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Plant Growth-Promoting Bacteria (PGPB): A Potent Source of Heavy Metal Stress Management in Plants

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Abstract

Heavy metals or metalloids are toxic elements found throughout the crust of the earth's surface. The gradual increase of heavy metal concentration in soil and water due to some natural and anthropogenic activities like application of agrochemicals, waste disposal, industrial activities, mining, smelting, lead-based paints, etc cause stress to the local vegetation. Soil microorganisms play a critical part in the remediation of heavy metal contaminated soil and thereby exert direct or indirect promotion to plant growth. Plant growth-promoting bacteria (PGPB), specially the Plant growth-promoting rhizobacteria (PGPR), are a natural, sustainable, and eco-friendly solution for mitigating stress challenges. They can boost plant growth by alleviating heavy metal toxicity through various mechanisms such as metal sequestration, metal immobilization, and production of metal chelating compounds, which reduce metal toxicity and enhance plant growth. This review summarizes the effect of heavy metal stress on plants, the response of plants to heavy metal stress, mechanisms involved in metal stress tolerance by soil bacteria, and their application in managing heavy metal stress in plants.

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Introduction

Heavy metals (HMs) are naturally occurring toxic elements widely distributed in the environment. Due to some anthropogenic activities, the concentration of the HMs on the earth's surface is increasing gradually, sometimes crossing the normal limits, causing remarkable harm to the environment.[1] Heavy metals, after entering the soil, their persistence become a long-term threat to soil microbiota and vegetation, resulting in ecosystem malfunction. HMs in the soil may be present due to natural processes or anthropogenic activities. In natural processes, HMs in soil are derived from soil parent materials such as metal-enriched rocks, serpentine, and black shale, etc. The anthropogenic sources of heavy metals tend to be more mobile than the

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natural lithogenic sources.[2] Mining, smelting, sewage & sludge supplementation (biosolids), application of agrochemicals and lead-based paints, leaded petrochemicals, etc. are the major anthropogenic sources of HM in the soil.[3]

Pb, Ni, Hg, Cr, Cu, As, Cd, Zn, etc. are the most common heavy metals responsible for contamination of agricultural soil.[3] In spite of their essence being in trace amounts, some HMs are poisonous to the living system at their higher concentrations. Others may be toxic in lesser amounts also. The level of HMs in the soil beyond certain limits exhibits toxic effects on plants and human health.[4] In addition to contamination of food chains, absorption of HMs by plants results in chlorosis, inhibition of growth and photosynthesis, low biomass accumulation, altered water balance, etc., and at greater quantities, it leads to the death of the plant.[5] Heavy metals, when they reach the water bodies, their removal by natural processes becomes very difficult and time consuming. In such cases, it may stimulate the ROS (Reactive Oxygen Species) formation causing remarkable damage to aquatic organisms.[6]

Microorganisms in the soil play a pivotal role in preserving soil fertility and plant productivity. PGPB holds a key position in this environment by promoting plant growth through fixing nitrogen, controlling detrimental microorganisms, enhancing soil nutrients, and helping plants cope with various stresses in both natural ecosystems and agriculture. The rhizosphere, where plants and microorganisms interact, is a dynamic ecosystem with a diverse array of impacts on both the partners. PGPR are a group of PGPB that colonize specially the rhizosphere and augment plant growth and development via multiple pathways, including mitigation of HM stress. The ability of various PGPB species to support heavy metal cleaning, and enhance crop performance under abiotic stress has been discovered. Numerous PGPB have shown the potential to bioremediate heavy metals from contaminated soils, including *Mesorhizobium* sp., *Burkholderia phytofirmans*, *Variovorax paradoxus*, *Bacillus pumilus*, *Azotobacter* spp., *P. libanensis*, and *P. reactants.*[7] Due to their biological characteristics, PGPB may develop a tolerance to HMs or use direct detoxification, leading to resistance. The presence of *Bacillus thuringiensis*, for example, boosted the efficiency of the *Alnus firma* in removing metals like Zn, Cd, As, Cu, Pb, and Ni, or reduced their harmful effects by accumulating these metals in the seedlings of this plant.[8] PGPB have an excellent potential to promote plant growth via different pathways, including the synthesis of plant growth regulators (IAA, GA3), production of ACC Deaminase, solubilisation of minerals (N, P) etc. For instance *Cellulosimicrobium* sp., with various plant growth promoting traits enhanced growth of Alfalfa under metal stress condition.[9] The elevated concentration of HM in the ecosystem significantly affects the microbial communities.[10] Many bacteria die due to exposure to these contaminants, despite the fact that some microbes, like PGPB, have evolved numerous defense mechanisms against the toxicity of HMs. Thus, PGPB, when used as biofertilizers, helps enhance the growth of plants grown in HM-contaminated soil.[11] The present review aims to study the responses of plants to HM stress, mechanisms adopted by microbes to overcome HM stress, and management of HM stress by using PGPB for sustainable agriculture.

Materials and Methods

This paper uses academic databases, libraries, and online resources to gather relevant research articles, reviews, and other scholarly materials related to microbes' heavy metal stress management mechanisms and their role in managing HM stress in plants, mostly from 2010 onwards. Critical analysis of the responses of PGPB and plants to HM, mechanisms responsible for managing HM stress in plants and microbes, and application of PGPB in managing heavy metal stress are the key points selected for this article.

Responses of Plants to Heavy Metal Stress

Plants have different defense mechanisms that are activated during stress conditions; they also maintain the critical metal homeostasis required by plants.[12] The responses of plants to the toxicity of different HMs vary from species to species. HMs such as Pb, As, Hg, Cd, Cr, etc encountered in contaminated soil are toxic in both chemically combined and elemental forms.[13] The first line of defense of plants against toxicity is to minimize metal uptake when toxicity is encountered. This is performed with the aid of cellular and root exudates, that can change the pH of the rhizosphere.[12] As a second line of defense, plants use various molecular and physiological systems, including separation, chelating metal production, accumulation, exclusion, and manufacture of osmoprotectants, etc.[14] HMs are chelated and sequestered by compounds such as phytochelatins, metallothioneins, and antioxidants such as superoxide dismutase (SOD) and peroxidase in the cytosol.[15]

To survive under stress conditions, complicated signal transduction processes are activated within the plant cell. These signaling pathways help to induce the transcription of various metal stress-responsive genes. For instance, signaling pathways of hormone and ROS, MAPK (Mitogen-activated protein kinase) cascade, and Ca–Calmodulin pathway, etc. are activated in response to different metal stresses.[12] In the Ca-Calmodulin pathway, Ca acts as a second messenger, eliciting responses to diverse biotic and abiotic stress signals. These signals initiate downstream events that lead to a change in gene expression like ABA (Abscisic acid)-responsive genes, MIR genes, metal transporters, etc., and the adaptation of plants to stress tolerance. In response to HM stress, NO (Nitric Oxide) is known to be associated with raising the level of Ca^{2+}, which in turn regulates the elevation/ control of NO concentration, along with elicitation of specific physiological responses to a given signal, thus having a combined function in HM or abiotic stress regulatio.[16] Nitric oxide is a very effective and widely used signaling molecule responsible for reducing oxidative stress as it participates in the breakdown of oxygen radicals to hydrogen peroxide and oxygen, and it might also serve as a signal that stimulates the activities of ROS-scavenging enzyme under abiotic stress. Nitric oxide can detoxify the free radicals in the cell as it is itself an antioxidant and also promotes the synthesis of antioxidant enzymes.[17] ROS not only causes damage to DNA and the cell membrane but also serve as a vital signaling chemical that regulates plant growth and plant protection against HM. It has been reported that ROS production that is induced by heavy metals is known to activate MAPK signalling, which works downstream processing of ROS.[18]

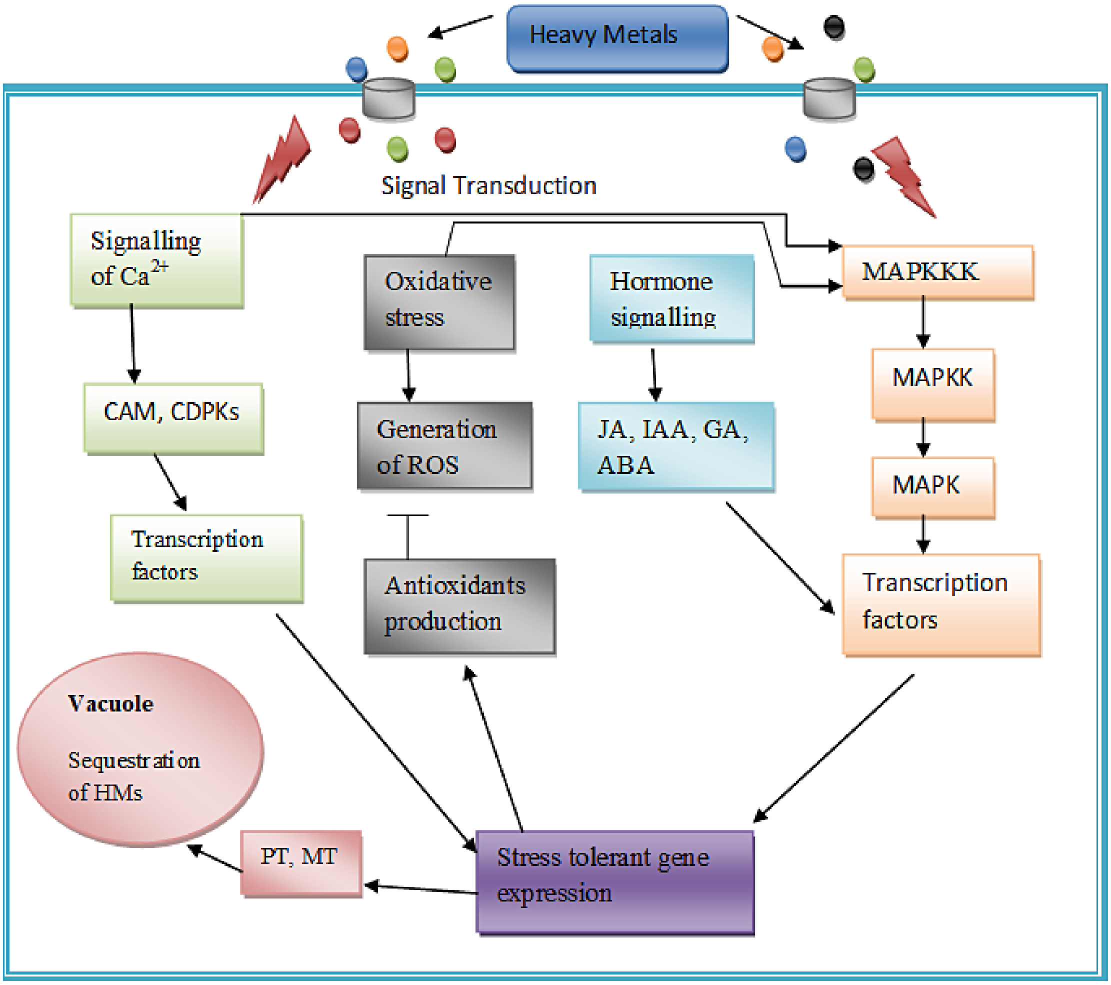
Proline, an amino acid accumulated by a plant in response to HM stress acts as an osmoprotectant, ROS quencher, and HM chelator. Proline increases the tolerance of a plant to HM stress by various mechanisms. When plants are exposed to heavy metals, the activity of proline increases antioxidant enzyme activities, reconstruction of Chlorophyll, as well as regulation of intracellular pH, etc.[19] The formation of phytochelatin that can chelate HM to decrease its toxicity is induced by Proline.[20] According to Xu *et al*. (2009) pre treatment of proline protected the plasma membrane of the callus subjected to Cd stress by reducing the level of ROS, thereby improving the Cd tolerance in *Solanum nigrum.* It has been shown that, inhibition of enzyme activity (glucose-6-phosphate dehydrogenase and nitrate reductase) caused by Cd and Zn was protected by exogenous application of proline.[20]

Various studies have shown that phytohormones play a vital role during stress. Exposure of plants to HM intensifies complicated signal transduction networks and synthesizes stress-related phytohormones.[22] Some of the plant hormones related to heavy metal contamination are Gibberellic acid (GA), Auxin (IAA), Abscisic acid (ABA), ethylene, etc. Abscisic acid is an essential phytohormone that has been linked with tolerance to adverse environmental conditions having a role in abiotic stresses. Endogenous ABA concentration in plant tissue is known to rise in response to HM exposure, which, by activating specific signaling pathways, modulates gene expression levels in plants.[15] Exogenous ABA enhances tolerance to excess Zn and increases the expression of a gene to HM detoxification. A previous experiment has shown an increase in ABA levels in the roots of *Phragmites* and *Typha* when they are treated with Cd and also noted the involvement of ABA in the activation of O-acetyl serine, which is responsible for cysteine biosynthesis[23]

IAA is reported as an important mediator for plant growth and development in both regular stressfull conditions. Auxin homeostasis within the plant may be disturbed by HM, for instance, Cd stress leads to change in auxin homeostasis in *Arabidopsis* seedlings.[23] Exogenous application of IAA alleviates HM stress while maintaining endogenous IAA homeostasis.[25] To alleviate the effect of HM toxicity in plants, auxin has been observed to cross-talk with the ROS detoxification system. As (Arsenic) toxicity in Arabidopsis, elevates the H_2O_2 content which is responsible for promoting the transportation of auxin through *AUX1*. Additionally, it causes a decrease in the transcript levels of catalase-3 *(CAT3)*. Thus the cross-talk between auxin and ROS could potentially be crucial in the mechanisms that enable tolerance to HM stress.[22,26]

Ethylene is a gaseous phytohormone that is involved in numerous biological processes such as floral senescence, abscission of leaves, ripening of fruit, etc. When the plant faces HM stresses, the rate of ethylene synthesis increases, which is associated with a decline in plant growth. In Arabidopsis, Cd induces the activation of ethylene biosynthesis genes ACS2 [1-aminocyclopropane-1-carboxylic acid (ACC) synthase] and ACS6, which leads to an increase in ethylene production via Yang's cycle. On the contrary, the acs2-1acs6-1 double knockout mutant failed to display higher ethylene production under Cd stress[15,27]

GA (Gibberellic acid) is responsible for seed germination, stem elongation, fruit development, etc. They promote plant tolerance levels to HM stress and enhance antioxidant effectiveness, thereby minimizing the toxicity of metals like Cd, Ni, Cr, and Fe, etc. Degradation of DELLA (Aspartic acid, Glutamic acid, Leucine and Alanine) a negative regulator of GA signaling protein is induced by GA. It has been noted that under Cd and Pb stress, exogenous application of GA in *Chlorella vulgaris* increased protein content and cell number.[14]



Abbreviations- PC-phytochelatins; MT-metallothion, CaM/CDPK- Calcium-dependent protein kinases,

Fig. 1: Crosstalk of several signaling pathways working during heavy metal stress that regulate expression of stress related genes.[28]

Heavy Metal Resistant Soil Microorganisms

The huge amounts of mine waste reduce the biological activity of soil microorganisms due to the discharge of HMs from the minerals by high amount of sulfuric acid. It has been observed that HM contamination affects the microbial communities both for shorter and longer durations. However, different microbial communities have varying levels of resistance to soil heavy metal toxicity.[29] Microorganisms have a vital function in the remediation of environments contaminated with HMs through the biogeochemical cycling of metals. Microbes can alter the mobility and bioavailability of HMs by releasing chelating substances (siderophores), dissolving metal phosphate, altering redox potentials, and acidifying soil.[29,30] It was established that the population and occurrence of HM-resistant bacteria increased with increasing concentrations of HM.[31] They have the ability to reduce the toxicity level of HM. Additionally, by bringing certain HMs down to a lower redox state, microorganisms can keep them out of polluted soils. These microbes are renowned as dissimilatory metal-reducing bacteria. In anaerobic respiration, they utilize metals as terminal electron acceptors in anaerobic respiration.[11] EPS (extracellular polymeric substances) are fundamental constituents of biofilms that provide support and protect the microbial communities from harsh environmental conditions. These substances potentially increase microbial resistance to HM concentrations. These are composed mainly of polysaccharides but may also include proteins, extracellular DNA, lipids, and humic substances. EPS have the capability to remove HM and emulsify hydrophobic compounds in the remediation process.[31]

Heavy Metal Resistance Mechanism of Bacteria

Tolerance of bacteria to HM stress depend upon several factors such as localization of metal resistance genes, types of metal ion transport into the cell, etc. There are five main mechanisms of HM-resistant bacteria. These are-

Extracellular Barrier

A bacterial cell's capsule, it's cell wall, and plasma membrane act as an extracellular shield to inhibit the entry of metal or metal ions into the cell. Metal ions can be absorbed by some bacteria via the ionizable cell walls or capsule groups such as phosphate, amino, carboxyl, and hydroxyl groups). Several authors have found that non-viable cells of some bacterial species, like *Bacillus* sp., *Pseudomonas putida*, and *Brevibacterium* sp., possess a significant amount of passive biosorption of HM ions.[32] The plasma membrane's altered permeability may restrict metal ions from entering the cell. Silver ion accumulation inside the cell was found to be low in *Escherichia* coli mutants that lack porins, which are membrane proteins that operate as transport channels for hydrophilic substances.[33] Gram-positive bacteria have a thick murein coating that can keep a hazardous component out of the cell. Due to the presence of mycolic acid, some specific gram-positive genera, including *Dietzia*, *Corynebacterium*, *Rhodococcus, Nocardia, Tsukamurell*, and *Skermania,* are incredibly resistant to poisonous substances.[34]

Active Transport of Metal Ions

Efflux pump system or active transport corresponds to protein-rich transport and is represented as the largest group of HM resistance systems of bacteria. They exploit this mechanism to decrease the accumulation potential and concentration of cellular detoxification. Some metal ions are transported inside the cell via a system liable for the absorption of vital components. Previous studies have shown that Cd, Co, Zn, etc. enter the cell via the Mg transport system of *Alcaligenes eutrophus.*[33]

Efflux systems containing proteins are afflicted into five major families, comprising the major facilitator superfamily, the small multidrug resistance family included in the larger drug/metabolite transporter superfamily, the RND family (Resistance, Nodulation, division), the multidrug and toxic compound extrusion family, and the ATP-binding cassette superfamily.[36] These efflux pumps are energy-dependent as they transport substrates against the concentration gradient. They draw energy from ATP hydrolysis or from chemical gradients. ABC transporters play a significant role in nutrient uptake and in the expulsion of harmful substances from the cell, and are considered as an important virulence factor, they also secrete peptides, lipids, hydrophobic drugs, etc.[37] P-type ATPase and CDF (cation diffusion facilitators) proteins are involved in bacterial immunity.[34,37] P-type ATPase mainly transfers metal ions with high affinity, while CDF-proteins specifically interact with divalent metal ions.

Metal-efflux is a mechanism by which membrane-bound CDF proteins contribute to bacterial metal tolerance. The RND protein family has tripartite organizations that transport HMs, proteins, and other substances from the periplasm across the plasma membrane[37,38]

Extracellular Sequestration

Extracellular sequestration describes the complexation of metal ions into insoluble compounds or the accumulation of metal ions by cellular components in the periplasm or the cell's outer membrane.[32] This process involves the secretion of chelating agents like phosphate, siderophores, sulfide, oxalate etc.[38] Copper-resistant strains *Pseudomonas syringae* synthesize membrane proteins such as CopA, CopB, and CopC that can bind to copper ions as an outcome of metal accumulation. Studies have shown that the accumulation of copper by a resistant strain was in a complex form, whereas the accumulation of copper done by a sensitive strain in a free ionic form is highly hazardous to the cell.[33]

Intracellular Sequestration

Intracellular sequestration refers to the complexation of metal ions by various compounds in the cytoplasm of a cell. As a result of association with ligands on the surface followed by sluggish transport, the metal concentration of the cell could rise. Through the influx mechanism, HM detoxification by bacterial cells is developed, and metallothioneins sequester it intracellularly.[37] The cyanobacterium *Synechococcus* sp. PCC 7942 has provided evidence that prokaryotic cells can synthesize metallothionein and is encoded by the genes *smtA* and *smtB*, which are triggered by cadmium and zinc ions.[40] With the aid of cysteine-rich proteins, the cadmium-tolerant strain *Pseudomonus putida* is able to sequester Cu, Cd, and Zn ions inside its cells. In *Rhizobium leguminosarum* cells, glutathione was found to intracellularly sequester Cd ions.[41]

Reduction of Metal Ions

By changing the oxidation states of metal ions, microbial organisms can lessen their noxiousness. Some bacteria produce energy by using metallic elements and metalloids as electron donors or acceptors. During bacterial anaerobic respiration, oxidized metals might behave as terminal acceptors of electrons.[32,33] Enzymatic metal ion reduction could lead to the creation of less hazardous forms of chromium and mercury. For instance, some *Bacillus* sp can reduce the toxicity level of Pb by transforming it from $Pb(NO_3)$ to a less toxic PbS form.[37] Reduction or biotransformation of toxic Cd to Cds by *Pseudomonas aeruginosa* provided an eco-friendly circumvention for toxicity removal, as reported by Mahle *et al*., (2020).

HM Resistance Genes in Bacteria

The mechanisms applied by microbes in response to HM stress are encoded by genes present in chromosomes and on plasmids. Several Metal Resistance Genes (MRG) are reported in bacterial communities from wide habitats.[44] Abou-Shanab *et al*., (2007) isolated forty-five bacteria from Ni-rich soil and analyzed several metal-resistant genes present in those bacteria, specifically five cultures such as *Rhizobium mongolense*, *Arthrobacter rhombi*, *Clavibacter xyli, Variovorax paradoxus*, and *Microbacterium arabinogalactanolyticum* were tolerant to nine different metals. They found that *ncc, czc, chr,* and *mer* genes are responsible for resistance to Cr, Ni, Zn, and Hg by using different molecular techniques such as PCR, RFLP, and DNA-DNA hybridization. According to Abdelatey *et al*., (2011) both gram-positive and gram-negative bacteria, including *Staphylococcus aureus*, *Bacillus subtilis, Bacillus cereus, Pseudomonas* sp., and *Bordetella* sp., showed metal tolerance against Cd^{2+} and Co^{2+}. The MRGs such as c*hr, czc, mer*, and *ncc* were shown to be present in these bacteria by using the semi-quantitative reverse transcription-PCR. Previously, *Pseudomonas putida* was isolated from sewage sludge samples, which were found to be resistant to Cd. The MRG involved in tolerance to Cd came from three gene clusters such as *czc*CBA1, *cad*A2R, and *col*RS.[47] Some more Gram-negative bacteria, like *Pseudomonas aeruginosa* and *Cupriavidus metallidurans* have the ability to tolerate Cd, and the *czc*ABC gene is responsible for (cobalt/zinc/cadmium) resistance. The *czc* gene cluster identified in *Alcaligenes eutrophus* was plasmid-encoded, whereas the homologous gene cluster (*czc*) called *czr* identified in *Pseudomonas aeruginosa* was chromosomal coded and resistant to Cd, Zn, and Co.[48]

Table 1: Use of PGPB in heavy metal detoxification and its role in alleviation of plant HM stress

Heavy metal	PGPB strain	Host plant	Main PGP trait	Effects	Reference
Cu, Cd, Pb and Zn	*Alcaligenes faecalis* MG257493.1, *Bacillus cereus* MG257494.1 and *Alcaligenes faecalis* MG966440.1	*Sorghum bicolor,* L.	Siderophores, Chelating agents, EPS	Increased plant height, photosynthetic pigments and enhanced plant growth.	62
Cr	*Myroides odoratimimus* TCR22, *B. cereus* TCR17, *Providencia rettgeri* TCR21,	*Sorghum bicolour*	IAA, siderophores.	Stimulated plant growth, increased pigment contents, protein, antioxidant (Superoxide Dismutase, Catalase).	63
Zn	*Serratia* sp. ZTB	*Zea mays*	IAA, siderophores, ACCD, and solubilisation of phosphate(P) and potassium(K)	Enhanced plan growth, improved antioxidant enzyme activities. Under Zn stress, accumulation of Zn was reduced in maize plantlet.	64
Cd	*B. contaminans*	*Glycine max*	P-solubilization, ACCD, siderophores, and IAA	Increased nitrogen content and plant tolerance to Cd, promoted plant dry biomass.	65
Cd	*P. fluorescens*	*Sedum alfredii*	IAA	promoted a lateral root formation of its host plant, efficiency of higher Cd phytoremediation.	66
Zn, Al and Pb	*Halobacillus* sp. SB2, *Bacillus* sp. SB1	*Arachis hypogaea*	N_2-fixation, P solubilisation	It had a positive impact on different plant physiological processes.	67
Ni	*Psychrobacter* sp., *Bacillus* cereus SRA10, *Bacillus weihenstephanensis* SRP12	*B. juncea, B. Oxyrrhina*	Siderophore, ACCD, IAA, P- solubilisation	Directly improves phytoextraction efficiency by increasing metal accumulation in plant tissues.	68
Cu, Cd, Pb	*Ochrobactrum cytisi, Bradyrhizobium sp.* 750,	*Lupinus luteus*	N_2 fixation	Boost plant yield and N-content, and lower plant metal accumulation.	69
Mn	*B. thuringiensis, B. cereus*	*Broussonetia papyrifera*	Siderophores IAA, and P solubilization,	Enhanced biomass, increased total length of root, surface area	70

				of the plant and also improved soil environment.	
Co, Cd, Cu, Cr, Ni, Zn	*B. vietnamensis* AB403, *Kocuria flava* AB402	*O. sativa*	EPS, IAA, siderophores	increased rice seedlings growth in As-amended hyper saline soil.	71
Cd, Zn	*Rhodobacter sphaeroides*	*T. aestivum*	IAA	Decreased the metal accumulation in plants.	72
Cu	*P. thivervalensis, B. Cepacia, Microbacterium oxydans,*	*Brassica napus*	Siderophores, P solubilisation, IAA, ACCD	Increased the antioxidant contents such as Ascorbic acid, Glutathione, enhanced plant biomass.	73
Cd	*Serratia sp.*	*Zea mays*	IAA, P-solubilization	Enhanced plant growth, increased biomass accumulation, decreased ROS production.	74
Cu, Cr, Cd	*P. aeruginosa* CPSB1	*T. aestivum*	IAA, HCN, siderophore, ACCD, P solubilisation	Enhanced production of wheat, showed metal tolerance capability.	75
Cd, Cu, Zn, and Pb	*Streptomyces pactum* Act 12	*Triticum aestivum*	IAA, ACCD, siderophores	Promoted plant growth, raised plant biomass and decreased antioxidant activities.	76
Cd	*Pseudomonas fluorescence* PGPR-7 and *Trichoderma sp.* T-4	*Cicer aeietinum*	Siderophore	Enhanced plant growth, increased seed germination, content of Chlorophyll and carotenoid.	77

Application of HM-Resistant PGPB in Plant Stress Management

The association between plants and microorganisms may involve several mechanisms that are important for both plants and microbial communities, this interaction may be harmful, beneficial, or neutral. Among rhizosphere microorganisms, PGPB may directly enhance plant growth by either regulating phytohormone levels or facilitating resource acquisition, or indirectly by acting as a biocontrol agent.[50]

Bacteria are the most crucial microorganisms for the treatment of soil contaminated with HMs. Several studies have demonstrated the role of PGPB in the elevation of crop yield either directly or indirectly due to their stimulatory impacts on soil nutrients, boosted nutrient uptake, overall physiological processes, and coping with stressfull situations by plants, and plants' resistance against pathogens.[7,50–52] The mechanism by which PGPB influences plant development and growth differs among species or strains; that includes restoration of soils, nitrogen and phosphate solubilization, and generation of plant hormones and siderophores, among others.[7] By generating 1-aminocyclopropane-1-carboxylate deaminase (ACCD), which dissolves insoluble mineral nutrients like potassium, phosphorus, nitrogen, etc, PGPB can lower the metal toxicity, change the bioavailability of metal in soils, and improve both abiotic and biotic stress resilience.[53] *Rhizobium, Pseudomonas*, *Azospirillum, Alcaligenes, Bacillus*, *Arthrobacter, Agrobacterium, Azotobacter, Burkholderia, Klebsiella*, and *Enterobacter* species are among a group of PGPB that are resistant to metals and have the potential to promote plant growth in metal-contaminated soil.[53] It has been reported that *Pseudomonas fluorescens* can enhance the growth of *Sedum alfredii* when exposed to stressors Zn and Cd by generating IAA.[54]

PGPB can also increase plant growth and development under HM-stress situations by fixing nitrogen, dissoluting phosphorus and potassium. For instance, *Klebsiella variicola*, one of the PGPB can increase the bioavailability of phosphate in the rhizosphere by transforming insoluble phosphate to soluble form with the aid of enzymes C–P lyases and phosphonates.[55] The stress hormone ethylene acts at low concentrations and regulates plant growth and development. Many recent investigations aim to minimize the ethylene level in plants through the activity of the bacterial enzyme ACCD which controls the ethylene generation by converting ACC into α-keto butyric acid and ammonia.[56]

Metal bioavailability in soil can be reduced by the combination of the metal with extracellular substances, thereby reducing metal absorption by plants through the root system. This mechanism is done by some PGPB through precipitation, alkalization, and complexation processes. To form insoluble precipitates, PGPB secretes some inorganic acids that can react with dissolved metals like Cu, Fe, Zn, Pb, etc.[57]

Siderophores (chelator agents) are produced by bacteria to overcome nutritional Fe limitations as they have a high affinity for chelating Fe^{3+}. Thus, they aid in the enhancement of plants growth and also protect against phytopathogen. Depending on their chemical nature, siderophores are divided into different groups that include, catecholates, hydroxamates, phenolates, carboxylates, and mixed types. Pseudobactin and pyoverdine, a mixed type of siderophore are synthesized by various *Pseudomonas* sp.[58] A hydroxamate type of siderophore, mainly pyoverdine, is produced by *Pseudomonas aeruginosa*.[61] da Costa *et al*., (2014) observed that the bacterial genera such as *Grimontella* and *Burkholderia*, had strains that produced a lot of siderophores, while other genera such as *Stenotrophomonas*, *Herbaspirillum* and *Citrobacter* had strains that produced a lot less siderophores.[56] According to de Souza *et al*., (2013) isolates of the genera *Enterobacter* and *Burkholderia* produced the most siderophores.

Discussion & Conclusion

The review has demonstrated that PGPB play a pivotal role in enhancing HM tolerance in plants. Various mechanisms employed by PGPB, such as enhancing nutrient uptake, metal chelation, and reducing HM uptake and translocation, contribute to reducing the toxic effects of HM on plants. This not only improves the overall health and growth of plants but also helps in maintaining crop productivity under HM-contaminated conditions. The utilization of PGPB as biofertilizers and bioremediation agents offers a promising and environmentally friendly alternative to traditional approaches for managing HM stress in plants. Continued research development in this field hold the potential to transform agriculture and contribute to sustainable environmental conservation.

Due to fast industrialization, sophisticated agricultural practices, and expanding anthropogenic activities, the toxicity of HM in soil has now emerged as one of the most important issues in the globe's history. A lot of work or experiments have been done to decrease, eliminate, and deteriorate the HMs from the soil. Heavy metal accumulation in plants affects various biological functions like hormonal imbalance within plants. The exogenous application of phytohormone boosts the yields and production of crops exposed to HM. However, some microorganisms present in soil can minimize the toxicity level of HM. Among them, PGPB may directly enhance the growth and development of plant by various processes. The use of these PGPBs has great potential in the remediation of HM-contaminated sites. Thus further studies are required in the future to find more beneficial bacteria that can diminish stress.

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