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Review

Microbial-assisted alleviation of chromium toxicity in plants: A critical review

Freeha Fatima Qureshi [a], Muhammad Arslan Ashraf [a,*], Rizwan Rasheed [a], Iqbal Hussain [a], Muhammad Rizwan [b,*], Muhammad Iqbal [a], Jean Wan Hong Yong [c,*]

[a] Department of Botany, Government College University Faisalabad, Faisalabad 38000, Pakistan
[b] Department of Environmental Sciences, Government College University Faisalabad, Faisalabad 38000, Pakistan
[c] Department of Biosystems and Technology, Swedish University of Agricultural Sciences, 23456 Alnarp, Sweden

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ABSTRACT

Soil contamination with chromium (Cr) is a serious and burgeoning environmental problem. The infiltration of excess Cr into the food chain causes a number of human health issues, including respiratory disorders, cardiovascular diseases, renal failure, and several types of cancer. The Cr pollution can be contained by different physical, chemical, and biological remediation approaches. Physical and chemical methods are costly and hazardous to the environment as they cause secondary pollution. Biological approaches such as bioremediation that employ plants (phytoremediation) and microbes are eco-friendly, efficient, and cost-effective. Nonetheless, conventional phytoremediation encounters limitations in large-scale applications due to a restricted pool of hyperaccumulator plant species, slow growth rate, limited biomass production, plant-contaminant specificity, and contaminant-mediated oxidative stress in plants. Interestingly, microbes such as bacteria and fungi have the potential to survive and thrive under extreme environmental conditions. Plant growth-promoting bacteria (PGPB) utilize siderophores, organic acids, biosurfactants, redox mechanisms, and biomethylation to convert metals into soluble and bioavailable forms. Further, these bacteria are involved in synthesizing phytohormones and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, acquisition of iron, nitrogen fixation, and phosphorus solubilization, which improve plant growth and strengthening eco-physiological resilience, thereby aiding in phytoremediation. This literature review encompasses a breadth of research conducted over the preceding decade, underscoring the contemporary remedial approaches with a primary focus on the crucial role of microbes in facilitating the phytoremediation of Cr. Moreover, this article revealed the underlying and plausible mechanisms involved in the microbe-assisted phytoremediation potential of plants grown under Cr-contaminated soils.

Introduction

Rapid industrialization and urbanization resulted in an escalation of heavy metal and metalloid pollution in the environment (Clemens and Ma, 2016; Ifediegwu et al., 2021; Song et al., 2022). As a result, heavy metal-contaminated soils have become an alarming issue throughout the globe (Keller et al., 2015; Hussain et al., 2022; Zaynab et al., 2022; Rasheed et al., 2024). Heavy metals and metalloids, including cadmium (Cd), chromium (Cr), mercury (Hg), lead (Pb), molybdenum (Mo) and arsenic (As, a metalloid), have been found in natural sources like water and soils. Exposure to these toxic metals and metalloids results in considerable damage to water supplies, soil-borne animals, microbes as well as plants and ultimately affects human health via the food chain (Yong et al., 2010; Liu et al., 2012; Tow et al., 2018;Rizwan et al., 2016; Song et al., 2019; Vardhan et al., 2019; Guo et al., 2021; Ahammed and Yang, 2022). Among the heavy metals, Cr is a highly hazardous

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Abbreviations: Cr^{6+}, hexavalent chromium; Cr^{3+}, trivalent chromium; ROS, reactive oxygen species; $O_2^{\bullet-}$, superoxide radicals; •OH, hydroxyl radicals; PGPM, plant growth promoting microbes; PGPR, plant growth promoting rhizobacteria; AMF, arbuscular mycorrhizal fungi; MG, methylglyoxal; Gly-I, glyoxalase I; Gly-II, glyoxalase II; SPB, siderophore producing bacteria; ACC, 1-aminocyclopropane-1-carboxylate deaminase; PAL, phenylalanine ammonia lyase; GR, glutathione reductase; DHAR, dehydroascorbate reductase; MDHAR, monodehydroascorbate reductase; IAA, indole-3-acetic acid.

* Corresponding authors.

E-mail addresses: marslanashraf@gcuf.edu.pk (M.A. Ashraf), mrazi1532@yahoo.com (M. Rizwan), jean.yong@slu.se (J.W.H. Yong).

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non-essential metal that may be found in various environments (Sun et al., 2023). Chromium contamination has been documented all over the world, causing irreversible harm to microorganisms and plants (Khan et al., 2012). Chromium ranks 17th in terms of abundance in the earth's crust. Although Cr is needed at minimal levels by humans and animals, it is a major environmental contaminant at elevated levels (Kumar et al., 2016; Srivastava et al., 2021; Irshad et al., 2023). Chromium is considered a significant source of soil pollution due to its vast application in several industrial processes, such as plating, alloy, stainless steel welding, leather tanning, and the production of pigments, cement, steel, and nuclear weapons. The excessive discharge of untreated quantity of wastewater (Cr-bearing wastewater and solid sludge) from these industries is one of the primary sources of Cr pollution in the soil (Prasad et al., 2021; Bao et al., 2022). Furthermore, several fertilizers, fungicides, plastic films, and smoke released from vehicles are also the major contributors to Cr toxicity in water and soil (Constantin et al., 2021).

Chromium has a valence shell chemistry and complex electronic configuration due to its ability to switch from one oxidation state to another (Shahid et al., 2017). Chromium is often found in hexavalent (Cr^{6+}) and trivalent (Cr^{3+}) states in soil. Hexavalent Cr is more hazardous than Cr^{3+} and is classified as a group-1 human carcinogen by the International Agency for Research on Cancer (Alvarez et al., 2021). Moreover, the U.S. EPA (United States Environmental Protection Agency) also classified Cr^{6+} as the most toxic contaminant owing to its life-threatening effects (Shakya et al., 2019; Manoj et al., 2020).

Being a carcinogenic and mutagenic species, Cr^{6+} can cause multiple human disorders, such as chromosomal aberrations, skin problems, and DNA damage. Besides, Cr^{3+} plays a crucial role in glucosidic digestion occurring in the human body. Cr^{3+} also controls the blood glucose level via the breakage of insulin (Ali et al., 2021b) . Although Cr^{3+} is a micronutrient for humans, its elevated level results in health problems (Dimitroula et al., 2015). In nature, Cr^{3+} can oxidize, converting into its more hazardous form, Cr^{6+} (Vendruscolo et al., 2017). Higher toxicity of hexavalent Cr was attributed to its greater solubility, mobility, dominance, and permeability through the plant cell membrane (Siddiqa and Faisal, 2018). Cr^{6+} enters the cell via the sulfate transport system and interacts with proteins and nucleic acids in plants. Cr^{6+} pollution disturbs the structure of microbial communities, thereby diminishing their growth (Mishra and Bharagava, 2016). Cr^{6+} toxicity perturbs normal plant metabolism and hampers seed germination, growth, biomass, photosynthesis, water relations, nutrient uptake, and yield. Also, Cr^{6+} stress favors lipid peroxidation through reactive oxygen species (ROS) generation in plants (Sangwan et al., 2015; Brasili et al., 2020; Sharma et al., 2020a). Cr^{6+} stress negatively affects plant health due to its higher cell membrane permeability and consequent disruption rates and ROS generation, which intensifies such effects compared to Cr^{3+} (Ukhurebor et al., 2021). Chromium also causes alterations in subcellular compartments of plant cells, such as cell walls and membranes, plastids, mitochondria, vacuole, and nuclei bodies. Plant cell cycle, cell division, and enzymatic activities are also adversely affected by Cr stress (Wakeel and Xu, 2020). Chromium toxicity has been reported to severely impair plant root architecture, thereby obstructing water and nutrient acquisition leading to growth retardation.

Notably, several reports have demonstrated the harmful impacts of Cr toxicity on plant metabolism, limiting their growth potential to survive under such adverse environments. Hyperaccumulator plants are known to accrue significantly higher metal content in different tissues due to their efficient metal tolerance mechanisms . However, some reports have demonstrated that excess metal accumulation in hyperaccumulator plants instigates severe oxidative stress by generating ROS such as singlet oxygen ($^1O_2$), superoxide radicals ($O_2^{\bullet-}$), hydroxyl radicals ($\bullet$OH), and hydrogen peroxide (H_2O_2) that deteriorates cellular metabolism and infrastructure leading to diminished plant growth alongside their phytoremediation potential (Hussnain et al., 2023; Kumar and Seth, 2022; Malik et al., 2021; Mallhi et al., 2020; Zaheer et al., 2020). Microbes possess significant potential in mitigating the phytotoxic impacts of excess Cr and promoting growth by regulating crucial physiological and biochemical processes in plants. Also, microbes exhibit enzymatic detoxification capabilities, exemplified by processes like reducing Cr^{6+} to Cr^{3+}, rendering it less toxic to plants. Therefore, researchers introduced multiple solutions to tackle the issue of Cr pollution aimed at alleviating its deleterious effects.

The approaches employed to tackle the problem of Cr pollution may be broadly divided into physical, chemical, and biological techniques. Physical and chemical strategies involve excavation, landfill placement, thermal treatment, leaching, and electro-reclamation. These methods are fast but inadequate, expensive, altered soil properties, and leading to secondary pollution (Liu et al., 2018). In comparison to physical and chemical processes, bioremediation of Cr pollution through microbes has manifested as a cost-effective and environment-friendly method (Verma and Kuila, 2019). However, the efficiency of this process is significantly influenced by environmental conditions such as the availability of moisture, optimum temperature, and pH, which govern the metabolic activity and growth of microbes (Kuanar et al., 2022).

Various bacterial species have demonstrated the capacity to mitigate Cr phytotoxicity by converting Cr^{6+} to Cr^{3+} and limiting its absorption into above-ground plant parts, thereby primarily contributing to Cr phytostabilization. For instance, a strain of *Pseudomonas* sp. (NT27) significantly improved plant biomass and redox homeostasis with a concomitant increase in root Cr content of *Medicago sativa* plants, exhibiting potential for Cr^{6+} phytostabilization (Tirry et al., 2021). Various strains belonging to the genus *Stenotrophomonas maltophilia* and *Bacillus thuringiensis* caused a noteworthy accumulation of Cr in the roots of chickpea plants relative to controls (Shreya et al., 2020b). Likewise, *Bacillus species* notably suppressed the Cr uptake by chickpea plants. This strain also effectively augmented the plant growth, chlorophyll contents, nodulation, leghaemoglobin, grain protein, and seed yield under Cr^{6+} stress (Wani and Khan 2010). According to Sundar et al. (2011), *Bacillus subtilis* attained 64% Cr^{3+} remediation potential. Likewise, a bacterial strain, *Staphylococcus arlettae*, reduced up to 98% of Cr^{6+} (100 mg L^{-1}) in wheat plants after 24 h. Besides, the strain significantly lowered the Cr^{6+} levels, such as 500 and 1000 mg L^{-1} by 98% and 75%, respectively, in 120 h (Sagar et al., 2012). Upadhyay et al. (2017) reported that microbes reduce the Cr^{6+}stress by using the Cr either as a final electron acceptor or by secreting specific soluble enzymes in plants. Similarly, Oves et al. (2013) isolated *Pseudomonas aeruginosa* strain that removed 100% of Cr from chickpea plants grown in Cr-contaminated soil. The results also manifested that the strain improved the accumulation of dry matter, symbiotic characteristics including nodule formation, yield of grain, and protein contents of chickpea plants under Cr stress. Further, the strain also diminished Cr uptake in plant harvestable parts under Cr stress. In another study, plant growth-promoting rhizobacteria efficiently lessened the toxic impacts of Cr by reducing Cr^{6+} to Cr^{3+} in wheat plants. The bacteria demolished the Cr contents by 62% in the soil medium. Plants inoculation with these bacteria dramatically declined the Cr uptake up to 36% and 60% in root and shoots, respectively (Khan et al., 2013). Under Cr^{6+} stress, *Lens esculenta* plants were supplemented with three bacterial strains, namely, *Ochrobactrum intermedium, Bacillus cereus*, and *Brevibacterium* sp. It was found that strains effectively reduced the Cr^{6+} into Cr^{3+} under Cr^{6+} stress (Faisal 2013). In another study, the inoculation of effective microbes noticeably improved the *Zea mays* L. and *Vigna radiata* L. growth under Cr^{6+} stress. In comparison, *Z. mays* plants exhibited better growth in the form of higher chlorophyll and protein contents under Cr^{6+} stress. It also inhibited the Cr^{6+} uptake upon effective microbe application, thereby minimizing oxidative injury in plants under Cr^{6+} stress. Likewise, the effective microbes downregulated the superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activities in plants (Dheeba et al., 2014). Soni et al. (2014) examined the impact of bacterial (*Microbacterium* sp.) and fungal (Arbuscular mycorrhizal fungi, AMF) strains in maize under Cr^{6+} stress. The Cr-reducing bacterial strain improved the plant yield by lowering the bioavailability and uptake of Cr^{6+} in plants. Further, the bacterial strain also promoted nutrient availability via enhanced mycorrhizal colonization, which hindered Cr transport towards the aerial parts of plants under Cr^{6+} stress. Similarly, a bacterial strain, namely *Brucella* sp. decreased the Cr^{6+} level by 69.6% and 40% in vegetative and reproductive parts of okra plants. The strain also substantially enhanced the plant growth and yield regarding root length, fruit weight, number of fruits per plant, and plant height under Cr^{6+} toxicity (Maqbool et al., 2015). Besides, PGPB not only assists in improving plant growth but also facilitate heavy metal mobility and accessibility, trigger redox alterations, enhance phosphate solubility, encourage acidification, and synthesize chelating agents, thereby augmenting plant metal uptake and accumulation. For instance, *Bacillus cereus* inoculation has resulted in a manifold increase in Cr concentration in the aerial parts of *Brassica nigra* plants while keeping the Cr-associated oxidative damage at a minimum (Akhtar et al., 2021).

Therefore, it is imperative to find out new, improved, economical, and eco-friendly approaches for alleviation of Cr contamination from soil to avert detrimental effects on human health and the ecosystem. The objective of this article is to conduct a comprehensive review of previously published studies in the last decade that focus on the role of bacteria in phytoremediation efficacy. This review also highlights the significance of bacterial mechanisms in facilitating and optimizing the phytoremediation process. The review strategy opted for this study involves an extensive search for peer-reviewed published original research papers using multiple keywords on different databases such as Google Scholar, Web of Science, Sciencedirect, Researchgate, and Scopus. The keywords used to filter relevant research studies were “Cr toxicity”, “phytotoxicity”, “remediation techniques”, “microbes”, “plant growth promoting rhizobacteria”, “bioremediation”, “nutrient acquisition”, “inoculation”, “antioxidant system”, “glyoxalase system”, “osmolytes”, “chromium”, “chlorophyll”, “plant biochemistry”, “phytoextraction”, “phytostabilization”, and “phytoremediation”.

Techniques for the remediation of chromium-polluted soil

The remediation of toxic heavy metals is needed to avoid harmful environmental effects and to safeguard the functionality of ecosystems for future generations. Removing toxic heavy metals and metalloids is expected to be challenging with regards to technical difficulty, operational processes, and expense. Over the years, multiple soil remediation procedures have been employed for heavy metal remediation (Ashraf et al., 2017; Clemens and Ma, 2016; Yan et al., 2020). Hexavalent Cr (Cr^{6+}) is among the most frequent environmental pollutants because of its extensive industrial usage. Being a heavy metal, it is non-biodegradable and, hence, a significant subject of concern. Thus, it is essential that the remediation procedures bring Cr levels below permissible limits before the discharge of effluents (Jobby et al., 2018). In this context, several techniques have been employed for the Cr remediation. These include physical, chemical, and biological methods (García-Hernández et al., 2017).

Physical and chemical strategies to clean up chromium-polluted soil

The physical method is a way of eliminating Cr from polluted soil by employing physical engineering procedures. It is typically ideal for prompt remediation of Cr. Chemical approaches entail adding appropriate chemical agents to contaminated soil to change the form and valence of Cr. Chromium mobility and toxic effects are also reduced due to these changes (Bao et al., 2022). The physical methods include drying, sedimentation, ball milling, crushing, filtration, sieving, and absorbing toxic metals like Cr from sludge to remove pollutants with 50% removal efficiency. Ion exchange, reverse osmosis, and chemical precipitation are the well-known chemical approaches for Cr removal from industries and household sludge with 98–99% removal efficiency (Kumar et al., 2021b). Other approaches such as adsorption, electrocoagulation, electrodialysis, and membrane separation are also widely used for Cr remediation. These technologies, however, have several limitations, such as low efficacy, high operating and maintenance costs, and the production of secondary pollution in the form of sludge, which restricts their use in real-world situations. Additionally, it also causes hardness in water and passive reaction rate. Chemical expense, high labor, and tools make them not feasible for Cr remediation. The filtration is also unsuitable due to expensive membrane management and additional chemicals needed to convert Cr^{6+} to Cr^{3+}. In this process, before filtration, the Cr^{6+} was converted to Cr^{3+} by using ferrous sulphate, followed by coagulation. Further, the reverse osmosis and ion exchange are restrained by increased cost and membrane ultrafiltration, and low stability (Alemu et al., 2018; Pakade et al., 2019). Generally, Cr^{6+} in industrial wastewaters is subjected to reduction and, following chemical precipitation, to less toxic Cr^{3+} by employing reductants such as $FeSO_4$, $Na_2S_2O_5$, and SO_2 or electrochemical methods including electro-reduction, and electro-deionization. Additionally, another method such as adsorption on adsorbents (activated carbons or zeolites) is also employed for Cr removal. It showed various benefits, including ease of use, cheap cost, and high efficacy. Although, this technique also has some drawbacks, such as the demand for adsorption media regeneration and not effectively converting the Cr^{6+} to Cr^{3+}. Additionally, despite the widespread use of traditional techniques for Cr^{6+} polluted area rehabilitation, the soil excavation, and groundwater pump and treat (P&T) are energy-consuming processes. They are also chemical demanding and require massive costs. Further, the P&T approach also becomes inefficient when dealing with polluted wastes at minimum Cr^{6+} levels. This approach includes extracting affected water from the aquifer and treating it above-ground (Beretta et al., 2019). Furthermore, physical and chemical methods often degrade soil properties, biodiversity and impair microbial biota, which has an impact on environmental health (Bahadur et al., 2017; Das et al., 2021). In fact, the mobility, distribution, level, and presence of Cr species in the sources influence the selection of the most appropriate approach for Cr remediation (Nayak and Kale 2020).

Biological strategies to remediate chromium-contaminated soil

Since multiple remediation techniques have been employed to remediate soil pollution with different degrees of effectiveness over the years. However, the research scientist argues that no one universal remediation approach will be adequate for all types of soil and contaminants. This is because of the complexity of soils and the diversity of pollution (Yan et al., 2020). Alternatively, an efficient remediation program may need two or more technologies in combination (Hassan et al., 2016). In this context, biological approaches for toxic metal removal, including Cr, might be an appealing alternative to physical and chemical methods (Dixit et al., 2015). Biological approaches are defined as the employment of living organisms (animals, plants, and microbes) to remove heavy metals, such as Cr, from the soil (RoyChowdhury et al., 2018; Bao et al., 2022; Gulzar and Mazumder, 2022). Generally, biological remediation is a green technology solution to the problem of environmental contamination. It is described as applying microbes or plants to detoxify or eliminate organic and inorganic xenobiotic substances from the environment. It is a cost-effective and natural process that provides a long-term solution for metal removal due to the complete mineralization of toxins. It also offers less exposure of workers to dangerous pollutants, safeguarding public health (Abioye 2011). Further, biological approaches, due to their environment-friendly nature, are broadly accepted by the public (Pinto et al., 2016). These technologies can help reduce energy usage and the use of hazardous and expensive chemicals, allowing long-term environmental restoration (Ossai et al., 2022). Biological approaches are further classified into two categories, bioremediation and phytoremediation, which can be used either alone or in combination for effective metal removal (Dhaliwal et al., 2020; Raj and Maiti, 2020; Yan et al., 2020).

Bioremediation is the implementation of microbes that play an essential role via decomposing, mineralizing, and accumulating a variety of hazardous and biodegradable contaminants from the environment and converting them into less toxic forms (Patel et al., 2022). Microorganisms that carry out the process of bioremediation are known as bio-remediators (Kensa, 2011). For example, bacteria, yeast, fungi, and algae have been found as efficient bioremediation agents (Biswas, 2015; Kumar and Dwivedi, 2021). This method has proven practical and trustable due to its environmentally favorable characteristics (Azubuike et al., 2016; Mohanty and Rath, 2020). Bioremediation is further categorized into in-situ and ex-situ bioremediation methods; bioventing, bioaugmentation, biosparging, biostimulation, and phytoremediation are among the *in-situ* bioremediation techniques. Besides, bioreactors, composting, biopiles, and land farming are *ex-situ* approaches to bioremediation of metal removal (Prabhu et al., 2017; Sayqal and Ahmed, 2021). The basic principle of bioremediation is the degradation and conversion of contaminants to less toxic forms. Bioremediation performance, either ex-situ or in-situ, depends on a variety of factors such as cost, site attributes, nature, and level of a contaminant (Sharma, 2020). *Ex-situ* bioremediation entails the removal of polluted substances that have been treated elsewhere, while *in-situ* bioremediation is the treatment of polluted substances in the same place (Kumar et al., 2018; Arantza et al., 2022). The excess application of fertilizers, pesticides, and herbicides has resulted in low agricultural productivity as well as soil fertility, adverse economic returns, food poisoning, soil impairment, loss of biodiversity and severe environmental threats (Alori et al., 2017). Besides, bioremediation is the feasible and alternative method for decontaminating polluted soils more cleanly and safely (Pant et al., 2021). It is a non-invasive method (Khalid et al., 2017). The bioremediation process can be active or passive (Clemens and Ma, 2016; Kramer, 2010). The methods that are adopted through microbes in bioremediation are bioaccumulation, biotransformation, bioleaching, biosorption, and biomineralization (Tekere, 2020). Biological elimination of Cr^{6+} is considered a viable approach for the cleanup of substantially less toxic and less mobile Cr^{3+} compared to chemical processes of polluted streams and soils (Pradhan et al., 2017). In this context, the bioremediation of Cr^{6+} can take place through two mechanisms; biosorption and biotransformation. Biosorption refers to the sorption and retention of Cr^{6+} by biologically generated materials and living organisms, lowering Cr^{6+} levels. However, the biotransformation involves the conversion of Cr^{6+} into Cr^{3+}. These two ways can limit Cr migration capability and bioavailability, as well as Cr absorption by crops and other biota in the food chain (Xia et al., 2019). Through bioremediation techniques, multiple classes of pollutants can be mitigated in comparison to conventional physical and chemical processes that are ineffective and need high cost (Ojuederie and Babalola, 2017; Uma Maheshwari Nallal et al., 2022). Most researchers, however, recommended that microorganisms can be used instead of organic materials to eliminate or decrease heavy metal concentrations in polluted locations. Microbial communities have successfully used this intrinsic capacity to lessen, decompose, or immobilize hazardous pollutants and clean up contaminated conditions (Jacob et al., 2018).

Likewise, phytoremediation, is also an innovative method that may be employed to remediate polluted areas by using plants. In the present scenario, inoculation of plants with their symbiotic and effective microorganisms have attracted interest for phytoremediation of metals contaminated soils. In this way, the technique, phytoremediation, is gaining attraction to detoxify polluted soils on a broad scale (Ratna et al., 2021). Some of the famous on-field success stories of bioremediation by employing plants and microbes can be seen in the reclamation of radioactive polluted land due to the Chernobyl nuclear disaster in 1986 and Fukushima Daiichi nuclear disaster in 2011 (Sasaki et al., 2013; Tamaoki et al., 2016; Khan, 2020; Li et al., 2023).

Phytoremediation of chromium-affected soils

Phytoremediation is a green technique that uses plants to remove contaminants from the environment (Gajić et al., 2018; Nguyen et al., 2021). It is a cost-effective, environment-friendly, and widely accepted technique for toxic metal and metalloid removal (Yong et al., 2010; Malaviya et al., 2020; Haokip and Gupta, 2021; Kafle et al., 2022). The phytoremediation of heavy metals and metalloids from polluted sites typically occurs through one or a combination of the ensuing techniques such as phytoaccumulation, phytostabilization, phytovolatilization, and phytodegradation (Clemens and Ma, 2016; Yan et al., 2020). The description of these phytoremediation techniques is presented in Table 1S. Plants have been identified as a potential feedstock for generating biofuels as a source of renewable energy. Within this context, phytoremediation serves as a metal remediator and an energy generator from the resultant phytoremediator plants. When this strategy is implemented on the large scale, plants utilized in phytoremediation can assist in improving climatic conditions, lowering greenhouse gas emissions, and ecologically restoring metal-affected lands and water. Plants belonging to Brassicaceae, Asteraceae, Fabaceae, and Poaceae are generally efficient in extracting metal ions from the soil. Only those plants are chosen that accumulate metals or have substantial resistance to metal accumulation in a stressed environment. They can efficiently transport metal ions from root to shoot so that the plant biomass can be harvested and further treated from metal-polluted sites (Adrees et al., 2015; Amin et al., 2019). Therefore, plants with fast growth rate, larger above and below ground biomass, and easy cultivation processes are ideal candidates for phytoremediation (Patra et al., 2020; Chen et al., 2021; Wang et al., 2022). In this context, hyperaccumulator plants have been widely employed for successful remediation of hazardous metals. Hyperaccumulators are plants that can survive and grow in metalliferous soils, while actively absorbing and accumulating many heavy metals in their aerial organs without presenting phytotoxic signs (Song et al., 2021; Sytar et al., 2021; Zhang et al., 2022). Currently, over 400 plant species have been identified as metal hyperaccumulators, accounting for less than 0.2% of all angiosperms (Haldar and Ghosh, 2020). For this reason, phytoremediation is mainly based on the utilization of hyperaccumulator plants that may remove toxic chemicals and metals from the soil through assimilation or adsorption (Amna et al., 2015; Liu et al., 2022). Because of its ease of use and high metal removal effectiveness, phytoremediation has also shown to be a practical approach for reclaiming Cr-contaminated soil and wastewater. Plants that are hyperaccumulators tend to convert highly toxic Cr^{6+} into less hazardous $Cr^{3+}$with diminished mobility. It exploits a plant's natural process to bioaccumulate and store the maximum amount of Cr in its roots and aerial parts. Chromium hyperaccumulator plants can accumulate up to 1000 mg kg^{-1} Cr content dry weight in their tissues. In the pursuit of effective Cr phytoremediation, a number of parameters assume significance, encompassing soil physio-chemical attributes, the bioavailability of Cr, plant root exudates, microbial interactions, and the inherent capacity of plants to uptake, translocate, and accumulate Cr (Sinha et al., 2018). Therefore, it is imperative to ascertain the optimal plant species suitable for utilization as hyperaccumulators alongside their compatible microbes in the exploration of Cr phytoremediation (Halder and Anirban, 2022). In this context, Adiloğlu et al. (2021) discovered that the Malabar spinach was a hyperaccumulating species , effectively remediated Cr^{6+} from Cr affected soil. Similarly, *Spirodela polyrrhiza* (L.) Schleid. proved a good phytoremediator of Cr^{6+}. The plant can effectively accumulate a large quantity of Cr^{6+} in roots rather than fronds, thereby protecting fronds from phytotoxic impacts of Cr^{6+} (Singh and Malaviya 2019). Kundu et al. (2018) reported that *Plantago ovata* Forsk displayed substantial accumulation of Cr^{6+} and thus served as a potential candidate for phytoremediation. The phytoremediation of Cr^{3+} by *Tagetes erecta* plants was significant. This plant acts as an extreme Cr^{3+} accumulator and is a good candidate for Cr^{3+} removal grown in nutrient solution (Coelho et al., 2017). *Lemna minor* L. plant

Table 1
Effect of microbes on plant growth under Cr stress. Abbreviations: IAA, indole-3-acetic acid; ACC, 1-aminocyclopropane-1-carboxylate; Cr, chromium; PGPR, plant growth promoting rhizobacteria; VOC, volatile compounds; EPS, exopolysaccharides.

Plant species	Cr Level	Microbial strain	Mechanism used	Plant response	Reference
Medicago sativa L.	2.30 mM	*Bacillus pseudomycoides*	IAA, auxin, siderophores	The inoculation of this PGPR on alfalfa under induced Cr^{6+} stress boosted seed germination and root and shoot length.	Knežević et al. (2021)
Solanum lycopersicum L.	50 mg kg^{-1}	*Klebsiella* and *Enterobacter* sp.	IAA and ACC deaminase, phosphorus, and nitrogen solublization, protection from phytopathogens	Cr^{6+} stress showed a negative correlation with plant growth attributes. However, the inoculation of tomato plants with Cr^{6+}-tolerant *Enterobacter* sp. increased the root and shoot length and their fresh and dry weights compared to *Klebsiella* sp.	Gupta et al. (2020a)
Brassica nigra L.	Cr^{3+}20 mg L^{-1}	*Bacillus cereus*	ACC deaminase, phosphate solublization, siderophore, organic acid hydrogen cyanide	Inoculation of plants with *Bacillus cereus* strain improved seed germination percentage by 28.07%, root length by 19.11%, and shoot length by 35.86%. Also, fresh and dry biomass increased by 48 and 62.16%, respectively, under Cr^{3+} stress.	Akhtar et al. (2021)
Medicago sativa L.	300–600 mg L^{-1}	*Pseudomonas* sp.	Siderophore, IAA, phosphorus solublization,	PGPR markedly enhanced Cr^{6+} tolerance in the *Medicago sativa* plants, resulting in maximal root and shoot dry weight at 300 mg kg^{-1} Cr^{6+}level.	Tirry et al. (2021)
Zea mays L.	Soil contaminated with 300 mg kg^{-1} of Cr	PGPR isolated from root nodules of *Phaseolus lunatus* (LCC69 and LCC41)	IAA, phosphate solublization	Maize plants supplemented with bacterial strain LCC69 stimulated the shoot dry weight under Cr^{6+} stress. However, bacterial strain LCC41 exhibited higher root dry weight in plants against Cr^{6+} stress.	Silva et al. (2021)
Abelmoschus esculentus L.	20 mg kg^{-1}	*Pseuomonas* sp.	By converting Cr^{6+} into Cr^{3+}	The PGPR increased the root and shoot length. It also escalated the root and shoot fresh and dry weight. Fruit fresh and dry weight was also improved under Cr^{6+}stress with PGPR inoculation.	Mushtaq et al. (2021)
Festuca arundinacea	250 mg L^{-1}	*Bacillus* sp. AK-1 and *Lysinibacillus* sp.	IAA, siderophores and solubilization of phosphate	Improved plant biomass, root, and shoot length	Peng et al. (2021)
Zea mays L.	100 ppm	Trichoderma (*T.viride*), rhizobium (*R. trifoli)* and mycorrhiza (AMF, *Glomus* species)	By improving nutrient and water availability	Plant leaf area was increased	Devi and Kumar (2020)
Prosopis laevigata L. and *Arabidopsis thaliana* L.	100 mg L^{-1} (*A. thaliana*) 2500 mg L^{-1} (*P. laevigata*)	*Bacillus* sp.	Ammonia and VOCs (2,4-di-tert-butyl phenol, heneicosane, hentriacontane, and Tetracosane	Improved seed germination of both plants	Ramírez et al. (2020)
Sesbania sesban L.	50, 100, and 200 mg kg^{-1}	*Bacillus xiamenensis*	EPS, acidification, ACC deaminase, synthesis of enzymes for chelating the potassium, iron, phosphorus	Under Cr^{6+} stress, this bacterium had a positive effect on root and shoot length. It also boosted the root and shoot fresh and dry weights under Cr^{6+} stress.	Din et al. (2020)
Helianthus annuus L.	300 ppm	*Staphylococcus arlettae*	Cr^{6+} into Cr^{3+} conversion	It deliberately augmented the plant growth in the form higher root and shoot length under Cr^{6+} stress	Qadir et al. (2020)
Capsicum annum L.	100 mg kg^{-1}	*Bradyrhizobium japonicum*	Auxin and cytokinin. IAA	A marked improvement was seen in root and shoot length, fresh and dry weight after inoculation with PGPR under Cr^{6+} toxicity	Nemat et al. (2020)
Zea mays L.	50 and 100 mg kg^{-1}	*Agrobacterium fabrum*	IAA, and organic acid	The strain enhanced the height, leaves, root and shoot length of maize plants under Cr^{6+} stress. Further, root and shoot dry weights were also ameliorated by strain inoculation under Cr^{6+}stress in plants	Danish et al. (2019)
Eruca sativa	150, 250 and 500 ppm	*Pseudomonas putida*	Siderophore, IAA, ACC deaminase	Plants administered bacterial inoculation showed higher root and shoot length under Cr^{6+} stress. Likewise, root as well as shoot fresh and dry weights were also improved under Cr^{6+}stress.	Kamran et al. (2017)
Phaseolus vulgaris L.	1200 µg mL^{-1}	Rhizobacterial strain AR6 homology with *Cellulosimicrobium funkei*	IAA	The authors isolated Rhizobacterial strain AR6 homology with *Cellulosimicrobium funkei* that can tolerate Cr (1200 µg/L) after grown in Cr contaminated soil. The strain efficiently increased the root length of plant through IAA production under Cr stress. Since IAA is responsible for maximal root cell elongation and division.	Karthik et al. (2017)
Zea mays L.	1000 µg mL^{-1}	Auxin-producing bacterial isolates (*Bacillus cereus, Halomonas* sp. (AST), *Bacillus* sp. (EIV), *Arthrobacter mysorens* (AHA), and EIII)	Auxin, ACC deaminase	Maize root and shoot length, leaves number and fresh weight was positively correlated with auxin producing bacterial strain under Cr^{6+} stress.	Fatima and Ahmed (2016)

(*continued on next page*)

Table 1 (*continued*)

Plant species	Cr Level	Microbial strain	Mechanism used	Plant response	Reference
Cicer arietinum L.	2000 μg ml^{-1}	*Pseudomonas aeruginosa*	Phytohormone, siderophore, and EPS	This bacterial strain significantly enhanced the root and shoot dry weight, nodule formation and grain yield under Cr^{6+} stress.	Oves et al. (2013)
Cicer arietinum L.	68 mg kg^{-1}	*Bacillus* species	IAA	The *Bacillus* strain improved the *Cicer arietinum* L. plant growth in the form of higher roots along with shoot length, nodule number and dry weight. It also increased the total dry weight of plants under Cr^{6+}stress.	Wani and Khan (2010)
Brassica Juncea L.	25 mg L^{-1}	*Pseudomonas* and *Bacillus* sp.	IAA, siderophores and solubilization of phosphate	*Pseudomonas* sp. showed more improvement in root and shoot length of plants. It also increased the fresh and dry weight of plants.	Rajkumar et al. (2006)

exhibited the potential to remediate Cr^{6+} polluted soil (Sallah-Ud-Din et al., 2017).

Sajad et al. (2020) evaluated different species for their phytoremediation potential on the basis of their bioconcentration factor, translocation factor, bio-accumulation coefficient and Cr concentration in shoot and found that six species namely *Allium griffithianum, Catharanthus roseus, Himalaiella heteromalla, Geranium rotundifolium, Marrubium vulgare,* and *Solanum nigrum* are Cr hyperaccumulators. In another study, *Brassica juncea* L. displayed significant potential for Cr^{6+} phytoremediation by hyperaccumulating it (Mahmud et al., 2017). A considerable Cr^{6+} uptake and accumulation potential were evident in *Nymphaea alba* L. plants grown under Cr stress (Khan et al., 2016). *Chrysopogon zizanoides* L. displayed marked potential for Cr^{6+} phytoremediation from electroplating wastewater (Nugroho et al., 2021). *Spartina argentinensis* plant depicted maximal phytoremediation tendency for Cr^{6+} (Redondo-Gómez et al., 2011). Chen et al. (2020) reported the Cr phytoremediation potential of *Pennisetum sinese* as it accumulated 150.99 mg kg^{-1} DW in the aerial part and 979.03 mg kg^{-1} DW in the root under 2000 μM Cr^{6+} treatment. In the study by Kumar and Seth (2022), *Helianthus annuus* L. emerged as a viable candidate for Cr^{6+} accumulation when cultivated under 15, 30, and 60 mg Cr^{6+} kg^{-1} of soil, owing to its excellent tolerance mechanisms against the harmful effects of Cr^{6+} toxicity. Interestingly, another study on *Helianthus annuus* L. showed significant Cr accumulation in the aerial parts with no translocation to the seed oil making it a valid phytoremediation candidate (Stoikou et al., 2017). *Melia azedarach* L. treated with 20 mg L^{-1} Cr^{6+} demonstrated significant Cr accumulation of 131.2 mg kg^{-1} in aboveground parts and 824.7 mg kg^{-1} in roots, showcasing its potential as a phytostabilizer and a promising candidate for phytoremediation applications (Yan et al., 2020). Recently, *Pteridium aquilinum*, a member of *Dennstaedtiaceae* family, discovered as a novel hyperaccumulator of Cr^{6+}. The gametophytes accumulated up to 915 mg kg^{-1} Cr content DW, while the sporophytes accumulated up to 11,854 mg kg^{-1} Cr content DW in the underground parts, displaying good potential for phytoremediation of Cr contamination (Eslava-Silva et al., 2023).

Microbe-assisted phytoremediation of chromium

Researchers have utilized various assistive phytoremediation strategies, including the use of organic (composts, biochar, digestates) and inorganic compounds through seed priming, foliar applications, and soil supplements (Sani et al., 2023; Yan et al., 2020). Nevertheless, certain compounds are costly and require additional field-level trials. Microorganisms, on the other hand, exhibit a cosmopolitan distribution across diverse environments. They can survive and thrive under a spectrum of environmental conditions, such as soil, air, water, deserts, and extreme temperatures (Ullah et al., 2015). Bioremediation of metal-polluted soils through microbial action is preferable to chemical applications due to its ability to minimize residual effects, leverage microbial diversity for comprehensive remediation, and adapt to variable metal concentrations. The promotion of soil health, synergistic microbial interactions, and avoidance of chemical runoff further contribute to its societal appeal. Additionally, microbial activities in bioremediation may support carbon sequestration and exhibit resilience to environmental changes, providing a sustainable and environmentally friendly approach to metal pollution remediation (Atuchin et al., 2023).

The rhizosphere is the narrow soil area surrounding plant roots, significantly influenced by their presence. In this zone, a multitude of macro and microorganisms, including bacteria, fungi, viruses, protozoa, algae, nematodes, and micro-arthropods, coexist, participating in various interactions among themselves and with the plants (Prashar et al., 2014; Munir and Faisal, 2016; Kour et al., 2019). However, among microbial communities, bacteria, fungi, protozoa, and algae in the rhizosphere are the most abundant organisms (Cetin et al., 2011). The interaction of plant roots with a diverse spectrum of soil bacteria, particularly in the rhizosphere, is one of the essential factors of phytoremediation capability. The performance of associated plant-microbe symbioses in polluted soil is controlled by both the micro-partner, i.e., plant-associated microorganisms, and the host plant (Mandal et al., 2016). Because plant root exudates supply nutrients and energy to soil bacteria, where they build intricate communication networks with them in the rhizosphere. Plant growth-promoting microorganisms (PGPMs) are beneficial bacteria and fungi that can minimize toxic metal impacts and encourage plant development in both direct and indirect ways. These bacteria cause the activation of defense systems against phytopathogens in indirect ways. Besides, they directly solubilize the mineral nutrients such as N, P, K, and Fe and stimulates the generation of phytohormones (plant growth-promoting chemicals), and secrete particular enzymes such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Dotaniya et al., 2018; Ma et al., 2016b; Tak et al., 2013). Plant growth promoting microbes such as plant growth-promoting bacteria (PGPB) and rhizobacteria (PGPR), nitrate fixation bacteria (NFB), arbuscular mycorrhizal fungi (AMF), and siderophore producing bacteria (SPB) are among the microorganisms that are valuable to plants (Ahammed et al., 2023). Among PGPB *Pseudomonas, Enterobacter, Arthrobacter, Glucanoacetobacterium, Flavobacterium, Beijerinkia, Klebsiella, Erwinia, Bacillus, and Serratia* are commonly employed and investigated to improve plant growth. Plant-microbe interactions also include other quorum-sensing-derived mechanisms. For instance, acylated homoserine lactones (AHLs), regulate bacterial traits like symbiosis, virulence, competence, conjugation, mobility, sporulation, biofilm, and antibiotic production. They provoke tissue-specific gene expression, plant growth homeostasis, and defensive responses when they are identified by plant (Arantza et al., 2022). Several fungal species have also been widely exploited for hazardous metal removal in plants, including arbuscular mycorrhizal fungi (AMF), *Aspergillus, Penicillium, Fusarium, Yarrowta*, and *Mucor* (Jagtap et al., 2016; Ahammed et al., 2023). In a nutshell, both PGPB and AMF can enhance phytoremediation and plant growth in metal-polluted soils (Gamalero et al., 2009).

The interaction between plants and microorganisms is significant in the phytoremediation of toxic metals, particularly Cr^{6+}. These microorganisms can improve the phytoremediation process by methylation, changing soil pH, facilitating redox reactions, and secreting chelators (siderophores and organic acids) and biosurfactants (Franchi et al., 2017; Das et al., 2021). Microbes can advance phytoremediation by lowering metal availability in the soil through a process known as phytoextraction. They encourage metal transfer directly from the ground to root (bioaccumulation) or indirectly from root to shoot tissues (translocation). Additionally, microbes can tolerate high metal levels in natural (serpentine soil) and anthropogenic polluted ecosystems (e.g., mine waste and fly ash). Another reason behind using microbes along with phytoremediation is that the microbial metabolites generated in the rhizosphere (*in situ*) are biodegradable and less toxic (Ma et al., 2016b). The efficacy of phytoremediation is based on the plant's potential to produce high biomass and tolerate metal toxicity. However, in rhizospheric soil, metal bioavailability is a critical element in determining the tendency of metal translocation. In this context, microbial assisted phytoremediation improves the bioavailability of metal through adopted several mechanisms including acidification, precipitation, chelation, complexation, and redox reactions, thereby improving the plant metal uptake capability. Plant-microbe interaction enhanced the plant nutrient uptake, cell elongation, and mitigated the biotic and abiotic stress in plants. Further, the rhizosphere microbes augmented the mobility of metal ions (Rajkumar et al., 2012; Ma et al., 2016a). As a result, makes metal available to plant roots through their catabolic mechanism of metal tolerant behavior (Nayak et al., 2018). In the rhizosphere, the microbes secreted H^+ ions and generated an acidic environment, thereby improving the metal bioavailability in plants. Similarly, organic compounds may also release organic acids. These organic acids not only improve the metal bioavailability but also strengthen the root physical, chemical, thermal and microbial attributes in plants under heavy metal stress (Jagtap et al., 2016). By following the acidification process, the microbes improve metal (Cr^{6+}) phytoavailability by causing modification in soil pH (Das et al., 2021). The bacterial strains, through redox processes, abridged the toxic metal impacts via stabilizing them in soil and converting them into a non-toxic form (Ma et al., 2016c). For instance, wheat plants were amended by bacterial strain (*Bacillus cereus* and *Pseudomonas japonica*) and biochar under Cr^{6+}stress. The bacterial strain and biochar retained 90% of Cr^{6+} in soil media. The strains also declined the Cr phytotoxic impacts by reducing $Cr^{6+}$to Cr^{3+}. Exposure of both bacterial strains resulted in maximal Cr^{6+} reduction into Cr^{3+}than biochar (Arshad et al., 2017). The more significant potential of microbes in the absorption of Cr also benefits plants in the process of phytoremediation. The Cr sorption by microbes can occur through either a passive or active process. In the passive sorption process, the Cr binds with the functional group on the surface of dead microbial cells. Besides, the active sorption process includes live microbial cells absorbing Cr from the soil through several methods. For instance, metallothionein inside the microbial cells binds to Cr and promotes their sequestration in specific intracellular organelles. Further, several microbes also generate amphiphilic chemicals known as biosurfactants. These biosurfactants may desorb Cr from the soil, raising their solubility and mobility. As a result, making Cr bioavailable for plant uptake (Fenibo et al., 2019; Das et al., 2021; Sharma et al., 2022b). For instance, Karnwal and Bhardwaj (2014) reported that the bacterial species gram-negative *Bacilli* isolated from heavy metal polluted soil and water. The strain produced 'rhamnolipid' (biosurfactant), which effectively reduced up to 41 ppm of 80 ppm Cr^{6+} under Cr stress. Similarly, the bacterial strain *Pseudomonas aeruginosa* produced rhamnolipid (biosurfactant) resulted in 99% removal of Cr (10 $mg^{-}1$ L) (Ozturk et al., 2012).

Consequently, phytoremediation in combination with microbes has become not only the most popular and promising strategy. But also, the safest, cost-effective, and ecologically friendly approach for the reclamation of metal-affected soil. As previously stated, microorganisms can boost metal mobility and bioavailability. Thus, microbial-mediated phytoremediation enhances ion exchange capacity, metal valence conversion potential, immobilization and extraction ability of plants. Further, improve performance, plant growth as well as biomass and heavy metal ion accumulation, with the potential to shorten the plant growth cycle (Liu et al., 2020). Therefore, bacteria or fungi with the physiological and metabolic capacities to break down pollutants are the ideal microorganisms in the bioremediation of pollutants. Additionally, bacteria and fungus are natural recyclers that can convert both natural and synthetic substances into energy and essential materials for their own development. This means that biological processes can be used in addition to chemical or physical treatment. For that reason, bioremediation is becoming increasingly crucial for the cleanup of polluted soils worldwide (Juwarkar et al., 2010).

Mechanisms involved in microbe-assisted phytoremediation of chromium

There has been a growing fascination with the utilization of microbes in aiding the phytoremediation of heavy metals, both through direct and indirect mechanisms. Direct processes involve the augmentation of bioavailability, solubility, and the accumulation of heavy metals and metalloids, induced by microbes. On the other hand, indirect approaches encompass microbial-mediated enhancements in plant growth and defense against different environmental constraints, thereby fostering the accumulation of heavy metals. The detailed discussion on how microbes improve morpho-physiobiochemcial characteristics of plants to counteract Cr toxicity and assist in Cr phytoremediation is given below and is illustrated in Fig. 1.

Seed germination and plant growth

Chromium being a toxic heavy metal, inhibited plant growth and development. In plants, seed germination is the first physiological mechanism affected by Cr, because the capacity of a seed to germinate in a Cr-bearing media would reveal its level of tolerance to this metal (Nagajyoti et al., 2010; Gill, 2014; Asati et al., 2016). Cr^{6+} has been reported to decline seed germination in okra (Amin et al., 2013), pigeon pea (Dotaniya et al., 2014), wheat (Datta et al., 2011; Lei et al., 2021) and tomato (Hafiz and Ma, 2021) plants. Generally, plant seed germination is dependent on appropriate water availability in the growth medium. However, Cr toxicity limited the water uptake that, in turn, diminished the seed germination, thereby decreasing the plant growth and biomass (Singh and Rathore, 2019). Cr^{6+} hindered the transportation of sugars to the embryo axis, which is responsible for declined seed germination of plants. Further, Cr^{6+} stress upregulated the protease activity and deteriorated the α and β-amylase activities which, in turn, demolished the seed germination of plants. The hydrolysis of starch by amylase is required to provide sugar to growing embryos. Under Cr treatment, a drop in amylase activity lowers sugar availability to developing embryos, which may lead to seed germination suppression. Because amylase hydrolysis would provide the essential sugar for growing embryos. Thus, direct Cr application may diminish sugar availability, posing a direct or indirect threat to the seed germination of plants. Additionally, Cr^{6+} stress impaired the permeability of seed coat, thereby declining the seed germination of plants (Medda and Mondal, 2017). Cr stress negatively influenced the plant roots and shoots. However, plant roots are more affected owing to their direct contact with Cr. It might be because elevated levels of both Cr species (Cr^{3+} and Cr^{6+}), impaired either the cell division/elongation or both in the tips of roots. Further, both Cr species caused a reduction in the mitotic index in developing root tips. Cr^{6+} has more toxic impacts on cell division rather than Cr^{3+}. Cr^{6+} prolongs the cell cycle, which impedes cell division and thus root development. As a result, the reduced root development lessens the water and nutrient absorption and their transfer to aerial parts, thereby inhibiting the plant shoot growth (Singh et al., 2013). Cr has several toxic impacts on plant roots, including (1) decreased length, biomass, and diameter, (2) injury to the growth cone, (3) destruction of root hairs or lowering in root numbers, (4) improved or decreased lateral root formation, (5) higher lignification, and (6) alterations in the hypodermis and endoderm structure. Cr stress adverse impacts on shoot

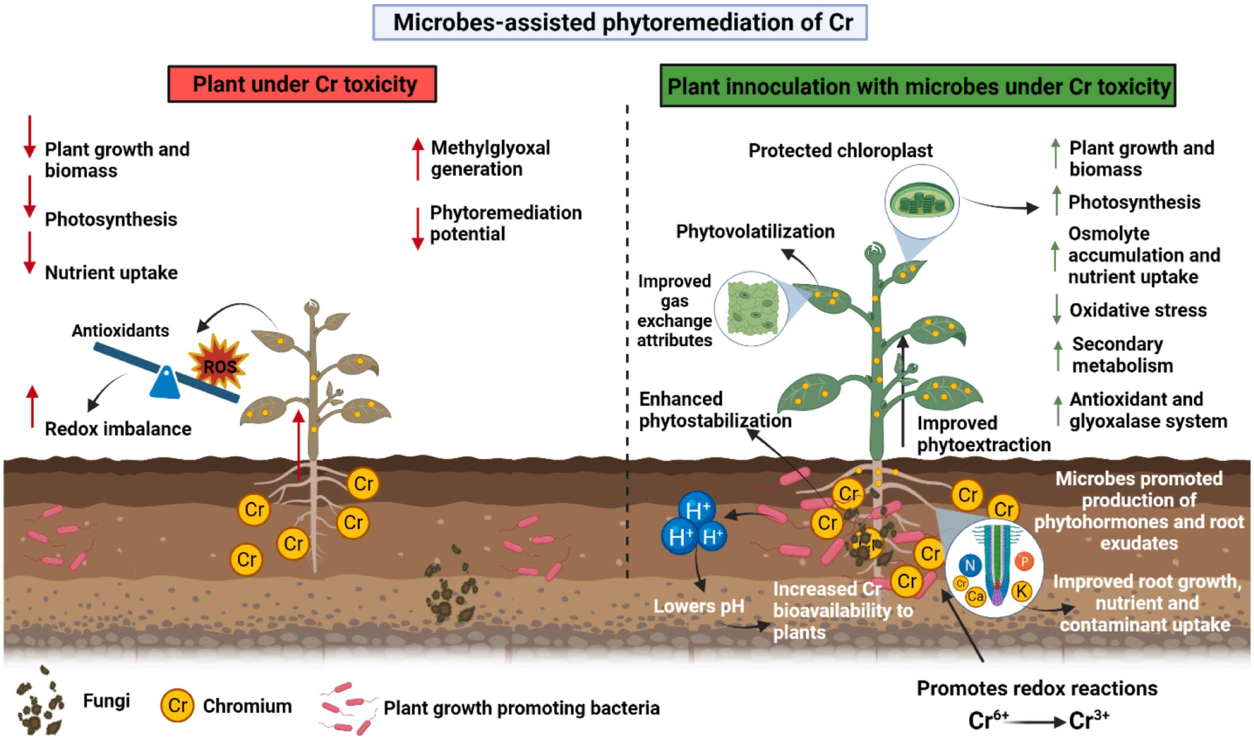

Fig. 1. The mechanistic representation of microbes-assisted phytoremediation of chromium.

growth may include a reduction in the size of flowers and fruits (Stambulska et al., 2018). However, the application of PGPR improved plant growth by (i) improving root growth, (ii) making the availability of soil nutrients to plant roots, and (iii) fixing atmospheric nitrogen and encouraging soil fertility under heavy metal stress conditions. Additionally, microbial-assisted plants demonstrated enhanced plant growth and nutrient uptake and regulated several soil-borne diseases via several means. These include the synthesis of phytohormone (indole acetic acid, cytokinins, and gibberellic acid), exopolysaccharides and osmoprotectants, organic acid, siderophores, ACC deaminase enzyme (to decrease the concentration of ethylene in growing plant roots, where ACC is the precursor of ethylene), phosphorus and potassium solubilization, antifungal metabolites or lytic enzymes, biosorption of toxic metals and augmented resistance of plants against toxic metal stress (Egamberdieva et al., 2016; Etesami and Maheshwari, 2018). Generally, ACC deaminase promotes plant growth by suppressing ethylene in growing roots and lowering ACC in Cr-stressed plants. Because ACC deaminase uses the ammonia (NH_3) produced from ACC as a nitrogen source, causing its limitation in plants (Fatima and Ahmed, 2016). Generally, the rhizosphere is a nutrient-dense environment with nutrients, amino acids, carbohydrates, fatty acids, and other organic substances which attract bacteria that consume the nutrients discharged by the root. After that, microbes produce physiologically active substances such as phytohormones (auxins, cytokinins, gibberellins, and ABA), antifungal compounds, enzymes, and compatible solutes. In this way, microbial metabolites improve the plant growth and development under stressful conditions (Egamberdieva et al., 2017). These microbes also improve plant growth through solubilization of minerals, conversion of nutrient elements and hydrogen cyanide production in plants under Cr stress (Shahzadi et al., 2013; Tirry et al., 2018). Karthik et al. (2016) observed a reduction in seed germination, root as well as shoot length, and total biomass in *Phaseolus vulgaris* under Cr^{6+} stress. However, Cr-stressed plants inoculation with bacterial strain (*Cellulosimicrobium funkei*-like) manifested improved seed germination by 89.5%, root as well as shoot length by 60% and 74.5%, respectively, and total biomass by 52.5%. Bacterial strains provide an ample quantity of indole acetic acid (phytohormone) that boosts the activity of hydrolytic enzymes (α-amylase and protease) involved in seed germination under Cr^{6+} stress. Because bacterial strains improve the phytohormone synthesis and nutrient uptake from soil by the plant, which, in turn, enhances the growth of plants under Cr^{6+} stress. Also, the rhizosphere bacterial strains can tolerate Cr^{6+} stress that protects plants from the lethal impacts of Cr^{6+}. Yasin et al. (2018) reported that these bacteria operate as soil conditioners, improving soil structure and chelating heavy metals, allowing plants to absorb them. As a result, improve the plant growth under Cr stress. Table 1 summarizes the strategies that PGPR employs to enhance plant growth and their phytoremediation capability under Cr stress.

Photosynthesis

Photosynthesis is a biological process that produces complex chemical molecules by utilizing solar energy (Siddiqui et al., 2018). Photosynthesis occurs not just in green leaves of plants but also in aquatic and terrestrial plant embryos and in microbes (bacteria). Photosynthesis drives several metabolic events in plants by activating the conversion of light energy into chemical energy (Muhammad et al., 2021). However, abiotic stresses such as heavy metal ions can change the cellular and molecular functions of plants by: removing critical components from macromolecules, inhibiting enzyme functional groups and their active sites, disrupting membranes, and changing transcription patterns (Sharma et al., 2020b). Heavy metals affect the photosynthetic process by oxidizing the photosystem II (PSII), disrupting the electron transport chain (ETC) and mineral metabolism in plants (Seneviratne et al., 2019). Cr stress influence the photosynthesis in terms of CO_2 fixation, electron transport, photophosphorylation, and enzyme activity in plants. Chromate is used as Hill reagent by isolated chloroplast (Shanker et al., 2005; Edelstein and Ben-Hur, 2018; Shahzad et al., 2018; Chaudhary and Sharma, 2019). Cr^{6+} stress produces ultrastructural alterations in the chloroplast, leading to photosynthetic suppression (Panda and Choudhury, 2005). Several studies documented Cr-induced ultrastructural changes in the chloroplast of tomato, maize, red bean, black gram, and

canola plants (Li et al., 2018; Gupta and Seth, 2021; Mahajan et al., 2021; Mahdavian, 2021; Tiwari and Singh, 2021). Similarly, Sharma et al. (2020b) reported that Cr stress caused altered chloroplast ultrastructure in plants. Possibly because, Cr stress resulted in poor lamellar organization, few grana with widely spaced thylakoids, starch grain loss, and plastoglobuli formation. Further, Cr^{6+}-mediated less chloroplast volume and autofluorescence are also responsible for the inhibition of photosynthesis in plants (Bibi et al., 2014; Dongre, 2021). Cr stress also distorted the chloroplast membrane, and influenced the light/dark reaction by hindering the Hill reactions, thereby abridging the plant photosynthesis. Another possible reason behind decreased photosynthesis is the production of electrons generated during photochemical responses that may not be primarily utilized to fix carbon under Cr^{6+} stress. Cr^{6+}-mediated hindered electron transport might be owing to redox changes in the Cu and Fe carriers or Cr binding to the heme group of cytochromes in plants. Cr^{6+} also decreased the cytochrome oxidase activity via binding to cytochrome-a_3 of complex IV in ETC. Furthermore, due to its high oxidizing potential, Cr^{6+}inhibited photosynthesis by generating ROS as an alternative electron sink via oxygen reduction in plants (Shahid et al., 2017; Wakeel et al., 2020). Plant gas exchange attributes such as CO_2 assimilation (A), stomatal conductance (g_s), evapotranspiration (E), and internal carbon dioxide concetration (Ci) are also affected under Cr stress (Santos and Rodriguez, 2012). For instance, Cr^{3+}stress resulted in water imbalance and affects the stomatal opening, thereby caused reduced stomatal conductance in plants. Elevated level of Cr also disintegrated the activities of various enzymes such as Rubisco, leading to lower the photosynthetic yield in plants (da Conceicao Gomes et al., 2017). Ertani et al. (2017) reported that Cr-induced changes in the cellular structure of spongy parenchyma and, as a result, a decline in stomatal size present on the mesophyll cells might be encouraged lowered stomatal conductance in plants. Cr stress lessened the transpiration rate by affecting water movement in the xylem of plants. Singh et al. (2015) investigated that Cr toxicity affected the biomass accumulation in barley plants. It might be due to ultrastructure disturbances in leaves, including irregular chloroplast thickening and swelling, expanded plastoglobuli, and deteriorated thylakoid membrane. All these factors resulted in a drop in net stomatal conductance, cellular CO_2 concentration, transpiration rate, photochemical efficiency, and net photosynthetic rate, thereby reduced the plant biomass under Cr stress. Bashir et al. (2021) observed that Cr^{6+} stress negatively influenced the maize plant gas exchange attributes, including CO_2 assimilation, stomatal conductance, and evapotranspiration rates. Similarly, Habiba et al. (2019) found that maize cultivars (9108 and 6103) given Cr^{6+} (0, 5, and 10 mg $kg^{-1)}$ manifested reduced stomatal conductance, net photosynthetic, and transpiration rate. In this context, Cr^{6+} (10 mg kg^{-1}) pronounced a more toxic effect on gas exchange attributes in cultivar 9108 than 6103. Likewise, Ali et al. (2013) examined that when barley plants were administered Cr^{6+} stress (100 μmole L^{-1}), a visible decline in net photosynthetic rate (Pn), internal carbon dioxide, stomatal conductance, and transpiration rate (Tr) was observed. In the present scenario, plant inoculation with PGPR enhanced the photosynthetic process by improving the gas exchange parameters. The PGPR enriched the rate of intracellular CO_2 that, in turn, improved the gas exchange attributes of plants under heavy metal stress. Also, PGPR upregulated the efficacy of photosynthetic enzymes such as Mg^{2+}-ATPase, Ca^{2+}-ATPase, and rubisco. Further, PGPR advanced the overexpression of photosystem-linked genes in plants, thereby augmenting the gas exchange attributes of plants under heavy metal stress (Khanna et al., 2019b). Zeng et al. (2020) reported that plant inoculation with Cr^{6+} resistant bacterial strain (*Staphylococcus aureus*) improved the gas exchange attributes (Pn, g_s, and Tr) of wheat plants.

Photochemical efficiency

Though numerous physiological, biochemical, and molecular mechanisms work together to determine plant productivity. However, it is considered that stable photosynthetic performance is critical for healthy plant growth and development. Chloroplast being the house of both light/dark reactions of photosynthesis, is adversely affected by the abiotic stresses such as heavy metals in plants (Ma et al., 2021). Chlorophyll fluorescence measurement is a highly sensitive and non-invasive method for assessing plant responsiveness to various stress conditions. The attributes of chlorophyll fluorescence are important measures of plant photosynthetic health (Faseela et al., 2020). The significance of this method stems from its ability to detect changes in photosystem (PS) II photochemical proficiency before they have an impact on overall plant growth. Fv/Fm is one such parameter, which represents the maximum efficiency of PSII. This ratio often declines under metal toxicity, indicating damage to the photosynthetic machinery (Athar et al., 2015). Effective quantum yield (ΦPSII) is another key metric that indicates the actual efficiency of PSII in converting light energy into chemical energy. Metal stress frequently decreases ΦPSII by impairing the efficiency of the electron transport chain (Kalaji et al., 2018). Photochemical quenching (qP) shows the proportion of open PSII reaction centers and can decrease when metal stress is applied, suggesting decreased photochemical efficiency. Electron transport rate (ETR) represents the rate of electron transport through the photosynthetic electron transport chain and is usually abridged in plants under metal toxicity (Ashraf and Ashraf, 2012). Overall, metal stress has a negative impact on chlorophyll fluorescence metrics because it causes oxidative stress, disrupts the electron transport chain, and compromises plant photosynthetic activity. It has been reported that abiotic stresses remarkably influence PSI, PSII, electron transport chain (ETC), and chlorophyll production in plants (Song et al., 2020;Muhammad et al., 2021). Heavy metal toxicity is a significant abiotic constraint that results in photooxidation due to ETC over-reduction in plants (Gururani et al., 2015). Therefore, higher plants must absorb enough light energy to avoid molecular damage to pigments and proteins that comprise their photosynthetic system. However, abiotic stresses can further impede the utilization of absorbed light energy, resulting in photoinhibition of PSII. Non-photochemical quenching (NPQ), one of the critical photoprotection responses in higher plants, dissipates excess chlorophyll excitation energy inside the light-harvesting antennae of PSII (Yuan et al., 2014). When plants are exposed to high levels of certain heavy metals, the breakdown of photosynthetic pigments is prevalent. Because of the loss of pigments, the light-harvesting ability of the plant suffers, which, in turn, decreases the photosynthetic efficiency (Hayat et al., 2012). Photosystem II is more vulnerable to environmental perturbations than the photo-damage process itself in the thylakoid membrane. By contrast, PSI is less prone to be affected due to a very effective photoprotection system that can prevent photoinhibition. PSI is affected when the supply of electrons from PSII exceeds the potential of PSI to receive electrons. When PSI is photo-damaged, the recovery procedure is lengthy and, in some situations, not completely reversible (Guidi et al., 2019). Photosynthetic parameters (PSI, PSII, and intersystem electron carriers) are determined from the light-induced kinetics of prompt chlorophyll *a* fluorescence under Cr^{6+} stress (Todorenko et al., 2020). Because Cr inhibits photosynthetic activities, therefore, chlorophyll fluorescence parameters can exhibit inhibition at various stages in the photosynthetic apparatus (Mathur et al., 2016). Further, the chlorophyll fluorescence parameters also helped us to comprehend better the photochemical and non-photochemical activities that take place in chloroplast thylakoid membranes under Cr (Cr^{3+} and Cr^{6+}) stress in plants (Vernay et al., 2008). Ayyaz et al. (2021) reported that Cr^{6+} stress remarkably lessened the PSII and PSI activity of two *Brassica napus* L. cultivars. Cr^{6+}stress significantly lowered PSII photochemical yield in terms of quantum yield. Furthermore, both cultivars showed a considerable drop in electron donation efficiency to PSI (*Fv/Fo*). Cr^{6+}stress had a significant impact on *the Fv/Fm* ratio with more severe effect evident in sensitive cultivar (DGL) compared to tolerant one (AcExcel). *Fv/Fm* ratio is usually confirmed by chlorophyll concentration and cell shape. Both of which can be influenced by various variables that alter PSII activity.

Cr^{6+} harmed the reaction center, ETC, resulting in a lower net PSII quantum yield. Cr^{6+} stress hampered photosynthesis by lowering one or more structural and functional components of the photosynthetic system, either directly or indirectly. In this study, the authors observed that Cr^{6+} stress diminished the PSII system including ETR, ΦPSII, *Fv/Fm, Fv/Fo*, qP, and NPQ of hybrid Napier grass plant. Cr^{6+} stress led to the shutdown of specific PSII centers and lowered the efficiency of open PSII centers, thereby declining the qP and *Fv/Fm* ratio, respectively, in plants. Also, Cr^{6+} stress limited the number of active PSII centers and, as a result, lowered its density. Furthermore, a fall in qP is correlated with an increase in qN. Cr^{6+}-mediated maximal increment in qN was due to the dissipation of a large quantity of excitation energy. Additionally, after the Cr^{6+}-induced decrease in CO_2 absorption, higher qN limits NADPH and ATP consumption culminating in photosynthetic ETR damage. The reduced ETR indicates that electron flow has been disrupted. Under Cr^{6+} stress, rice seedlings have been found to have obstructed electron transport from the reaction center to the quinone pool. Cr^{6+}-induced reduction in the activity of water-splitting complex, is evidenced by a decrease in *Fv/Fo* ratio. It might be one of the causes of reduced electron flow in the current investigation. The reduced *Fv/Fo* ratio also implies structural damage in the chloroplast, such as the loss of thylakoid membranes in plants (Ram et al., 2019). ΦPSII describes the number of electrons transported across a PSII reaction center per mole of quantum absorbed (Oliveira, 2012). Cr^{6+} stress also affected the photochemical efficiency by replacing the co-factor Ca^{2+} (an essential element for water splitting) at PSII, thereby disturbing the oxygen-evolving complex (OEC) of plants. Cr^{6+} ions, along with OEC, interacted with several electron acceptor proteins such as Q_B located in the electron transport of PSII. Cr^{6+} stress also impaired the PSI efficiency through interactions with mono and multimeric subunits. Hence, disturb the electron pathway in ETC that ultimately reduces the energy conversion potential of PSII in plants under Cr^{6+} stress (Ayyaz et al., 2020). In consideration of Cr influence on plant fluorescence variables, Jan et al. (2020) found that tomato plants exposed to Cr^{6+}showed inhibition in *Fv/Fm*, ΦPSII, and qP up to 40.0, 33.9, and 46.2%, respectively. However, the NPQ level was increased up to 40.0% compared to control. The fall in *Fv/Fm* ratio might be due to Cr adverse impact on photochemical processes. Cr reduces the efficiency of photochemistry in PSII by down-regulating the ETC. Further, the reduction in photosynthesis is owing to the demolition of the leaf PSII reaction center. Cr has also been shown to disable the water oxidizing centers (WOC) linked with PSII through the blockage in Mn and Ca^{2+}absorption, which are essential components of WOC. In another study, Lu et al. (2020) reported that Cr stress dramatically decreased the *Fv/Fm* ratio and qP by inhibiting the electron transport and photochemical efficiency of PSII in wheat plants. However, Cr stress markedly improved qN, indicating that wheat plants maintained their photoprotective capacity under Cr stress. The authors suggested an inherent connection between plant growth and chloroplast function, arguing that this association is tied to the correlation between antioxidant levels and photosynthetic pigments, both integral to the crucial role of chloroplasts. This connection was underscored by their observation that exposure to Cr stress resulted in a diminished photosynthetic activity of chloroplasts in plants. Likewise, *Lolium perenne* L. plants showed decreased *Fv/Fm, Fv/Fo*, ΦPSII, qP and increased NPQ under Cr^{6+}stress (Vernay et al., 2007). Interestingly, microbes have the capacity to compensate the deleterious impacts of Cr on chlorophyll fluorescence indexes. In this context, Vishnupradeep et al. (2022) reported that inoculation of *Zea mays* with the bacterial strains (TCR05 and TCR20) notably improved the performance of PSII and PSI by enhancing Fv/Fm, ETR, ΦPSII and qP compared to uninoculated counterparts under Cr toxic conditions. Similarly, wheat plants treated with a consortium of four *Actinobacterium* sp. manifested notably improved Fv/Fm under Cr toxicity, which was ascribed to the potential of the microbes in managing the portion of excitation energy reaching the reaction centers in PSII and circumvent photodamage in leaves during periods of Cr toxicity (Albqmi et al., 2023). Thus, fluorescence attributes of chlorophyll have a unique function in detecting detrimental impacts on photosynthesis, describing inherent photosynthetic traits. They are used as an internal probe to explore the link between photosynthesis and the environment (Li et al., 2015). In light of these findings, it is evident that microbes have the potential to protect photosynthetic machinery by regulating chlorophyll fluorescence parameters, thereby promoting plant growth and phytoremediation potential under Cr polluted soils.

Chlorophyll pigments

Chlorophyll is the green pigment that gives plants their distinctive appearance. Chlorophyll is the central part of chloroplast and is associated with plant photosynthetic rate. Any alteration in chlorophyll contents can determine plant health and responses to environmental stresses (Alharby and Ali, 2022). Environmental constraints and nutrition availability influence the amount of chlorophyll in leaf tissues (Palta, 1990; Yong et al., 2010). Abiotic stresses are all known to cause a decrease in photosynthetic pigment molecules, particularly chlorophyll, in plants. This decline happens due to changes in pigment production or degradation under stress condition. Furthermore, the severity of these effects is contingent upon type and duration of stress, plant species and their stress tolerance potential. Carotenoids are also crucial for photoprotection in photosynthesis occurring in plants under abiotic or biotic stress (Shareef et al., 2020). Heavy metals stress also affect the chlorophyll contents of plants. Chlorophyll contents can be easily measured and are widely used for regulatory purposes to detect stress in plants. Generally, metal sensitivity is found in two essential enzymes of the chlorophyll *b*iosynthesis pathway namely γ-aminolaevulinic acid (ALA)-dehydratase and protochlorophyllide reductase (Aggarwal et al., 2012). Heavy metals such as Cr stress also impeded the chlorophyll contents of plants. For instance, Alam et al. (2021) found that Cr^{6+} reduced the total chlorophyll contents in tomato plants. This is because Cr^{6+} reduced the chlorophyll *b*iosynthetic enzyme (d-aminolaevulinic acid dehydratase and protochlorophyllide reductase) activities in plants. Further, Cr^{6+} also inhibited the uptake of Mg ions, an integral part of the chlorophyll molecule, thereby resulting in its deficiency in plants. Chlorophyll *a* and *b* are the most critical leaf pigments for transforming light energy into chemical energy and are needed for the production of oxygen. However, Cr^{6+} stress deliberately affected the chlorophyll *a, b*, total chlorophyll and carotenoids contents of bread wheat plants. The reason behind lowered chlorophyll contents was the higher activity of chlorophyll degrading enzyme as chlorophyllase under Cr^{6+}in plants. Cr^{6+}-induced ROS is also responsible for chlorophylls degradation in plants (Akcin, 2021). Cr also compete with Mg and Fe ions for absorption and transportation towards aerial parts of the plants. As a result, affected the chlorophyll *b*iosynthetic mechanism of plants. Additionally, Cr-induced ROS affected the pigment-protein complexes found in the thylakoid membrane, followed by pheophitinization (replacement of Mg by H^+ ions) of chlorophylls and disintegration of the thylakoid membrane of plants (Oliveira, 2012). However, plant inoculation with PGPR improves the plant chlorophyll contents under heavy metal stress. PGPR, through the secretions of phytohormones and growth regulators (siderophores, indole-3-acetic acid, and gibberellins), enhanced the chlorophyll contents (Zafar-ul-Hye et al., 2020). Similarly, plant inoculation with microbial strains also effectively improved the chlorophyll contents of plants under Cr^{6+} stress. In this context, rice plants were treated with Cr^{6+}-resistant bacterial strain namely *Staphylococcus aureus* under Cr stress. Cr^{6+} at 100 mg kg^{-1} level remarkably lowered the chlorophyll *a, b*, total chlorophyll, and carotenoids contents in rice plants. Besides, plant inoculation with bacterial strain exhibited improved chlorophyll contents of plants. It might be due to PGPR positive role in detoxification of Cr^{6+} into less toxic Cr^{3+} from their metabolic process in plants. PGPR can enhance the tolerance mechanism of plants against Cr^{6+} stress. Also, PGPR reduced the availability of Cr to plants for uptake thereby enhanced the chlorophyll contents of plants under Cr stress (Alharby and Ali, 2022). In another study, elevated levels of Cr^{6+} stress diminished the chlorophyll (Chlorophyll *a, b*, total chlorophyll, and carotenoids) contents by generating oxidative stress in wheat plants. Plant inoculation with *Bacillus subtilis* may increase the plant chlorophyll contents by increasing their tolerance against Cr^{6+} stress (Seleiman et al., 2020). Likewise, Saif and Khan (2018) observed that Cr^{6+} (400 µg mL^{-1}) negatively affected the chlorophyll contents of chickpea plants. Plants supplementation with *Pseudomonas aeruginosa* (Cr resistant strain) boosted the chlorophyll contents of plants under Cr^{6+} stress. The chlorophyll *a/b* ratio is linked to the photosystem II (PSII) core and light-harvesting complex II (LHCII) ratio, indicating plant metabolic efficiency. PSII cores receive the excited energy from LHCII. As a result, the chlorophyll *a/b* ratio represents the photosynthetic mechanism in plants. Cr stress inhibits the *a/b* ratio, whereas bacterial inoculation improves the *a/b* ratio in plants under Cr stress (Shahzad et al., 2021). A number of studies on microbial-mediated improvement in photosynthetic attributes of different plants exposed to Cr toxicity are given in Table 2.

Reactive oxygen species (ROS) generation and lipid peroxidation

Plants are dependent on oxygen to produce energy during photosynthesis. The formation of ROS is an indispensable part of normal metabolic functioning in plants (Garcia-Caparros et al., 2021). In optimal environmental conditions, ROS are produced at modest levels, functioning as signaling molecules and influencing other biomolecules and hormones involved in growth, development, and stress tolerance regulation (Nadarajah, 2020). However, different biotic and abiotic environmental constraints aggravate ROS generation, which causes oxidative stress in plants. Oxidative stress is the consequence of an imbalance between ROS production and its quenching by antioxidants thereby impacting plant cellular processes and eventually causing plant death (Zulfiqar and Ashraf, 2023). Therefore, a balance between ROS generation and quenching is vital in terms of its utilization as a defense molecule under stressful environments (Hasanuzzaman et al., 2019, 2020). The higher accumulation of ROS in plant cells is an early sign of oxidative stress under Cr stress. Besides, the process of ROS-mediated toxicity is highly unique, most likely relying on the existence of free radicals reacting with parts of the living organism. ROS family comprised of singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), hydroxyl ($OH^{\bullet}$), and superoxide ($O_2^{\bullet-}$) radicals. They are all different due to their chemical attributes (Yu et al., 2017). The generation of ROS is governed by two primary processes. The primary mechanism of O_2 activation in most biological systems is the reduction of O_2 to produce $O_2^{\bullet-}$, H_2O_2, and $OH^{\bullet}$ radicals. Besides, the generation of $^1O_2$ by the photosynthesis process is also crucial in plants. In plants, the major sites of ROS production are the ETC of mitochondria and chloroplast, owing to electron leakage (Sgherri et al., 2017). Among heavy metals, Cr is the highly toxic metal influencing soil, water, and plants through ROS production, resulting in oxidative damage. Cr-mediated ROS induces cytotoxic, genotoxic, and photosynthetic modifications in plants (Sahoo et al., 2021). Cr stress resulted in ROS generation through the Cr^{6+}reduction to intermediates viz Cr^{5+}, Cr^{4+}, and Cr^{3+} by following Fenton or Haber–Weiss type reactions in plants. As a result, a wide range of ROS ($O_2^{\bullet-}$, H_2O_2, and $OH^{\bullet}$) is produced during the one-electron reduction of Cr^{6+} to the ultimate stable product Cr^{3+}. ROS generation via these reactions caused lipid peroxidation in plants (Shi, 1999). Lipid peroxidation is considered as an indicator of oxidative damage in plants (Bali and Sidhu, 2021). Notably, chloroplasts contain a complicated structure of

Table 2

Effect of microbes on the photosynthetic traits of plants under Cr stress. Abbreviations: Cr, chromium; AMF, arbuscular mycorrhizal fungi; PSII, photosystem II.

Plant species	Cr level	Microbial strain	Plant response	Reference
Oryza sativa L.	0, 50, and 100 mg kg^{-1}	*Staphylococcus aureus*	This strain significantly improved the plant photosynthetic rate, stomatal conductance, transpiration rate, and water use efficiency of plants. Further, chlorophyll *a, b*, total chlorophyll, and carotenoids were also augmented under Cr stress.	Alharby and Ali (2022)
Ricinus communis L.	0 µM, 100 µM, 200 µM	*Staphylococcus aureus* and *Bacillus subtilis*	*Staphylococcus aureus* more prominently escalated the gas exchange attributes (photosynthesis rate, stomatal conductance, transpiration rate, and water use efficiency) of plants. It also enhanced the chlorophyll *a, b*, total chlorophyll, and carotenoid contents of plants.	Ali et al. (2021b))
Zea mays L. and *Vigna radiata* L.	0–1500 mg *L*$^{-1}$	*Bacillus subtilis*	Improved the chlorophyll *a*, *a* + *b*, and *a/b* levels in maize compared to the *Vigna radiata*.	Shahzad et al. (2021)
Sesbania sesban L.	Cr (25–75 mg *L*$^{-1}$) Cd (100–200 mg *L*$^{-1}$)	*Bacillus anthracis*	Chlorophyll *a, b*, and total chlorophyll content were conspicuously increased in plants.	Ali et al. (2021a))
Zea mays L.	Industrial polluted water	*Bacillus* sp. in combination with biochar	Increased the plant chlorophyll contents (56%) and gas exchange attributes, including transpiration rate (45%), stomatal conductance (62%), and photosynthetic rate (57%) under Cr toxicity.	Abubakar et al. (2020)
Cicer arietinum	Cr-contaminated soil containing 0.11–0.24 mg kg^{-1}	*Stenotrophomonas maltophilia, Bacillus thuringiensis B. cereus*, and *B. subtilis*	The plant exhibited maximal total chlorophylls and carotenoid contents.	(Shreya et al. (2020b))
Vicia faba L.	500 ppm	*Corallina officinalis*	Chlorophyll *a, b*, and total chlorophyll contents were enhanced by bacterial inoculation in plants.	Bouhadi et al. (2019)
Brassica napus L.	20 mg kg^{-1}	*Burkholderia phytofirmans*	It enhanced the photosynthetic rate, transpiration rate, stomatal conductance, sub-stomatal CO_2 concentration, water use efficiency, and chlorophyll contents of plants.	Nafees et al. (2018)
Zea mays L.	0.86, 350, and 500 ppm	*Burkholderia vietnamiensis*	Plants manifested higher chlorophyll *a, b*, and carotenoid contents.	(Ali et al., 2018)
Zea mays L.	200, 400, and 600 µg mL^{-1}.	*Bacillus pumilus, Bacillus atrophaeus, Bacillus cereus, Staphylococcus lentus*	*Bacillus pumilus* augmented the chlorophyll *a, b*, and total chlorophyll content of plants.	Habib and Ahmed (2018)
Vigna radiate	0–400 mg kg^{-1}	*Enterobacter* sp.	The bacterial inoculation stimulated the chlorophyll *a* and *b* content of Cr-affected plants.	Subrahmanyam et al. (2018)
Triticum aestivum L.	50–1000 ppm	*Bacillus megaterium-*	Improved chlorophyll *a* and *b* content.	Aslam et al. (2016)
Capsicum annum L.	2 mM	*Cellulosimicrobium cellulans*	It eminently boosted the chlorophyll contents of plants.	Chatterjee et al. (2009)
Helianthus annuus L.	Cr^{3+}: 12 mmol Cr^{6+}: 0.1 mmol	AMF fungal strain (*Glomus intraradices*)	AMF inoculation remarkably improved the net photosynthetic rate and stomatal conductance of plants under Cr^{3+} compared to Cr^{6+} stress in plants.	Davies et al. (2002)

membranes rich in polyunsaturated fatty acids, which can be potentially peroxidized by ROS. Therefore, controlling chloroplastic antioxidants appears to be a crucial technique under Cr stress (Rodríguez et al., 2007). Lipid peroxidation is the irreversible oxidation of lipid, protein and DNA damage in plants under heavy metal stress (Rusinowski et al., 2019). Lipid peroxidation changes the structure of membranes and, as a result, modulates their enzymatic and transport activities in plants under Cr stress. The malondialdehyde (MDA) is an indicator of lipid peroxidation of biological membranes of plants under Cr stress (Sinha et al., 2005). Since MDA is a by-product of lipid peroxidation, the increased MDA content represents membrane damage caused by the peroxidation of the membrane's lipid content in the presence of ROS (Suthar et al., 2014). However, microbes (fungi) protect plants from Cr-induced ROS lethal impacts by stimulating SOD and CAT activity (Wani et al., 2018b). It was shown that copper (Cu) stress eminently enhanced the ROS (H_2O_2) and MDA (lipid peroxidation) contents of lentil plants. Besides, Cu-stressed plants inoculation with PGPB lowered the H_2O_2 and MDA contents in plants. Possibly because microbes protected the plant against harmful impacts of Cu stress (Islam et al., 2016a). Bruno et al. (2020) investigated the catastrophic impact of Cr^{6+}-induced MDA contents and its alleviation by Cr reducing-thermotolerant PGPB strain in *Sorghum bicolor* plants. Cr^{6+} stress enhanced the lipid peroxidation of the plant membrane by increasing the MDA contents. However, plant inoculation with PGPB lowered the MDA contents in plant. It might be due to PGPB-mediated decreased lipid peroxidation and oxidative injury in plants under Cr^{6+}stress. Additionally, PGPB inoculation depressed the ROS generation that, in turn, reduced the MDA contents and improved plant growth under Cr^{6+} stress. Su et al. (2018) administered Cr^{6+} contaminated aqueous wastes to photosynthetic bacterial isolates. The results manifested that Cr^{6+} stress boosted the ROS (H_2O_2 and $O_2^{\bullet -}$) production that, in turn, increased the MDA and electrolyte leakage in the solution. The authors advocated that Cr^{6+} favors ROS generation due to its partial reduction to Cr^{3+} highly unstable radicals. However, plant treatment with photosynthetic bacterial isolates lowered the ROS generation and MDA contents. Less MDA contents mirrored low oxidative damage to cells and strong resistance to Cr damage. Several studies depicting the role of microbes in regulating oxidative defense mechanism in Cr-affected plants are summarized in Table 3.

Glyoxalase system

Plants, as sessile organisms, are mostly subjected to multiple environmental stresses, which can result in a variety of physiological problems and even death. Oxidative stress, one of the most prevalent effects of abiotic stress, resulted in ROS production in plants. Oxidative stress occurs when the production of ROS exceeds the capability of the antioxidant defense system in plants. Plants similar to ROS also produced methylgyloxyal (MG) contents under abiotic stresses such as heavy metals. MG is a highly reactive αβ-dicarbonyl ketoaldehyde. It is produced by following non-enzymatic pathway from photosynthetic intermediates (glyceraldehyde-3-phosphate) and dihydroxyacetone phosphate (DHAP) as a by-product of glycolysis. MG may be found in the chloroplast, mitochondrion, and cytosol. Plant cells possess a modest quantity of MG under normal development conditions; nevertheless, MG synthesis gradually increases under several types of abiotic stress. MG at lower concentration promotes plant growth and other physiological mechanisms in plants. These include seed germination, root growth, shoot morphogenesis, photosynthesis, stomatal closure, pollination, programmed cell death, and stress tolerance. MG played a role as a signaling molecule through ROS, Ca^{2+}, abscisic acid, and K in plants. However, under abiotic stresses, various plant species produce 2–6 times more MG. MG promotes oxidative stress by catalyzing the photoreduction of O_2 to $O_2^{\bullet -}$in PSI that, in turn, enhanced the oxidative injury in plants. MG is a powerful reactive cytotoxin that causes lipid peroxidation and protein and fatty acid oxidation in plants. It also impaired the plant membrane structures and functions under heavy metal stress. MG denatures proteins via the production of advanced glycation. Higher

Table 3
Effect of microbial inoculation on oxidative defense mechanism of plants under Cr toxicity. Abbreviations: ROS, reactive oxygen species; H_2O_2, hydrogen peroxide; $O_2^{\bullet -}$, superoxide radicals; OH•, hydroxyl radicals; MDA, malondialdehyde; SOD, superoxide dismutase; POD, peroxidase; CAT, catalase; APX, ascorbate peroxidase; DHAR, dehydroascorbate reductase; GST, glutathione-S-transferase; GPOX, glutathione peroxidase; GR, glutathione reductase; GSH, reduced glutathione; IAA, indole-3-acetic acid.

Plant species	Cr level	Microbial strain	Plant response	Reference
Brassica juncea L.	0.5 mM	*Pseudomonas aeruginosa* and *Burkholderia gladioli*	Decreased production of ROS such as H_2O_2, $O_2^{\bullet -}$, diminished EL and MDA contents, maximal ascorbic acid contents, stimulated the activities of SOD, POD, CAT, APX, DHAR, GR and GST, declined GPOX activity.	Sharma et al. (2022a)
Triticum aestivum L.	0, 50, 100 and 200 mg kg^{-1}	*Staphylococcus aureus*	Lower H_2O_2, MDA, and EL, higher SOD, POD, CAT, and APX activities	Ahmad et al. (2022)
Brachiaria mutica		*Rhizophagus irregularis*	Higher levels of protein as well as proline, increased CAT, APX, and glutathione peroxidase activity	Kullu et al. (2020)
Macrotyloma uniflorum	0–3000 mg L^{-1}	*Bacillus aryabhattai* and *Rhizobium pusense*	Inhibition in ROS (H_2O_2, $O^{2\bullet -}$, OH•) and MDA accumulation, higher activities of SOD, POD, CAT, APX, more phenolics, and flavonoid contents in plants.	Dhali et al. (2021)
Solanum lycopersicum L.	Cr: 500 μg g^{-1} Cd: 100 μg g^{-1}	*Aspergillus niger*	Increment in IAA, phenols, flavonoids, sugars, proteins, proline, CAT, and ascorbic acid oxidase activity,	Aziz et al. (2021)
Ricinus communis L.	0 μM, 100 μM, 200 μM	*Bacillus subtilis* and *Staphylococcus aureus*	Reduction in H_2O_2, MDA, and electrolyte leakage, enhancement in SOD, POD, CAT, and APX activities in plants	Ali et al. (2021a, b))
Triticum aestivum L.	2.5 mg kg^{-1}	*Bacillus* spp	Higher accumulation of proline and soluble sugars, enhanced SOD activity	Mazhar et al. (2020)
Helianthus annuus (L.)	50, 100 and 200 mg L^{-1}	*Klebsiella* and *Enterobacter* sp.	Maximal SOD, and POD activity, decreased CAT activity	Gupta et al. (2019)
Lycopersicon esculentum L.	Cd: 0.4 mM	*Pseudomonas aeruginosa* and *Burkholderia gladioli*	Resulted in the buildup of phenolics, flavonoids, total carbohydrates, reducing sugars, total osmolytes, glycine betaine, proline, free amino acid contents	Khanna et al. (2019b)
Helianthus annuus L. and *Solanum lycopersicum* L.	0, 50, 100, and 200 mg kg^{-1}	*Pseudomonas* sp.	Diminished MDA contents. upraised SOD, POD, and CAT activities	Gupta et al. (2018)
Glycine max L	5 mM	*Sphingomonas* sp.	Abridged MDA content, increased GSH levels, alongside SOD, POD, and CAT activities.	Bilal et al. (2018)
Glycine max L.	100 μg ml^{-1}	Penibacillus sp.	Declined MDA contents, as well as total SOD and CAT activity	Wani et al. (2018a)
Medicago truncatula	2.5 μg mL^{-1}	AMF *Rhizophagus irregularis*	Improved phosphorus uptake in plants	Gil-Cardeza et al. (2017)
Cicer arietinum L.	50–500 μg mL^{-1}	*Mesorhizobium*	Boosted the plant grain proteins and nitrogen accumulation	(Wani et al., 2008)

levels of MG also caused inhibition of germination and cell proliferation in plants. It also disrupted the antioxidant defense system and other metabolic dysfunctions in plants. The elevated level of MG also caused DNA damage and resulted in mutation in plants. To detoxify MG, plants have the glyoxalase system. The glyoxalase system, which consists of two enzymes, Gly-I (lactoylglutathione lyase) and Gly-II (hydroxyacylglutathione hydrolase), and GSH, work together to remove MG. Under a limited amount of GSH, more MG is accumulated in plants. This MG elimination process is also known as a GSH-dependent glyoxalase pathway because of GSH involvement. Plants, through the glyoxalase system, protect DNA and protein by converting MG into D-lactate (Hossain et al., 2011; Hasanuzzaman et al., 2017; Mostofa et al., 2018). Higher MG accumulation further strengthened the ROS synthesis through interfering with physio-metabolic processes, including inactivation of the antioxidant defense system under heavy metal stress (Hossain et al., 2012). Therefore, the improved glyoxalase system is important for conferring tolerance in plants against MG-mediated oxidative injury under heavy metals stress. The accumulation of MG dependent on the period and intensity of heavy metal stress in plants. Mahmud et al. (2017) found that 0.3 mM Cr^{6+}stress in *Brassica juncea* L. deliberately enhanced the MG accumulation. Higher MG accumulation was associated with maximal Gly-I but minimal Gly-II activity in plants under Cr^{6+} stress. Alam et al. (2021) reported that higher MG contents reacted with GSH, resulting in its limitation in plants. Moreover, MG converts the GSH into hydroxyacylglutathione, which, in turn, hinders the ascorbate-glutathione cycle of plants. Because GSH is the principal part of this cycle. The inhibition in the Gly-II system might be due to a reduction in GSH recycling in plants. Cr^{6+}-induced decrement in Gly-II system was owing to proteolytic deterioration of enzymes. Similarly, Kamran et al. (2021) performed an experiment with *Brassica parachinensis* L. under 0, 150, and 300 μM Cr^{6+} stress. The findings revealed that Cr^{6+} at 300 μM remarkably augmented the MG (114.6%) and Gly-I activity (28%) in plants. However, Cr^{6+} (300 μM) conspicuously declines the Gly-II activity (58.4%) in plants. According to the author, the glyoxalase system is involved in the recycling of GSH, which is vital for maintaining GSH homeostasis and subsequent ROS removal in plants. Higher MG accumulation demonstrates that the detoxifying ability of the glyoxalase system (Gly-I and II) is inadequate to neutralize Cr stress in plants. The drop in Gly-II activity might deplete GSH, resulting in a buildup of cytotoxic S-lactoylglutathione. In another study, exposure of *Pisum sativum* L. plants to Cd stress manifested higher MG accumulation. The authors advocated that a higher MG level is an indicator of metal toxicity in plants (Jan et al., 2018). However, Kaur et al. (2022) reported that *Arabidopsis* plants exhibited lowered MG levels and improved glyoxalase system under abiotic stress in response to microbial application. Stressed plants were treated with *Pseudomonas* sp. and *Bacillus marisflavi* strains. In this context, *Pseudomonas* sp. was more effective in MG detoxification compared to *Bacillus marisflavi* under dicarbonyl stress. Besides, *Bacillus marisflavi* considerably detoxified the MG level in plants under salt stress. *Pseudomonas* sp. has more glyoxalase (both Gly-I and II) activity, while *Bacillus marisflavi* manifested improved MG-induced Gly-II activity in plants. The microbes improved plant growth by mitigating MG levels and improved the glyoxalase system in plants. As a result, activating the defense system of plants under stress conditions.

Antioxidative defense system in plants

Non-enzymatic antioxidants

Antioxidants are substances that, when present in small amounts, can delay or prevent the adverse effects of free radicals. Antioxidants act as free radical quenchers, lessening free radical damage to organisms under abiotic stresses. Antioxidant system is comprised of enzymatic and non-enzymatic in plants. The non-enzymatic antioxidant system consists of phenolics, flavonoids, anthocyanins, and ascorbic acid in plants. They all are active quenchers of ROS produced in plants. Phenolic acids are secondary metabolites found primarily in plants. Phenolics act as antioxidants by donating hydrogen, quenching $^1O_2$, and $O_2^{\bullet-}$ radicals. They also functioned as metal ion chelators for peroxynitrites, superoxide anions, and peroxyl and hydroxyl radicals in plants. Flavonoids are biological phenolic substances produced by all plants in response to biotic and abiotic stresses. The antioxidant capability of flavonoids, such as scavenging ROS and RNS are dependent on the functional groups present in plants. The antioxidant action of flavonoids is due to a combination of free radical scavenging activity and inhibition of ROS-producing enzymes such as NADH oxidase, mitochondrial succinoxidase, microsomal monooxygenase, and glutathione S-transferase. Vitamin C including ascorbic acid and tocopherol protect biological membrane from toxic effects of ROS in plants. The antioxidant ability of carotenoids and anthocyanins content are attributed to the polyene backbone, which combines with $^1O_2$ and free radicals to quench them and provide protection against oxidative injury in plants. Carotenoids consist of α-carotene, β-carotene, β-cryptoxanthin, zeaxanthin, lutein, and lycopene in plants. Anthocyanins are pigments that consist of polyhydroxy or polymethoxy groups, which along with phenolic rings or conjugated double bonds, contribute to their antioxidant properties in plants. They prevent membrane lipid peroxidation by scavenging peroxyl radicals (Kumar et al., 2021a; Ahmed et al., 2023). Plant-microbe interaction is a critical component of the soil ecosystem. It helps plants to cope with a variety of challenges. The soil amendment with these microorganisms has a considerable influence on heavy metal stress tolerance and alleviation. Flavonoids are predominantly released from root tips and root hair zones. Both of these areas are the target sites for the symbiotic connection between plant and bacterium. Soil- microbes generally improve the host plant's biotic and abiotic stress tolerance by raising or lowering the activity of ascorbic acid (Khanna et al., 2018). It was found that maize plants produced a lower amount of phenolics and flavonoid contents under Cr^{6+} stress. Cr^{6+} stress resulted in the malfunctioning of necessary enzymes that played an essential role in phenol biosynthesis in plants. Besides, maize plants inoculation with the PGPR (*T2Cr and CrP450*) strain effectively enhanced the phenolics and flavonoid content under Cr^{6+} stress. It might be due to PGPR positive role in plant metabolic activity that, in turn, caused higher phenolics production in plants under Cr^{6+} stress. The PGPR-induced elevated quantity of flavonoid contents might be owing to enhanced exudation, biochemical metabolites, and afterward active mineral nutrition in plants. This improvement resulted from the relationship between plants and microbes in the root zone (Islam et al., 2016b). In another study, Jinal et al. (2021) observed higher phenolics and ascorbic acid contents in maize plants under Zn stress. Additionally, Zn-stressed plants inoculation with PGPR (*Lysinibacillus* spp.) also exhibited higher phenolics and ascorbic acid contents. The author advocated that higher phenolic content chelates metals, hinders lipid peroxidation, and depresses the Fe ions uptake via lower ROS production in plants. An elevated amount of ascorbic acid contents function as a ROS quencher and lower oxidative injury in plants. An increment in phenolics, flavonoids and anthocyanins content was seen in *Brassica juncea* L. plants under Cr^{6+} stress. Cr^{6+} stress boosted the glutathione *S*-transferase activity which is responsible for higher anthocyanins content in plants. Cr^{6+} stress accelerated the PAL (phenylalanine ammonia lyase) activity that, in turn, upregulated the phenolics and flavonoids contents in plants (Handa et al., 2019). Plants inoculation with PGPR caused upregulation in anthocyanins content under heavy metal stress. It might be due to PGPR involvement in phosphate solubilization that resulted in higher anthocyanin contents via stimulating the phenylpropanoid pathway as a defense response in plants (Khanna et al., 2019a). Several reports of microbes modulating non-enzymatic antioxidants in plants under Cr stress are given below in Table-3

Enzymatic antioxidants

The enzymatic antioxidant system includes superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX) and glutathione reductase (GR) to quench ROS under heavy metal stress in plants. Plant oxidative injury is specified by the levels of ROS ($O_2^{\bullet-}$, H_2O_2 and $OH^{\bullet}$). SOD is the first line of defense involved in the dismutation of $O_2^{\bullet-}$ to H_2O_2 in plants under heavy metal stress. The resultant H_2O_2 is quenched by POD, CAT, and APX in plants (Gratão et al., 2005; Jia-Wen et al., 2013). For estimating the consistent flow of $O_2^{\bullet-}$ radicals and H_2O_2, the balance between SOD and APX or CAT activity in cells is critical. This equilibrium, along with metal ion sequestration, is crucial in preventing the generation of the very dangerous $OH^{\bullet}$ via metal-dependent Haber–Weiss or Fenton reactions (Bhaduri and Fulekar, 2012). Kanwar et al. (2015) reported that plant enzymatic antioxidant activities are primarily dependent on the metal as well as plant species type and period of metal exposure under Cr^{6+} stress. In this context, *Brassica juncea* L. exhibited maximal increment in SOD and APOX activity grown under hydroponic conditions after 60 days of exposure to Cr^{6+} stress. However, the activities of CAT, POD, GR (glutathione reductase), DHAR (dehydroascorbate reductase), and MDHAR (monodehydroascorbate reductase) were lowered after 60 days of Cr^{6+} stress in plants. Zhang et al. (2010) described that Cr^{6+} stress remarkably diminished the SOD, POD, CAT, and APX activities of wheat plants after 48 h. In another study, 30 days of exposure to Cd, Pb, and Cr^{6+} stress markedly enhanced the SOD and POD activities in *Typha angustifolia* plants. However, CAT, APX, and GPX activities were higher under Pb stress than other stress treatments in plants. Cr^{6+} toxicity diminished the APX and GPX activities of plants (Bah et al., 2011). *Catharanthus roseus* plant enzymatic antioxidant system including SOD, POD and CAT was enhanced under Cr^{6+} stress. Further, plant inoculation with bacterial strain such as *Bacillus fortis* also triggered the enzymatic activities under Cr^{6+}. It might be due to PGPR-mediated amplification in gene/mRNA expression of plant enzymatic antioxidant under Cr^{6+} (Yasin et al., 2018). Khanna et al. (2018) reported that plant-microbe symbiosis allows the buildup of stress-responsive phytohormones and the activation of antioxidative defense genes, both of which help plants to survive under metal stress. In another study, plant inoculation with PGPR improved the SOD, POD, CAT, and APX activities by removing ROS in plants under heavy metal stress. It could be due to PGPR influential role in the stimulation of *de novo* synthesis of enzymes. Further, PGPR inoculation minimizes the detrimental impacts of toxic metals by advancing symbiotic relationships in legumes (Ju et al., 2019). Shah et al. (2021) observed that *Cucumis melo* plants displayed higher SOD, POD and CAT activities under Cd stress. However, plant inoculation with *Bacillus fortis* further enhanced the SOD, POD and CAT activities through minimizing oxidative stress in plants. The impact of application of microbes on plant enzymatic antioxidant system has been listed in the Table 3.

Osmolyte accumulation

Plants have evolved various strategies to protect themselves under stressful conditions. For instance, heavy metal stress resulted in the buildup of ROS, lipid peroxidation, and inert solutes in plants. These inert or non-harmful compatible solutes are called osmolytes. These metabolites are synthesized and accumulated to protect plants against the detrimental impacts of abiotic stresses. Therefore, the osmolytes are also called as cytoprotectants of plants (Jogawat, 2019). There are two types of osmolytes, such as organic solutes and inorganic ions, that play a critical role in osmotic adjustment against abiotic stresses. Organic solutes are also known as compatible solutes, including proline, sugars, polyols, and quaternary ammonium compounds like glycine betaine. They reduce or balance the osmotic potential of extracellular and intracellular ions to resist osmotic stresses in plants. Inorganic ions such as K and Ca are also the significant contributors to osmotic adjustment in plants. Organic compatible solutes are involved in the stabilization of enzymes/proteins and maintain the integrity of membranes. Besides, their production needs energy cost and might be one of the factors affecting plant development. However, the accumulated ions should be stored as an osmoticum in the vacuoles to avoid ion toxicity in plants (Patade et al., 2011). Osmolytes also control cell turgor and modulate the cell signaling system of plants. Further, these are also recognized as water-soluble low-molecular-weight compounds with no net charge under physiological pH and do not disrupt normal cellular metabolic functions. They are active quenchers of ROS and upregulate the enzymatic antioxidant activities in plants under stress conditions (Ali et al., 2021b; Ejaz et al., 2020). Higher plants accumulate proline, sugars and glycine betaine in considerable amounts in response to stress conditions. Proline is an active quencher of OH• radical produced under heavy metal stress. By controlling ROS, it minimizes oxidative damage in plants under heavy metal stress. Proline played its influential role as an antioxidant, signaling molecule, safeguarding photosynthetic apparatus, controlling cellular homeostasis, providing energy for plant growth, and effects programmed cell death (Anjum et al., 2023). Proline synthesis catalyzes activities in the pentose phosphate pathway. As a result, it serves as a source of $NADP^+$ for redox cycling, ensuring that antioxidant defense mechanisms operate properly during stress in plants. Under stressful conditions, glycine betaine (GB) prevents protein production and breakdown in plants. Because GB reduces ROS tolerance to repair photosystem II by shielding specific proteins (Ali et al., 2020). In plants, sugars have two opposing functions in terms of ROS. Firstly, higher synthesis of sugars owing to photosynthetic activity caused more cytosolic H_2O_2 production in plants. Secondly, sugars contribute to ROS quenching by producing NADPH necessary for glutathione production during the oxidative phase of the pentose phosphate cycle (Ejaz et al., 2020). Sugar contents are also necessary for osmoprotection, homeostasis and ROS quenching in plants under metals stress (Ali et al., 2013; Jan et al., 2019). Plants have shown variable responses in term of osmolytes accumulation under metal stressed conditions. A number of studies have demonstrated that plants amplify osmolytes accumulation in order to circumvent the phytotoxic effects of heavy metals including Cr (Alam et al., 2023; Handa et al., 2018; Kaur et al., 2024; Pirzadah et al., 2019). Contrarily, some studies displayed reduction in osmolytes production in metal-stressed plants. In this context, Zainab et al. (2021) found that *Sesbania sesban* plants grown under industrially polluted soil (Cu, Zn, Cr, and Ni) displayed significant abridge in proline content. However, bacterial inoculation (*Bacillus gibsonii* and *B. xiamenensis*) amplified proline production in metal-stressed plants. Plants inoculation with *B. xiamenensis* produced (117%) more proline than *B. gibsonii* (112%) under heavy metal stress. Another report suggested that Cr stress increased proline content in *Vigna radiata* plants. However, inoculation of Cr-stressed plants with rhizobacterial strain M2 diminished proline and H_2O_2 content and promoted phytostabilization of Cr (Srinivas Ravi et al., 2022). Likewise, Din et al. (2020) suggested that *Bacillus xiamenensis* PM14 inoculation considerably subsided the oxidative stress and reduced proline accumulation in *Sesbania sesban* which resulted in enhanced Cr uptake by 44.73% as compared to uninoculated plants. *Brassica nigra* L. plants exposed to Cr toxicity displayed increased accumulation of proline and sugars, which was further exacerbated by the inoculation of *Bacillus cereus* resulting in enhanced Cr bioaccumulation and translocation. The authors propose *Bacillus cereus* as a promising microbial strain for augmenting the phytoextraction capabilities of plants under metal toxicity (Akhtar et al., 2021). Malook et al. (2017) reported that inoculation of spinach with *Bacillus* spp. and *Corynebacterium* spp. improved proline, glycine betaine, and sugar content showing their role in mitigating oxidative stress, which also underscore the substantial role of these microbes in bioremediation. Moreover, arbuscular mycorrhizal fungi (*Rhizophagus irregularis)* enhanced osmolytes accumulation in *Brachiaria mutica* under Cr6+ toxicity. Further, mycorrhizae inoculated plants accumulated considerable amount of Cr in their roots showing the efficiency of this fungi to be used in the Cr phytoremediation programs (Kullu et al., 2020). The literature recommends that microbes represent promising contenders for phytoremediation of Cr contamination. This is attributed to their capacity to transform Cr into less toxic form (Cr^{3+}), facilitating its bioavailability for plant uptake. Additionally, microbes exhibit the potential to fine-tune the accumulation of osmolyte and alleviate oxidative stress, thereby enhancing their plant resilience to metal stress. Some examples of microbes mediated regulation of osmolytes in different plants under Cr toxicity has been listed in Table 3.

Nutrient acquisition

Apart from deriving carbon (C), hydrogen (H), and oxygen (O) from CO_2 and water, terrestrial plants commonly rely on a spectrum of elemental nutrients from the soil to foster robust growth and development. These indispensable nutrients encompass nitrogen (N), phosphorus (P), potassium (K), sulfur (S), magnesium (Mg), and calcium (Ca), collectively classified as macronutrients due to their larger quantities essential for plant structure and functionality. Additionally, there are micronutrients, including iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), boron (B), molybdenum (Mo), chlorine (Cl), and nickel (Ni), collectively designated as micronutrients due to their relatively limited requirement in plants. Insufficiency in any of these macronutrients or micronutrients can result in varied biological consequences at molecular, physiological and phenotypic levels in plants (Tripathi et al., 2014; Shi et al., 2019). Each nutrient has a specific function in the life cycle of plants, and its requirements vary depending on the species and stage of development. For instance, nutrients like N, P, K, Mg, Mn, Cl, and Fe are directly engaged in photosynthetic processes (Shi et al., 2019; Yong et al., 2010). Whereas, Ca, B, Cu, Fe, Mn, Zn, and Mo are crucially involved in enzymatic activities. Protein synthesis requires both N and S in plants. These nutrients also play several other vital roles in plant biology and physiology (Song et al., 2020). For example, the abiotic stress-induced limited usage of light energy and CO_2 fixation intensifies the inevitable generation of ROS during photosynthesis. In this context, nutrients such as N, K, Ca, Mg, and Zn have been reported to support the utilization of light and CO_2 fixation and other photosynthetic activities to a certain level. K and Zn, in particular, have been found to interfere with the NADPH-oxidizing enzyme and hence provide protection against ROS-induced damage under abiotic stress (Hasanuzzaman et al., 2018). Among heavy metals, Cr is a nonessential and poisonous element for plant health. An elevated amount of Cr suppresses the nutrient uptake (Ca, P, B, Mg, K, and Cu) in plants. Cr also hampers the uptake of Fe and S due to ionic resemblance and competition with them. Cr stress diminishes the nutrient uptake by impeding the plasma membrane H^+-ATPase activity in plants. Cr also reduces N uptake by interfering with critical enzymes in its metabolism in plants (Duman, 2012). Further, Cr^{6+} is transformed to its less hazardous form, Cr^{3+}, under reducing conditions. This conversion indirectly affects and shifts soil pH to both alkalinity and acidity extremes, depending on the prevailing situation in the soil subsurface. This might affect nutrient bioavailability and their sorption in plants (Emamverdian et al., 2015). Bacterial inoculation can improve the nutritional needs of micronutrients and macronutrients of plants by affecting host physiology and changing the root absorption system under heavy metal stress such as Cr (Ali et al., 2021a,b). PGPR shows potential as a component in strategies for ensuring adequate plant nutrition. As a result, lowering fertilizer-related negative environmental consequences under abiotic stresses. Plant growth stimulation by certain PGPR has been linked to phosphate solubilization and absorption. PGPR also causes root development (increment in root surface area and number of root tips) through the synthesis of phytohormones such as indole-3-acetic acid (IAA). Consequently, it improves the nutrient uptake in plants under abiotic stresses. PGPR also triggers the ATPase proton pump activity in plants (Yang et al., 2009). PGPR bacteria establishes a symbiotic relationship with plant roots, emitting growth-promoting chemicals that make essential nutrients available to plants and enabling them to deal with stress (Gupta et al., 2020; Ramírez et al., 2020). Notably, PGPR produces IAA as well as siderophore and stimulates the activity of ACC deaminase that, in turn, made the availability of Fe to plant under heavy metal stress (Selvakumar et al., 2012). Similarly, Hidangmayum and Dwivedi (2018) also reported that a fungal strain isolated from *Trichoderma* spp. enhanced the plant Fe uptake through siderophore production under abiotic stresses. They further suggested that siderophores synthesized through microbes are thought as a beneficial tool for Fe uptake in plants, particularly in calcareous soil. Likewise, Akhtar et al. (2021) found that PGPR-discharge siderophores and organic acid that augments the iron uptake and phosphorus availability in the rhizosphere, respectively. Dimkpa et al. (2009) further explained that rhizobacteria respond to root exudates by chemotaxis toward the reservoir of the exudate. Then efficient bacteria in this situation tend to modify their metabolism to maximize nutrition uptake in plants (Ali et al., 2015). Khan et al. (2020) in his findings observed the impact of PGPR strains (*Planomicrobium chinense* and *Bacillus cereus*) on nutrient uptake in maize plants under drought stress. PGPR strain effectively improved the levels of nutrient ions such as Ca, K, Mg, Na, Cu, Co, Fe, and Zn in drought-stressed plants. Fe and Zn are essential components of several enzymes and pigments in plants. They play a crucial role in DNA synthesis, photosynthesis, and respiration, as well as assisting in the energy generation of plants under abiotic stresses. Cu deficiency in plants causes poor growth, delayed flowering, and sterility, as well as expanded exposure to diseases. However, plant inoculation with PGPR advanced the Cu contents in plants under drought stress. Higher Cu contents stimulated the lignification process of plants that, in turn, raised strength and declined lodging in cereal crops. In the rhizosphere, PGPR produces chelating chemicals that influence the availability and mobility of essential nutrients. In another study, *Bacillus amyloliquefaciens* inoculation resulted in higher Ca and P content in maize plants under stress conditions. This is because PGPR application improves the solubilization and mobility of Ca and P in the rhizosphere, increasing their accumulation in plants (Okoroafor et al., 2022).

Conclusion and future perspectives

The presence of heavy metals and metalloids has significant adverse effects on the plant biosphere, highlighting an urgent need to identify effective solutions for the removal of these pollutants from the environment. Various physicochemical and biological approaches are being utilized to address the issue of heavy metal and metalloid removal from contaminated soils. Among these methods, phytoremediation stands out as an innovative, cost-effective and environmentally safe approach to manage heavy metals and metalloids. The effectiveness of phytoremediation is further augmented by the symbiotic partnership of compatible microbes. Phytobacterial extraction of heavy metals and metalloids offers a secure method to manage these pollutants with minimal negative effects on the environment. Compatible plant growth-promoting bacteria and fungi play a crucial role in converting heavy metals into bioavailable forms, increasing metal solubility and thereby faciliatating phytoremediation. Researchers have examined various bacterial and fungal species that augment metal accumulation in plants. Additionally, the application of genetically modified microbes holds promise for the remediation of heavy metals and metalloids. Functionally, microbes possessed diverse traits such as biomethylation, initiation of redox reactions, and heightened production of biosurfactants, siderophores, and organic acids. These beneficial characteristics collectively amplify the ability of plants to metabolize and later hyperaccumulate the toxic heavy metals and metalloids. Additionally, plant growth-promoting bacteria and fungi contribute to the synthesis of phytohormones and osmolytes and have the potential to regulate photosynthesis, gas exchange attributes, antioxidant and metal detoxification systems in plants, thereby improving resilience and growth durong exposure, and indirectly improving the efficiency of phytoremediation. In this scenario, the amalgamation of diverse bacterial and fungal diversity could prove more efficient in improving the rehabilitation of contaminated soils. It is crucial to formulate novel and sustainable strategies for the effective removal of pollutants from our environment, aiming to deliver high liveability for our future generations .

CRediT authorship contribution statement

Freeha Fatima Qureshi: Conceptualization, Project administration, Supervision, Writing – original draft. **Muhammad Arslan Ashraf:** Writing – original draft, Writing – review & editing. **Rizwan Rasheed:** Conceptualization, Writing – review & editing. **Iqbal Hussain:** Writing – original draft, Writing – review & editing. **Muhammad Rizwan:** Conceptualization, Project administration, Supervision, Writing – original draft. **Muhammad Iqbal:** Project administration, Supervision, Writing – original draft. **Jean Wan Hong Yong:** Project administration, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Supplementary materials

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