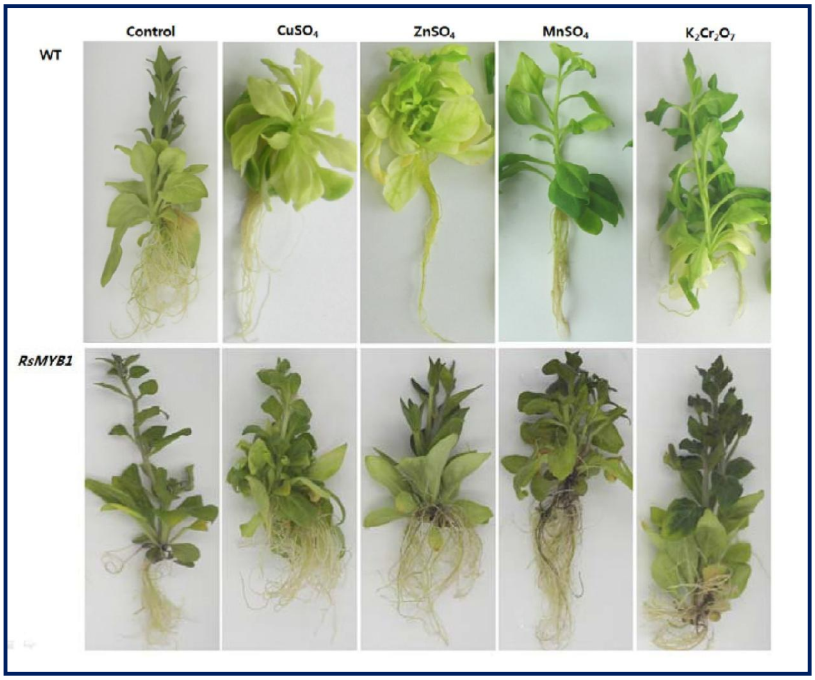


Fig. 62: Comparisons of severity of toxicity in RsMYB1-overexpressing plant and WT caused by different heavy metals stress. Photos were taken on 30th day after starting of the experiments. After: Ai *et al.,* (2021)

Ai *et al.,* (2021) reported that the RsMYB1 transcription factor (TF) controls the regulation of anthocyanin in radish (*Raphanus sativus*), and its overexpression in tobacco and petunia strongly enhances anthocyanin production. However, no data exists on whether RsMYB1 is involved in the mechanism that leads to abiotic stress tolerance. Under normal conditions, transgenic *petunia* plants expressing RsMYB1 and WT were able to thrive by producing well-developed broad leaves and regular roots. In contrast, a reduction in plant growth was observed when they were exposed to heavy metals ($CuSO_4$, $ZnSO_4$, $MnSO_4$, and $K_2Cr_2O_7$). However, RsMYB1-overexpressing plants were found to be more tolerant to the stresses than the WT plants because the expressions of stress tolerant genes (GSH and PCs) and antioxidant genes (SOD, CAT, and POX) were enhanced. In addition, according to the phylogenetic analysis, RsMYB1 has a strong sequence similarity with other MYB TFs that confer different abiotic stresses. These results showed that overexpression of RsMYB1 enhances the expression levels of metal-induced stress tolerance genes and antioxidant genes, and the resultant increase in gene expression improved heavy metal stress tolerance in *Petunia*.

The engineering of transcription factors (TFs) that control the synthesis of important metabolic chemicals also has an impact on the Cr stress tolerance in addition to the previously described essential regulators of metal tolerance. Many TF gene families play a vital role in the ability of HMs to withstand stress, including R2R3-type MYB, ZAT6, Zinc-Finger type, bZIP, GeBP-LIKE 4 (GPL4), and NAC Khan *et al.,* (2021); Raza *et al.,* (2021). It was noted that transgenic rice that overexpresses OsMYB-R1 has a noticeable increase in lateral roots, which was assumed to be related to improved tolerance to Cr Tiwari *et al.,* (2020). Further supporting the role of lateral roots in Cr tolerance is the correlation between the increase in lateral roots and a corresponding increase in auxin accumulation in transgenic lines as compared to wild type plants. Along with that, it was also thought that the OsMYB-R1 over-expressing lines had significantly higher antioxidant activity and proline accumulation, which were likely mediated by salicylic acid (SA) signaling and contributed to the transgenic rice's ability to tolerate Cr Tiwari *et al.,* (2020). Fig. (63). As a result, TFs are essential molecular regulators that help plants tolerate Cr stress and lessen the negative effects of exposure to metals, which supports plant growth and development. However, the identification and functional confirmation of several additional TFs from diverse TF families, many of which are still mostly unknown, could, therefore, be helpful in creating enhanced plant types with high HM tolerance.

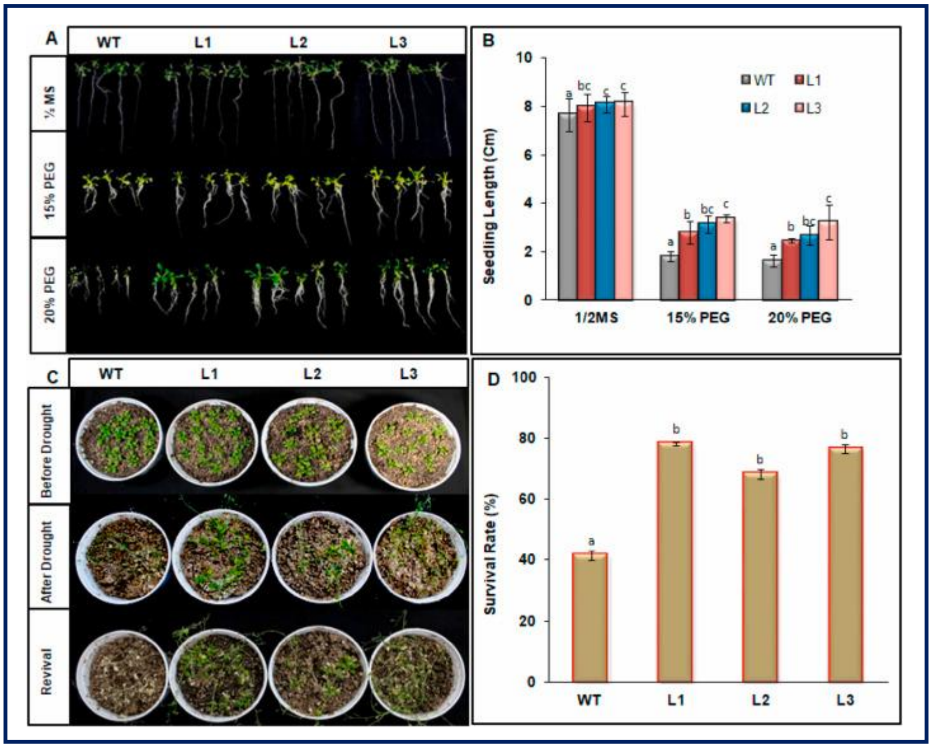


Fig. 63: Plate and simulated pot experiment of transgenic *Arabidopsis* lines and wild-type plants under PEG and drought stress. (A) Transgenic lines over-expressing OsMYB-R1 and wild type plants grown

under controlled conditions for 5 days in ½ MS and then treated with 15% PEG and 20% PEG; and pictures were taken after 18 days of treatment. (B) Seedling length of WT and transgenic lines recorded after 18 days of non-treatment, 15% PEG and 20% PEG treatment. (C) Transgenic lines over-expressing OsMYB-R1 and wild type plants grown under controlled conditions for 15 days and then inculcating drought stress by withholding water for 30 days. The picture was taken after reviving plants for 7 days. (D) The survival rate of transgenic lines compared to WT. Data are expressed as the mean of triplicate values and error represent the SD. Values marked with similar letters are not significantly (Duncan's test: $p \leq 0.05$) different. After: Tiwari *et al.,* (2020)

Conclusion and Future Perspectives

Chromium pollution is becoming a serious problem to the ecosystem and a major health risk to the biota. Additionally, the detrimental effects of chromium on our agriculture are a serious concern for food security and safety. Chromium toxicity in plants provides a review of related research on chromium toxicity in the environment, mainly in water and soil. Chromium exists primarily in three oxidative states: chromium (0), chromium (III), and (VI) which are the most stable form of Cr. Chromium (0) is the metallic kind, the kind of chromium (III), and (VI) is the most preponderant in soil and water. The current review looked at the various negative impacts of Cr exposure in plants, both morphologically and physiologically. Chromium can cause a variety of hazardous consequences in plants, including changes in the germination process and root, stem, and leaf growth, as well as detrimental impacts on morphological and physiological systems like photosynthesis, water relations, and mineral nutrition. The hazardous qualities of Cr (VI) stem from its action as an oxidizing agent and the generation of free radicals during the reduction of Cr (VI) to Cr (III) that happens within the cell. Apart from generating reactive oxygen species (ROS), Cr (III) in the contrary can induce hazardous effects when present in large amounts because of its propensity to coordinate diverse chemical molecules, resulting in inhibition of metalloenzymes systems. Hence, there is a need to find a long-lasting remedial tool kit for its removal from the environment. This requires a deep understanding of chromium accumulation, translocation, and plant defense responses in both model and crop systems. When Cr enters plant cells through the pathways of necessary nutrients like Fe, sulphate, and phosphate, it might result in physiological and molecular alterations. Chromium buildup affects nutrient intake, photosynthesis, growth, development, and seed germination. High concentrations of chromium can cause oxidative stress in plants and alter the structure of cell nuclei and chloroplasts. Overproduction of ROS could disrupt cell homoeostasis, stop cell division, harm DNA, and even cause cell death. Organic and inorganic reductants have been widely employed for the in-situ remediation of chromium (VI) - contaminated soil to lessen the hazard of chromium (VI) to soil-plant systems. We discussed chromium toxicity in plants, its signaling cascades, and various mitigation approaches. However, many questions about chromium perception and signal transduction warrant future attention. For example, how cell wall receptor kinases and ion channels respond to chromium stress. How chromium triggers Ca^{2+} and ROS signaling cascades and how it modulates different intracellular signaling cascades in roots. The functions of the many ion transporters that promote chromium transport as well as the several carriers that assist in its movement from the roots to various compartments require future consideration. Moreover, how chromium stress triggers hormonal activation or how it regulates cross talk can have different outcomes in terms of plant growth and defense. Additionally, genetic engineering and advanced breeding tools, such as genome editing, can also provide the best approaches to develop long-lasting chromium -tolerant crop cultivars for sustainable agriculture.

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