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Microbes-mediated alleviation of heavy metal stress in crops: Current research and future challenges

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ABSTRACT

Heavy metals (HMs) pollute the environment on a global scale and have different harmful effect on ecosystem. Outstripping accumulation of diverse toxic HMs in soils has altered the diversity, structure and function of microflora, degraded soils, reduces growth and yield of plant, and entered the food chain. HM treatment is necessary for maintaining the agricultural soil health. Many procedures and approaches have been used to recover contaminated soils in recent time, however, most of them were too pricey not environmentally friendly, and negatively affected soil properties. Usage of microbes was found as cost affective and ecofriendly approach for bioremediation of HMs. Microbes increased sustainability in agriculture soil health, which is essential to uninterrupted plant growth or improvement in stress full condition through mechanism likes productions phytohormones, organic acids, biosurfactants, exopolymers, antioxidant enzymes; and solubilization of phosphorus. It is well known that plant growth-promoting microbes enhance crop productivity and plant resistance to HM stress. In this following review, deep insight have has provided on mechanism of alleviation of HM stress by microbes and enhancement of plant growth promotion.

1. INTRODUCTION

Pollution is a persistent global issue which is caused by various hazardous pollutants including heavy metals (HMs), xenobiotics, polyaromatic hydrocarbons, agro-chemicals, and industrial effluents. HMs, the metals and metalloids having a density more than 5 g/cm^3 are one of the serious environmental pollutants due their non-biodegradable characteristics. They are characterized into three classes' namely toxic metals (arsenic, cadmium, copper, nickel, chromium, cobalt, lead, mercury, tin, and zinc), precious metals (gold, platinum, ruthenium, palladium, and silver) and radionuclides (americium, radium, thorium, and uranium) [1]. They are mainly spread by various human activities such as mining, dye and pigment manufacturing, electroplating, and fossil fuel combustion [2,3]. HMs spread through diverse modes such as surface runoff, food chain, atmospheric deposition, and also adopt different chemical forms including carbonate-bound, exchangeable, iron manganese oxide-bound, residual, and organic-bound [4].

Around the globe, the HM accumulation in the environment possesses a threat to the fertility of soil, plant, animal, and humans due to its highly toxic, mutagenic, carcinogenic, and teratogenic nature. In humans, HMs ingestion and inhalation may cause damage to the mental health, genetic makeup, and central nervous system. The HM direct contact could also escalate the cancer risk in the human population [5,6]. HMs have also a harmful impact on the ecological dynamics of the rhizosphere niche [7]. At the same time, they also have a negative impact on the growth of plants, biomass disposal, photosynthesis, and long-term production of food [2]. In plants HMs may result in the disruption of enzymatic function and nucleic acid structure; and hindrance of essential metals movement and absorption from their normal binding sites which leads to deficiency and nutrient imbalance [8]. After analyzing the serious and harmful impact of the HMs on the environment, environmentalists have come up with strategies such as physicochemical and biological approaches. The

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biological approaches have proved to be more efficient due to cost-effective and eco-friendly approach. In biological approach, plant and microbes are used and among them, microbes are applauded more. Plant allied microbes; especially plant growth-promoting (PGP) beneficial rhizobacteria are playing a significant role in plant growth promotion, mobilization, and phytoremediation of HM from soil [9,10].

Recently, HM tolerant PGP microbes are known for their potential role in mitigating the HM stress for the plant growing in metal stressed soil and enhance their growth [11,12]. Multiple HM resistant-PGP rhizobacteria indicated multiple reactions to metal ions such as metal bioaccumulation, enzymatic transformation, deposition, complexation, precipitation, and oxidation/reduction, and; thus reducing HM ion toxicity towards plants [8]. In general, PGP rhizobacteria have caused a decrease in metal bioavailability on inoculation into different plants and different environments. The present review deals with the different mechanism of the microbes which helps in the mitigation of the HM stress in the plants for agro-environmental sustainability.

2. APPROACHES FOR REMEDIATION OF HMS

Mitigation of HM is an urgent need to reduce the pollutant spread via the food chain, thus decreasing the health-related risks. Removal of HM from the soil is a challenging task with respect to technical complexity and a variety of methods have been adopted for the elimination of toxic HM [13,14]. Several strategies such as physicochemical and biological are available to decontaminate the soil from HM [15]. Basic impurity immobilization and removal methods have evolved into current biological elimination approaches [16]. Traditional physicochemical treatment methods could not resolve the pollution problem due to their detrimental effects and intrinsic drawbacks including their cost, amendment of soil properties, secondary pollution, and structural and functional changes in microbial communities [17].

2.1. Physico-chemical Approaches

Soil vitrification and replacement both are included in physical remediation method [18]. Physio-chemical approaches include electro-reclamation, leaching, landfill, thermal treatment, excavation, soil physicochemical properties change such as redox and pH potential by the addition of organic matter, chemical reagents, and curing agents [19]. This strategy of HM removal is fast but expensive and moreover causes detrimental effect on physio-chemical and other biological properties of soil and results in increasing secondary pollution. These approaches fail to remove the complete pollutants [20].

2.2. Biological Approaches

The bioavailability and solubility of HM could be increased by microbiota of soil [15,21]. The biological method of HM removal is a suitable approach due to an environmentally friendly process, reasonability, and higher public receipt. Moreover, the microbial use also conserves natural soil properties [22]. A biological approach includes bioleaching, bioaugmentation, biostimulation, bioreactors, bioventing, composting, bioremediation, phytoremediation, and land forming [23]. Phytoremediation is a biological method by which the efficacy of HM remediation could be increased if it is combined by microbes. Various microbes from diverse habitats have been reported for the effective removal of HMs from the soil. In a report, fungal species *Phanerochaete chrysosporium,* isolated from sewage contaminated soil have been reported for bioremediation of nickel and chromium up to 57% and 64.25%, respectively, in *in vitro* condition via biosorption mechanism [24]. In another report, a bacterium, *Bacillus* sp. isolated from HM contaminated soil was shown resistant to toxic HM such as Cr(VI), Cr(III), Cd^{2+}, Co^{2+}, Cu^{2+}, Ni^{2+} and Zn^{2+}. This bacterium was reported for effective detoxification of hexavalent chromium [25].

In an investigation, bacterial strain, *Cupriavidus metallidurans* from Pb-Zn mine showed to biosorbent the HM including Cr (4%), Cd (53%), Co (52%), Mn (74%), and Zn (48%) [26]. Bhattacharya and Gupta [27] reported *Acinetobacter* sp. for the detoxification of Cr (VI) up to 67% within 24h of incubation. In another report, *Bacillus subtilis* was reported for the immobilization of Cd metal through bio-augmentation technology. The inoculation of this strain in the carrot grown in cadmium contaminated soil was reported for alleviation of Cd stress along with enhancing the plant shoot (16%) and root (55%) [28]. Gan *et al*. [29] reported thermophile consortium of *Acidithiobacillus caldus* and *Sulfobacillus thermotolerans* for bioleaching of HM including, Zn, Cu, Mn, Cd, As, Hg, and Pb. Similarly, the bioleaching of HM was reported by fungus *Aspergillus niger* isolated from HM contaminated sediments. The fungus particularly leaches Pb by 11.5% from the polluted sediments along with Cd (93.5%), Cu (62.3%) and Zn (68.2%) [30]. Emenike *et al*. [31] reported the microbial blend of bacteria including *Rhodococcus* sp., *Lysinibacillus* sp., and *Bacillus* sp. for the bioremediation of HM such as Cu, Zn, and Pb by 86%, 73%, and 71% in leachate contaminated soil, respectively. The removal of HM was reported by the bacterial endophytes of *Tridax procumbens* identified as *Paenibacillus* sp. This bacterium was reported for detoxifying Zn, Pb, and As [32].

In a different report, the phytoremediation of Cd was reported by the Cd resistant bacteria namely *Arthrobacter* sp., *Micrococcus* sp., and *Pseudomonas* sp. The phytoremediation of Cd metal through bacteria was assisted by biostimulation and bioaugmentation. The inoculation of these bacteria on the *Glycine max* L. growing in Cd contaminated soil was reported for increasing the growth parameters [33]. Satyapal *et al*. [34] noted that reported *Pseudomonas* for remediation of arsenic in water. The particular strain was reported for the attendance of *aoxB, aoxR,* and *aoxC* genes, which play a significant role in arsenic bioremediation. Moreover the bacterial isolate *Pseudomonas* was reported for the bioremediating other metals including Hg(II), Ag(I), Ni(II), Cr(IV), Co(II), Cd(II), Cu(II), and Pb(II). Similarly, *Pseudomonas* sp. sorted out from the Cd contaminated soil was reported for the Cd transformation at 6.0 pH and 50°C [35]. HM Cr bioremediation was reported by the soil bacteria namely, *Pseudomonas fluorescens* and *Bacillus safensis* by 84% and 72% respectively [36]. Diba *et al*. [37] reported halophilic bacteria *Bacillus* sp., *Oceanobacillus* sp. and *Salinicoccus* sorted out from the Khara salt lake in Iran for detoxification of lead and nickel.

3. MECHANISMS OF HM RESISTANCE/TOLERANCE IN MICROBES

Resistance and tolerance of HM by the microbes are the most important mechanisms as the resistance helps in reducing and mobilizing the toxic HMs by 99.9%. Microbes show resistance in several environmental conditions including soil, water, and industrial and municipal waste. HMs resistance in microbes is majorly governed by the variety of transposon, chromosomal and plasmid-mediated resistance systems [Figure 1]. The maximum of the resistance mechanism is mediated by the plasmid which is highly effective to a particular anion and cation. Microbes using the various

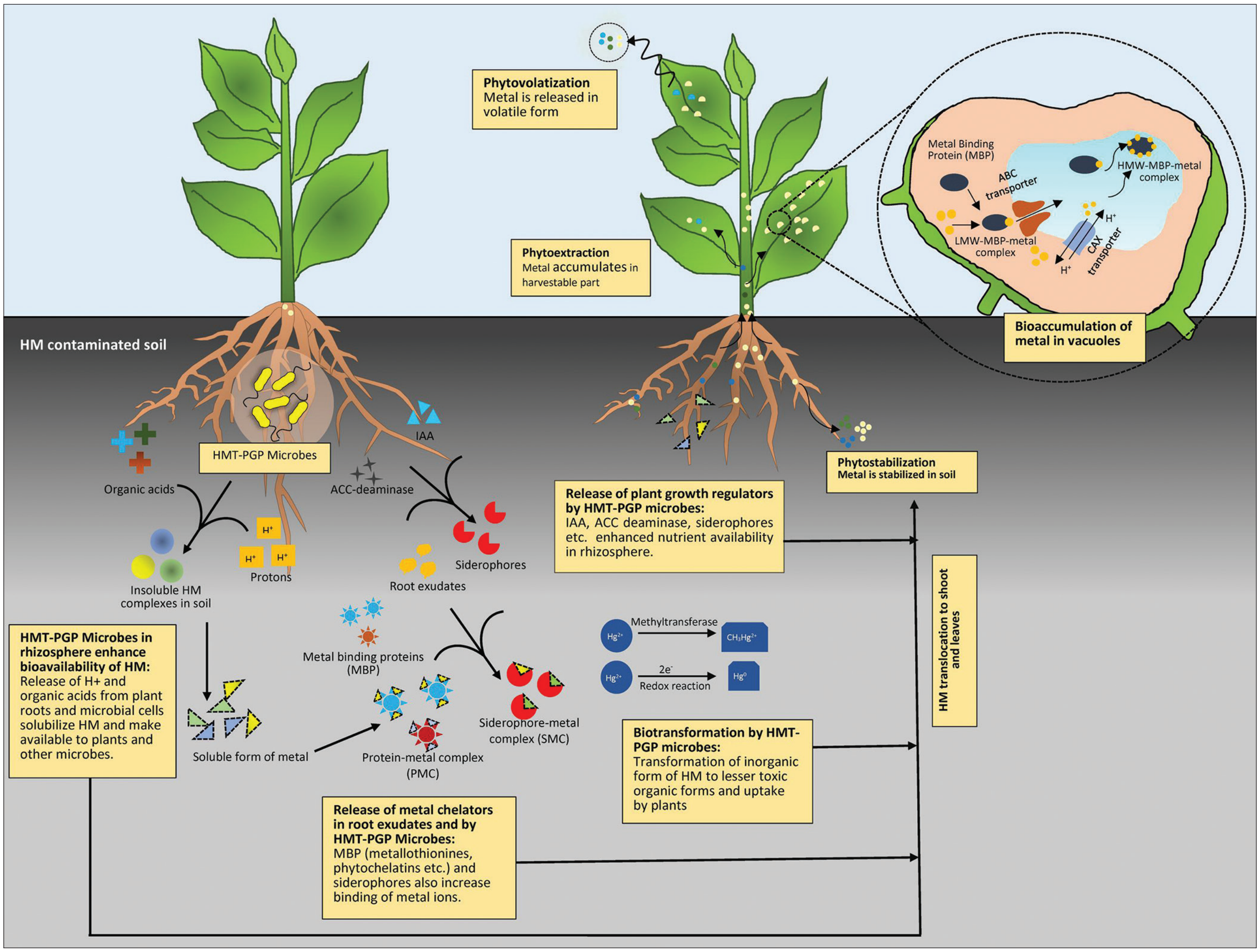

Figure 1: Mechanisms involved in remediation of heavy metal contaminated soil by beneficial microbes. Adapted from Mishra *et al*. [176].

systems tolerate the HM through mechanisms [38]. In the metal exclusion mechanism, microbes create modifications in the cell wall and envelop the membrane and surface layer. In this mechanism, the microbe protects its metals sensitive cellular components [39,40]. Microbes protect the cellular component by passively absorbing the high level of the HM on the cell *via* charge-mediated attractions. The non-specific binding on the outer membrane, envelop, surface layer; and extracellular polymeric substances (EPS) of the HMs prevent the entry of these metals inside of the microbial cell and hinder the essential components interference of the cell [41]. Absorbing the HM on the surface of the microbes may cause the metal local detoxification due to the metal's mobilization caused by to the coating of the polysaccharides on the surface layer of the microbes [42]. Another HMs tolerance mechanism in microbes is extracellular sequestration which is known to withstand the HM in the microbial cell. In particular type of mechanism, microbes produce several types of metabolites such as siderophores and biosurfactants that result in the metal precipitation. These secreted metabolites efficiently bind to the toxic HM and it subsequently detoxifies metals simply by complex formation or by the formation of the effective barrier around the cell of microbes [43].

In a report, endophytic bacteria *Bacillus thuringiensis* was reported for the siderophores production and reported for the detoxifying the toxic HM [44]. In a similar report, siderophores producing *Bacillus* sp. was reported for assisting phytoremediation of HM including iron, copper, zinc, cadmium, manganese, nickel, lead, and arsenic [45]. Detoxification of the metals through the mechanism of intracellular chelation refers to the metals deposition within the cytoplasm to prevent revelation to vital cellular components. A few of the microbes follow the cytosolic sequestration mechanism for protecting themselves from the toxic nature of the HM. Intracellular proteins can also decrease the concentration of free ion with the cytoplasm and sequester HMs which finally results in detoxification of the toxic HMs.

The detoxification of the metals through the enzymatic cation mechanism is another mechanism of the microbes which convert the toxic HM to less toxic forms. In this mechanism, various types of reaction such as oxidation, reduction, methylation, and demethylation are involved [46]. The reaction methylation of the HMs including Pb Sn, Se, and Te, could be converted into the gaseous state by the addition of the methyl group that helps in the methylated metal diffusion away from microbial cell due to its volatile nature. This mechanism results in less toxic environmental conditions for the microbial cell. Mechanism of HM alleviation was also reported by the active transports or efflux system. The system is considered the largest category of HM resistance systems in which microbes export the toxic metals out of the cytoplasm. This mechanism is plasmid or chromosomal encoded. The system works ATPase and non-ATPase-linked and highly specific for cations and anions and with the use of ATPase/chemiosmoticion/

proton pumps, microbes actively eliminate the toxic metals from its microbial cell [47].

4. MECHANISM OF MICROBIAL MEDIATED ALLEVIATION OF HMS IN PLANTS

4.1. Production of Phytohormones

Modification in the phytohormones content plays an essential role in the plant survivability. The changes in the level of phytohormones in the plant during the hostile environmental conditions may lead to perturbations of plant health and growth [48,49]. Microbes play a significant role in the mitigation of the HM stress by modulating the level of the phytohormones by producing different plant growth regulators (PGRs) such as auxin, gibberellins, and cytokinin [50]. In literature several types of the microbes have been known to produce the PGRs which also help in the alleviation of the plants stress caused by toxic HMs [51]. In a report, bacterium *Burkholderia* sp. sorted out from the metal contaminated soil was reported for the production of PGR, indole-3-acetic acid (IAA) along with 1-aminocyclopropane-1-carboxylate (ACC) deaminase and siderophores. This bacterium was reported for alleviating the HM stress in plant *Sedum alfredii* after inoculation and also enhanced the plant biomass as compared to uninoculated control [52].

Similarly, bacteria *Serratia marcescens* and *Rhodotorula mucilaginosa* was reported for producing IAA, siderophores, and exhibits the activity of ACC deaminase which helps in remediating the toxic HM such as zinc, cadmium, and lead in the macrofungus *Tricholoma lobynsis* [53]. In an investigation, *Polygonum pubescens* endophyte *Rahnella* sp. was reported for alleviating cadmium, zinc, and lead in plant *Brassica napus* by producing, IAA, siderophores, and ACC deaminase He *et al*. [54]. In an investigation, *Enterobacter* sp. And *Klebsiella* sp. sorted out from the *P. pubescens* gown in metal-polluted soil was reported for producing IAA, alleviating the cadmium, zinc, and lead toxicity and improving the growth parameters of rapeseed [55]. Singh *et al*. [56], have isolated *Pseudomonas putida* and *B. safensis* from the *Phylllnathus urinaria* rhizosphere, and these strains were reported for the production of IAA and alleviation of HM stress [Table 1].

In another investigation, *Pseudomonas protegens* have been reported for producing IAA, chitinase, polymer degrading enzymes, and siderophores which helps in the alleviation of HM stress [57]. In a report, *Leifsonia xyli*, the rhizospheric bacterium was reported for mitigating copper metal stress in tomato by the producing two different PGRs i.e. gibberellins and IAA [58]. In different report, microbial consortium of a fungus and bacterium namely, *Paecilomyces formosus* and *Sphingomonas* sp. was reported for producing gibberellins and the co-inoculation in soybean was reported for alleviating the stress caused by metal aluminum and zinc. The microbial consortium also reported for reducing the concentration of abscisic acid and jasmonic acid (JA) which helps the plant to survive and grow well in stressful conditions [59 1788].

In another report, IAA producing fungal endophyte, *Penicillium roqueforti* was reported for alleviating HM stress in wheat crop growing in the HM contaminated soils [60]. Similarly, Bilal *et al*. [61], have concluded gibberellins and IAA producing endophytic fungus *Penicillium funiculosum* for alleviating the toxic effect of the HMs by hormonal modulation in the crop *G. max* L. Another report has reported phytohormones producing rhizobacterium identified as *Staphylococcus arlettae* alleviated the chromium stress in sunflower plant [62]. Bilal *et al*. [63] have reported two fungal endophytes i.e. *P. formosus* and *P. funiculosum* for the producing gibberellins and IAA which helps in mitigating multi-metal toxicity in soybean.

4.2. Synthesizing ACC Deaminase

Exposure of plant to HM stress causes an increase of ethylene biosynthesis which results in the declination of the root elongation, induction of apoptosis, and accumulation of hydrogen peroxide. The ACC deaminase synthesis by the microbes is one of the most important and accepted mechanisms for conferring the HM stress in plants. The production of the enzyme, ACCD enhances the root growth of the plants by hydrolyzing ACC which is the immediate precursor of the ethylene (produced during exposure to HM stress) to ammonia and α-ketobutyrate and reduces the ethylene level in the plant [64]. The inoculation of the ACC deaminase synthesizing diverse group microbes has reported for successfully alleviating the HM in stress [65,66]. In a report, bacterial endophyte namely, *Pantoea agglomerans, Pseudomonas thivervalensis*, and *Ralstonia* sp. were concluded for having the capability to synthesize the ACC deaminase enzyme and siderophores. These strains inoculation in the plant *B. napus* was reported for enhancing the growth of plant and alleviating the copper accumulation [67].

In another report, ACC deaminase enzyme-producing endophytic yeast *Cryptococcus* sp. isolated from rapes were reported as potential strain for mitigation of the multiple metal stress in plant *Brassica alboglabra* growing in multiple-metal contaminated soil i.e. cadmium, lead, and zinc [68]. Guo and Chi [69], reported PGR rhizobacterium *Bradyrhizobium* sp. for alleviating HM stress in *Lolium multiflorum* and *G. max*. In another report, ACC deaminase synthesizing *Sinorhizobium meliloti* was reported conferring Cu tolerance in *Medicago lupulina* [70]. Rizvi and Khan [71], have reported *Pseudomonas aeruginosa* for the production of ACCD enzyme along with hydrogen cyanide (HCN), ammonia, siderophores, and IAA. This strain was mitigating the HM stress in wheat plant and enhancing the crop root structure.

In a report, *Pantoea* sp. from the rhizosphere of *Ziziphus nummularia* was reported for synthesizing the ACC deaminase enzyme and it was alleviating copper stress for wheat crop [72]. Danish *et al*. [73], reported *Agrobacterium fabrum* and *Leclercia adecarboxylata* for the production ACCD enzyme and helps in alleviating the chromium stress in the crop *Zea mays* growing under Cr stressful conditions. In a report, *Bacillus xiamenensis* was reported for producing ACC deaminase enzyme and alleviating the toxic HM in soil contaminated by industries and enhancing the growth of flax plant [74]. In another report, copper accumulating bacteria *Pseudomonas* sp. was reported for producing ACCD and enhancing *Helianthus annuus* L. plant growth [75].

4.3. Production of Siderophores

Siderophores, the iron-chelating compounds are produced by both microbes and plants for the sequestration of the mineral iron from the surrounding soil. This compound helps in combating the nutrient (fulfilling the iron mineral requirement), biotic (pest and pathogens), and abiotic stresses such as HM stress. Siderophores confer the stress exerted by abiotic factors by reducing the accumulation of the HM in plant that helps in enhancement [76]. The exposure of the HM to plant may affect plants negatively which leads to lower siderophores production. On the other hand, microbial siderophores help in alleviating the stress for plant [77,78]. Numerous microbial species have been found producing siderophores and combating the metal stress

Table 1: PGP bacteria enhanced phytoremediation of heavy metals.

PGP bacteria	Associated Plant (s)	Heavy Metal	PGP attributes	References
Achromobacter xylosoxidans A×10	*B. juncea*	Cu	ACC deaminase, IAA, *P* solubilization	Ma *et al*. [154]
Azotobactor chroococum	*Zea mays*	Pb	IAA, dercrease soil pH	Hadi and Bano [155]
Bacillus mucilaginosun HKK-1	*B. juncea*	Cd	IAA, Gibberellins	Wu *et al*. [156]
Bacillus pumilus E2S2	*Sedum plumbizincicola*	Cd	IAA, ACC deaminase, siderophores	Ma *et al*. [157]
Bacillus thuringiensis GDB-1	*Alnus firma*	As	ACC deaminase, IAA, Siderophores	Babu *et al*. [158]
Burkholderia sp. J62	*Lycopersicum esculentum*	Pb	Phosphate solubilization, IAA, ACC	Jiang *et al*. [159]
Cupriavidus taiwanensis	*M. pudica*	Pb	Biodegradation, biosorption	Chen *et al*. [160]
Cupriavidus taiwanensis	*M. pudica*	Cu	Biodegradation, biosorption	Chen *et al*. [160]
Cupriavidus taiwanensis	*M. pudica*	Cd	Biodegradation, biosorption	Chen *et al*. [160]
Enterobacter sp. JYX7	*Polygonum pubescens*	Cd	IAA, siderophores, ACC deaminase	Jing *et al*. [55]
Enterobactor cloacae CAL2	*B. napus*	As	IAA, ACC deaminase	Nie *et al*. [161]
Meshorhizobium huakuii B3	*Astragalus sinicus*	Cd	Production of metallothioneins	Sriprang *et al*. [162]
Micrococcus sp. MU1	*Helianthus annus*	Cd	IAA, ACC deaminase	Prapagdee *et al*. [163]
Paenibacillus macerans NBRFT5	*B. juncea*	Cu	Siderophores, organic acids, protons	Tiwari *et al*. [164]
Pseudomonas aeruginos	*Orychophragmus violaceus*	Cd	Improve plant growth	Liang *et al*. [165]
Pseudomonas fluorescens G10	*B. napus*	Pb	IAA, ACC deaminase	Sheng *et al*. [166]
Pseudomonas jessenii PjM15	*Ricinus communis*	Zn	Biosorption, ACC deaminas, IAA,	Rajkumar *et al*. [167]
Pseudomonas putida 06909	*Helianthus annuus*	Cd	Production of metal-binding peptide	Wu *et al*. [168]
Pseudomonas putida KT2440	*Triticum aestivum*	Cd	Production of phytochelatins	Yong *et al*. [169]
Pseudomonas sp. LK9	*Solanum nigrum*	Cd	Biosurfactants, siderophores	Chen *et al*. [170]
Pseudomonas tolaasii ACC23	*B. napus*	Cd	ACC deaminase, siderophores and IAA	Dell'Amico *et al*. [153]
Pseudomonas veronii	*S. alfredii*	Zn	IAA, decrease soil pH, supply *P* and Fe	Long *et al*. [171]
Psychrobacter sp.SRA1	*B. juncea*	Ni	ACC deaminase, IAA, *P* solubilisation	Ma *et al*. [172]
Rahnella sp.	*Amaranthus*	Cd	IAA, siderophores, ACC deaminase	Yuan *et al*. [173]
Rhizobium leguminozarum	*B. juncea*	Zn	Metal chelation	Adediran *et al*. [174]
Staphylococcus arlettae	*B. juncea*	As	IAA, siderophores, ACC deaminase	Srivastava *et al*. [175]

B. juncea: *Brassica juncea*, *M. pudica*: *Mimosa pudica*, *B. napus*: *Brassica napus*. PGP: Plant growth promoting, IAA: Indole-3-acetic acid, ACC: 1-aminocyclopropane-1-carboxylate

in the plants [79]. In a report, rhizospheric bacterium *Burkholderia* sp. was reported for having siderophores production along with IAA and ACCD. The inoculation of the strain in the *Salix caprea* plant growing under the Cd and Zn contaminated soil was found to lower the uptake of metal in roots and promoted the plants growth [80].

Similarly, Zhang *et al*. [81], have reported bacterial endophytes *Agrobacterium tumefaciens* and *Bacillus* sp. of *Commelina communis* plants for the production of iron chelating compound, ACC deaminase, and IAA which helps in mitigating the effects of lead in the plant. In another report, siderophores producing *Pseudomonas* sp. were reported for alleviating Pb and Cd stress in *Oudemansiella radicata* plant [82]. Gaonkar and Bhosle [83] have reported *Bacillus amyloliquefaciens* for the production of iron chelating agent, siderophores which were having a capability for mitigating arsenic, lead, aluminum, and cadmium stress. Similarly, *Acinetobacter* sp. and *P. putida* having attributes of producing siderophores, IAA, and phosphorus solubilization was reported for alleviating copper stress in maize and enhanced its growth by increasing the biomass and chlorophyll content [84]. In another report, HM stress in soil is mitigated by siderophores producing microbe *Streptomyces lividans* and *Streptomyces mirabilis* [85].

In a report, siderophores producing isolate *Brevundimonas diminuta* from rice crop was reported for alleviating arsenic stress in crop rice *via* increasing biomass, chlorophyll, and MDA content [86]. In a report, Chen *et al*. [87] reported *Enterobacter* sp. for the alleviating cadmium and iron stress in *Hibiscus cannabinus* through exhibiting PGP activity of siderophores production and IAA. In another report, siderophores producing *Klebsiella pneumonia* were reported for the alleviation of cadmium stress in *Vigna mungo* [88]. Similarly, an investigation reported *Pseudomonas orientalis* and *Chaetomium cupreum* for the siderophores production, mitigating metal stress, and growth promotion of *Eucalyptus globulus* [89]. In another report, consortium of ACCD and IAA producing strain *Pseudomonas* and *Bacillus* was reported for alleviating the cadmium, lead, and zinc content and improving the spinach growth [90]. In another report, siderophores producing bacterium *Rhizobium* with a combination of root endophytic fungi *Piriformospora indica* was reported for alleviating cadmium stress in alfalfa plant [91].

4.4. Phosphorus Solubilization

Phosphorus (P) solubilization is another microbial mediated mechanism for the HM stress alleviation in the plants. Microbes have the capability to solubilize the mineral phosphate complexes such as Al-P Ca-P and Fe-P present in soil which enhances the phosphorus availability that rapidly immobilizes the HMs in soil [92]. The immobilization of the HM enhances the plant tolerance towards the HM stress through the formation of the insoluble HM phosphate complex. In literature, various microbial species have been found for the exhibiting this mechanism and alleviating HM stress [47,93]. In a report, microbial endophytes were sorted out from the *Solanum nigrum* L. which were *Acinetobacter* sp. *Enterobacter* sp., *Enterobacter aerogenes* and *Serratia nematodiphila.* These isolates were found to solubilize the phosphorus along with synthesizing siderophores, ACCD, and IAA which was efficiently mitigating cadmium stress in the plants *S. nigrum* and enhances its growth [94,95].

In another study, phosphorus solubilizing fungus *Trichoderma harzianum* were reported for mitigation of the cadmium stress in chickpea [96]. El-Deeb *et al*. [97], reported *Enterobacter* sp. an endophytic bacterium of aquatic hyperaccumulator plant, *Eichhornia crassipes* for alleviating cadmium and zinc metal stress. This strain was reported for solubilizing the mineral P and producing siderophores and IAA. In another report, tricalcium phosphate solubilizing, IAA, and exopolysaccharides producing *P. aeruginosa* was reported for the mitigating the toxicity of chromium metal stress in chickpea [98].

Fungus, *Trichoderma virens* from rhizospheric soil of plant growing in the mine tailing soil was reported for phosphorus solubilization and exhibiting the phytase activity. The strain was also reported for synthesizing siderophores for the sequestration of the iron and ACCD enzyme. All these activities exhibited by the microbe were reported for the bioleaching of the cadmium, arsenic, zinc, copper, and lead and enhance maize physiological and growth parameters such as chlorophyll, total soluble sugar, starch, protein, root, and shoot length [99]. In a report by Sukweenadhi *et al*. [100], *Paenibacillus yonginensis*, phosphate solubilizer, and siderophores producer were reported for ameliorating of aluminum, drought as well as salinity stress in plant *Arabidopsis thaliana*. Marzban *et al*. [101] have reported *P. putida* as efficient solubilizer and producer of phosphorus and IAA, respectively. The strain inoculation in maize crop growing in lead, copper, and cadmium contaminated soil was reported for mitigating metal stress and increased dry weight of the plant.

In a similar investigation, bioaccumulation and biosorption of the HM was reported by the phosphorus solubilizing bacterium namely, *Ensifer adhaerens*. The strain was also reported for secreting IAA, siderophores, HCN, and ammonia under *in vitro* conditions [102]. Similarly, Mitra *et al*. [103] have reported *Enterobacter* sp. for solubilizing phosphorus and also mitigating cadmium stress in rice crop growing in the cadmium stressed soil. In another report, phosphate solubilizing bacteria *Achromobacter xylosoxidans* was reported for reducing chromium metal stress in HM contaminated soil [104]. In a report, HM chromium immobilization was found to be done by the phosphorus and potassium solubilizing microbes *B. thuringiensis*, *B. cereus*, *B. subtilis* and *Stenotrophomonas maltophilia* [105]. Pramanik *et al*. [106] have reported *Pseudomonas* sp. from a metal contaminated rice rhizosphere for solubilizing phosphorus, nitrogen fixation and IAA production under cadmium stress.

4.5. Production of Organic Acids

HMs have the ability to produce organic acid such as citric, gluconic, oxalic and succinic acid in many PGR microbes have been reported [107,108]. It was certified that the organic acid-producing PGPMs can reduce metal-induced stress in plant and help to increasing the survivability of plant in HM polluted soil [109]. The complex form of an organic acid-like metal oxalate crystal can turn and deactivate cytology and reduce the free metal ion effect, later plants provide to toxic metals. Microbial organic acids are known to have a higher affinity for chelating HM than essential nutrients. Stimulate the production of organic acid via plants uncovered to HM that help the formation of more complexes using HM [110,111]. The acetate, citrate, malate, and oxalate are incorporated by a complex reaction (HM detoxification) to dissolve the HM of the soil's solid phase (mineral weathering) and thus make them unavailable for stressed plant regeneration. "Conferring benefits in the sequestration of important nutrients" [112]; "modifying antioxidant enzyme reactions shown through plants" [109]; and "dissolve mineral phosphate and releasing P" [113], the resulting insoluble HM phosphorus precipitates (eg, Cd and Pb) [8].

Several microbes have been reported for the remediating HM via the production of organic acids such as *Enterobacter* sp. and *Pantoea* sp. was reported immobilizing Pb and P solubilizing [114]. In a report, tartaric acid-producing bacterium *Burkholderia cepacia* was reported for alleviating Cd stress in *S. alfredii* plant [115]. Similarly, *Enterobacter asburiae* PSI3 was reported and producing gluconic acid and remediating Cd [109]. In a report, rhizobacteria *B. cepacia, Enterobacter cancerogenes*, and *Microbacterium seperdae* were reported for producing organic acid including oxalic acid, acetic acid, formic acid and tartaric acid which helps in the mobilization of Cd and Zn metal [116]. Gao *et al*. [117] reported citric acid producing fungus *Purpureocillium lilacinum* for detoxification of Cd and Pb. The fungal strain inoculation on the *S. nigrum* L. growing under HM stressed soil. Similarly, the organic acid, oxalic acid-producing endophytic bacteria *Sphingomonas* was reported for the detoxification of Pb and Zn. The inoculation of this strain in the *S. alfredii* was enhancing the plant growth parameters in HM stress [118]. Khanna *et al*. [119] reported *Burkholderia gladioli* and *P. aeruginosa* for remediating HM stress via producing the organic acids such as succinic acid, malic acid, fumaric acid, and citric acid. The strains were also reported for increasing the seedling growth of tomato in HM stressed plants.

4.6. Production of Bio-surfactants

Biosurfactants are the extensive group of structurally different surface-active compounds composed of fatty acids, lipoprotein, glycolipids, mycolic acid, and phospholipid. These are amphiphilic compounds with hydrophobic and hydrophilic portions [120]. They are synthesized as metabolites by different groups of microbes in the exponential or stationary phase of the microbial growth. Microbial biosurfactants are found to be having a countless advantages in the biodegradability of pollutants including HM [121]. Biosurfactants-mediated toxic metal bioremediation is promoted in two basic ways in solid phases. The first way is mediated by the complexation of metals free forms in a solution which is followed up by desorption based on Le Chatelier's principle. Another way is the metal accumulation with the biosurfactants under the reduced interfacial tension conditions which allow direct contact between the sorbed metal and biosurfactants. HM extraction through the microbial biosurfactants is achieved by counter binding, precipitation-dissolution, and ion exchange. In the ion exchange mechanism, biosurfactants carrying negative charge form a stronger bond with positive charge carrying metal ions which make them non-toxic and reduces the toxicity of the metals [122]. Some scientist has investigated that HM was alleviated from soil via bio-surfactants of di-rhamnolipids, rhamnolipids, and sophorolipids secreted by *B. subtilis*, *P. aeruginosa,* and *Torulopsis bombicola* [123,124].

In a report, bacterium isolated from the marine environment *Bacillus* sp. was reported for detoxifying the effect of hexavalent Cr through the biosurfactants production and extracellular enzyme reductase [125]. Sriram *et al*. [126] isolated bacterium *Escherichia fergusonii* from oil-contaminated soil. This bacterium was reported for having a potential to produce the lipopeptide biosurfactants which successfully remediated HM such as Cu, Mn, Pb, Fe, Ni, and Zn. In an investigation report, biosurfactant mediated HM bioremediation was reported by the yeast, namely, *Candida lipolytica*. The lipoprotein produced by the yeast was reported for removing 96% of Cu and Zn and also helped in the reducing the concentration of Pb, Cd, and Fe [127]. Similarly, lipopeptide biosurfactant consisting of fengycin and surfactin obtained from *B. subtilis* was reported for biodegrading the HM including Cd, Cu, Co, Pb, Ni, and Zn by 44.2%, 26.2%, 35.07%, 40.3%, 32.2%, and 32.07% respectively [128]. de França *et al*. [129] reported HM detoxifying bacterium *B. subtilis* for producing biosurfactant. Similarly, remediation of Cr was mediated by the biosurfactant marine bacterium *B. subtilis* [130]. In another report, *Bacillus* sp. was reported for producing biosurfactants which help in the alleviation of HM stress [131]. Bacterium *Citrobacter freundii* was also reported for the producing biosurfactant and bioremoval of HM [132]. In an investigation, biosurfactant mediated HM detoxification was reported by the bacterium *B. subtilis*. The bacterium was able to produce the lipopeptide biosurfactant [133].

4.7. Production of Exopolymers

EPS are high-molecular weight natural polymers liberated via microbes into the environment. They are made up of homo and hetero-polysaccharides (such as mucopolysaccharides, proteins humic, and substances) that adhere to the bacterial cell surface. The polysaccharides composition which makes EPS varies in diverse species of microbes, but galactose, glucose, and mannose may be mentioned as monomers. Other EPS molecules are amino sugar, natural sugars, organic ester-linked substituents, pyruvate ketals, and uronic acid [134-136]. The ionic property of exopolymers is attributed to its acyl group, which increases the lipophilicity of the compound and, consequently, alters its interactions with other cations and polysaccharides [137]. Microbial EPS plays a vital role in the complexing of toxic HM and reducing their mobility and plant accessibility [138]. EPS generated by PGP rhizobacteria has been demonstrated to bind potentially harmful trace elements and trap precipitated metal oxides and sulfides, resulting in the organic metal complexes development and increased trace element resistance [139]. In this study, Xu *et al*. [139] was reported EPS secreted by bacterium *P. putida* converted the bioavailable Cd^{2+} into organic species through complexation. Cd^{2+} binding capacity of EPSs released by *P. putida* was shown to be primarily due to phosphate and carboxyl groups [140]. PSB could immobilize HM via absorption of metal to EPS. In another study, EPS producing *Azotobacter* spp. were found to inhibit Cd and Cr absorption by wheat via binding Cd (15.2 mg g^{-1}) and Cr (21.9 mg $^{g-1}$) of., and subsequently, immobilizing them [141]. Similarly, Wang *et al*. [142] reported *Desulfovibrio desulfuricans* for detoxification of HM by EPS. The bacterium was reported for alleviating HM such as Cu^{2+}, $Cu^{2+}$and Zn^{2+}.

4.8. Induction of Plant Production of Antioxidant Enzymes

Toxic HM could cause oxidative stress by releasing oxygen-based radicals, known as reactive oxygen species (ROS). ROS generally considered existing in this form like “oxygen-derived free radicals including alkoxyl (RO•), hydroxyl (HO•), superoxide anion ($O_2^{\bullet -}$), and peroxyl ($RO_2^{\bullet}$) or oxygen-derived nonradical such as hydrogen peroxide (H_2O_2), organic hydroperoxide (ROOH), and singlet oxygen ($½O_2$) [143,144]. All of these species which are oxygen-based toxics are ROS; however, not all ROS species are not oxygen radicals. ROS are reactive molecules with unpaired valence shell electron, which are short-lived, unstable, and chemically reactive [145]. ROS is reactive in nature because ROS such as hydroxyl radicals, (H_2O_2), superoxide radicals (O_2^-) and peroxides (O_2^{2-}), radicals, and singlet oxygen quickly attack all types of biomolecules such as lipids, amino acids, nucleic acids, and proteins, causing irreversible metabolic dysfunction and cell death [146]. HMs toxicity, such as other abiotic stressors, causes plants to produce ROS [147]. To defend against oxidative stress, plant cells produce antioxidant enzymes including ascorbate peroxidase, catalase, dehydroascorbate reductase, glutathione reductase, glutathione-S-transferase, glutathione peroxidase, peroxidase, and superoxide dismutase and nonenzymatic antioxidants such as atocopherol, asascorbate, glutathione, and proline [148]. According to certain research, PGP microbes cause plants to produce antioxidant enzyme in response to stress exerted by abiotic factors. In this study, *P. aeruginosa* were reported under Zn stress an uptake of N and P and increases in total soluble protein, leaf chlorophyll, and biomass of wheat [149]. In another study, Afridi *et al*. [150] were reported microbes *Kocuria rhizophila* and *Cronobacter sakazakii*, carry SOD and CAT higher activity under salt stress condition in wheat.

4.9. Induction of HM Resistance Genes

HM resistance genes in microbes can respond to the encouragement of HM. The co-occurrence of HMs resistance gene in long-term HM contamination area is still poorly assumed. Some of the genes have been identified that gene involved in induced systematic tolerance (IST) and stimulating IST in plant host. It has been known that few microbes have the capability to trigger IST in plant host, analogous to those for triggering ISR in plants. Microbes are involved in the ISR induction produces some metabolites such as antibiotics, bio-surfactants, siderophores, and lipopolysaccharides from bacterial outer membranes, and volatile organic compounds. These metabolites have led to the stimulation of resistance against their pathogens in many plants. Systemic defense responses emanating from bacteria are controlled via signal network.

These metabolites result in the resistance initiation in several plants against their plant pathogens. Systemic defense responses from microbes are controlled via a signal network. In this network, phytohormones including ethylene, JA, and salicylic acid play a significant role [150,151]. Some of the phenomena have linked with IST. Plant-associated microbe is affecting the appearance of few genes coding for proteins associated with HM tolerance. In an investigation by Ouziad *et al*. [152], *Glomus intraradices* increased the tomato growth cultivated under Zn stress condition. However, the expression of *LeNramP1* (for HM transporter) and *Lemt2* (coding for MTs) genes was reduced in the inoculated plant. This indicates that *G. intraradices* reduced the HM concentration in plant.

A large group of plants has been reported for their potential to deposit substantial level of HM. However, a lot of plants associated with phytoremediation (hyper accumulating plants) do not produce enough biomass to make this method effective. As a result, using PGPMs to facilitate phytoremediation is more suitable. A wide variety of PGPMs has been molecularly identified that successfully aid in phytoremediation of HM. As an example, Jing *et al*. [55] was isolated metal resistance PGPMs from *P. pubescens* grown in metal contaminated soil. These isolated strains were recognized as *Enterobacter* sp. and *Klebsiella* sp. that were inoculated into *B. napus* (Canola/Rapeseed) for HM accumulation and improve growth of plant and the accumulation of Cd and Zn. The same plant was also reported by Dell’Amico *et al*. [153] produced *Pseudomonas tolaasii*, *P. Fluorescens,* and *Mycobacterium* sp. and uptake Cd successfully.

5. CONCLUSION

The pollutant, HMs is one big concern of every environmentalist due to its harmful effect on whole global system. Anthropogenic activities such as industrialization, mining, and afforestation are the major cause of this environmental contaminant which is very hard to stop. As a result, remediation is one technique that could be used for mitigating this contaminant. Remediation through biological methods is a more effective method of mitigating HM in comparison to physical and chemical methods and biological methods phyto-microbial system is more preferred. Bioremediation through microbe's weather bacteria or fungi has reported as an effective approach to eliminate the HM or lowering the toxicity. According to the literature, microbes used a specialized mechanism of alleviating the HM that also helps in enhancing the plant growth promotion. Microbes enhance the plant growth by various mechanisms such as availing the nutrients by solubilizing, or chelating. Solubilization of phosphorus, chelation of iron through siderophores, production of organic acids, exopolysaccharides are some of the mechanism which helps in the enhancement of the plant growth. The use of microbes for the alleviation of HMs and enhancement of plant is an effective method and more effective microbial strain should be explored in future research.

6. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agreed to be accountable for all aspects of the work. All the authors are eligible to be an author as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

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The authors report no financial or any other conflicts of interest in this work.

9. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

10. DATA AVAILABILITY

Not Applicable.

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