



Plant Growth Promoting Rhizobacteria: Role in Heavy Metal Detoxification in Plants

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Abstract

Heavy metals in rhizospheric soil are difficult to break down and can easily migrate, endangering both human health and the environment. As a result, heavy metal pollution in rhizospheric soil is one of the most serious environmental problems facing the world. Plant growth-promoting rhizobacteria (PGPR) are rhizosphere microorganisms that can help plants grow and increase agricultural productivity. PGPR can alter heavy metal bioavailability in the rhizosphere microenvironment, and enhance the uptake of heavy metal, and phytoremediation efficiency in heavy metal-contaminated soils. Recent research has shown that PGPR can improve phytoremediation efficiency for heavy-metal-contaminated soil. This paper provides a systematic review of PGPR mechanisms that improve plant-heavy metal interactions, such as chelation, induction of systemic resistance, and increased bioavailability, as well as promote plant growth through nitrogen fixation, phosphorus solubilization, iron solubilization, potassium solubilization, and plant hormone secretion. Future research on PGPR should address the issues of heavy metal removal by phytoremediation

Keywords: *Plant-Growth-Promoting Rhizobacteria (PGPR); Rhizosphere; Heavy metal; Heavy metal detoxification; Bioremediation*

Introduction

Since the 20th century, as the social economy has grown rapidly, people have burned fossil fuels, extracted gold from deposits, and used pesticides, fertilizers, and other chemicals. As a result, there has been a noticeable increase in the intensity and geographic range of heavy metal pollution in the soil environment (Zhang & Wang, 2020). Heavy metals contaminate soil and groundwater when they reach the soil environment through fertilization, irrigation, atmospheric settling, and other processes (Hou, 2021). Ecological imbalance, biodiversity loss, soil erosion, desertification, acidification, salinization, decreasing soil fertility, soil consolidation, and soil subsidence are all signs of heavy metal-contaminated soil (Vaverkova, 2019). In soil, heavy metals will be absorbed and accumulate in plants due to their exceptional environmental persistence and through the food chain (Leong & Chang, 2020). Therefore, it is necessary to remove these harmful heavy metals from the soil. Different physicochemical methods like chemical solidification, washing, and replacing soil have partially stopped soil heavy metal migration to groundwater. Still, their use is restricted because of their high energy requirements, secondary pollution, and disintegration of soil aggregate structures (Padhan *et al.*, 2021). In the same way, bioremediation—which includes processes like biosorption and bioaccumulation—is a straightforward, sustainable, and eco-friendly technique that has attracted a lot of attention to improve the plant repair efficiency with high metal concentration. Plant Growth Promoting Rhizobacteria (PGPR) is a promising tool. It increases agricultural output via biotechnology and offers an easy, sustainable, and ecologically friendly substitute (Pantoja-Guerra *et al.*, 2023). By using PGPR as a bioinoculant, plant biomass and root growth are promoted by the ability to recycle nutrients, stabilize soil

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structure, and control the bioavailability and toxicity of heavy metals (Ahemad, 2019). PGPR establishes a positive interaction with plants and creates broad interest in heavy metal stress management in agricultural and environmental research.

PGPR: Plant Growth Promoting Rhizobacteria

German microbiologist Lorenz Hiltner used the term “rhizosphere” in 1904 and described how soil microorganisms are affected by plant root exudates (Hartmann, 2008). The group of microorganisms known as rhizosphere microbes consists primarily of bacteria, actinomycetes, fungi, viruses, and algae (Jha & Saraf, 2015). In the rhizosphere of plants, many beneficial free-living bacteria in the soil that are attached to plant roots are commonly referred to as PGPR (Barriuso et al., 2008). Because most plant roots can release significant amounts of nutrients, like amino acids, sugars, and organic acids, these provide energy for the growth and metabolism of bacteria. The concentration of rhizospheric bacteria is exceptionally high in plants (Kloepper, 1987). The term “PGPR” was initially introduced in 1978 by Kloepper and Schröth, who defined it as a group of microorganisms that invade the plant rhizosphere and stimulate plant development (Kloepper, 1987). The common species of PGPR and their mechanism for heavy metal extraction in plants are displayed in Table 1. PGPR in heavy-metal-contaminated soil can interact with heavy metals and increase phytoremediation's efficacy.

Table 1. Assistance of PGPR in the phytoextraction of heavy metals

Heavy Metals	PGPR	Test Plants	Plant-Growth-Promoting Mechanisms	Study
As	<i>Exiguobacterium</i> sp.	<i>Vigna radiata</i>	Secretes IAA and EPS.	Pandey, N. and Bhatt, R. 2016
As, Cd and Cr	<i>Pseudomonas</i> sp.	<i>Lens culinaris</i>	Secretes IAA.	Biswas, J.K. et. al. 2017
Ca	<i>Bacillus</i> spp.	<i>Brassica napus</i> L.	Secretes IAA, Siderophores and ACCD; phosphate solubilization	Samreen, T. et. al. 2019
Cd	<i>Azotobacter</i> sp.	<i>Triticum aestivum</i> L.	Secretes IAA and ACCD; nitrogen fixation; phosphate solubilization	Hassan, W. et. al. 2016
Cd	<i>Bacillus megaterium</i>	<i>Hybrid Pennisetum</i>	(ACCD); phosphate solubilization and nitrogen fixation.	Wu, J. et. al. 2019, Kamal, N. et. al. 2021
Cd	<i>Bradyrhizobium</i> sp.	<i>Lolium multiflorum</i> Lam.	Secretes IAA, siderophores, and ACCD; phosphate solubilization.	Guo, J. and Chi, J. 2014
Cd	<i>Ochrobactrum</i> sp.	<i>Oryza sativa</i>	Secretes siderophores and ACCD.	Pandey, S. et. al. 2013
Cd, Pb	<i>Enterobacter bugandensis</i> and <i>Bacillus megaterium</i>	<i>Lactuca sativa</i> L.	Secrete IAA and siderophores.	Wang, T. et. al. 2020
Cd, Zn	<i>Bacillus</i> sp.	<i>Oryza sativa</i>	Secretes indole-3-acetic acid (IAA), 1-aminocyclopropane-1-carboxylate (ACC)	Liu, A. et. al. 2022
Cd, Pb and As	<i>Klebsiella michiganensis</i>	<i>Oryza sativa</i>	Secretes IAA and ACCD; nitrogen fixation; phosphate solubilization.	Mitra, S. et. al. 2018
Cr	<i>Pseudomonas</i> sp.	<i>Medicago sativa</i>	Secretes IAA and siderophores; produces ammonia, cellulase, pectinase, chitinase, and ACCD;	Wang, T. et. al. 2020

			phosphate solubilization; nitrogen fixation.	
Cr	<i>Klebsiella</i> sp.	<i>Lathyrus sativa</i> L.	Secretes IAA, ammonia, siderophores, and HCN	Gupta, P. et. al. 2018
Cr	<i>Agrobacterium fabrum</i>	<i>Zea mays</i>	Secretes siderophores, IAA, and potassium; phosphate solubilization.	Danish, S. et. al. 2019
Cr, Cd	<i>Azotobacter</i> sp.	<i>Lepidium sativum</i>	Solubilizing of phosphorous; improves the dissolution and retention of iron in the growth medium; nitrogen fixation; produces plant hormones.	Sobariu, D.L. et. al. 2017
Cu	<i>Kocuria</i> sp.	<i>Saccharum spontaneum</i>	Secretes IAA, product ammonia, and hydrogen cyanide (HCN); phosphate solubilization.	Biswas, J.K. et. al. 2017
Ni	<i>Bacillus</i> spp.	<i>Althea rosea</i> L.	Secretes IAA; siderophore production; phosphate solubilization.	Hansda, A. and Kumar, V. 2017
Ni	<i>Bacillus subtilis</i>	<i>Brassica juncea</i>	Secretes IAA; phosphate solubilization.	Khan, W. U. et. al. 2017
Ni, Pb, Cd and Cr	<i>Pseudomonas putida</i>	<i>Zea mays</i>	Increases the availability of Fe, Zn, K and Ca. Secretes IAA, siderophores, ACC deaminase (ACCD); phosphate solubilization and nitrogen fixation.	Liu, A. et. al. 2022, Asadullah, A.B. and Javed, H. 2021
Ni, Zn and Fe	<i>Psychrobacter</i> sp. and <i>Pseudomonas</i> sp.	<i>Brassica juncea</i> and <i>Ricinus communis</i>	Secretes siderophores, ACCD, and IAA; phosphate solubilization.	Sobariu, D.L. et. al. 2017
Pb	<i>Luteibacter</i> sp. and <i>Variovarax</i> sp.	<i>Lathyrus sativus</i> L.	Secretes IAA, siderophores, and HCN; phosphate solubilization.	Hassan, W. et. al. 2016
Pb, As	<i>Bacillus</i> sp.	<i>Oryza sativa</i>	Secretes siderophores and ACCD.	Pandey, N. and Bhatt, R. 2016
Zn	<i>Pseudomonas aeruginosa</i>	<i>Triticum aestivum</i> L.	Secretes IAA, ACCD, and siderophores; phosphate solubilization.	Ma, Y. et. al. 2015
Zn	<i>Proteus mirabilis</i>	<i>Zea mays</i>	Secretes IAA, siderophore, and ACCD; phosphate solubilization.	Guo, J. and Chi, J. 2014

PGPR: Promote Plant Growth

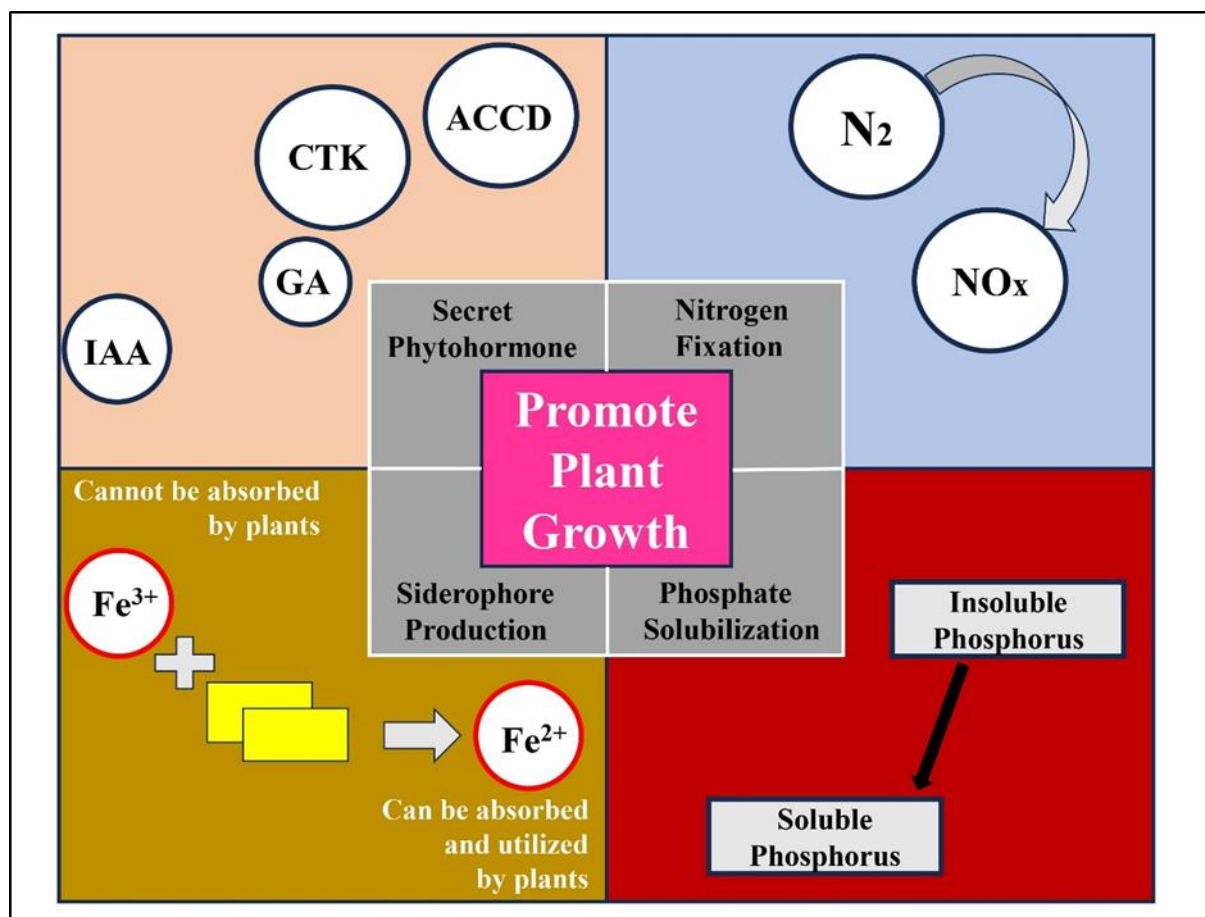


Figure 1. Growth-promoting mechanism of PGPR

Biological Nitrogen Fixation

N_2 is one of the most important nutrients for plant growth, flowering, and fruiting. It is also a necessary component of membrane amino acids, lipids, chlorophyll, protein, nucleic acids, ATP, NADH, co-enzymes, and other substances (Wagner, 2011). Only 30-50% of Nitrogen fertilizers are adopted by the plants; the rest seep into the water and cause eutrophication (Hodge *et al.*, 2000). PGPR is an invaluable tool for application in agriculture and environmental rehabilitation since it functions as a bacterium that can coexist with plants to fix nitrogen. The procedure by which nitrogen-fixing microorganisms transform atmospheric nitrogen into ammonia that is available to plants is known as biological nitrogen fixation or BNF. Numerous *Rhizobium* species, *Acetobacter* species, *Arthrobacter* species, *Citrobacter* species, *Clostridium* species, *Streptomyces* species, etc. are common nitrogen-fixing bacteria (Olenska *et al.*, 2020). *Rhizobia* is the most common N_2 fixing, symbiotically associated bacteria with leguminous plants. These bacteria formed root nodules with the roots of these plants. Nitrogenase enzyme is responsible for N_2 fixation but is sensitive to O_2 and causes inhibitory activity. The root nodule provides a hypoxic condition so that N_2 fixation smoothly takes place. *Rhizobia* obtain nutrients, carbon energy, and a healthy living environment from the host plant; while plants receive nitrogen nutrients from them (Mus *et al.*, 2016). Studies show that rhizobia and legumes contribute about 70% of biological nitrogen fixation and that rhizobia supply 90% of the nitrogen needed by these plants (Olenska *et al.*, 2020). One of the key functions of PGPR in boosting plant vitality is nitrogen fixation, which plays a significant role in stimulating plant growth. Cakmakcı *et al.*, 2007, reported that six common PGPR significantly helped in the growth of wheat and spinach. Additionally, it was confirmed that the PGPR inoculation greatly enhanced the nitrogenase activity of *Dalbergia sissoo* seedlings and encouraged their growth (Dhiman *et al.*, 2022). Generally, legume growth, nodules, nitrogenase activity, and nitrogen-fixing properties can all be negatively impacted by heavy metals (Hao, 2014). This has given researchers ideas for choosing rhizobia that are resistant to heavy metals. It was discovered that co-inoculation of *Rhizobium* (*Sinorhizobium*) and *Agrobacterium tumefaciens* could notably raise plant biomass and nitrogenase activity by alleviating heavy metal stress from excessive concentrations of heavy metals such as Cu^{2+} and Zn^{2+} while without nodule formation and inoculation of nitrogenase activity was reduce (Jian *et al.*, 2019). The same

results were also obtained by Chen et. al., in *Medicago sativa* seedlings in which *Rhizobium* increases N_2 activity and alleviates heavy metal stress (Chen et al., 2018). Inoculation with *Burkholderia* sp. reduced Cd contents in their roots and leaves by 58.11% and 64.54%, respectively, in rape seed and by 72.89% and 70.03%, in uninoculated plants (Shen et al., 2023). PGPR by enhancing shape and surface area of root, nitrogen uptake, and plant-growth-promoting qualities and increasing nitrogen bioavailability.

Solubilization of Phosphate

Phosphorus is an essential component for plant metabolism and nutrient cycling, second only to nitrogen in importance (De Zutter et al., 2021). Aside from nitrogen, phosphorus is a key nutrient required for plant metabolism and nutrient cycling. A lot of phosphorus is present in the soil. Still, in its insoluble form, it frequently binds to other ions such as calcium, iron, and aluminium, making it difficult for plants to absorb and utilize (Mehta et al., 2019). Fertilizers are frequently used in agriculture to improve crop yields. However, too much phosphorus has led to major problems with environmental degradation, such as water eutrophication, an imbalance in the soil microbial community, and a reduction in soil fertility (Schmidt, 2023). Hence, there is an immediate demand for an economical and ecologically friendly substitute for phosphorus fertilizers. Using phosphorus-solubilizing microbes is one of the most promising ways to create safe and reliable technologies (Ma et al., 2016). It is crucial for the cycling of phosphorus and for encouraging plant growth. Research has shown that PGPR acts as a PSM to convert insoluble phosphorus into a soluble form that is utilized by plants (Saha et al., 2016). Mostly by releasing organic acids (such as gluconic acid, citric acid, and oxalic acid), chelating metal ions to create soluble complexes (like calcium, iron, and aluminium phosphates), and generating enzymes (pyridoxal phosphatase, phytanase, and C-Plyase) that hydrolyze soil's organic phosphorus into inorganic forms. The phosphorus dissolving pathways with the help of PGPR are summarized in Figure 2. Common PSM present in agricultural soil are *Pseudomonas* species, *Enterobacter* species, *Bacillus* species, *Serratia* species, *Arthrobacter* species, *Burkholderia* species, *Aspergillus* species, *Gongronella* species, *Penicillium* species, *Talaromyces* species, and many others (Tank & Saraf, 2009).

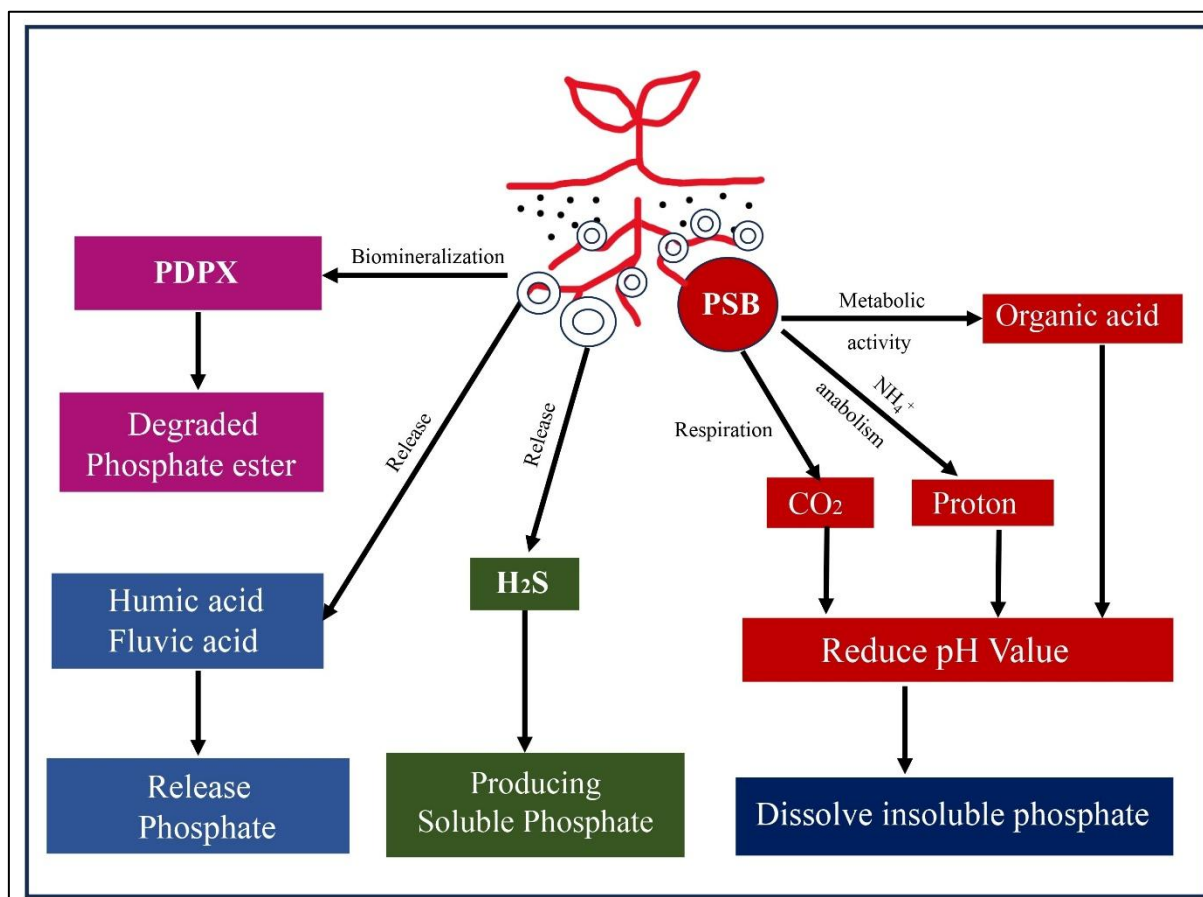


Figure 2. Mechanism of PSM in bio-dissolving insoluble phosphates.

Production of Siderophore

Iron is an essential nutrient required for proper growth and the development of cellular processes in plants. Iron is present in the soil in large quantities, but it is usually in an insoluble oxidation form, so very difficult for plant roots to absorb and utilize it (Amara *et al.*, 2015). Certain microbes and plants might produce siderophores, which are low-molecular-weight organic molecules with a great affinity for iron when there is little iron stress (Amara *et al.*, 2015). As a result, an iron absorption system is established, with a siderophore serving as the primary component. The siderophore and insoluble iron form a complex, which is then transported across the microbial membrane by the membrane receptor. Fe³⁺ linked to the iron carrier is released again when the cell's enzyme system reacts (Saha *et al.*, 2016). Siderophores can chelate with additional harmful metal ions to lower their concentration. Research has indicated that Fe-S clusters can be destroyed by intracellular reactive species of hydrogen peroxide (H₂O₂) or superoxide (O₂⁻), which releases excess free Fe²⁺ from the damaged cluster. *Pseudomonas aeruginosa* can be protected from oxidative damage by Pyoverdine (PVDI), a fluorescent iron carrier, which chelates with liberated ferrous to prevent the generation of OH (Jin *et al.*, 2018). When consumed by iron-stressed seedlings, the DCY119T ginseng rhizosphere strain can generate siderophores and eliminate excess ROS, reducing oxidative stress (Huo *et al.*, 2021). When it comes to limited iron supplies, PGPR can compete with harmful rhizospheric bacteria (Di Francesco & Baraldi, 2021).

Production of Different Phytohormones

PGPR-released phytohormones such as auxin (IAA), gibberellin (GA), cytokinin (CTK), and ethylene (ETH) (Manoj *et al.*, 2020) stimulate plant development when heavy metal stress is present (Yu *et al.*, 2020).

Auxin

Auxin is found naturally in plants and plays a crucial role in several activities, including the elongation of buds, the development of organs, and root hair (Du *et al.*, 2020; Chen *et al.*, 2017). Numerous PGPR have been documented to assemble IAA, including *Rhizobium* sp., *Arthrobacter* sp., *Bradyrhizobium* sp., *Azospirillum* sp., *Alcaligenes* sp., *Klebsiella* sp., *Enterobacter* sp., *Acetobacter* sp., *Bacillus* sp., *Pseudomonas* sp., *Xanthomonas* sp., *Rhizobium* sp., *Arthrobacter* sp., and *Bradyrhizobium* sp. By secreting IAA, PGPR can advance plant root growth in contaminated soil by increasing heavy metals. This boosts the surface area of plant roots, their ability to absorb nutrients from the soil, and the number of heavy metals that accumulate in their roots—all of which raise the efficiency of the plant's ability to absorb the heavy metals (Ma *et al.*, 2016). PGPR raised the Zn and Cu content in *Brassica oxyrrhina* by 61% and 146%, respectively discovered by Ma *et al.*, 2016. They also discovered that inoculating maize and sunflowers with the PGPR strain greatly enhanced the amount of copper in the shoots (Abbaszadeh-Dahaji *et al.*, 2021). Bacterial strains produced more IAA, which gave plants more heavy metals and nutrients in plants in addition to increasing the length and surface area of their roots, was connected to a higher capacity for heavy metal accumulation in PGPR-infected plants. Rhizospheric soil bacteria are thought to secrete and aid in IAA absorption of heavy metals from the soil.

Gibberellins

A diterpenoid plant hormone called gibberellin (GA) is bioactive and involved in complicated biosynthesis at several phases of plant growth. such as fruit ripening, flowering, germination, and an increase in root hairs (Nagel *et al.*, 2018). More than 130 different types of GAs have been identified GA₃, GA₁, GA₄, and GA₂₀ are the most common types of gibberellins produced by PGPR. *Acetobacter* sp., *Azotobacter* sp., and *Bacillus* sp. are common PGPR species capable of producing GA (Amara *et al.*, 2015). GA provides adaptation of the plants under heavy metals toxicity. In the pea (*Pisum sativum* L.) seedling toxicity of Cu stress was reduced after application of GA₃ (Massoud *et al.*, 2018). GA greatly enhanced the dry biomass of leaf, stem, root, and shoot in the *Sedum alfredii* heavy metals such as Cd and Pb were observed significantly. Hence this plant can used for heavy metal phytoremediation (Liang *et al.*, 2021).

Aminocyclopropane-1-Carboxylate (ACC) Deaminase

Ethylene, a gaseous plant hormone, is a key growth regulator. Ethylene promotes flowering, fruit ripening, leaf aging, and seeding. The high amount of ethylene inhibits normal plant growth and promotes senescence (Olenska *et al.*, 2020). However, when exposed to heavy metals, plants can produce a lot of ethylene. As a result, for plants under severe metal stress to thrive, the right management of the ethylene level is essential (Olenska *et al.*, 2020). The synthesis of ethylene involves two distinct enzymatic reactions. In the first reaction, ACC synthetase (ACS) converts the substrate S-adenoyl-L-methionine (SAM) to ACC and 5'-

methylthioadenosine (MTA) in the first step but in the second reaction, ACC oxidase (ACO) converts ACC to ethylene, CO₂, and cyanide levels can be regulated by controlling ACC levels (Pattyn *et al.*, 2021). To some extent, ethylene production could be controlled by lowering the activity of ACS and ACO. In *Zea mays* ACS and ACO activities dramatically decreased PGPR inoculation (Misra & Chauhan, 2020). Volatile organic chemicals released by *Bacillus subtilis* (strain SYST2) inhibited the transcription of the ACO1 gene and decreased the endogenous ethylene levels in tomato seedlings (Tahir *et al.*, 2017). An enzyme that can break down ethylene by ethylene precursor lowering ethylene levels, ACC deaminase (ACCD). Studies suggested that PGPRs are responsible for heavy metal accumulation in different plants, like in the presence of *Bacillus safensis* [FO-036b (T) strain] and *Pseudomonas fluorescens* (p.f.169), which contains ACC deaminase, sunflowers acquired more Pb and Zn and grew significantly better (Mousavi *et al.*, 2017). *Serratia* K120, *Escherichia coli* N16, *Klebsiella* Mc173, and *Enterobacter* N9 which is the strain of rhizobia produce ACCD. Significantly lengthened the roots and shoots of cauliflower, hence these PGPR are used for the phytoremediation of metals like copper, zinc, nickel, lead, and arsenic. In conclusion, it is clear that PGPR, especially those that can produce ACC deaminase, is important for supporting and enhancing heavy metal consumption and plant growth.

Cytokinin

Cytokinin is found in many bacteria, algae, and higher plants. Cytokinin (CTK) is the second most significant phytohormone after IAA (Li *et al.*, 2020). In plants, stimulating cell division, expansion, and tissue growth, cytokinin is essential for the development of chloroplasts, vascular systems, and bud differentiation (Kieber & Schaller, 2018). Many authors reported that PGPR can produce cytokinin and induce plant growth in heavy metal-contaminated soil (Wang *et al.*, 2018). In *Acutodesmus* obliquus growth inhibition was much reduced by cytokinin, according to Piotrowska, and its capacity to resist lead toxicity under lead stress was increased (Piotrowska-Niczyporuk *et al.*, 2018). Similarly, the extremely prolific plant *Sedum alfredii*'s biomass and cadmium absorption efficiency is significantly increased by cytokinin are found by Yu *et al.*, 2024. *Azotobacter chocoocum* which was inoculated with plants showed a notable improvement in growth status, as demonstrated by Nieto and Frankenberger.

Interaction of PGPR with Heavy Metals

Chelation

Production of Exopolysaccharide (EPS)

Exopolysaccharides are a type of naturally occurring polymer with a large molecular weight that is secreted by microbes. These compounds include lipids, proteins, sugars, and amino acids. EPSs form on the bacterial cell surface and function as a protective barrier against damaging external elements such as pathogen attachment, phagocytosis, pH, drying, and heavy metals (Manoj *et al.*, 2020). EPSs adsorb heavy metals through ion exchange, surface precipitation, electrostatic contact, complexation, redox, and other interactions lowering toxicity (Vimalnath & Subramanian, 2018). The mechanism of EPSs shields cells from heavy metal ions is shown in Figure 3. Without EPS metal ions will directly come in contact with the cell and react with particular proteins or enzymes, which will eventually cause the cell damage and lose their activity. The EPSs produced by PGPR (*Azotobacter* sp.) combine with the heavy metals cadmium and chromium to reduce their migration potential alleviate the pressure on wheat development and help in reducing heavy metals. According to reports, the components of EPS bind Cr (VI) and interact with the hydroxyl and carboxyl groups due to the enzymatic reduction of Cr (VI) (ref). It is possible because the protein components of EPSs reduced Cr (VI). Moreover, the main functional groups that can bind Cr (VI) to protect cells from its harmful effects include COO⁻ and OH⁻ groups in EPSs (Lu *et al.*, 2018).

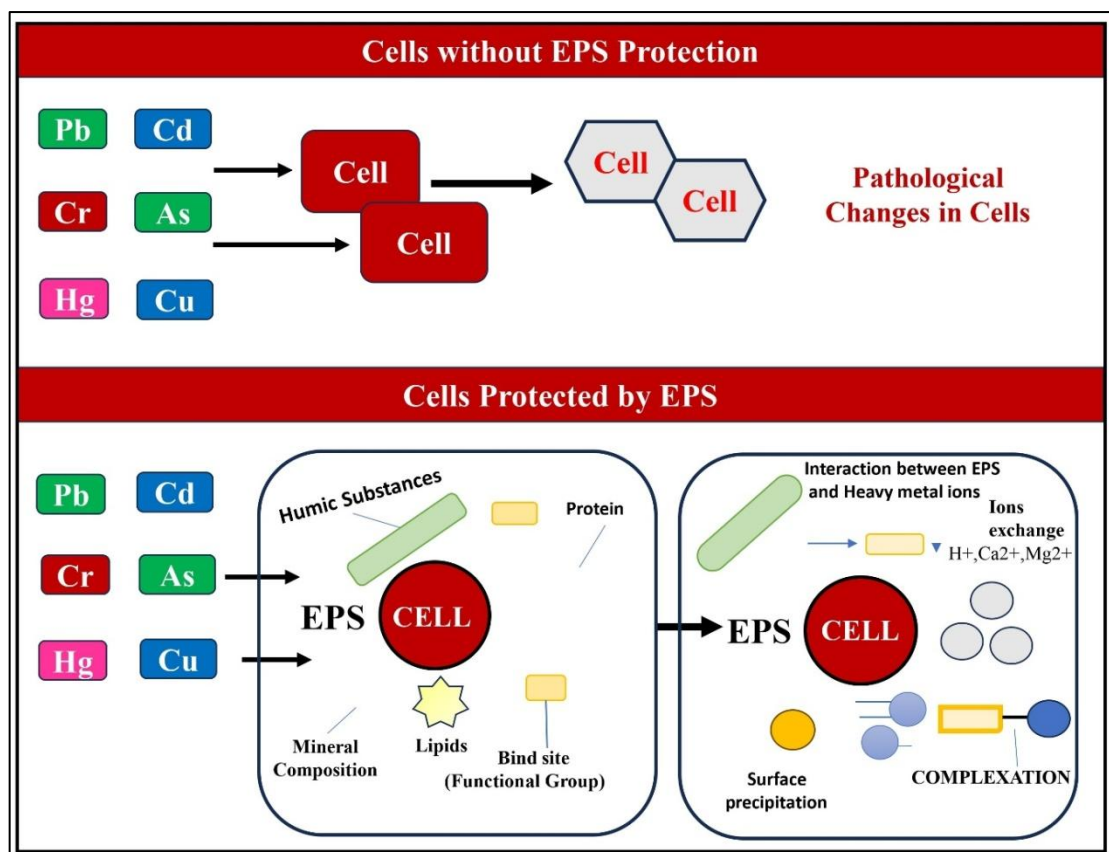


Figure 3.

Schematic mechanism of metal-EPS interactions.

Production of Metallothionein

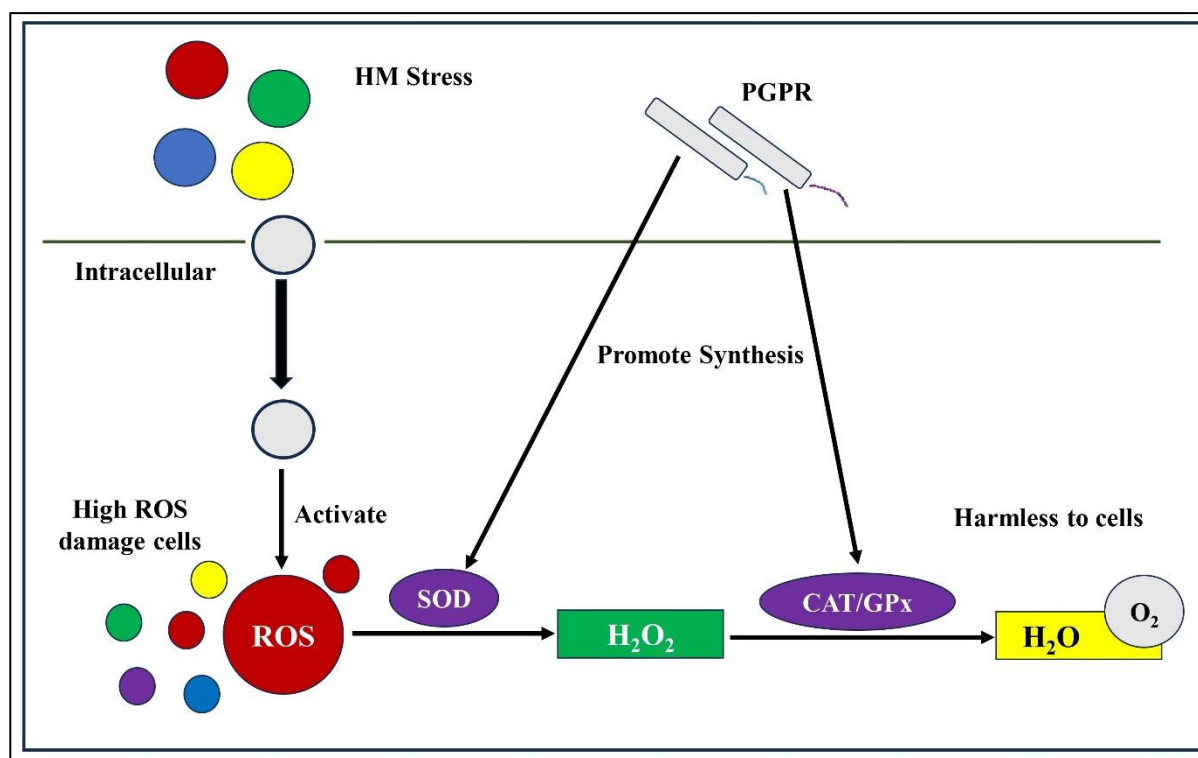
Cystines make up around one-third of the amino acid makeup of metallothioneins (MTs), a class of ubiquitous low-molecular-weight proteins (Bataineh *et al.*, 1986). Metallothioneins are commonly found in eukaryotes and some prokaryotes. MTs bind to different metal ions like Zn^{2+} , Cd^{2+} , and Cu^{2+} and from sulfur-based metal clusters through the thiol group and cysteine and are helpful in detoxification (Si & Lang, 2018). These clusters are essential for controlling the dynamic equilibrium and plant metal ion detoxification. Plants with PGPR strains carrying bacterial MTs discovered that their bioremediation process in metal-contaminated soil was improved, and heavy metal removal, such as Pb^{2+} , exhibited encouraging results. MTs in tobacco leaves can regulate silene's response to Cu stress (Hussain *et al.*, 2022).

Production of Soil Organic Acid

Acetic acid, formic acid, succinic acid, tartaric acid (TA), citric acid (CA), oxalic acid (OA), and gluconic acid (GA) are among the organic acids that are secreted by some PGPR can emit. For example, strains of PSM found in soil can release a lot of gluconic acid, which increases the bioavailability and improves the mobility of cadmium (Yang *et al.*, 2018). Similarly, treatment with citric acid, tartaric acid, oxalic acid, and malic acid, increased root and stem Cd concentrations significantly in comparison to the control, which had a positive effect on the soil's ability to absorb total Cd (Yu *et al.*, 2020). Exogenous CA administration in a growth medium containing Cd considerably reduced the deleterious effects of Cd on plants, according to research that explored the effects of various dosages of CA on stress tolerance and heavy metal accumulation in *Brassica juncea L.* (Al Mahmud *et al.*, 2018). In Cr-contaminated soil, applying 5-aminolevulinic acid and citric acid together might enhance photosynthesis, gas exchange properties, and biomass of sunflowers (Farid *et al.*, 2019). Similarly, acid malic or tartaric acid can greatly enhance the developing potential of hybrid flowers under conditions of Cd stress (Chen *et al.*, 2020). Increasing the levels of succinic acid, citric acid, fumaric acid, and malic acid, in tomato seedlings inoculated with *Burnetidia eriagladlioli* and *Pseudomonas aeruginosa* decreased Cd-induced toxicity. According to this study, PGPR is essential for plants to secrete organic acids that reduce heavy metal stress (Khanna *et al.*, 2019).

Induced Systematic Resistance (ISR)

Plants can develop a defense against pathogens known as induced systematic resistance, which is brought about by a variety of agents, including rhizosphere bacteria (Loon *et al.*, 1998). ISR triggers several possible defense mechanisms, like boosting the activity of peroxidase, β -1,3 glucanase, and chitinase; accumulating low molecular antimicrobial substances like phytoalexins; and forming protective biopolymers like hydroxyproline-rich glycoprotein, lignin, and callose (Annapurna *et al.*, 2013). It was discovered that by boosting antioxidant enzyme activity, PGPR can complete the ISR process (Jorquera *et al.*, 2016). As illustrated in Figure 4, increased ROS generation by plant cells under heavy metal stress leads to oxidative damage. To counteract this oxidative damage, plant cells synthesize a range of antioxidant enzymes, including ascorbic peroxidase (APX), catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD). This is good for plant growth and can efficiently eliminate ROS from plant cells (Miller *et al.*, 2010). Two PGPR strains, *Bacillus firmus* (strain 40), and *Bacillus pumilus* (strain DH-11) were isolated from the potato rhizosphere by Gururani *et al.* These strains increased the plant's tolerance to zinc by increasing the amounts of gene transcription of ROS-scavenging enzymes (SOD, APX, CAT, GR, and DHAR,) in potato plants (Gururani *et al.*, 2013). A consortium of rhizobium and PGPR could reduce ROS accumulation, boost antioxidant enzyme activity, and improve tolerance to copper in alfalfa plants (Ju *et al.*, 2020). Despite *Pseudomonas* sp. inoculation, sunflower, and tomato can increase SOD production, CAT minimize the formation of ROS and improve Cr tolerance (Gupta *et al.*, 2018).



Figure

4. Systemic resistance

Transform the Toxicity of Heavy Metals

Heavy metals can be changed by soil bacteria (PGPR) into an easily soluble form and increase bioavailability so that plant roots can easily absorb it and are helpful in phytoremediation (Prapagdee *et al.*, 2020). Plants may accumulate more selenium when bacteria convert selenium acetate to organic Se into selenate (Zayed & Terry, 1988). *Bacillus megaliium* considerably raised the exchangeable Cd content of rhizosphere soil (Prapagdee *et al.*, 2013). For example, *Pseudomonas aeruginosa* BS2 produces biosurfactants that cause Pb and Cd to become soluble (Juwarkar *et al.*, 2007). The availability of soluble zinc in soil and accumulation of zinc in plants were enhanced by *Bacillus subtilis*, *B. cereus*, *Pseudomonas aeruginosa*, and *Flavobacterium* sp. (He *et al.*, 2010).

Conclusions

PGPR-aided phytoremediation of heavy metal pollution seems to be a potentially advantageous method in terms of both environmental and economic benefits. PGPR can improve the efficacy of soil heavy metal

remediation by promoting plant growth through metabolic processes that include nitrogen fixation, phosphorus dissolution, plant growth hormone secretion, and increased heavy metal bioavailability. In addition, secreting high-affinity siderophores increases the supply of iron, induces ISR, activates plant antioxidant enzymes, and competitively limits heavy metal uptake by plant roots, as well as affecting heavy metal absorption, transportation, and intracellular distribution. These actions can decrease heavy metal stress, boost endurance to heavy metals, and ultimately increase the efficacy of phytoremediation. In addition to helping plants absorb and acquire heavy metals or immobilize the soil under a variety of heavy metal stress scenarios. In rhizosphere soil, PGPR is essential for the mobility and processing of heavy metals. Some of the future research directions for PGPR include the development of the strains themselves, plans for the cooperative use of multiple strains, procurement of mixtures of multiple strains directly from natural habitats, and the development of macromolecular materials like biochar in conjunction with PGPR for phytoremediation.

Author's contributions

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data.

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REFERENCES

1. Abbaszadeh-Dahaji, P., Atajan, F. A., Omidvari, M., Tahan, V., & Kariman, K. "Mitigation of copper stress in maize (*Zea mays*) and sunflower (*Helianthus annuus*) plants by copper-resistant *Pseudomonas* strains." *Current Microbiology* 78 (2021): 1335–1343.
2. Ahemad, M. "Remediation of metalliferous soils through the heavy metal resistant plant growth promoting bacteria: Paradigms and prospects." *Arabian Journal of Chemistry* 12 (2019): 1365–1377.
3. Al Mahmud, J., Hasanuzzaman, M., Nahar, K., Bhuyan, M. B., & Fujita, M. "Insights into citric acid-induced cadmium tolerance and phytoremediation in *Brassica juncea* L.: Coordinated functions of metal chelation, antioxidant defense, and glyoxalase systems." *Ecotoxicology and Environmental Safety* 147 (2018): 990–1001.
4. Amara, U., Khalid, R., & Hayat, R. "Soil bacteria and phytohormones for sustainable crop production." In *Bacterial Metabolites in Sustainable Agroecosystem* (2015): 87–103. Springer International Publishing.
5. Annapurna, K., Kumar, A., Kumar, L. V., Govindasamy, V., Bose, P., & Ramadoss, D. "PGPR-induced systemic resistance (ISR) in plant disease management." In *Bacteria in Agrobiolgy: Disease Management* (2013): 405–425. Springer Science & Business Media.
6. Asadullah, A. B., & Javed, H. "PGPR assisted bioremediation of heavy metals and nutrient accumulation in *Zea mays* under saline sodic soil." *Pakistan Journal of Botany* 53 (2021): 31–38.
7. Barriuso, J., Ramos Solano, B., Lucas, J. A., Lobo, A. P., García-Villaraco, A., & Gutiérrez Mañero, F. J. "Ecology, genetic diversity and screening strategies of plant growth promoting rhizobacteria (PGPR)." In *Plant-Bacteria Interactions: Strategies and Techniques to Promote Plant Growth* (2008): 1–17. John Wiley & Sons.
8. Bataineh, Z. M., Heidger, P. M., Thompson, S. A., & Timms, B. G. "Immunocytochemical localization of metallothionein in the rat prostate gland." *The Prostate* 9 (1986): 397–410.
9. Biswas, J. K., Mondal, M., Rinklebe, J., Sarkar, S. K., Chaudhuri, P., Rai, M., Shaheen, S. M., Song, H., & Rizwan, M. "Multi-metal resistance and plant growth promotion potential of a wastewater bacterium *Pseudomonas aeruginosa* and its synergistic benefits." *Environmental Geochemistry and Health* 39 (2017): 1583–1593.
10. Çakmakçı, R., Erat, M., Erdogan, Ü., & Dönmez, M. F. "The influence of plant growth-promoting rhizobacteria on growth and enzyme activities in wheat and spinach plants." *Journal of Plant Nutrition and Soil Science* 170 (2007): 288–295.
11. Chen, B., Luo, S., Wu, Y., Ye, J., Wang, Q., Xu, X., Pan, F., Khan, K. Y., Feng, Y., & Yang, X. "The effects of the endophytic bacterium *Pseudomonas fluorescens* Sasm05 and IAA on the plant growth and cadmium uptake of *Sedum alfredii* Hance." *Frontiers in Microbiology* 8 (2017): 2538.

12. Chen, H.-C., Zhang, S.-L., Wu, K.-J., Li, R., He, X.-R., He, D.-N., Huang, C., & Wei, H. "The effects of exogenous organic acids on the growth, photosynthesis and cellular ultrastructure of *Salix variegata* Franch. under Cd stress." *Ecotoxicology and Environmental Safety* 187 (2020): 109790.
13. Chen, J., Liu, Y.-Q., Yan, X.-W., Wei, G.-H., Zhang, J.-H., & Fang, L.-C. "Rhizobium inoculation enhances copper tolerance by affecting copper uptake and regulating the ascorbate–glutathione cycle and phytochelatins biosynthesis-related gene expression in *Medicago sativa* seedlings." *Ecotoxicology and Environmental Safety* 162 (2018): 312–323.
14. Danish, S., Kiran, S., Fahad, S., Ahmad, N., Ali, M. A., Tahir, F. A., Rasheed, M. K., Shahzad, K., Li, X., & Wang, D. "Alleviation of chromium toxicity in maize by Fe fortification and chromium-tolerant ACC deaminase-producing plant growth-promoting rhizobacteria." *Ecotoxicology and Environment* 185 (2019): 109706.
15. De Zutter, N., Ameye, M., Debode, J., De Tender, C., Ommeslag, S., Verwaeren, J., Vermeir, P., Audenaert, K., & De Gelder, L. "Shifts in the rhizobiome during consecutive *in planta* enrichment for phosphate-solubilizing bacteria differentially affect maize P status." *Microbial Biotechnology* 14 (2021): 1594–1612.
16. Dhiman, V. K., Rana, N., Pandey, H., Verma, P., & Singh, D. "Effect of rhizobial isolates and nitrogen fertilizers on nursery performance, nodulation behavior and nitrogenase activity of *Dalbergia sissoo* Roxb. seedlings." *Plant Stress* 4 (2022): 100080.
17. Di Francesco, A., & Baraldi, E. "How siderophore production can influence the biocontrol activity of *Aureobasidium pullulans* against *Monilinia laxa* on peaches." *Biological Control* 152 (2021): 104456.
18. Du, M., Spalding, E. P., & Gray, W. M. "Rapid auxin-mediated cell expansion." *Annual Review of Plant Biology* 71 (2020): 379–402.
19. Farid, M., Ali, S., Saeed, R., Rizwan, M., Bukhari, S. A. H., Abbasi, G. H., Hussain, A., Ali, B., Zamir, M. S. I., & Ahmad, I. "Application of citric acid and 5-aminolevulinic acid improved biomass, photosynthesis and gas exchange attributes of sunflower (*Helianthus annuus* L.) grown on chromium-contaminated soil." *International Journal of Phytoremediation* 21 (2019): 760–767.
20. Guo, J., & Chi, J. "Effect of Cd-tolerant plant growth-promoting rhizobium on plant growth and Cd uptake by *Lolium multiflorum* Lam. and *Glycine max* (L.) Merr. in Cd-contaminated soil." *Plant and Soil* 375 (2014): 205–214.
21. Gupta, P., Kumar, V., Usmani, Z., Rani, R., & Chandra, A. "Phosphate solubilization and chromium (VI) remediation potential of *Klebsiella* sp. strain CPSB4 isolated from chromium-contaminated agricultural soil." *Chemosphere* 192 (2018): 318–327.
22. Gupta, P., Rani, R., Chandra, A., & Kumar, V. "Potential applications of *Pseudomonas* sp. (strain CPSB21) to ameliorate Cr⁶⁺ stress and phytoremediation of tannery effluent-contaminated agricultural soils." *Scientific Reports* 8 (2018): 4860.
23. Gururani, M. A., Upadhyaya, C. P., Baskar, V., Venkatesh, J., Nookaraju, A., & Park, S. W. "Plant growth-promoting rhizobacteria enhance abiotic stress tolerance in *Solanum tuberosum* through inducing changes in the expression of ROS-scavenging enzymes and improved photosynthetic performance." *Journal of Plant Growth Regulation* 32 (2013): 245–258.
24. Hansda, A., & Kumar, V. "Cu-resistant *Kocuria* sp. CRB15: A potential PGPR isolated from the dry tailing of Rakha copper mine." *3 Biotech* 7 (2017): 132.
25. Hao, X. "Phytoremediation of heavy and transition metals aided by legume–rhizobia symbiosis." *International Journal of Phytoremediation* 16 (2014): 179–202.
26. Hartmann, A. "A pioneer in rhizosphere microbial ecology and soil bacteriology research." *Plant and Soil* 312 (2008): 7–14.
27. Hassan, W., Bashir, S., Ali, F., Ijaz, M., Hussain, M., & David, J. "Role of ACC-deaminase and/or nitrogen-fixing rhizobacteria in growth promotion of wheat (*Triticum aestivum* L.) under cadmium pollution." *Environmental Earth Sciences* 75 (2016): 267.
28. He, C. Q., Tan, G., Liang, X., Du, W., Chen, Y., Zhi, G., & Zhu, Y. "Effect of Zn-tolerant bacterial strains on growth and Zn accumulation in *Orychophragmus violaceus*." *Applied Soil Ecology* 44 (2010): 1–5.
29. Hodge, A., Robinson, D., & Fitter, A. "Are microorganisms more effective than plants at competing for nitrogen?" *Trends in Plant Science* 5 (2000): 304–308.
30. Hou, D. "Sustainable remediation in China: Elimination, immobilization, or dilution." *Environmental Science & Technology* 55 (2021): 15572–15574.

31. Huo, Y., Kang, J. P., Ahn, J. C., Kim, Y. J., Piao, C. H., Yang, D. U., & Yang, D. C. "Siderophore-producing rhizobacteria reduce heavy metal-induced oxidative stress in *Panax ginseng* Meyer." *Journal of Ginseng Research* 45 (2021): 218–227.
32. Hussain, I., Afzal, S., Ashraf, M. A., Rasheed, R., Saleem, M. H., Alatawi, A., Ameen, F., & Fahad, S. "Effect of metals or trace elements on wheat growth and its remediation in contaminated soil." *Journal of Plant Growth Regulation* 42 (2022): 2258–2282.
33. Jha, C. K., & Saraf, M. "Plant growth promoting rhizobacteria (PGPR): A review." *Journal of Agricultural Research and Development* 5 (2015): 108–119.
34. Jian, L., Bai, X., Zhang, H., Song, X., & Li, Z. "Promotion of growth and metal accumulation of alfalfa by coinoculation with *Sinorhizobium* and *Agrobacterium* under copper and zinc stress." *PeerJ* 7 (2019): e6875.
35. Jin, Z., Li, J., Ni, L., Zhang, R., Xia, A., & Jin, F. "Conditional privatization of a public siderophore enables *Pseudomonas aeruginosa* to resist cheater invasion." *Nature Communications* 9 (2018): 1383.
36. Jorquera, M. A., Maruyama, F., Ogram, A. V., Navarrete, O. U., Lagos, L. M., Inostroza, N. G., Acuña, J. J., Rilling, J. I., & de la Luz Mora, M. "Rhizobacterial community structures associated with native plants grown in Chilean extreme environments." *Microbial Ecology* 72 (2016): 633–646.
37. Ju, W., Liu, L., Jin, X., Duan, C., & Fang, L. "Co-inoculation effect of plant growth-promoting rhizobacteria and rhizobium on EDDS-assisted phytoremediation of Cu-contaminated soils." *Chemosphere* 254 (2020): 126724.
38. Juwarkar, A. A., Nair, A., Dubey, K. V., Singh, S., & Devotta, S. "Biosurfactant technology for remediation of cadmium and lead contaminated soils." *Chemosphere* 68 (2007): 1996–2002.
39. Kamal, N., Liu, Z., Qian, C., Wu, J., & Zhong, X. "Improving hybrid *Pennisetum* growth and cadmium phytoremediation potential by using *Bacillus megaterium* BM18-2 spores as biofertilizer." *Microbiology Research* 242 (2021): 126594.
40. Khan, W. U., Yasin, N. A., Ahmad, S. R., Ali, A., Ahmed, S., & Ahmad, A. "Role of Ni-tolerant *Bacillus* sp. and *Althea rosea* L. in the phytoremediation of Ni-contaminated soils." *International Journal of Phytoremediation* 19 (2017): 470–477.
41. Khanna, K., Jamwal, V. L., Sharma, A., Gandhi, S. G., Ohri, P., Bhardwaj, R., Al-Huqail, A. A., Siddiqui, M. H., Ali, H. M., & Ahmad, P. "Supplementation with plant growth-promoting rhizobacteria (PGPR) alleviates cadmium toxicity in *Solanum lycopersicum* by modulating the expression of secondary metabolites." *Chemosphere* 230 (2019): 628–639.
42. Kieber, J. J., & Schaller, G. E. "Cytokinin signaling in plant development." *Development* 145 (2018): dev149344.
43. Kloepper, J. W. "Plant growth-promoting rhizobacteria on radishes." In *Proceedings of the 4th International Conference on Plant Pathogenic Bacteria* (1987): 879–882. INRA, Angers, France.
44. Leong, Y. K., & Chang, J.-S. "Bioremediation of heavy metals using microalgae: Recent advances and mechanisms." *Bioresource Technology* 303 (2020): 122886.
45. Li, S. M., Zheng, H. X., Zhang, X. S., & Sui, N. "Cytokinins as central regulators during plant growth and stress response." *Plant Cell Reports* 40 (2020): 271–282.
46. Liang, Y., Xiao, X., Guo, Z., Peng, C., Zeng, P., & Wang, X. "Co-application of indole-3-acetic acid/gibberellin and oxalic acid for phytoextraction of cadmium and lead with *Sedum alfredii* Hance from contaminated soil." *Chemosphere* 285 (2021): 131420.
47. Liu, A., Wang, W., Zheng, X., Chen, X., Fu, W., Wang, G., Ji, J., Jin, C., & Guan, C. "Improvement of the Cd and Zn phytoremediation efficiency of rice (*Oryza sativa*) through the inoculation of a metal-resistant PGPR strain." *Chemosphere* 302 (2022): 134900.
48. van Loon, L. C., Bakker, P. A. H. M., & Pieterse, C. M. J. "Systemic resistance induced by rhizosphere bacteria." *Annual Review of Phytopathology* 36 (1998): 453–483.
49. Lu, Y.-Z., Chen, G.-J., Bai, Y.-N., Fu, L., Qin, L.-P., & Zeng, R. J. "Chromium isotope fractionation during Cr(VI) reduction in a methane-based hollow-fiber membrane biofilm reactor." *Water Research* 130 (2018): 263–270.
50. Ma, Y., Oliveira, R. S., Freitas, H., & Zhang, C. "Biochemical and molecular mechanisms of plant-microbe-metal interactions: Relevance for phytoremediation." *Frontiers in Plant Science* 7 (2016): 918.
51. Ma, Y., Rajkumar, M., Rocha, I., Oliveira, R. S., & Freitas, H. "Serpentine bacteria influence metal translocation and bioconcentration of *Brassica juncea* and *Ricinus communis* grown in multi-metal polluted soils." *Frontiers in Plant Science* 5 (2015): 757.

52. Ma, Y., Rajkumar, M., Zhang, C., & Freitas, H. "Inoculation of *Brassica oxyrrhina* with plant growth-promoting bacteria for the improvement of heavy metal phytoremediation under drought conditions." *Journal of Hazardous Materials* 320 (2016): 36–44.
53. Manoj, S. R., Karthik, C., Kadirvelu, K., Arulselvi, I., & Rajkumar, M. "Understanding the molecular mechanisms for the enhanced phytoremediation of heavy metals through plant growth-promoting rhizobacteria: A review." *Journal of Environmental Management* 254 (2020): 109779.
54. Massoud, M. B., Sakouhi, L., Karmous, I., Zhu, Y., El Ferjani, E., Sheehan, D., & Chaoui, A. "Protective role of exogenous phytohormones on redox status in pea seedlings under copper stress." *Journal of Plant Physiology* 221 (2018): 51–61.
55. Mehta, P., Sharma, R., Putatunda, C., & Walia, A. "Endophytic fungi: Role in phosphate solubilization." In *Advances in Endophytic Fungal Research: Present Status and Future Challenges* (2019): 183–209. Springer International Publishing.
56. Miller, G., Suzuki, N., Ciftci-Yilmaz, S., & Mittler, R. "Reactive oxygen species homeostasis and signaling during drought and salinity stresses." *Plant, Cell & Environment* 33 (2010): 453–467.
57. Misra, S., & Chauhan, P. S. "ACC deaminase-producing rhizosphere-competent *Bacillus* sp. mitigate salt stress and promote *Zea mays* growth by modulating ethylene metabolism." *3 Biotech* 10 (2020): 119.
58. Mitra, S., Pramanik, K., Ghosh, P. K., Soren, T., Sarkar, A., Dey, R. S., Pandey, S., & Maiti, T. K. "Characterization of Cd-resistant *Klebsiella michiganensis* MCC3089 and its potential for rice seedling growth promotion under Cd stress." *Microbiological Research* 210 (2018): 12–25.
59. Mousavi, S. M., Motesharezadeh, B., Hosseini, H. M., Alikhani, H., & Zolfaghari, A. A. "Root-induced changes of Zn and Pb dynamics in the rhizosphere of sunflower with different plant growth-promoting treatments in a heavily contaminated soil." *Ecotoxicology and Environmental Safety* 147 (2017): 206.
60. Mus, F., Crook, M. B., Garcia, K., Costas, A. G., & Peters, J. W. "Symbiotic nitrogen fixation and challenges to extending it to non-legumes." *Applied and Environmental Microbiology* 82 (2016): 3698–3710.
61. Nagel, R., Bieber, J. E., Schmidt-Dannert, M. G., Nett, R. S., & Peters, R. J. "A third class: Functional gibberellin biosynthetic operon in beta-proteobacteria." *Frontiers in Microbiology* 9 (2018): 423.
62. Olenska, E., Małek, W., Wójcik, M., Świecicka, I., Thijs, S., & Vangronsveld, J. "Beneficial features of plant growth-promoting rhizobacteria for improving plant growth and health in challenging conditions: A methodical review." *Science of the Total Environment* 743 (2020): 140682.
63. Padhan, D., Rout, P. P., Kundu, R., Adhikary, S., & Padhi, P. P. "Bioremediation of heavy metals and other toxic substances by microorganisms." In *Soil Bioremediation: An Approach towards Sustainable Technology* (2021): 285–329. John Wiley & Sons.
64. Pandey, N., & Bhatt, R. "Role of soil-associated *Exiguobacterium* in reducing arsenic toxicity and promoting plant growth in *Vigna radiata*." *European Journal of Soil Biology* 75 (2016): 142–150.
65. Pandey, S., Ghosh, P. K., Ghosh, S., De, T. K., & Maiti, T. K. "Role of heavy metal-resistant *Ochrobactrum* sp. and *Bacillus* sp. strains in bioremediation of a rice cultivar and their PGPR-like activities." *Journal of Microbiology* 51 (2013): 11–17.
66. Pantoja-Guerra, M., Valero-Valero, N., & Ramírez, C. A. "Total auxin level in the soil–plant system as a modulating factor for the effectiveness of PGPR inocula: A review." *Chemical and Biological Technologies in Agriculture* 10 (2023): 6.
67. Pattyn, J., Vaughan-Hirsch, J., & Van de Poel, B. "The regulation of ethylene biosynthesis: A complex multilevel control circuitry." *New Phytologist* 229 (2021): 770–782.
68. Piotrowska-Niczyporuk, A., Bajguz, A., Zambrzycka-Szelewa, E., & Bralska, M. "Exogenously applied auxins and cytokinins ameliorate lead toxicity by inducing antioxidant defence system in green alga *Acutodesmus obliquus*." *Plant Physiology and Biochemistry* 132 (2018): 535–546.
69. Prapagdee, B., Chanprasert, M., & Mongkolsuk, S. "Bioaugmentation with cadmium-resistant plant growth-promoting rhizobacteria to assist cadmium phytoextraction by *Helianthus annuus*." *Chemosphere* 92 (2013): 659–666.
70. Prapagdee, B., Chanprasert, M., & Mongkolsuk, S. "Effects of plant growth-promoting bacteria on EDTA-assisted phytostabilization of heavy metals in a contaminated calcareous soil." *Environmental Geochemistry and Health* 42 (2020): 2535–2545.
71. Saha, M., Sarkar, S., Sarkar, B., Sharma, B. K., Bhattacharjee, S., & Tribedi, P. "Microbial siderophores and their potential applications: A review." *Environmental Science and Pollution Research* 23 (2016): 3984–3999.

72. Samreen, T., Zahir, Z. A., Naveed, M., & Asghar, M. "Boron-tolerant phosphorus-solubilizing *Bacillus* sp. MN-54 improved canola growth in alkaline calcareous soils." *International Journal of Agriculture and Biology* 21 (2019): 538–546.
73. Schmidt, W. "Iron solutions: Acquisition strategies and signaling pathways in plants." *Trends in Plant Science* 28 (2023): 188–193.
74. Shen, S., Li, Y., Chen, M., Huang, J., Liu, F., Xie, S., Kong, L., & Pan, Y. "Reduced cadmium toxicity in rapeseed via alteration of root properties and accelerated plant growth by a nitrogen-fixing bacterium." *Journal of Hazardous Materials* 449 (2023): 131040.
75. Si, M., & Lang, J. "The roles of metallothioneins in carcinogenesis." *Journal of Hematology & Oncology* 11 (2018): 1–20.
76. Sobariu, D. L., Fertu, D. I. T., Diaconu, M., Pavel, L. V., Hlihor, R.-M., Drăgoi, E. N., Curteanu, S., Lenz, M., Corvini, P. F.-X., & Gavrilescu, M. "Rhizobacteria and plant symbiosis in heavy metal uptake and its implications for soil bioremediation." *New Biotechnology* 39 (2017): 125–134.
77. Tahir, H. A., Wu, H., Wu, L., & Gao, X. "Plant growth promotion by volatile organic compounds produced by *Bacillus subtilis* SYST2." *Frontiers in Microbiology* 8 (2017): 2360.
78. Tank, N., & Saraf, M. "Enhancement of plant growth and decontamination of nickel-spiked soil using PGPR." *Journal of Basic Microbiology* 49 (2009): 195–204.
79. Vaverková, M. D. "Environmental consequences and the role of illegal waste dumps and their impact on land degradation." *Land Use Policy* 89 (2019): 104234.
80. Vimalnath, S., & Subramanian, S. "Studies on the biosorption of Pb(II) ions from aqueous solution using extracellular polymeric substances (EPS) of *Pseudomonas aeruginosa*." *Colloids and Surfaces B: Biointerfaces* 172 (2018): 60–67.
81. Wagner, S. C. "Biological nitrogen fixation." *Nature Education Knowledge* 3 (2011): 15.
82. Wang, J., Zhang, Y., Jin, J., Li, Q., Zhao, C., Nan, W., Wang, X., Ma, R., & Bi, Y. "An intact cytokinin-signaling pathway is required for *Bacillus* sp. LZR216-promoted plant growth and root system architecture alteration in *Arabidopsis thaliana* seedlings." *Plant Growth Regulation* 84 (2018): 507–518.
83. Wang, T., Wang, S., Tang, X., Fan, X., Yang, S., Yao, L., Li, Y., & Han, H. "Isolation of urease-producing bacteria and their effects on reducing Cd and Pb accumulation in lettuce (*Lactuca sativa* L.)." *Environmental Science and Pollution Research* 27 (2020): 8707–8718.
84. Wu, J., Kamal, N., Hao, H., Qian, C., Liu, Z., Shao, Y., Zhong, X., & Xu, B. "Endophytic *Bacillus megaterium* BM18-2 mutated for cadmium accumulation and improving plant growth in hybrid *Pennisetum*." *Biotechnology Reports* 24 (2019): e00374.
85. Yang, P., Zhou, X.-F., Wang, L.-L., Li, Q.-S., Zhou, T., Chen, Y.-K., Zhao, Z.-Y., & He, B.-Y. "Effect of phosphate-solubilizing bacteria on the mobility of insoluble cadmium and metabolic analysis." *International Journal of Environmental Research and Public Health* 15 (2018): 1330.
86. Yu, G., Liu, J., Long, Y., Chen, Z., Sunahara, G. I., Jiang, P., You, S., Lin, H., & Xiao, H. "Phytoextraction of cadmium-contaminated soils: Comparison of plant species and low molecular weight organic acids." *International Journal of Phytoremediation* 22 (2020): 383–391.
87. Yu, S., Zehra, A., Sahito, Z. A., Wang, W., Chen, S., Feng, Y., He, Z., & Yang, X. "Cytokinin-mediated shoot proliferation and its correlation with phytoremediation effects in Cd-hyperaccumulator ecotype of *Sedum alfredii*." *Science of the Total Environment* 912 (2024): 168993.
88. Zayed, A., & Terry, N. "Accumulation and volatilization of different chemical species of selenium by plants." *Planta* 206 (1988): 284–292.
89. Zhang, Q., & Wang, C. "Natural and human factors affect the distribution of soil heavy metal pollution: A review." *Water, Air, & Soil Pollution* 231 (2020): 350.

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