



REVIEW ARTICLE

Rhizosphere dynamics in contaminated soils: Unravelling plant, metal and microbe relationships

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Abstract

Heavy metal contamination from both natural and anthropogenic sources poses a significant environmental challenge, impacting human and animal health, as well as microbial populations. Microbes exposed to elevated metal concentrations develop resistance mechanisms, involving both physiological and genetic adaptations, to detoxify and transform metals. Recent advancements have elucidated the roles of metal-metabolizing bacteria and transport proteins during metal detoxification. Microbial inoculation with phytoremediation is termed as rhizoremediation, which enhances degradation of toxic compounds in soil, offering a promising solution to contamination issues. The synergistic relations between plants and microbes in the rhizosphere highlight the importance of root exudates in mediating microbial communities for plant nutrition and metal biotransformation. It is for these reasons that it is imperative to better understand these interactions in order to design more effective convention for the detoxification of metals for enhanced soil quality. The potential application of plant-microbe synergism in the remediation of metal pollutants using environmentally friendly and economically viable methods in soil remain scarce.

Keywords: biotransformation; ecological restoration; heavy metal detoxification; microbial resistance; root exudates

Introduction

Technological advances in the fields of food production, health, infrastructure, transportation and communications have been made possible by human beings since the beginning of the twentieth century. These endeavours demand a large number of novel resources and energy, which destroy natural environmental components and produce massive amounts of waste that degrades the environment (1). Severe harm to the ecosystem and related life is caused by the presence of toxic metals as well as metalloids in wastes produced by the industrial, residential and agricultural sectors (2). Because of their high mobility and solubility, the pollutants have the potential to bioaccumulate in the food chain and cause significant harm when their levels rise (3).

These toxins can cause several serious illnesses that can be fatal when they enter the body, viz., atherosclerosis, cancer, kidney and bone diseases, cardiovascular disorders, hypertension, low birth weight, Alzheimer's disease etc (4). The release of these hazardous elements poses a significant threat to human health, living organisms and ecosystems. Because metal does not biodegrade, it accumulates in biological tissues and is difficult to eliminate, which pose a serious threat to world health (5).

A decrease in soil fertility and water-holding capacity, microbial diversity and soil enzyme activity, as well as an increase

in bulk density and pH, are all consequences of metal contamination on the physicochemical and biological properties of soil (6). They are also responsible for changing microbial populations, which sheds light on the ecosystem equilibrium and interferes with the biogeochemical cycles (7). Some of the indirect and direct impacts on plant growth are chlorosis, necrosis, root damage, decreased carotenoids content, oxidative stress, moderated enzyme activity, osmotic stress, reduced photosynthesis and nutritional status affected by heavy metals (HM's) like Arsenic (As), Mercury (Hg), Nickel (Ni), Chromium (Cr), Lead (Pb) and Copper (Cu) (8). Additionally, due to the adverse effects that metals have on the environment, constant efforts are made to remove surplus and toxic metals responsibly to stabilize the ecosystem.

Microbes can improve phytoremediation in several ways, including by accelerating plant biomass, enhancing or decreasing the availability of metals in the soil (phytoextraction or phytostabilization) and facilitating the translocation of metals from the soil to the roots (bioaccumulation) or from the roots to the shoot tissues (9). Microbes can develop resistance mechanisms and withstand relatively high metal concentrations in both naturally occurring (serpentine soil) and artificially contaminated (mine waste, fly ash) environments (10). Because the microbial metabolites produced in the rhizosphere *in situ* are less toxic and biodegradable, employing plant growth promoting microorganisms

(PGPMs) in phytoremediation has various advantages over applying chemical amendments (11). In phytoremediation, the relationships between root exudates and rhizosphere microorganisms have been identified as a crucial element of plant growth (12). The mechanisms underlying the interactions between plants, microbes and metals are yet unknown, though. This article aims to review recent progress and applications in understanding the biochemical and molecular mechanisms underlying plant-microbe interactions, with a focus on their role in metal transformation processes.

Dynamics of rhizosphere region

The soil compartment that is impacted by plant growth is known as the rhizosphere. This effect arises from the plant's discharge of organic materials, known as rhizodeposition, which is primarily made up of plant waste and metabolites, or exudates (13). Fig.1. gives the schematic diagram of the rhizosphere microenvironment. A significant portion of the photosynthetically fixed carbon (between 20 % and 40 %) allotted to the underground root system is lost due to this carbon loss (14). Consequently, rhizosphere soils are characterized as mesotrophic, favouring the growth of populations of bacteria, archaea, microbial viruses and fungus, whereas most bare soils are considered oligotrophic settings (15). The selected microorganisms have a variety of effects on the plant and the general functioning of the rhizosphere. They either recycle carbon molecules or serve as prey for larger organisms like nematodes or amoebae. They also play a role in the carbon cycle. They can promote plant growth and protect plants from infections and some of them can even be plant pathogens. Microbial activity can alter plant rhizodeposition both quantitatively and qualitatively, which in turn impacts the microbial component. This may be referred to as the natural feedback loop of the rhizosphere that helps sustain its activity at a stable level. Such an intertwined connection leads to ask whether the rhizosphere, which meets at the interface between plant root and soil, can be manage to promote plant growth, or to minimize the impact of different types of biotic or abiotic stresses - a fact of high interest in the current scenario of global change and necessity of more sustainable

agricultural production (16). In essence, it is possible to modify all three rhizosphere components. The microbial populations can be selected to support plant development and health. The plant can be modified to select or introduce a novel trait of interest and the soil can be altered to modify its physicochemical characteristics or enhance its overall quality.

Role of root exudates

For water, nutrients and mechanical support, plants depend on their roots (17). From previous studies (18), organic matter (5-21 %), proteins, amino acids, fatty acids, carbohydrates, vitamins, nucleotides, phenolic compounds and polysaccharides are among the metabolites released by plant roots. The compounds that are discharged are referred to as root exudates and the process is known as root exudation. In order to influence the phytoremediation process, root exudates might change the rhizosphere's physical and chemical properties or increase the pollutants' bioavailability there (18).

Exudates from roots help microorganisms with their metabolic processes by providing a carbon source. Root exudates facilitate microbial biodegradation through physical processes such as nutrient assimilation, pollutant biotransformation and breakdown, microbial attachment sites and soil aeration. It can improve rhizosphere activity by using ectoenzymes to break down organic molecules. Root exudates can change the chemical presence of contaminants by increasing the bioavailability of pollutants, promoting soil microorganisms and reducing environmental concerns (19).

Heavy metal - soil's silent threat

Environmental pollution is regarded as one of the major issues facing the modern world and is one of the most important environmental concerns. The most dangerous pollutants in the environment are heavy metals (around 65 metals) (20). Chemical elements with an atomic mass of more than 20 u and a density greater than 5 g/cm³ or specific gravity at least five times that of water are referred to as heavy metals (HMs) (21). HMs could be

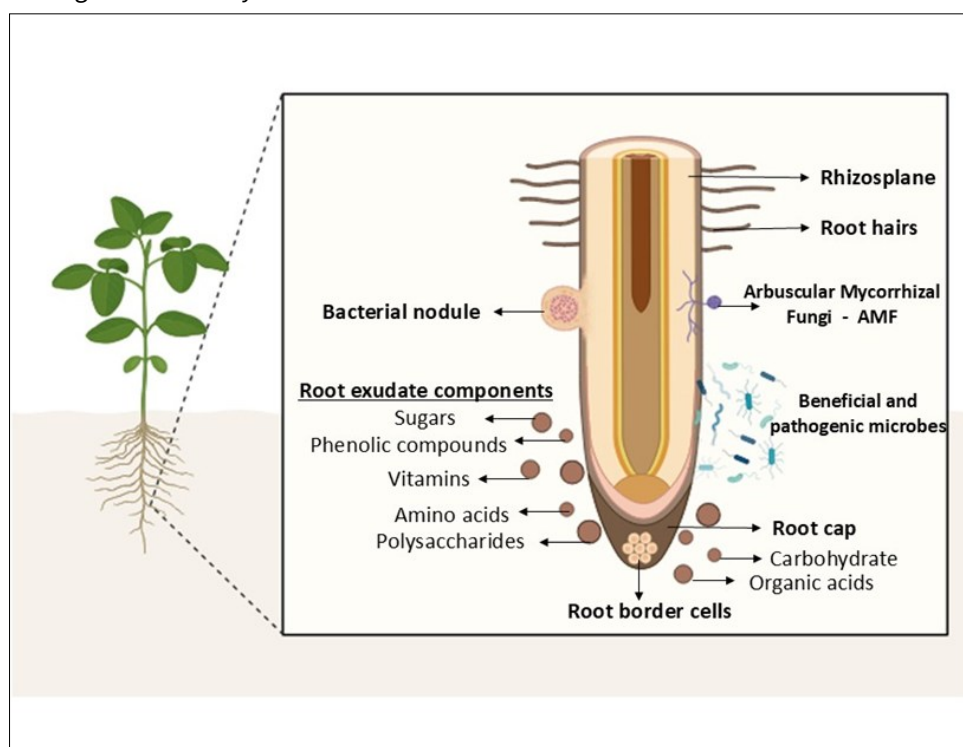


Fig.1. Schematic diagram of the rhizosphere microenvironment.

divided into necessary and harmful constituents from a biological standpoint. Several plant and animal micronutrients, including Zn, Fe, Ni and Cu, are referred to as essential metals (or metalloids in some situations), yet they turn poisonous at specific levels (22). Conversely, non-essential metals that are extremely harmful even at low quantities are known as toxic elements (23). Despite being ubiquitous trace elements in all environmental compartments, these metals-both essential and non-essential-accumulate in a specific location because of human activities including mining, smelting, urbanization, industrialization and agriculture (24). Due to their ubiquity, lack of biodegradability, toxicity, accumulation and persistence, increased heavy metals (HMs) in soil and the environment have garnered significant attention globally (25). It is commonly known that HMs have detrimental impacts on the physicochemical, biological and biochemical characteristics of soil (26). Table 1 gives a comparative study of major heavy metals and they're on the environment. Furthermore, hazardous metals enter the food chain due to the cohabitation and permanence of heavy metals in the soil, which poses serious health risks to living things (27). By removing the current soil vegetation and establishing new vegetal cover, HMs significantly disrupt soil horizons, soil structure, soil fertility, nutrient biogeochemical cycles and soil microbial communities (28). By changing the size, makeup and activity of the microbial population, HMs has an indirect impact on soil enzymatic activities (29). Fig. 2. gives the diagrammatic representation of sources and effects of heavy metal in soil. By interfering with important microbial metabolic functions, such as respiration, denitrification and enzymatic activity, HMs has harmful impacts on the microbial population (30). Additionally, HMs alters the organization of microbial communities and decreases the abundance of particular microbial populations (29).

Moreover, HMs negatively impacts the distribution of cell membranes and prevents microbial cell division, transcription and protein denaturation (31). Several variables, such as soil texture, clay and organic matter levels, pH, inorganic anions and cations and the metal's chemical forms and speciation, affect how much of an impact metals have on soil biological characteristics (32). Plant quality and yield, as well as soil fertility, are all significantly impacted by HM contamination. HMs significantly impair several physiological and biochemical functions in plants, including stomatal conductance, water balance, photosynthesis, electron transport, CO₂ assimilation, antioxidant scavenging enzymes, solute accumulation, mineral nutrition and stunted growth. In the end, these conditions may result in plant death (28). Furthermore, high metal toxicity inhibits plant cells' cytoplasmic enzymes and damages cell structures through oxidative stress, which in turn impacts plant growth and metabolism (33). Food insecurity results from the ongoing reduction in plant development, which lowers yield. Because they can penetrate other environmental compartments like groundwater, rivers and crops, heavy metals (HMs) that have accumulated widely in soils pose a threat to human health (34). Researchers have demonstrated that HMs that surpass the permissible limits deteriorate water quality and make it unfit for drinking and irrigation purposes (35). By direct ingestion or contact with a polluted environment, the food chain, or drinking contaminated water, HMs can enter the human body (36). Humans are negatively impacted by prolonged consumption of certain metals and the associated harmful effects become apparent after many years of exposure (37).

Table 1. Comparative table of major heavy metals and their effects on the environment

| Heavy Metal | Primary Sources | Concentration in contaminated Soils (mg/kg) | WHO/EPA Toxicity Threshold (mg/kg) | Soil Persistence (years) | Effects on Soil Health | Effects on Rhizospheric Microbes | Effects on Human Health | References |
|----------------------|---|---|--|--------------------------|--|---|---|------------|
| Cadmium (Cd) | Mining activities, phosphate fertilizers, industrial processes, battery manufacturing, electroplating | 3-50 (agricultural); 50-500 (industrial sites) | 3.0 (WHO); 1.4 (EPA residential) | 75-380 | Reduces enzymatic activity, alters pH, decreases organic matter decomposition, inhibits nitrification | Reduces microbial biomass by 40-60 %, inhibits nitrogen fixation, alters community structure | Kidney dysfunction, bone disease, cancer, cardiovascular effects | (38) |
| Lead (Pb) | Paint, gasoline additives, mining, smelting, battery manufacturing, ammunition, old plumbing | 100-1000 (urban areas); 500-5000 (mining areas) | 400 (EPA residential); 300 (WHO agricultural) | 150-5000 | Inhibits plant growth, reduces nutrient availability, affects soil structure, decreases microbial activity | Decreases bacterial diversity, inhibits phosphatase activity, reduces mycorrhizal | Neurological damage, developmental delays, cardiovascular disease, renal dysfunction | (39) |
| Arsenic (As) | Mining, smelting, pesticides, wood preservatives, coal combustion, natural geological sources | 20-200 (agricultural); 200-2000 (mining sites) | 10 (WHO drinking water); 0.39 (EPA residential soil) | 1000-3000 | Phytotoxicity, reduced crop yields, altered nutrient cycling, soil acidification | Shifts microbial community composition, reduces methane oxidation, inhibits sulfate-reducing bacteria | Cancer (skin, lung, bladder), skin lesions, cardiovascular disease, diabetes | (40) |
| Chromium (Cr) | Leather tanning, electroplating, stainless steel production, wood preservation, textile industry | 50-500 (industrial areas); 500-5000 (tannery sites) | 230 (EPA residential); 100 (WHO agricultural) | 100-1000 | Cr(VI) highly toxic to plants, reduces root development, inhibits photosynthesis, alters soil pH | Cancer (lung), skin irritation, respiratory problems, liver damage (Cr VI) | Inhibits nitrification, reduces fungal biomass, alters enzyme activity | (41) |
| Nickel (Ni) | Stainless steel production, electroplating, mining, fossil fuel combustion, sewage sludge | 20-200 (urban soils); 200-2000 (industrial sites) | 1500 (EPA residential); 210 (WHO agricultural) | 80-480 | Phytotoxicity, chlorosis, reduced root growth, interferes with iron metabolism | Allergic reactions, respiratory cancer, dermatitis, cardiovascular effects | Reduces soil respiration, inhibits urease activity, affects bacterial community structure | (42) |

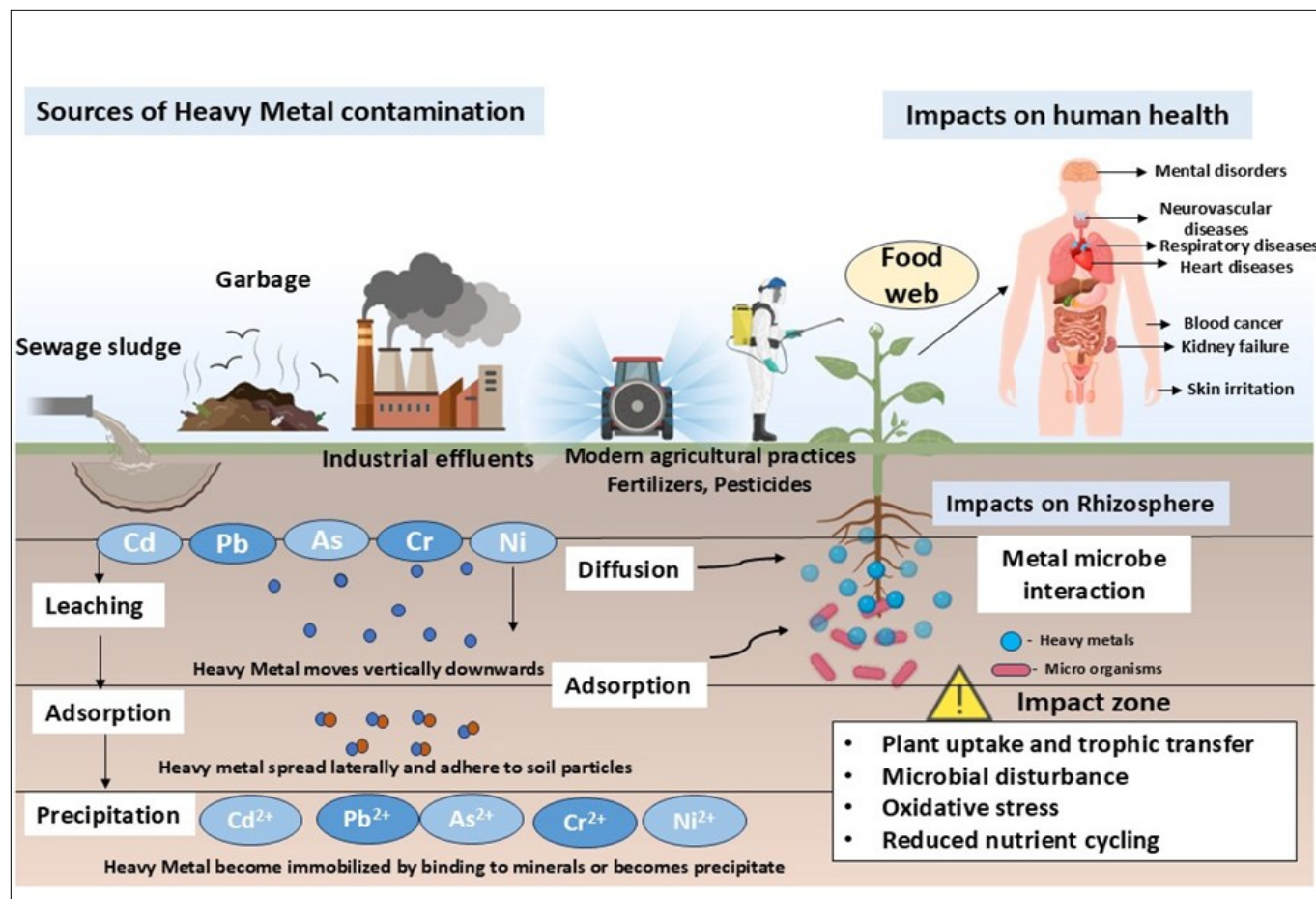


Fig. 2. Sources and impacts of heavy metals in soil.

Microbial techniques for heavy metal detoxification

Detoxification, degradation, mineralization and the conversion of harmful contaminants into less toxic forms are some of the methods used in bioremediation. The bioremediation technique we choose is dependent on several variables, including cost, site features, pollutant type and concentration and it can be carried out either in situ or ex-situ (43). In situ bioremediation involves treating contaminated materials at the source of contamination. Since this method doesn't require excavation, there is minimal to no soil disturbance. This method is inexpensive because there is no need to excavate (44). In contaminated areas, this method has successfully treated hydrocarbons, dyes, HMs and chlorinated solvents (45). In situ technology employs two distinct methods: intrinsic and artificial bioremediations. Because it involves stimulating native or naturally occurring microbial populations, intrinsic bioremediation is less costly and involves cleaning up contaminated soils without the use of external forces. Improved physicochemical conditions and modified microorganisms are used in engineered bioremediation to speed up the rate at which contaminants degrade (46).

Ex-situ digging up contaminants and moving them from contaminated places to another location for treatment is known as bioremediation. Ex-situ bioremediation strategies have been carried out according to the polluted site's location, treatment cost, pollutant type, degree of pollution and depth of contamination. This technique involves excavating pollutants and then relocating them to a separate treatment site (47). Ex-situ technology includes slurry-phase bioremediation and solid-phase treatment. In solid-phase bioremediation, HMs are remedied by releasing a bacterial inoculum into soil piles via pipes following

soil removal (48). Polluted soils are mixed with water, nutrients and oxygen in a bioreactor during slurry-phase bioremediation to provide an ideal environment for the microorganisms to effectively break down the soil pollutant. Fig. 3. provides the diagrammatic representation of the types of *ex situ* technology.

Countries are becoming more industrialized, which causes toxins to reach the environment more quickly. Since these pollutants are detrimental to living things, we should regulate those using natural means that have a good impact on living things. Regeneration of polluted sites using bioremediation is eco-friendly and (microbial process and beneficial microorganisms) has been proven effective (49). Using PGPRs for bioremediation is a natural technique that can be used to reduce the adverse effects of environmental pollutants(50). Previous researchers (50) isolated endophytic bacterial strains were surface sterilized before *S. nigrum*, a cadmium hyperaccumulator, was collected from a sewage discharge canal bank. The ability of bacterial strains to reduce the impacts of heavy metals (HMs) (Cd(II), Pb(II), Cu(II), Cr(VI) and Zn(II)) in soils was assessed after they were kept and activated in Lactose Broth (LB) medium. The 16S rDNA gene sequences were used to identify the chosen strains. The EB L14 strain, one of the 96 strains obtained in this study, was a member of the *Bacillus* species. The morphological, physiological and chemical traits of this strain performed exceptionally well in removing Pb (II) and Cd (II).

Microbial process in metal transformation

Heavy metal pollution poses serious problems for all due to its long-term, harmful impacts on the environment. Because contaminants and organic metals are durable, they can remain in the environment for a long time and, even at low quantities, have

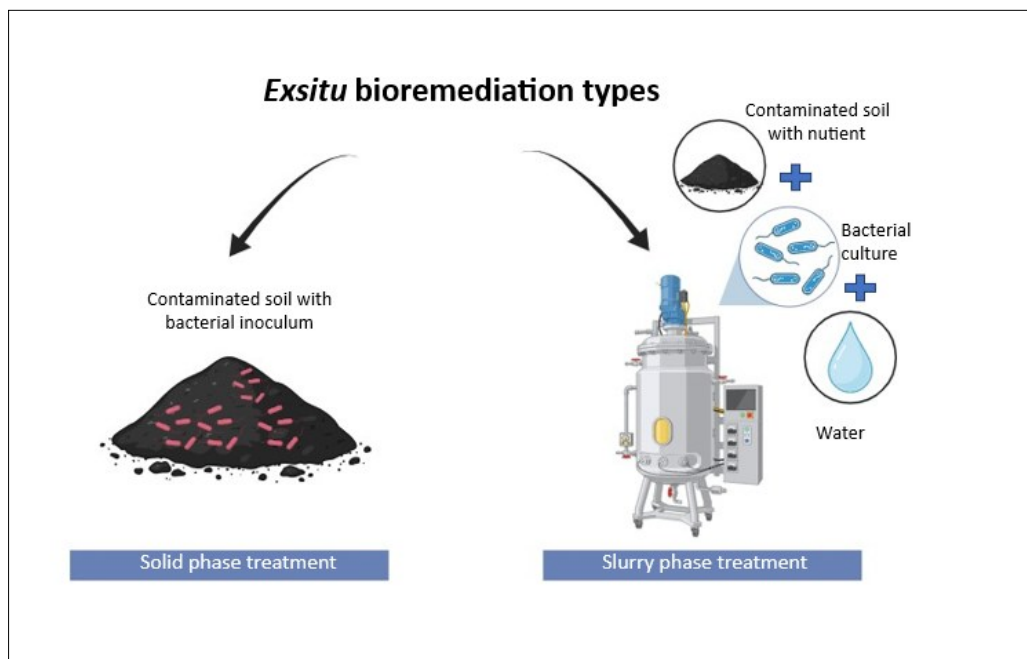


Fig. 3. Types of *ex situ* technology.

an adverse effect on species' food chains. Remediating the soil in contaminated regions using physical and chemical approaches is not cost-effective and generates a lot of chemical waste (51). Fig. 4. gives the schematic representation of microbial process in metal transformation. Both native and non-native microorganisms can be introduced to contaminated locations in a variety of methods when utilized in bioremediation. The most crucial strategy for resolving issues with the biodegradation and bioremediation of contaminants is the use of native microorganisms in contaminated areas (52). Bacteria's flexibility and biologically active processes make them ideal for the cleanup procedure. *Achromobacter sp*, *Alcaligenes sp*, *Corynebacterium sp*, *Flavobacterium sp*, *Mycobacterium sp*, *Nitrosomonas sp*, *Xanthobacter sp*, *Pseudomonas sp*, *Bacillus sp*, *Enterobacter sp*

and *Micrococcus sp*. are many bacterial species that have been studied for bioremediation. Their remarkable capacity for biosorption is explained by their high surface-to-volume ratio and perhaps active chemisorption sites (teichoic acid) on their cell wall (53). It has been reported that if the number of native microorganisms that can degrade the target contaminant is less than 105 CFU/g of soil, bioremediation will not proceed at a meaningful rate (54).

As a great soil conditioner, corncob powder is used as the carrier material for the carrier-based inocula. This carrier material has accelerated the pace of degradation by forming air pockets in the soil, which makes the soil porous and facilitates aeration for the introduced bacterial consortium's development and survival as well as bioremediation. The type of substrate (the treatment



Fig. 4. Microbial process in metal transformation.

containing the selected bacterial consortia and nutrients) and the inoculum concentration determine the maximum bioremediation response (55). The saprophytic survival of *Phytophthora drechsleri* was assessed using an experiment. Samples of the soils surrounding pistachio trees were taken at various locations in Rafsanjan, Iran. The results showed that fungal survival was significantly influenced by the kind of substrate (pistachio leaf and wheat straw), the duration of the incubation period and the inoculation density; hence, larger inoculum densities would result in longer *P. drechsleri* survivability (56).

Metal - microbe interaction in soil

Microorganisms' ability to break down pollutants is dependent on their metabolic system, which uses the redox process to change the pollutants into harmless forms (57). By sequestering metals in cell wall components, changing the metabolic pathway to prevent metal uptake, lowering the intercellular metal concentration through a precise efflux system and converting toxic metals into less hazardous forms, they assist plants in reducing metal toxicity (58). Microorganisms (such as bacteria and fungi) play a vital role in metal transformation process. Furthermore, several genes that encode heavy metal-resistant proteins and transporters are found on transposons and plasmids in microorganisms. Recently, the remediation of Cd, Pb and Cu from polluted soil was enhanced by the synergistic impacts of four bacterial strains: *Viridibacillus arenosus* B-21, *Sporosarcina soli* B-22, *Enterobacter cloacae* KJ-46 and *E. cloacae* KJ-47 was discovered (59). Furthermore, following 48 hrs of testing, the combination of bacterial strains demonstrated higher resistance and efficacy for metal transformation than a single strain. The bioremediation of contaminated environments depends on a variety of metabolites released by microorganisms (60). Siderophores produced by bacteria can reduce the bioavailability of metals and they are subsequently removed from polluted ground (61). It has been observed that bacteria can change their shape to produce more siderophores, which encourage the buildup of metals between cells (62). Cell wall biomolecules contain negatively charged functional groups such as carbonyl, hydroxyl and phosphate. These groups facilitate bioremediation by quickly bonding with hazardous metal ions (63). Moreover, bacteria are an ideal bioremediation agent since they can be cultivated and endure in harsh environmental circumstances (64).

Similarly, fungi may be cultivated in challenging environments and use accumulation, valence transformation and extracellular and intracellular precipitations to detoxify metal ions (65). In addition to the transformation process, fungi function as a promising biocatalyst by absorbing harmful substances into their mycelium and spores. Recently, Previous studies (66) shown the Ascomycota and Basidiomycota fungal consortia's capacity for bioremediation, indicating that fungal bioaugmentation aids in the removal of heavy metals from contaminated land. Numerous studies have been conducted to explore the potential of microorganisms for bioaccumulation and biosorption as effective strategies for remediating metal-contaminated environments. Numerous heavy metal-resistant microbes have recently been isolated by researchers from contaminated soils, abandoned and mining sites, industrial waste dumping yards and the rhizosphere of plants growing in metal-affected environments (67). The metal transformation process is significantly influenced by the isolated bacterial genera (*Arthrobacter*, *Enterobacter*, *Corynebacterium*, *Stenotrophomonas*, *Bacillus* and *Pseudomonas*) and fungi

(*Aspergillus flavus*, *Aspergillus awamori*, *Saccharomyces cerevisiae*, *Phanerochaete chrysosporium*, *Penicillium oxalicum* and *Trichoderma viride*). The metal transformation process is significantly influenced by the isolated bacterial genera (*Arthrobacter*, *Enterobacter*, *Corynebacterium*, *Stenotrophomonas*, *Bacillus* and *Pseudomonas*) and fungi (*Aspergillus flavus*, *Aspergillus awamori*, *Saccharomyces cerevisiae*, *Phanerochaete chrysosporium*, *Penicillium oxalicum* and *Trichoderma viride*).

Plant - microbe interaction in phytoremediation

Both the detoxification of pollutants and the resilience of plants to heavy metal stress are significantly influenced by microorganisms. Complex communities that facilitate beneficial species' colonization of plants are made possible by free-living microorganisms, organisms that are more firmly attached to roots and endosymbionts that invade the tissues inside plants (58). These animals may limit infections, encourage vegetative growth and aid in the removal of heavy metals (68). Certain plant species may have a unique microbial community that varies based on the stage of growth and location of the roots and plants help to form their own rhizobiomes (69). Under stressful conditions, such as the presence of heavy metals, or in contaminated soils, plants can form a special rhizobiome that makes them more resilient (70). For instance, previous researchers identified metal-microbe interactions that were specific to rice, soybeans, or maize, as well as crop-specific rhizosphere populations in HM-contaminated soils (71). In contaminated soils, plants change microbial communities by increasing their biomass, diversity and activity and by promoting bacterial heavy metal detoxification (72).

Root exudates are one of the many materials that metal-reducing bacteria can use as electron donors to aid in the detoxification of heavy metals (73). The advantageous "rhizosphere effect" can influence microbial populations in the bulk soil near roots, enhancing the soil's overall quality (74). Exudates increase the pH of the soil, which promotes bacterial detoxification and metal mobilization, enabling hyper accumulative plants to take up heavy metals (75). Compared to their non-accumulative counterparts, plants with hyper-accumulative ecotypes, such as *Sedum alfredii*, display different microbial community compositions. Additionally, the rhizospheres of these ecotypes show a decrease in soil HM content and an increase in enzymatic activity (76). In particular, bacteria that benefit plants are commonly characterized by their plant growth-promoting rhizobacteria (PGPR) (77). By producing secondary metabolites (such as siderophores, 3-indoleacetic acid: IAA and 1-aminocyclopropane-1-carboxylic acid: ACC), deaminase activity and the ability to solubilize phosphates, PGPR are directly linked to metal detoxification (78). Several metal-tolerant PGPR are employed in phytoremediation because they alter metal mobility, lessen plant metal toxicity and stress and encourage plant growth. In the PGPR, roots are associated with several species, such as *Bacillus*, *Pseudomonas*, *Enterobacter*, *Acinetobacter*, *Burkholderia*, *Arthrobacter*, *Paenibacillus*, *Agrobacterium*, *Lysinibacillus* and *Flavobacterium* and new genera are constantly being found (79).

Plant- microbe - metal interaction in contaminated soil

Plant-microbe remediation is becoming more and more common since it has a greater removal efficiency than plant-based remediation. These microorganisms have a variety of roles in biochemical processes, including the mineralization of carbon and nitrogen, the fixation of nitrogen and the breakdown of

organic matter, all of which support the creation of soil, the cycling of nutrients and the transmission of energy. In contaminated environments, HMs also have an impact on soil microbes. On the other hand, they often adapt to the constant exposure and acquire distinct characteristics with a limited number of particular microbial populations. Toxic metals from contaminated areas can be removed using these particular kinds of bacteria. Furthermore, the most productive species in the soil reclamation process are soil microbes that partner symbiotically with host plants. Various bioremediation techniques have made use of the close symbiotic relationship that mycorrhizal fungi have with their host plants (80). The most well-known symbiotic fungus, *Arbuscular mycorrhizae*, is widely employed in phytoremediation because of their widespread occurrence in soil.

Plant growth-promoting bacteria (PGPB) can increase plant development and assist plants in adjusting to the contaminated environment. The plant-microbe-based bioremediation approach has two components. First and foremost, by supplying nutrients, microbes aid the host plant in surviving in the hostile environment. Second, the plant is essential to the reclamation process because it sustains favourable environmental conditions that improve soil organic matter, accessible P, K and N and foster the growth of soil microorganisms that aid in the process. The benefits of the plant-microbe-based bioremediation approach have been emphasized in several recent studies. According to a study, *Trifolium repens* plant increases the soil enzymatic activity in areas contaminated with heavy metals (81). The planting of *Salix* in Cd-contaminated soil enhanced the diversity of beneficial microbes, including bacteria from the genera *Arthrobacter*, *Bacillus*, *Flavobacterium*, *Niastella*, *Novosphingobium*, *Niabella*, *Anaeromyxobacter*, *Rmlibacter* and *Solitalea*, as demonstrated by

(82). Fig. 5. Gives schematic overview of mechanism of plant - metal - microbe interactions

Root exudates interaction in contaminated soil

One of the most important elements that might influence the diversity and microbiological proliferation of microorganisms living in harmony in the rhizosphere is root exudates. Compared to non-rhizospheric soil, the microbial communities found in rhizospheric soil are more varied, dynamic and cooperative. Exudates from plant roots serve a variety of purposes, including promoting plant development and accelerating the breakdown or elimination of soil pollutants. Root exudates alter the physical and chemical characteristics of rhizospheric soil. They either raise the bioavailability of pollutants in the rhizosphere or acidify the rhizospheric soil by lowering the pH, which promotes the desorption of heavy metals from insoluble complexes to free ion form, which is preferable for improved heavy metal uptake (83).

The bioavailability of heavy metals can be improved for better plant uptake from the soil by using specific chemicals or metabolites of root exudates as metal chelators (84). The fact that plants use metal chelator chemicals to mobilize soil nutrients to promote plant development is well known. For instance, compared to other types of iron, phytochelators convert ferrous (Fe^{2+}) iron to ferric (Fe^{3+}) iron, which plants more readily absorb (85). In a similar vein, it has been observed that root exudates are essential for boosting the availability of phosphorus-solubilizing bacteria (PSB) so that soil may absorb more phosphorus. In order to modify the rhizospheric microbial diversity of soil, the rhizospheric microbial communities also exhibit a chemotactic response to root exudates and form a synergistic relationship.

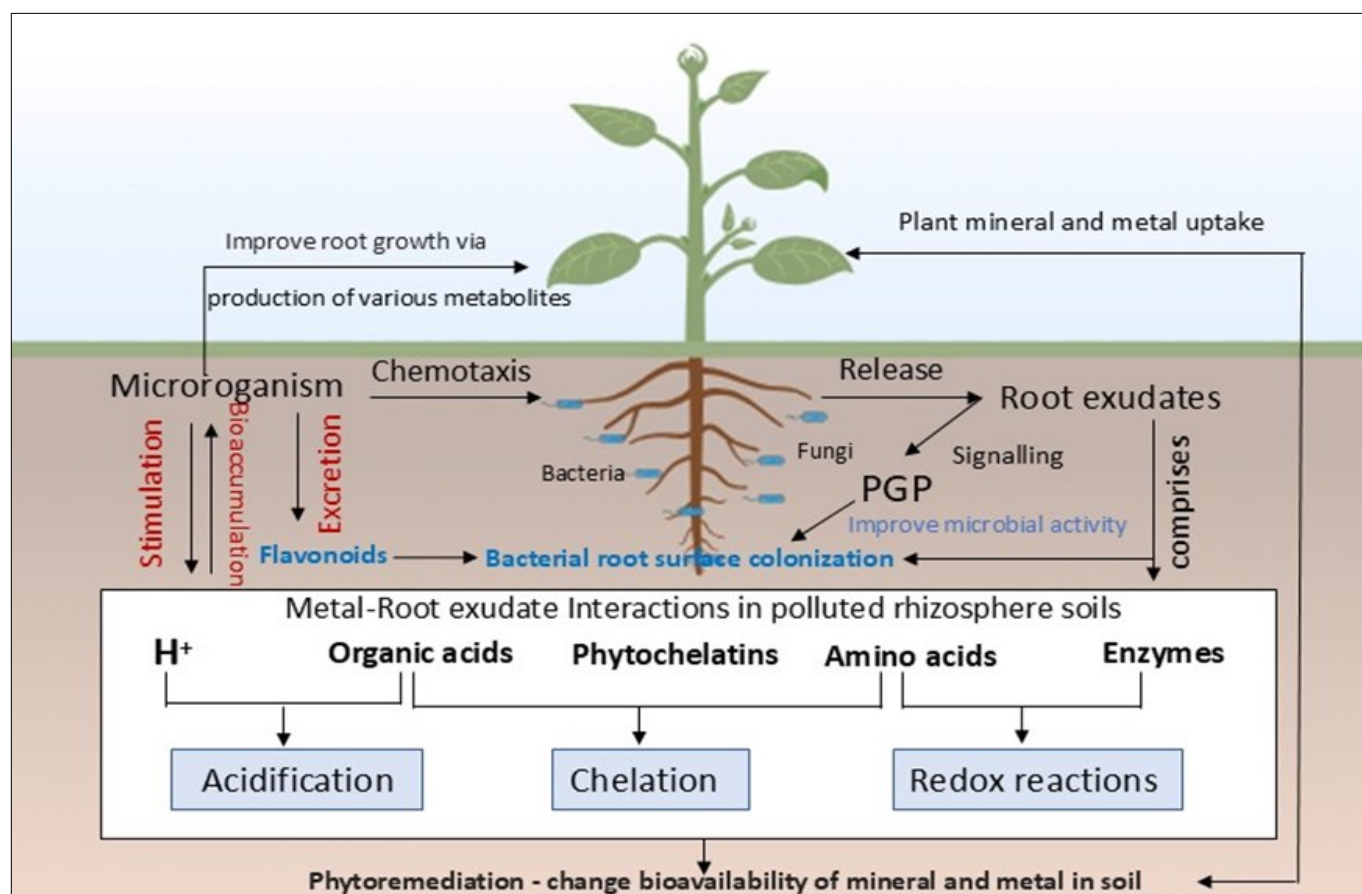


Fig. 5. Schematic overview of mechanism of plant metal microbe interactions.

Effect of root exudates on rhizosphere microbiology

By simulating the signals of quorum sensing metabolites, root exudates can change the diversity of microbes in the rhizosphere. By attracting advantageous specific microorganisms as PGPRs, mycorrhizal fungi, or nitrogen-fixing bacteria, root exudates mediate rhizosphere interactions. Using beneficial bacteria, plant roots and microorganisms in the rhizosphere communicate chemically, which promotes the growth of biofilm. Their chances of surviving even in hazardous situations with contaminants in the soil are increased by this film (86). Plants employ exudates to protect themselves against diseases and root exudates accelerate the process of converting carbon and nitrogen, thereby aiding in maintaining the rhizosphere's carbon-to-nitrogen ratio. In the rhizosphere, they serve as the microbial communities' ecological driver (87). Another method for improved phytoremediation is artificial root exudates, which sequester inorganic metal ions or alter their bioavailability in the soil to make them simpler for plant roots to absorb.

It is well known that root exudates acidify the rhizospheric zone, changing the pH of the soil and eventually causing heavy metals to release their free ions from insoluble complexes in the soil. Therefore, it is important to note that root exudates contribute significantly to soil concentration and bioavailability of heavy metals (88). Root exudate components and their roles in rhizosphere microbial interactions and heavy metal dynamics is noted in Table 2. Similar to this, it is also widely known that in rhizospheric soil, plants can release certain metabolites that help to dissolve metals, which can impact the chelation of heavy metals in the soil. These plant chemicals, which can influence the physiochemical characteristics of the soil as well as the bioavailability of heavy metals in the soil, include organic acids, carboxylates and certain phytosiderophores (89).

Rhizosphere engineering strategies

One of the limiting factors that restricts phytoremediation is the accessibility of contaminants to plant roots. Numerous factors affect this availability, such as the type of soil, the interactions between the pollutant and soil particles, the quantity of organic

matter present, pH, water content, temperature (96). The rate of action of phytoremediation is limited by low availability. Certain materials can be added to soils to alter the availability of pollutants. When phytostabilization is the best course of action for metal-polluted soils, organic amendments are often used. Organic amendments serve as a microbial inoculum, a slow-releasing nutrient that encourages plant growth and an immediate decrease in metal bioavailability, moreover, organic matter increases infiltration, reduces erosion and fortifies the soil's structure. The carbon-to-nitrogen (C: N) ratio of the organic amendment must be between 12:1 and 20:1. As organic additions, a variety of materials have been used, including wood chips, straw, charcoal, humic acids, agricultural or municipal compost, or manure. To improve plant development and immobilize metals, liming was also used as an inorganic amendment (96).

Because the biochemical environment in the rhizosphere is a combination of soil type, soil moisture level, associated microbial communities, plant physiology and their synergy altogether, farmers typically apply soil amendments and irrigate the soil well near the roots of the plants in order to modify the rhizospheric region (97). Plant development can be enhanced, nutrient uptake can be aided, tolerance to specific pollutants and heavy metals can be increased and other abiotic/biotic stressors can be resisted or infections suppressed by propagating beneficial microorganisms that are either native to that type of soil or exogenously given. Since the rhizosphere is the vital interface between the soil and the plant root system, it is home to a variety of microorganisms that are ultimately sensitive to changes in the rhizospheric zone's microenvironment (98). Thus, in phytoremediation operations, this zone is especially important. The rhizospheric microbiome plays a critical role in maintaining the phytoremediation process, which is directly related to plant-associated bacteria and plant tolerance to metals, according to numerous researchers working in this area. Therefore, better designs for phytoremediation strategies must be created and implemented in field experiments to increase the remediation efficiency of plants (99).

Table 2. Root Exudate Components and their Roles in Rhizosphere Microbial Interactions and Heavy Metal Dynamics

| S.No | Component | Microbial Role | Heavy Metal Interaction | Reference |
|------|---|--|--|-----------|
| 1. | Organic acids (e.g., citric, malic, oxalic) | Acidify rhizosphere, mobilize nutrients, attract beneficial microbes | Chelate & mobilize Cd in soil, enhancing phytoremediation efficiency by 66% with citric acid application | (90) |
| 2. | Amino acids (e.g., glycine) | Serve as carbon/nitrogen source, signaling for PGPR colonization | Synergy with citric acid enhances Cd uptake in plants (increased phytoremediation by ~35%) | (91) |
| 3. | Soluble sugars (e.g., fructose) | Fuel growth of rhizosphere microbes, help biofilm formation | Support metal-tolerant microbial populations, aiding soil detoxification | (92) |
| 4. | Phenolics/flavonoids | Antimicrobial action; signal with mycorrhizae & beneficial microbes | Affect microbial metal tolerance & rhizosphere signaling | (93) |
| 5. | Polysaccharides/mucilage | Enhance microbial adhesion & biofilm formation; support soil aggregation | Bind metals, buffer pH, improve rhizosphere stability under heavy-metal stress | (94) |
| 6. | Phytosiderophores (e.g., mugineic acids) | Mobilize Fe & shape microbial community | Chelate Fe, Cd, Zn, Ni, facilitating metal uptake in grasses | (95) |

Conclusion

The rhizosphere is a dynamic and biologically active zone where plant roots, soil microorganisms and heavy metals interact in a complex yet coordinated manner. This review emphasizes that root exudates-such as organic acids, amino acids, sugars, phenolics and secondary metabolites serve as essential regulators of rhizospheric ecology, rather than being mere metabolic waste products. They play a dual role: nurturing beneficial microbial communities and modulating the mobility and speciation of heavy metals. Microorganisms respond to these exudates by engaging in biochemical processes such as biosorption, redox transformation, chelation and bioprecipitation, thereby altering the bioavailability and toxicity of heavy metals. Moreover, microbial consortia, especially plant growth-promoting rhizobacteria (PGPR) and mycorrhizal fungi, enhance plant tolerance by improving nutrient uptake, hormone regulation and antioxidant activity, all of which are essential under heavy metal stress. The synergy among plant-microbe-metal systems contribute not only to phytoremediation but also to the restoration of soil health, fertility and microbial biodiversity in degraded ecosystems. Root exudates act as ecological gatekeepers in this synergy, selecting for metal-tolerant and functionally specialized microbial communities that drive soil detoxification and nutrient cycling. Thus, understanding and manipulating root exudation patterns can be a key strategy for improving the efficacy of bioremediation efforts. As metal contamination continues to threaten agroecosystems and food security globally, this integrated, nature-based approach offers a sustainable, cost-effective and environmentally friendly alternative to conventional remediation methods. The rhizosphere, when managed intelligently, can transform from a contamination site into a centre of biological resilience and recovery.

Way Forward

Future research should aim to deepen our understanding of the molecular and metabolic pathways through which root exudates interact with specific microbial taxa and heavy metals. Identifying key exudate compounds and engineering plants to selectively enhance the secretion of these metabolites could significantly improve phytoremediation efficiency. Similarly, isolating and applying custom microbial consortia that are well-adapted to root exudate profiles in contaminated soils can increase microbial resilience and metal-transforming activity. Moreover, integrating omics-based tools (metagenomics, metabolomics and transcriptomics) can unravel the underlying mechanisms of rhizosphere modulation. Field-scale studies, rather than confined pot trials, are essential to validate laboratory findings under real environmental conditions. Ultimately, a multidisciplinary approach combining soil science, plant physiology, microbiology and environmental biotechnology is vital to engineer rhizosphere systems that are robust, adaptive and capable of long-term remediation of heavy metal-polluted soils.

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Authors' contributions

SK carried out literature collection, conceptualization and writing original draft. BA carried out supervision, visualization and critical revision. KT, DP and MP carried out supervision and reviewing. All authors read and approved the final manuscript.

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