

12-2-2024

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Available at: <https://journals.tubitak.gov.tr/agriculture/vol48/iss6/2>



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Role of nanoparticles in mitigating chromium toxicity: implications, mechanisms, and future prospects

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Received: 13.07.2024 • Accepted/Published Online: 03.09.2024 • Final Version: 02.12.2024

Abstract: Chromium (Cr) is an extremely toxic metal for all living organisms and its concentration in the environment is constantly increasing due to human activities. Plants quickly absorb Cr. Subsequently, it enters the human food chain and poses serious health risks. Chromium toxicity causes a significant reduction in plant growth by inducing oxidative damage and disturbing protein synthesis, enzyme activity, and nutrient uptake. Plants use diverse mechanisms to mitigate Cr toxicity; however, they are inadequate in the face of higher concentrations of Cr. Thus, it is essential to decrease Cr toxicity and increase the ability of plants to tolerate Cr stress. Nanoparticles (NPs) mitigate the toxicity of Cr by reducing its uptake and accumulation and improving antioxidant activities, nutrient homeostasis, photosynthetic efficiency, osmolyte synthesis, and hormonal balance. The complex interactions between NPs and microbes, signaling molecules, and hormones also significantly counter Cr toxicity. The present review discusses the various mechanisms of NPs for mitigating Cr toxicity. This review also addresses various research gaps to encourage the better utilization of NPs to mitigate Cr toxicity and improve crop growth and yield. This review offers new insights into the role of NPs in mitigating Cr toxicity.

Key words: Chromium, gene expression, microbial activity, nanoparticles, nutrient homeostasis

1. Introduction

Rapid increases in urbanization, industrialization, mining, and agricultural practices have increased the bioaccumulation of heavy metals (HMs) and serious attention is needed to tackle this problem (Hassan et al., 2019; Haider et al., 2022). Chromium (Cr) is a toxic metal present in the environment in two forms, namely Cr(III), or chromite, and Cr(VI), or chromate (Ali et al., 2023). More than 2000 tons of Cr enter global water resources every year via different liquid wastes generated by factories. The chromium concentration in waste liquids can vary from 2000 to 5000 mg L⁻¹, far beyond the maximum allowable limit of 2 mg L⁻¹ (Wei et al., 2022). This increasing concentration has harmful impacts on humans when Cr enters the food chain (Ahmad et al., 2020). Chromium causes cancer, skin problems, kidney damage, asthma, and eye irritation in humans (Zeng et al., 2020). Thus, controlling the Cr levels in water resources

is essential in protecting the environment and human health.

Chromium is not an essential metal and it negatively affects plant physiological, chemical, and biochemical functioning (Ali et al., 2023). Chromium toxicity reduces root growth, disturbs nutrient homeostasis, decreases chlorophyll synthesis, and causes membrane damage by increasing reactive oxygen species (ROS) production (Ali et al., 2023). It negatively affects microbial and enzymatic activities and leads to significant reduction in yield and quality (Seleiman et al., 2020; AbdElgawad et al., 2023). Different nanoparticles (NPs) have been suggested to be promising in mitigating Cr toxicity and improving crop productivity.

NPs improve plant functioning due to their beneficial properties in promoting oxidation and reduction reactions. They improve seed germination, nutrient uptake, photosynthesis, and hormonal balance in the presence of

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drought and HM stress (Subbaiah et al., 2016). Various researchers have reported that NPs can increase plant growth and reduce HM toxicity (Prakash et al., 2022). The exogenous use of zinc-based NPs improved growth and nutrition and mitigated Cr accumulation in soybean (Basit et al., 2023a). NPs also reduce malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) production and increase osmolyte synthesis, which counteracts the toxicity of HMs (Basit et al., 2023b). In other studies, it was observed that NPs enhanced nutrient uptake and antioxidant defense mechanisms and reduced Cr uptake (Adrees et al., 2021; Ramzan et al., 2023). However, the impact of NPs largely depends on the plant species, type of NP, stage of plant growth, and the applied NP concentration. There is no comprehensive review available describing the use of NPs to mitigate the toxic impacts of Cr in plants. Thus, this review comprehensively describes the different NP mechanisms used to induce Cr tolerance in plants with the aim of filling knowledge gaps to benefit researchers working to mitigate Cr toxicity and increase crop productivity.

2. Methodology used in the literature review

Relevant studies were obtained using Google Scholar, Scopus, and Web of Science. Key words and phrases including “nano,” “NPs,” “nanomaterials,” “Cr,” “Cr toxicity,” “Cr pollution,” “toxic effect of Cr on plants,” “role of NPs to alleviate Cr toxicity in plants,” “NPs mitigate Cr toxicity in plants,” and “NPs enhance plant resistance to Cr” were used to identify relevant studies. Data were collected from peer-reviewed papers and the literature review was limited to include only studies published since the year 2000. Review articles and duplicate studies were excluded. Thus, a total of 100 research studies were incorporated in the present review. All reviewed studies were published in English.

3. Mechanism of Cr uptake in plants

The concentration of Cr is continuously increasing in the environment due to agriculture and industrial activities (Schiavon et al., 2008). Chromium has various uses in different industries. Therefore, significant quantities of Cr are released into the soil and water from cement factories, steel plants, electroplating, paints, dyes, timber production, and the paper industry (Zayed and Terry, 2003). The allowable Cr limit in soils is 64 mg kg^{-1} , but rapid industrialization has significantly increased soil Cr concentrations (Yang et al., 2020). Different natural sources including volcanic ash, rocks, soil, and gases serve as other important mechanisms for Cr entry into the environment (Quantin et al., 2008). Plants absorb various forms of Cr but the exact mechanisms of absorption are not clear. Plants uptake Cr via ion

transporters, and the active mechanism of Cr(VI) uptake involves the use of sulfate transporters (Cervantes et al., 2001). Chromium also competes with iron, sulfur, and phosphorous for carrier binding in the processes of transportation (Figure 1).

Chromium competes with enzymes involved in the sulfate assimilation pathway. This reduces both cysteine and methionine production, resulting in faulty protein translation and subsequently sulfur deficiency. For example, the use of metabolic inhibitors reduced Cr(VI) absorption, although there was no effect on Cr(III) uptake, which indicates that the uptake of Cr(VI) is energy-dependent while Cr(III) uptake is energy-independent (Shanker et al., 2005). It was also documented that sulfur-accumulating plants (e.g., *Brassica* spp.) have higher absorption of Cr, which indicates that mechanisms of sulfur uptake and translocation are involved in Cr transportation from root to shoot (Singh et al., 2020). Iron-accumulating plants (e.g., *Brassica* and spinach) also absorb higher levels of Cr, which is transported to aboveground plant parts. Excessive Cr in the roots and its immobilization in root cell vacuoles are known to be major reasons for Cr bioaccumulation in plants. Chromium inhibits root length and cell division, which limits nutrient and water absorption and thus leads to reduction in shoot growth.

Many researchers have found that Cr excessively accumulates in plant roots and this accumulation occurs due to Cr immobilization in root cell vacuoles (Oliveira, 2012). For instance, Wu et al. (2013) found that increasing Cr concentrations in *Brassica* increased Cr accumulation in the cells, nuclei, mitochondria, and plastids. Increased sequestration of Cr in roots leads to the production of insoluble Cr compounds. Different metal transporter gene families that can help transport metals from plant roots to shoots have been identified. However, the roles of different transport families are still unclear in the case of Cr despite their appreciable influence in the absorption, transport, sequestration, and tolerance of metals.

Further research in this field will help in understanding the role of Cr in signaling pathways, which will help in developing Cr-tolerant crops. Chromium toxicity causes detrimental effects for plant functioning and leads to stunted growth (Dotaniya et al., 2014). Chromium toxicity also decreases photosynthetic pigments and inhibits the cell cycle and water and nutrient uptake, nitrogen accumulation, and other metabolic processes (Ugwu and Agunwamba, 2020) (Figure 2). Furthermore, Cr also triggers ROS production, which causes the oxidation of cellular structures and leads to cell death (Patra et al., 2019).

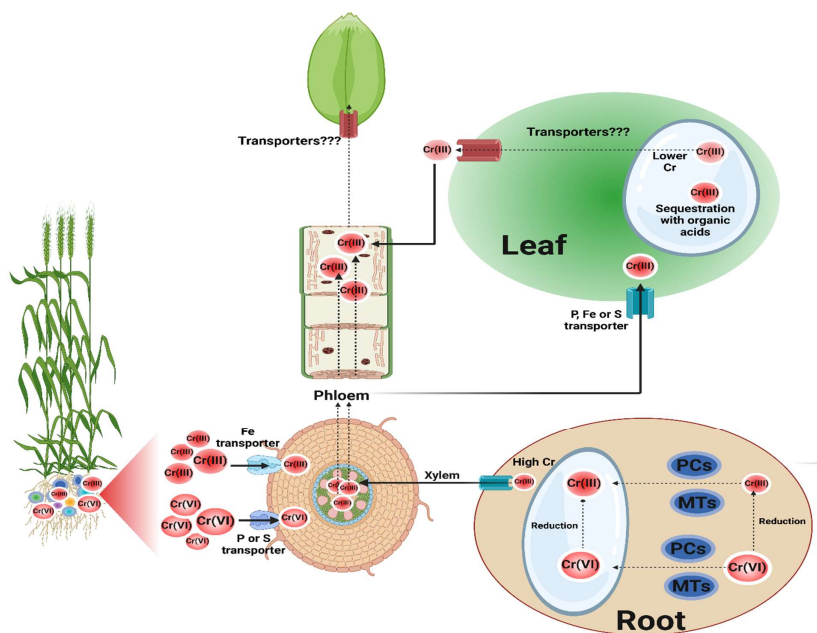


Figure 1. Mechanisms of Cr uptake and transport in plant parts. Cr(VI) uses sulfate and phosphate transporters while Cr(III) uses Fe transporters from the soil for transport. Furthermore, Cr(VI) is reduced to Cr(III), which is then transported to aboveground plant parts via xylem and phloem movements.

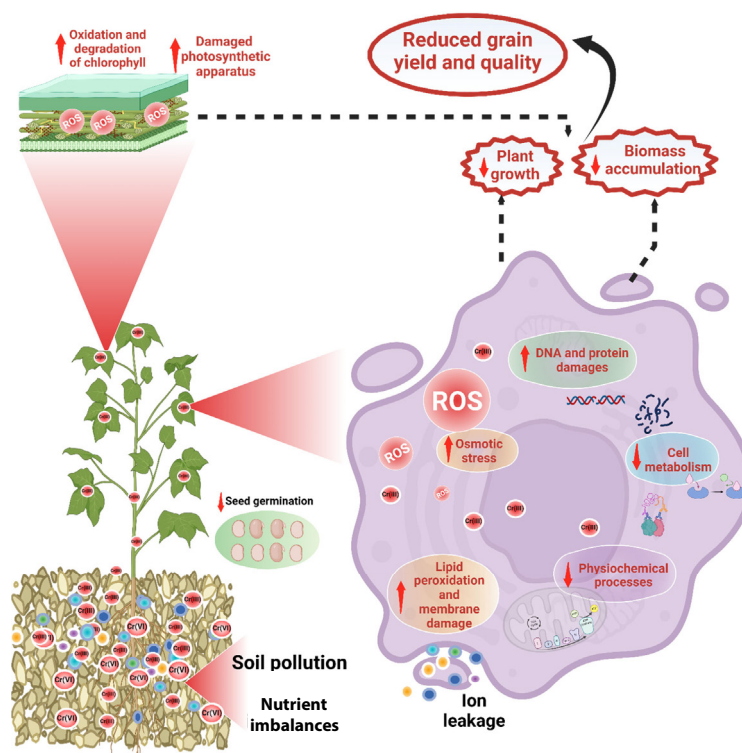


Figure 2. Toxic effects of Cr on plants. Chromium toxicity reduces seed germination, diminishes nutrient uptake, causes osmotic stress, and damages the photosynthetic apparatus, proteins, and DNA, resulting in substantial growth losses.

4. Cost of the synthesis of nanoparticles

NPs are economical and efficient solutions to remediate polluted soils. Globally, different techniques including chemical and physical methods are being used to produce NPs. The physical methods are costly and require more energy, while chemical techniques are economical. However, chemical methods are time-consuming and laborious, and they may also generate hazardous materials (Koul et al., 2021). Therefore, biological methods are increasingly gaining attention around the world. They have many benefits including quick synthesis, low production costs, and an environmentally friendly nature (Ingale and Chaudhari, 2013). Different microbes, plant extracts, and waste materials are used to synthesize NPs. The use of waste materials can decrease synthesis costs and dependence on the use of chemical substances (Sharma et al., 2019).

5. Nanoparticle uptake and translocation in plants

Nanotechnology has revolutionized the world as it provides effective solutions to manage environmental problems. NPs can be divided into different categories including metal oxides, polymers, carbonaceous materials, and dendrimers based on their structures and chemical compositions (Ealia and Saravanakumar, 2017). Distinct sizes, crystalline structures, and surface charges facilitate their application in diverse fields (Dasgupta et al., 2017). NPs can be applied to plants as a soil application, foliage spray, or seed treatment, but foliar sprays are more effective than the other application methods (Su et al., 2020).

The uptake of NPs is determined by soil properties, NP properties, and NP interactions with plant physiology. Plants absorb NPs through their leaves, and the NPs are then transferred to aboveground plant parts (Lv et al., 2019). With foliar sprays, the leaf stomata, cuticles, hydathodes, and trichomes can directly absorb NPs. NPs with sizes of 4–100 nm enter the leaves by penetrating the leaf cuticle (Larue et al., 2014), while NPs ranging in size from a few nanometers to over 100 nm also enter the stomata through apoplastic and symplastic pathways (Larue et al., 2014). It has been documented that NPs of 10–50 nm in size are transported symplastically, while NPs with sizes of 50–200 nm are transported apoplastically, following cell walls and intercellular spaces. After entering the leaves, NPs transported together with sugars will flow through the sieve tubes of phloem, which allows for the bidirectional movement and accumulation of NPs in roots, stems, fruits, and grains. Furthermore, the lipophilicity and hydrophilicity of NPs can affect the foliar pathways of their uptake (Popp et al., 2005).

In soil applications, different soil properties such as soil pH, soil microbes, organic matter, and root exudates impact NP uptake and availability. Different mechanisms such as pore formation, plasmodesmata, and carrier

proteins are being used for the internal movement of NPs inside plants. The plant anatomy and the surface charge of the NPs both affect the dispersion and translocation of NPs. NPs are absorbed on the surfaces of roots, and apoplastic and symplastic pathways are used for the uptake and transportation of NPs (Lv et al., 2019). However, the precise mechanisms through which NPs transverse physical barriers in plants are still unclear and more studies are needed to explore these mechanisms. When NPs are applied by soil application, the plant roots absorb the NPs, and NPs with sizes of 3–5 nm enter the cells of the root epidermis directly through the pores. However, NPs can also cross the Casparian strip barrier to enter the xylem. They cross that barrier using different mechanisms, such as the formation of pores and endocytosis or binding to protein carriers. Some NPs may fail to be internalized and accumulate on the root surfaces of the Casparian strip, which disturbs nutrient absorption (Ali et al., 2019).

Inconsistent results have been obtained by different authors regarding the impact of NP size on their uptake and translocation. Some authors found that plant roots take up small NPs while large NPs remain on the root surface. Lv et al. (2019) reported that tobacco roots took up gold NPs (Au-NPs) of 3.5 nm in size while Au-NPs with a size of 18 nm accumulated on the root surface. Larue et al. (2012) demonstrated that titanium dioxide (TiO_2) of >140 nm in size was not concentrated in wheat roots. Surface charge is an important factor that may significantly impact NP uptake by plants. For example, NPs with positive charges were shown to be absorbed on the mucilage layer while NPs with negative charges bypassed the mucilage layer and then translocated to root tissues (Sun et al., 2019).

The plant species and the growth stage also affect the uptake and transportation of NPs (Wang et al., 2023). For example, anatomical differences between monocot and dicot plants result in differences in NP absorption and transportation within plants (Sun et al., 2019). Dicot plants have higher cuticle permeability specific stomata shapes and cell wall architectures which affects the absorption and translocation of NPs in these plants (Sun et al., 2019). NPs also undergo different reactions including aggregation, dissolution, redox reactions, and interactions with macromolecules, and all of these processes affect the uptake and transportation of NPs (Lowry et al., 2012). Therefore, it is essential to have an understanding of NP uptake and transport in order to optimize their use in agriculture and the environment. This will allow for the development of appropriate measures to obtain the full benefits of NPs while reducing their risks. The uptake of NPs is very complex. Thus, future research must be aimed at exploring the impacts of different factors on the uptake of NPs.

6. Methods of NP application

NPs can be applied by soil application, foliar spray, hydroponics, or seed soaking. They can be applied to plants from sowing to harvesting, but their application is more effective at the germination and seedling growth stages (Fincheira et al., 2021). Seed treatment with NPs improves germination and seedling growth (Abbasi et al., 2021). Different authors have found that soil-applied copper oxide NPs (CuO-NPs) enhanced lettuce growth while ZnO-NPs improved the biomass and grain yield of wheat (Du et al., 2019). Other researchers found that a foliar spray of chitosan NPs improved antioxidant activity, protein synthesis, and photosynthesis in tomato plants (Faizan et al., 2021a). Cerium oxide NPs (CeO₂-NPs) mitigated the adverse impacts of Cd in hydroponic soybean plants (Rossi et al., 2018). Nanomaterials can also be used as carriers of fertilizers and pesticides; they have significant specific area, allowing them to deliver nutrients more effectively for improved solubility and bioavailability of nutrients and reduction in nutrient losses (Fincheira et al., 2021). Similarly, nanopesticides can ensure better release of drugs, resulting in better stability, solubility, and efficiency of pesticides (Bala et al., 2023).

7. Mechanisms of nanoparticles in mitigating chromium toxicity in plants

Many studies have explored the effects of NPs in mitigating Cr toxicity in plants. This section addresses the different mechanisms by which NPs mitigate Cr toxicity in plants.

7.1. Nanoparticles reduce Cr uptake by plants

Chromium toxicity is linked to its excessive accumulation in plants. However, NPs have been reported to decrease Cr uptake and transport in plants (Table 1). Different authors have reported that NPs can improve Cr resistance by decreasing Cr uptake and its subsequent transportation in plants. Zeng et al. (2010) showed that Cr in growth medium increased Cr accumulation in root apoplasts. The potential of ZnO-NPs was tested in rice plants grown under Cr stress (100 µM) and ZnO-NPs at 100 mg L⁻¹ were found to reduce the mobility of Cr in the root–shoot direction, therefore reducing its absorption and subsequent accumulation (Basit et al., 2022a). Basit et al. (2023b) also found that rice seedlings supplemented with ZnO-NPs at 25 mg L⁻¹ had reductions of 7.2% and 13.9%, respectively, in root and shoot Cr.

Table 1. Potential of NPs to mitigate Cr uptake and its accumulation in different plants.

Plant species	NPs	Mode of NPs	Cr concentration	Major effects	References
Wheat	Se-NPs (50 µmol)	Foliar spray	300 mM kg ⁻¹	Se-NPs reduced Cr uptake in roots (–30%) and shoots (–23%) of wheat plants.	Shah et al., (2024)
Maize	ZnO-NPs (50 mg kg ⁻¹)	Soil application	50, 100 mg kg ⁻¹	ZnO-NPs reduced Cr concentrations in roots by 68.21% and in shoots by 71.30% under Cr-50.	Mehmood et al. (2023)
Wheat, pak choi, beet	Fe-NPs (1%, 10%)	Soil application	747 mg kg ⁻¹	Application of nanoiron effectively reduced soil Cr concentration and decreased Cr availability and accumulation in all crops.	Li et al., (2023)
Barley	Ag-NPs (0, 15, 30 mM)	Foliar spray	0, 50, 100 mg kg ⁻¹	Exogenous Ag-NP spray reduced Cr concentrations in roots and shoots of barley compared with control plants.	Zhu et al. (2023)
Rice	Fe-NPs (0, 0.001%, 0.1% W/W)	Soil application	553 mg kg ⁻¹	Fe-NPs promoted Cr transport from roots to aerial parts. Cr accretion in roots and shoots increased after nanoiron application as compared to control.	Liu et al. (2023)
Sunflower	TiO-NPs (15 mg L ⁻¹)	Foliar spray	0, 15, 30, 60 mg kg ⁻¹	TiO-NP treatment reduced the Cr(VI) accumulation in roots and shoots. Furthermore, TiO-NPs reduced the bioaccumulation concentration and translocation factor compared to the control.	Kumar et al. (2023)
Barley	Fe-NPs (1%)	Soil application	6.26 mg kg ⁻¹	The use of nano-Fe decreased extractable Cr concentration and bioconcentration of Cr in barley plants.	Rodríguez-Seijo et al. (2022)
Wheat	ZnO-NPs (0, 50, 100 mg L ⁻¹)	Foliar spray	0, 50, 100, 200 mg kg ⁻¹	ZnO-NP (100 mg L ⁻¹) supplementation decreased the root and shoot Cr concentrations by 8.1% and 76.5%, respectively.	Ahmad et al. (2022)
Rice	Si-NPs (10 µM)	Nutrient medium	100 µM	The rice seedlings treated with Si-NPs showed a marked reduction in Cr concentration in both roots and shoots and reduced the negative effects of Cr toxicity.	Sharma et al. (2022)

Chickpea plants supplied with ZnO-NPs (25 μM) showed remarkable reduction in Cr uptake and accumulation in Cr-polluted soil (120 μM) (Singh et al., 2024). Furthermore, the NPs reduced Cr uptake and transport by negatively regulating organic acid exudates. However, more research is required to explore this mechanism. ZnO-NPs form a barrier that prevents Cr uptake, thereby reducing Cr absorption and subsequently its uptake (Singh et al., 2024).

Ma et al. (2022) tested the potential benefits of CeO_2 -NPs (0, 25, and 50 mg L^{-1}) for sunflower plants grown under Cr toxicity (0, 25, and 50 mg kg^{-1}). Chromium accumulation was increased in various plant parts, but the NPs decreased the Cr accumulation (Ma et al., 2022). However, it is still unclear how CeO_2 -NPs regulate Cr transporters to restrict Cr uptake and accumulation in plants. More studies must be conducted to discover the mechanisms behind the reduction in Cr uptake following CeO_2 -NP applications. Zeng et al. (2020) tested the impact of combined bacteria and NPs to mitigate Cr toxicity in wheat. The application of bacteria converted Cr(VI) to Cr(III) and reduced Cr bioavailability and its accumulation in roots and shoots. NPs can improve bacterial growth; therefore, combined applications of NPs and bacteria can provide better results for mitigating Cr uptake and improve plant performance (Timmusk et al., 2018).

A recent study determined the impacts of silicon NPs (50, 100, and 150 μM) on rapeseed plants grown hydroponically under Cr stress conditions (50 and 100 μM). Si-NPs (100 μM) increased leaf Si concentrations by 169% and decreased Cr accumulation in roots and leaves by 92% and 76%, respectively. Silicon in the leaf cells restricted Cr uptake and transportation, which reduced its accumulation. Furthermore, the Si-mediated increase in the expression of Cr transporter genes (*ST1* and *MT*) decreased Cr uptake and accumulation (Huang et al., 2024). It was also found that Si-NPs changed the activity of *ABC* and *MT* genes, which decreased Cr absorption (Nie et al., 2021). Park et al. (2012) studied different knockouts of *AtABCC1* in *Arabidopsis* and found that an increase in *ABC* gene expression decreased Cr uptake in plants. These findings indicated that NPs can reduce the absorption and accumulation of Cr. Foliar spray appeared to be an effective method for mitigating absorption and accumulation. Moreover, the concentration of the NPs is also crucial as it significantly affects Cr uptake and accumulation in plants. The aforementioned findings indicate that NPs reduce Cr uptake and accumulation, leading to improved plant performance. These outcomes provide guidance for mitigating Cr toxicity in crops while producing safer food. Nonetheless, more research is needed to understand the relationships between NPs and methods of NP application while considering differences in plant growth stages and plant species.

7.2. Nanoparticles improve nutrient homeostasis under Cr stress

Chromium interferes with different nutrients and decreases their uptake by inhibiting plasma membrane H^+ -ATPase (Kharbech et al., 2020; Zaheer et al., 2020). For instance, ZnO-NPs (100 mg L^{-1}) increased the concentration of Fe and Zn in rice plants under Cr stress (Basit et al., 2022). The increase in nutrient influx due to NP application substantially mitigated the adverse impacts of Cr (Table 2). Likewise, other researchers reported that an exogenous supply of NPs improved nutrient uptake and plant growth (Azimi et al., 2021). Recently, Singh et al. (2024) reported that applying ZnO-NPs to chickpea plants improved Ca, Fe, Mg, Zn, and K uptake. Ahmad et al. (2022) tested the impacts of ZnO-NPs (100 mg L^{-1}) and *S. aureus* K1 bacteria on wheat plants grown under Cr toxicity. Chromium toxicity (200 mg kg^{-1}) decreased the root, shoot, and grain Zn contents by 75.1%, 70.8%, and 87.3%, while ZnO-NPs (100 mg L^{-1}) enhanced the root, shoot, and grain Zn contents by 61.3%, 58.3%, and 79.9%, respectively. Basit et al. (2023a) also found that Cr administration reduced the Fe, Mn, and Zn uptake of soybean plants while ZnO-NPs (50, 75, and 100 mg L^{-1}) increased the uptake and accumulation. A particularly significant increase in the uptake of those nutrients was seen with 100 mg L^{-1} ZnO-NPs. These findings demonstrate the potential of NPs to increase nutrient uptake in plants growing in Cr-polluted soils. However, mechanistic studies are needed to explore how NPs affect nutrient uptake and transport in plants under Cr stress.

7.3. Nanoparticles improve photosynthetic efficiency under Cr stress

Chromium toxicity negatively affects photosynthesis by decreasing chlorophyll synthesis (Figure 3) and disturbing leaf gas-exchange characteristics (Table 2). However, the application of NPs improves photosynthesis, transpiration rates, and stomata conductance under Cr toxicity (Huang et al., 2024). Silicon improves the flexibility and plasticity of the cell wall, which affects the opening and closing of stomata (Vaculik et al., 2015). Therefore, nano-Si-mediated improvement in CO_2 uptake and O_2 exchange between leaves and the environment was shown to improve the photosynthetic rate under Cr toxicity. NPs can also improve chlorophyll synthesis; for example, CeO_2 -NPs enhanced the synthesis of chlorophyll and carotenoids, ensuring better photosynthesis (Etesami et al., 2021). Chromium toxicity disrupts the chloroplasts and ribulose biphosphate carboxylase (RuBisCO) activity, and it inhibits electron transport (Salam et al., 2022). However, exogenous applications to protect the chloroplasts maintain electron transport and nutrient acquisition and reduce ROS production, which enhances chlorophyll synthesis and the overall photosynthetic efficiency of plants (Basit et al., 2022).

Table 2. Effects of different NPs on plant growth, physiological activities, antioxidant defense, and nutrient homeostasis in the presence of Cr stress.

Plant species	NPs	Mode of NPs	Cr concentration	Major effects	References
Rice	CuO-NPs (0, 5, 10, 20 mg kg ⁻¹)	Soil application	0, 5, 10, 20 mg kg ⁻¹	CuO-NPs improved the root and shoot growth, photosynthetic pigment synthesis, and antioxidant activities, while reducing MDA and ROS production.	Ali et al., (2023)
Black cumin	SiO ₂ (200 mg L ⁻¹) and TiO ₂ (60 mg L ⁻¹)	Foliar spray	10 mg L ⁻¹	Combined SiO-NPs and Ti-NPs increased root biomass (26%), shoot biomass (25%), seed yield (36%), and chlorophyll concentration, while decreasing MDA (22%), EL (14%), CAT (32%), and SOD (33%) activities.	Chen and Kattab (2024)
Lemon balm	TiO ₂ -NPs (15 mg L ⁻¹)	Foliar spray	50, 100 mg kg ⁻¹	TiO ₂ -NP foliar spray reduced Cr toxicity and improved plant height, chlorophyll synthesis, total phenolic content, flavonoids, and rosmarinic acid, while reducing MDA and antioxidant activity.	Soliman et al. (2024)
Rice	Se-NPs (20 mg L ⁻¹)	Foliar spray	100 µM	Se-NP supplementation increases morphophysiological growth, leaf gas exchange traits, proline synthesis, and the expression of antioxidant genes, while reducing MDA and H ₂ O ₂ production.	Basit et al. (2023b)
Wheat	ZnO-NPs (10, 20, 30 mg kg ⁻¹)	Soil application	10 mg kg ⁻¹	ZnO-NPs improved leaf area, water use efficiency, chlorophyll and carotenoid synthesis, leaf gas-exchange characteristics.	Iqbal and Bhatti (2022)
Wheat	FeO-NPs (350, 450 mg L ⁻¹)	Foliar spray	350, 450 mg kg ⁻¹	FeO-NPs increased shoot length by 8% and 12%, shoot weight by 19% and 30%, and enhanced APX, CAT, POD, and SOD activities.	Zafar et al. (2024)
Rice	FeO-NPs (0, 10, 20 mg L ⁻¹)	Foliar spray	0, 50, 100 mg kg ⁻¹	FeO-NPs decreased oxidative damage and increased enzymatic and nonenzymatic activities, helping plants mitigate Cr toxicity.	Alharby and Ali (2022)
Rice	ZnO-NPs (5, 10, 15, 20, 25 mg L ⁻¹)	Seed priming	5 mg L ⁻¹	Seed primed with ZnO-NPs significantly improved in root and shoot growth, and reduction in bioaccumulation index of Cr.	Akhtar et al. (2021)
Lettuce	ZnO-NPs and FeO-NPs (0, 25, 50, 100 mg L ⁻¹)	Foliar spray	DNA	Foliar spray of combined Zn-NPs and Fe-NPs increased growth, photosynthetic performance, antioxidant activities, improved nutrient uptake, and reduced oxidative damage by activating antioxidant defense system.	Sameer et al. (2023)
Mungbean	Fe-NPs (0, 100, 1000 mg kg ⁻¹)	Soil application	50 mg kg ⁻¹	Addition of Fe-NPs to the growth medium increased plant fresh and dry biomass, total chlorophyll concentration, Fe uptake, and reduced Cr concentration.	Sun et al. (2020)

Table 2. (Continued.)

Wheat	CuO-NPs (25, 50, 100 mg kg ⁻¹)	Soil application	3.5 mg kg ⁻¹	Application of 25 and 50 mg kg ⁻¹ CuO-NPs promoted growth, biomass production, and decreased ROS and Cr translocation from roots to shoots by relieving the oxidative stress.	Noman et al. (2020)
Sunflower	Fe-NPs (0, 1%, 2%)	Soil application	0, 75, 150 mg kg ⁻¹	Treatment with Fe-NPs reduced Cr bioaccumulation, while enhancing growth and photosynthetic performance by increasing APX, CAT, POD, and SOD activities.	Mohammadi et al. (2020)
Chickpea	ZnO-NPs (25 µM)	Nutrient medium	0, 120 µM	ZnO-NPs increased plant growth, proline, soluble sugars, leaf gas-exchange characteristics, antioxidant activities, nutrient uptake, cell viability, and reduced MDA and ROS production.	Singh et al. (2024)
Mungbean	ZnO-NPs (2 ppm)	Nutrient medium	10 ppm	ZnO-NPs remarkably mitigated the adverse impacts of Cr, improved root and shoot growth, dry weight, antioxidant activity, and prevented the ultrastructural alterations.	Bhuyan et al. (2024)
Aloe Vera	Fe-NPs (DNA)	Soil application	15 mg kg ⁻¹	Application of Fe-NPs, in combination with Cr-tolerant bacteria, enhanced plant height, root area, leaf size, and gel concentration by 51%, 137%, 67%, and 49%, respectively. It also boosted CAT (125%), SOD (87%), POD (89%) activities, and proline synthesis (34%).	Komal et al. (2024)

DNA: Data not available.

It was found that supplementation of FeO-NPs (500 and 1000 mg L⁻¹) significantly increased chlorophyll synthesis and photosynthetic efficiency while mitigating the toxic effects of Cr (Brasili et al., 2020). Tripathi et al. (2015) tested the impact of Si-NPs (0 and 10 µM) on pea plants grown under Cr toxicity (100 µM). They found that Si-NPs ameliorated Cr toxicity and improved chlorophyll synthesis, photosynthesis, and nutrient uptake. Recently, Prakash et al. (2022) demonstrated that ZnO-NPs (25 µM) minimized Cr toxicity and improved the levels of photosynthetic pigments and subsequently photosynthetic efficiency by protecting the photosynthetic apparatus. They also reported that NPs reversed the inhibitory impacts of Cr and improved chlorophyll synthesis and quantum efficiency.

Basit et al. (2023a) noted a considerable reduction in Cr toxicity with ZnO-NPs and an improvement in the photosynthetic performance of soybean plants. They also found that the improved photosynthetic efficiency was linked to reduced oxidative damage with the administration of NPs (Basit et al., 2022). Ulhassan et al. (2023) found that Si-NPs markedly improved chlorophyll synthesis and electron transport efficiency. They also reported that

Cr stress upregulated the expression of *BnSAG12* by 2.7-fold, while Si-NPs downregulated the expression of that gene by 1.6-fold. The downregulation of *BnSAG12* by Si-NPs indicates that Si improved the chlorophyll levels and helped the plants overcome leaf senescence (Ulhassan et al., 2023). The findings of these studies suggest that NPs improve photosynthetic efficiency by reducing Cr toxicity, ROS production, and oxidative damage, leading to better assimilation and plant growth.

7.4. Nanoparticles improve antioxidant activities to counter the toxic effects of Cr

HMs increase the production of ROS, which damage cellular structures, plant metabolism, and physiological functioning, possibly even leading to cell death (Faizan et al., 2021b). Chromium toxicity significantly increases MDA and H₂O₂ production, which causes cell damage and lowers the cell viability of roots (Singh et al., 2024). However, ZnO-NPs (25 µM) reduced MDA and H₂O₂ production, which improved the cell viability (Singh et al., 2024). Furthermore, NPs can also alleviate ROS-induced damage by decreasing Cr uptake, and this phenomenon has been documented in rice, soybeans, and chickpeas (Basit et al., 2022; Singh et al., 2024). Alterations in antioxidant

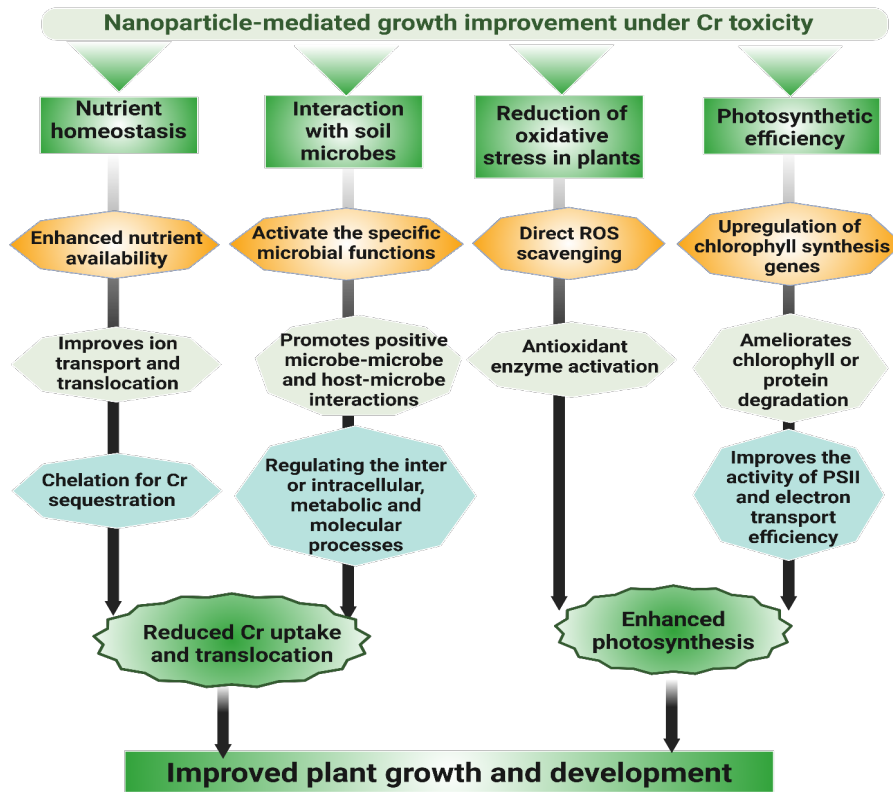


Figure 3. Mechanisms of NPs for improving plant growth and development under Cr stress.

activities and the ascorbate–glutathione (AsA–GSH) cycle in conjunction with Cr toxicity have been reported for many plants (Zeng et al., 2012). Prakash et al. (2022) reported that applying ZnO-NPs reduced catalase (CAT) and superoxide dismutase (SOD) activities in rice plants grown under Cr stress and that those reductions were linked to a reduction in oxidative stress. This indicates that lower antioxidant activities are associated with less production of oxidants following the application of ZnO-NPs. These authors also found that ZnO-NPs upregulated the AsA–GSH cycle by upregulating the dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), and glutathione reductase (GR) enzymes. Ma et al. (2022) stated that CeO₂-NPs reduced MDA and H₂O₂ production as well as EL by upregulating ascorbate peroxidase (APX) and SOD activity, which increased ROS scavenging and thus mitigated the deleterious effects of Cr as evidenced by lower rates of MDA and H₂O₂ production.

The potential benefits of zero-valent iron NPs (Fe⁰-NPs; 0%, 1%, and 2%) were studied in sunflower plants grown under Cr toxicity (0, 75, and 150 mg kg⁻¹). Fe⁰-NPs decreased Cr uptake and translocation and improved APX, CAT, and SOD activities (Mohammadi et al., 2020). In another study, a foliar spray of iron oxide NPs (FeO-NPs; 0, 10, and 20 mg L⁻¹) mitigated the toxic impacts of Cr by

improving enzymatic and nonenzymatic activities linked with reduced MDA and H₂O₂ production and EL. In tomato plants, the application of biochar-doped Fe⁰-NPs (0%, 0.5%, 1%, and 1.5%) minimized Cr accumulation and reduced H₂O₂ and MDA production. The possible mechanism of doped Fe⁰-NPs in reducing Cr accumulation was thought to be related to the absorption of Cr on the biochar surface (Naem et al., 2022). Earlier studies found that Si-NPs (0 and 10 µM) protected pea seedlings from Cr toxicity (100 µM) by increasing nutrient uptake (Ca, K, Mg, S, and P) and APX and SOD activities (Tripathi et al., 2015). Noman et al. (2020) used green synthesized CuO-NPs (0–15 mM) against Cr toxicity (0–100 mg kg⁻¹ soil) in wheat. They reported that CuO-NPs decreased the Cr-induced oxidative damage by increasing the uptake of essential nutrients and antioxidant activities (CAT, POD, and SOD).

The potential benefits of Si-NPs in mitigating Cr toxicity were tested in *Brassica* and the application of Si-NPs was found to increase SOD, CAT, APX, and GR activity in the roots and leaves. This indicated that the Si-NPs participated in the antioxidant defense system to ameliorate oxidative damage. Furthermore, the authors suggested that higher levels of antioxidants in the presence of Cr toxicity with Si-NPs would lead to

significant improvement in Cr tolerance (Ulhasan et al., 2023). Overall, NPs reduce ROS production by increasing antioxidant activities, but the effectiveness of NPs can vary depending on their concentration and type.

7.5. Nanoparticles cause ultrastructural changes and improve gene expression to mitigate Cr toxicity

Chromium toxicity damages the ultrastructure of plants, but exogenous application of NPs can cause favorable changes in plants to counteract Cr toxicity (Figure 3). For example, Basit et al. (2022) found that exogenous ZnO-NPs at 25 and 50 mg L⁻¹ slightly damaged the nucleolus structure, impaired thylakoid function, and caused chloroplast injury. However, ZnO-NPs at 100 mg L⁻¹ led to better chloroplast development, less damaged thylakoid granules, and better-developed nucleoli. These authors demonstrated that ZnO-NPs reduced cellular distortion by reducing ROS production and mitigating ultrastructural damage. This indicates that the concentration of NPs is an important variable in mitigating the adverse impacts of Cr.

Ulhasan et al. (2023) studied the impact of Si-NPs on thin sections of *Brassica* root tips. The tips of the roots showed well-developed cell walls, cell membranes, mitochondria, and chloroplasts with dense thylakoid granules under control conditions. However, Cr toxicity resulted in the swelling of the cell wall and cell membrane, with disrupted mitochondria and chloroplasts with abnormal shapes (Ulhasan et al., 2023). The application of Si-NPs resulted in thicker cell walls and cell membranes, better mitochondria, and well-shaped chloroplasts. Such benefits were attributed to Si-NPs reducing Cr-induced ROS production and maintaining cellular integrity, cell structure, and membrane stability (Manzoor et al., 2022). Singh et al. (2024) investigated the response of ZnO-NPs in chickpea plants grown under Cr toxicity and found that ZnO-NPs maintained the cell viability of the root tips. Manzoor et al. (2022) also reported that Si-NPs mitigated the deleterious impacts of Cr and resulted in better cellular ultrastructure, well-shaped chloroplasts with thylakoid granules, and distinct cell walls and cell membranes.

NPs have a significant ability to regulate gene expression. For instance, Prakash et al. (2022) found that Cr(VI) reduced the expression of *OsAPX*, *OsDHAR*, *OsMDHAR*, and *OsGR* by 29.11%, 32.5%, 25.5%, and 21.5%. However, exogenic ZnO-NPs increased the expression of those genes by 275%, 375%, 485%, and 205% under Cr stress. It was also observed that Si-NPs improved the expression of *BnSOD*, *BnCAT*, *BnAPX*, and *BnGR*, which improved Cr toxicity in *Brassica* plants (Ulhasan et al., 2023). In summary, NPs protect plant structures from the damaging impacts of Cr and improve gene expression to counteract Cr-induced damages.

7.6. Nanoparticles maintain hormonal balance and osmolyte accumulation to counter Cr stress

Osmolytes and phytohormones play crucial roles in plant adaptation to abiotic stresses (Banerjee and Roychoudhury, 2022). Limited research has been conducted to determine the crosstalk of hormones and NPs under Cr toxicity. In a recent study, the synergistic impact of indole acetic acid (IAA) and silicon NPs (Si-NPs) was evaluated in rice. The integrated use of Si-NPs and IAA enhanced biomass productivity and antioxidant activities, which mitigated ROS production (Sharma et al., 2022). This confirmed the protective role of Si-NPs and IAA in mitigating Cr toxicity, but it is still unclear whether Si-NPs can induce IAA biosynthesis genes for synergistic impacts with IAA in mitigating Cr toxicity. The interaction between Si-NPs and IAA should be studied in more detail at the molecular level. Moreover, additional studies are needed to explore the protective role of key hormones and signaling molecules together with NPs in mitigating Cr toxicity.

Mohammadi et al. (2018) investigated the effects of ethylenediaminetetraacetic acid (EDTA), FeO-NPs, and iron sulfate (Fe²⁺) on sunflower growth and physiological functions. They discovered that using FeO-NPs and Fe²⁺ produced marked reduction in Cr accumulation and oxidative damage together with an increase in chlorophyll synthesis. Furthermore, exogenously supplied EDTA exacerbated the negative effects of Cr by increasing MDA and H₂O₂ production. In general, chelating materials are used to enhance the mobility of HMs, resulting in better phytoextraction. However, in the study by Mohammadi et al. (2018), the increase in Cr uptake due to the use of EDTA and the positive correlation between FeO-NPs and Fe²⁺ revealed the increased phytoextraction capacity of sunflower plants. Another study found that combining *Bacillus* strains and an inorganic chelate (citric acid) mitigated the toxic impacts of Cr and ensured better wheat growth (Ilyas et al., 2022). The combined use of *Bacillus* and citric acid improved antioxidant activities and reduced Cr accumulation and excessive ROS production. However, it is still necessary to explore the crosstalk of *Bacillus* and citric acid with NPs under Cr stress.

Basit et al. (2022) found that ZnO-NPs increased the synthesis of brassinosteroids (BRs), which mitigated Cr stress by increasing the photosynthetic efficiency and decreasing ROS production. BR application improved the stomata regulation, photosynthesis, and growth of tomatoes under Cr stress (Jan et al., 2020). These findings indicate a positive relationship between ZnO-NPs and BRs for the mitigation of Cr toxicity. Another study found that ZnO-NPs improved the phytochelatin levels of soybean plants under Cr stress, which increased Cr tolerance (Diwan et al., 2010).

ABA plays crucial roles in seed development, leaf abscission, and vegetative growth (Vishwakarma et al., 2017). However, at higher concentrations it has antagonistic impacts on plants. Increased ABA in the presence of Cr toxicity is associated with reduced photosynthesis and plant biomass (Basit et al., 2022). ZnO-NPs (20, 50, and 100 mg L⁻¹) significantly reduced ABA synthesis, which was linked with improved Cr tolerance and better photosynthetic efficiency (Vishwakarma et al., 2017). Proline is a significant signaling molecule that plays a crucial role in stress tolerance. It has been documented that NPs increase proline synthesis, which helps plants counter Cr toxicity (Ramzan et al., 2023; Singh et al., 2024). However, there are few studies in the literature describing the impacts of NPs on signaling molecules and hormones under Cr stress. More detailed research is needed to explore the use of NPs and signaling molecules and hormones under Cr toxicity. This will help researchers develop strategies to improve plant resilience against Cr stress.

7.7. Nanoparticles interact with soil microbes to alleviate Cr toxicity

Soil microbes play important roles in maintaining soil fertility, nutrient cycling, and soil carbon sequestration (Bahram et al., 2018) as well as nutrient homeostasis and resistance to stress conditions (Vogel et al., 2021). Chromium toxicity has negative effects on microbial diversity and it also impairs the relationship between soil microbes and plants (Ao et al., 2022). NPs are an effective way to supply nutrients and activate soil microbial functions (Mishra et al., 2020). For example, silver NPs (Ag-NPs) enhanced the growth of nitrifiers, denitrifiers, and phosphorous-mobilizing bacteria (Mishra et al., 2020). In soil, microbes can reduce Cr(VI) to Cr(III) by different mechanisms such as biosorption and bioaccumulation, thereby remediating Cr toxicity (Ao et al., 2022). Ahmad et al. (2022) found that Cr-resistant *Staphylococcus aureus* applied together with ZnO-NPs decreased Cr accumulation while increasing chlorophyll synthesis, antioxidant activity, and nutrient uptake in wheat plants. However, the mechanism by which *S. aureus* and ZnO-NPs reduce Cr(VI) to Cr(III) remains unknown and more metabolic and molecular studies are needed. In another study, Alharby and Ali (2022) investigated the potential of *S. aureus* and FeO-NPs to reduce Cr toxicity in rice. Exogenous FeO-NPs increased growth, biomass production, and antioxidant activity and decreased Cr accumulation. These authors reported that the combination of *S. aureus* and FeO-NPs mitigated Cr toxicity in rice plants more effectively. Nevertheless, the efficacy of Cr-resistant microbes and NPs should be studied in different plants to explore the mechanisms used by microbes and NPs in addressing Cr toxicity.

NPs have attracted considerable attention in agriculture, but little is known about how NPs interact with microbial assemblages or homeostasis during Cr detoxification. Recently, the impact of NPs and microbes in regulating Cr toxicity was evaluated (Ahmad et al., 2022), but mechanistic genetic insights for the mitigation of Cr toxicity were not revealed. Such findings are vital to optimize the potential of NPs and microbes for bioremediation of Cr and the regulation of plant growth. For example, it is essential to discover whether plants recruit special microbial consortia when NPs are applied to mitigate Cr toxicity. Moreover, it is also necessary to determine whether NPs activate Cr detoxification genes in particular soil microbes to convert Cr(VI) to Cr(III). Such efforts will help achieve greater benefits for the remediation of Cr-polluted soils with the combined use of NPs and microbes.

7.8. Nanoparticles enhance plant growth under Cr stress

Chromium stress significantly reduces plant growth by inducing excessive production and disturbing nutrient uptake, photosynthesis, and plant-water relations (Xu et al., 2018). NPs work as slow fertilizers and are important sources of nutrients for plants, enhancing plant growth and development in polluted soils (Figure 3). For instance, a foliar spray of ZnO-NPs mitigated Cr toxicity and substantially increased the growth of soybean by mitigating Cr-induced oxidative damage and maintaining plant physiological activities and nutrient homeostasis (Basit et al., 2023a). Exogenous ZnO-NPs (50 mg L⁻¹) improved shoot weight (21%–77%), root weight (22%–45%), shoot length (3%–35%), root length (24%–154%), soluble sugars (19%–52%), and antioxidant activities in Cr-polluted soil (10, 15, and 20 mg kg⁻¹) (Ramzan et al., 2023). Furthermore, Si-NPs accelerated growth and germination by influencing antioxidant activities, physiological functioning, nutrient uptake, and the reduction of Cr accumulation (Ulhasan et al., 2023). Si-NPs form physical barriers in plant tissues that conserve water and allow for better root growth, thus resulting in better nutrient and water uptake and subsequent plant performance in the presence of stressors (Li et al., 2023). Tripathi et al. (2015) found that Si-NPs substantially reversed Cr toxicity and improved pea growth and development. They noted that soil-applied Si-NPs enhanced growth and photosynthetic activity and decreased Cr uptake and its translocation into plant parts. Sharma et al. (2021) reported that Si-NPs reduced Cr-induced oxidative damage and stimulated the growth of rice in Cr-polluted soils. Mohammadi et al. (2020) stated that Fe-NPs enhanced the antioxidant activities, growth, and development of sunflower plants grown in Cr-polluted soil. All of these studies indicated the potential of NPs to improve plant growth, but the effectiveness of NPs is significantly affected by their concentration and type, as well as the plant species.

8. Conclusion and future prospects

Chromium concentrations are soaring in the environment, which poses a serious threat to both plants and humans. NPs can decrease Cr uptake and Cr-induced oxidative damage and improve antioxidant activities and osmolyte accumulation, helping to maintain membrane stability, proteins, and lipids and safeguard the photosynthetic apparatus. These effects lead to better plant performance. The effects of NPs in mitigating Cr toxicity depend on the size, type, and concentration of the NPs and the growth stage and species of the plant. Despite recent achievements, future research is needed in this field to fill important gaps in the literature:

- The role of NPs in seed germination has not yet been fully explored; consequently, it is essential to explore the mechanisms underlying improvement in seed germination with NPs.
- Limited research has been conducted on the impacts of NPs on nutrient uptake under Cr stress. Therefore, understanding the effect of NPs on nutrient channels and nutrient signaling remains an important area of exploration.
- The effect of NPs on signaling molecules and plant hormones is poorly investigated. Understanding the impact of NPs on signaling molecules and plant hormones under Cr stress would open new avenues for the control of Cr toxicity.
- Efforts are needed to determine how NPs can downregulate different genes to reduce Cr accumulation in plants.
- It is still unclear how NPs regulate the compartmentalization of Cr in cell vacuoles by xylem or phloem loading and then transport the Cr into aboveground plant parts.
- The effect of NPs on soil properties is poorly studied; thus, more research is required to investigate these effects.

- NPs and microbes constitute a green and sustainable method for remediating polluted soils. More research is needed to discover Cr-resistant bacteria and the mechanisms of combined NPs and microbes in mitigating Cr toxicity.

- The use of NPs in combination with different osmolytes and hormones could be a viable approach for counteracting Cr toxicity.

- Generally, soils are contaminated by multiple toxic metals, and research should be aimed at determining the impact of NPs in soils with multiple types of contamination. Biosynthesized NPs could be a new and promising tool providing efficient results to counter Cr toxicity. Detailed studies are required before applying NPs in the environment to minimize possible damage to the ecological balance.

Conflict of interest

The authors have no conflicts of interest regarding this manuscript.

Funding

We are grateful to the National Key Research and Development Project of China (2016YFD0300208) and the National Science Foundation of China (41661070) for their financial support of this work. We express our gratitude to the National Key Research and Development Project of China (2016YFD0300208) and the National Science Foundation of China (41661070) for their financial support of this work.

Acknowledgments

The authors are thankful to Dr. Muhammad Aamer for his suggestions to improve the quality of the manuscript. The authors extend their appreciation to the Deanship of Research and Graduate Studies at King Khalid University for supporting this work through small group research under grant number RGP 1/7/45.

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