# Reconnoitering the Efficacy of Plant Growth Promoting Rhizobacteria in Expediting Phytoremediation Potential of Heavy Metals

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## Abstract

The abrupt release of heavy metals (HM) within environment by anthropogenic sources affect the living populations. Plants face many intricacies to survive under such conditions, therefore remediation of HM-contaminated soils is need of the hour. However, chemical processes are very costly and non-sustainable, henceforth HM-microbe associations play an integral role in reducing HM-stress from plants. Plants and microbes within rhizosphere are well adapted to metalliferous environment, thereby prove to be a best assistant for phytoremediation. Root exudates act as nutrients for microbes for establishment of inter-communication systems. Plant–microbe associations is a conducive dimension for phytoremediation, a low input, highly productive, and sustainable technology for maintaining HM-toxicity in soils. It is an emerging technology and is recommended for cleaning up the polluted sites, since plant growth promoting microbes (PGPM) have shown their effectively toward metal toxicity through their detoxification and resistance mechanisms along with growth promoting traits. Microbe-assisted phytoremediation is mainly facilitated either through direct or indirect manner. They synthesize various nutritional and phytohormonal substances namely, growth regulators, siderophores, enzymes, transformation of mineral nutrients (phosphate, potassium, nitrogen etc.). Further, they also modulate the metal detoxification, accumulation, and sequestration abilities of plants through secreting extracellular components, organic acids, biosurfactants, chelators etc. Besides, the metal bioavailability within soil is also modulated via different mechanisms like acidification, precipitation, complexation, or redox reactions. Apart from this, genetic engineering is a progressive approach that is combined with microbe-assisted phytoremediation to attain excellent results. The cumulative knowledge of transgenics, engineering designs, ecological knowledge is an essential element for phytoremediation using genetically engineered microbes. In this review, we have presented the advancement made hitherto for effective understanding of molecular, biochemical, and physiological mechanisms associated with plant–microbe interactions during phytoremediation. Along with this, we have shed light on the mechanisms involved in phytoremediation, therefore, this sustainable technology is widely accepted in reclaiming HM-toxicity to induce the yield and quality of soils and crops.

**Keywords** Heavy metals · Microflora · Phytoremediation · Growth stimulation · Metal detoxification · Sequestration · Transgenics · High-throughput sequencing

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## Introduction

With the advent of rapid industrialization and urbanization the agriculture sector has faced an abrupt elevation in heavy metal (HM) pollution globally. These are not degradable within soils and persist in soils for centuries that affect the entire ecosystem, agriculture, water bodies, soil microflora, and human health (Navarro-Torre et al. 2021; Kidd et al. 2012; Kong et al. 2019; Mishra et al. 2017). Excessive of HM concentrations within soil can be absorbed and accumulated by plants and can successfully enter the food chain

(Zhuang et al. 2014). HMs in plants inhibit enzymes, damage cell structures, generate oxidative stress by inducing reactive oxygen species (ROS) to disrupt the ionic homeostasis within plant cells (Sytar et al. 2013). Moreover, they also impede the metabolic activities of plants. However, plants possess certain defensive strategies to combat the toxicities but within certain limits, thereby, jeopardizing the plant (Clemens and Ma 2016). Therefore, it is crucial to de-contaminate the HMs from the environment so as to protect the soil and plant functioning and other organisms. In order to address this troublesome issue, there is an exigency for environmental cleanup of toxic metal contaminated soils. However, many of the remediation methods are chemical based that are costly as well as disparaging toward environment. Therefore, one of the best alternative is to use the hyperaccumulators assisted with friendly microflora as a promising approach to detoxify the environment through phytoextraction, phytostabilization, phytotransformation, phytovolatalization, and rhizoremediation, respectively (Ma et al. 2016a, 2016b; Nadeem et al. 2014; Mishra et al. 2017).

Since decades, several biological methods have been considerably used for remediation in which phytoremediation has attained a reputed position for HM removal. Phytoremediation employs plants with complete removal or stabilization of HMs or transform them into less toxic forms in situ. There are certain hyperaccumulators namely *Brassica juncea*, *Alyssum serpyllifolium*, *Sedum plumbizincicola*, *Arabidopsis halleri*, *Solanum nigrum*, *Solanum lycopersicum*, and *Thlapsi caerulescens* showing prominent results of phytoremediation (Wei et al. 2014; Ma et al. 2015; Yang et al. 2020). However, this technology has emerged more effective with the use of rhizospheric microbes. Rhizosphere is an area in the vicinity of roots with maximal microbial activity and root exudates play an essential role for microbial growth (Burdman et al. 2000; Kumar et al. 2022a, b, c). The root exudates and microbes maintains rhizospheric ecology and play substantial role in altering nutrient and metal bioavailability. They are chief source for nutrients and energy, while microbes in return boost exudation process (Feng 2022). Therefore, in this co-evolutionary process, microbe and plants either co-exist or compete with each other. They stimulate metal mobility through acidification caused by protons or by formation of complexes with organic acids, amino acids, or phytochelatins respectively. Other factors include electron transfer via enzymes (redox reactions) with which they stimulate phytoremediation efficacy (Sessitsche et al. 2013; Rabani et al. 2022). Soil microbes form complex networks within rhizosphere, subsequently participate in the ecological services and these interactions are conducive in determining the PGPM effectiveness for phytoremediation (Faust et al. 2016; Bhanse et al. 2022).

Microbe-assisted phytoremediation enables removal, detoxification, and sequestration of metal ions from polluted contaminants in an eco-friendly manner. Although, to understand its utilization it is necessarily important to focus on close interaction among plants and microbes (Fan et al. 2018; Navarro-Torre et al. 2021). Plant growth promoting microbes (PGPM) possess metabolic capacities for protecting plants against hazardous metal ions and preventing their accumulation within soil. For maintaining soil ecosystem, it is essential to improve the plant health and the microbial communities co-existing along with them. This is the most vital factor to enhance phytoremediation effectiveness (Ambrosini et al. 2016; Tiwari and Lata 2018; Rabani et al. 2022; Kumar et al. 2022a, b, c). Moreover, the PGPM nature, versatility, colonization ability, adaptability toward changing environment etc. are another factors that play integral role in effectiveness of this technique (Thijs et al. 2016). Researchers have found that PGPM mitigate metal toxicity and improve plant biomass in polluted soils (Ma et al. 2015; Arantza et al. 2022). Microbes stimulate phytoremediation in various ways, like expedition of plant biomass, phytostabilization, phytoextraction as well as bioaccumulation or translocation from soils (Ma et al. 2013). Strikingly, microbes possess resistant strategies due to their ability to produce an array of metabolites (Ma et al. 2015). Due to their properties of improving growth, metal toxicity alleviation, and other strategies they develop microbe-assisted and restoration phytoremediation strategies. Moreover, microbes also functions through the synthesis of phytohormones, siderophores, biosurfactants, organic acids, nutrient acquisition (nitrogen/potassium/phosphate), therefore, serve as bio-inoculants for assisted phytoremediation (Ahemad and Kibret 2014; Kumar et al. 2022a, b, c). There are various studies that are going on for assessing the microbial ecology, diversity and their potential to be used as phytoremediation agents. Hence, these interactions among plant roots and microbes within rhizosphere are critical part of phytoremediation. Bur the mechanisms underlying these processes are somehow elusive. Henceforth, in this review we have mainly focused on the understanding of biochemical and molecular basis of plant–microbe interactions with the special emphasis toward its role in phytoremediation. Moreover, the attention was given to microbe-mediated specific mechanisms for plant growth promotion, metal detoxification, mobilization, transformation, immobilization, accumulation, and translocation. Also, we have elaborated the mechanisms underlying interactions within rhizosphere (molecular signaling, perception, and quorum sensing). Finally, we have discussed about the role of genetic engineering or transgenics in the field of phytoremediation and various other strategies like illumina sequencing, high-throughput sequencing, and other strategies are also discussed in detail.

## Sources of Heavy Metals and Their Uptake/Toxicity in Plants

Within the environment, the HMs originates from variety of sources that are broadly categorized into natural and anthropogenic means. Natural includes particles from volcanic eruptions, sea salt, dust blown with winds, mineralization, wildfires, weathering of rocks, and vegetation. Weathering of rocks release high concentrations of metals like Cr, Pb, Cd, Ni, Mn, Hg, Zn, and Sn. Shale has high amount of HMs followed by sandstone and limestone (Nagajyoti et al. 2010).
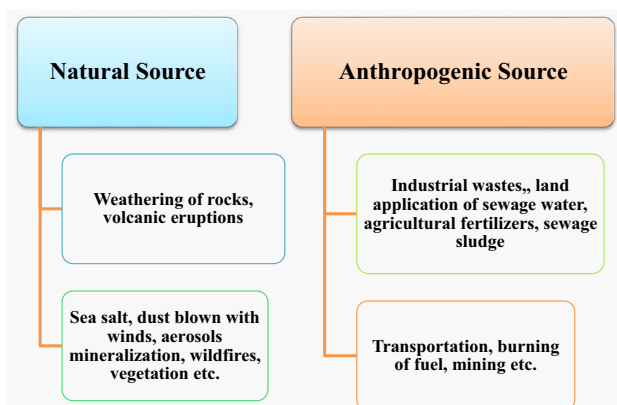


**Fig. 1** Schematic representation of Sources of heavy metals in environment

Wind-blown dusts, volcanoes, forest fires, marine aerosols also play role in transportation of HMs in ecosystem. Vegetation also act as mode of HM entry through decomposition of biomass, volatalization from leaves and stems. Anthropogenic means of HM includes industrial wastes, mining, land application of sewage water, agricultural fertilizers, sewage sludge transportation, and burning of fuel, Fig. 1. (Gupta et al. 2010; Edelstein and Ben-Hur 2018; Liu et al. 2022a, b). Coal mines, goldmines are major source of HM pollution as they release large amount of As, Hg, Fe, Cd etc. Mines wastes, industrial wastes, mine dust, accidental spilling, transportation, corrosion of metals etc. contaminate soil and water, making them unfit for agriculture and domestic purposes. HM-based pest killers are frequently applied to control pest attacks are also one of the major sources of HM pollution. Lead arsenate, a pesticide are used in orchards since decades contain higher amounts of Pb, Zn, and As (Nagajyoti et al. 2010). Many studies have documented the HM pollution in the environment through different means (Table 1).

Metals such as Fe, Cu, Mo, Zn, Co, Ni are important for plants and are considered as essential micronutrients or trace elements but when accumulated above the required amount results in toxicity (Gjorgieva Ackova 2018; Feng et al. 2022). In plants, some HMs show toxicity at very low concentration, whereas some plants have potential to bioaccumulate the toxins at higher levels without showing any toxic symptoms (Verkleij et al. 2009). Soil contaminated

**Table 1** Major sources of heavy metal pollution within ecosystem

| S. No | Source | Heavy metals | References |
|---|---|---|---|
| 1 | Coal combustion | Mn, Pb, Cd, As, Hg | Liang et al. (2017) |
| 2 | Petrochemicals | Cu, Zn, Cd | Xia et al. (2018) |
| 3 | Coal mining, Mining | Mn, Cr, Co, As, Cu, Ni | Klonowska et al. (2020) |
| 4 | Industrial means, Industrialized urban watershed | Pb, Cr, As, Cu, Zn, Cd | Xia et al. (2018) |
| 5 | Agricultural chemicals | Cu, Pb, Cd, Mn, As, Hg | Liang et al. (2017) |
| 6 | Livestock manure | Cu, Zn | Cheng et al. (2018) |
| 7 | Traffic | Cu, Zn | Cheng et al. (2018) |
| 8 | Geological minerals, ores, sulfide mineral | As, Pb, Mn, Cr, Cd, Hg | Cheng et al. (2018) |
| 9 | Volcanic eruption | Ni, Pb, Hg | Wu et al. (2020) |
| 10 | Dumped waste | Pb, Cu, Cd, Zn | Wu et al. (2020) |
| 11 | Indoor dust | Zn, Cr, Mn, Hg, Cu | Cheng et al. (2018) |
| 12 | Marine culture | Pb, Zn, Cu | Wu et al. (2020) |
| 13 | Textile/dyeing industries, electroplating industries | Cr, Cu, Cd, Pb, Ni, Co | Jiang et al. (2017) |
| 14 | Natural source, atmospheric deposition, industrial activities and agricultural activities | Zn, Cd, Cu, Hg, Pb, Sb, As, Mo, V, Mn, Fe, Cr | Liang et al. (2017) |
| 15 | Flood plain sites | Pb, Zn, Cu, Cd | Lamine et al. (2019) |
| 16 | Municipal solid waste | Cr, Pb, Cu, Zn | Vongdala et al. (2019) |

with HMs not only affects the quality of soil but also question the food quality and food safety.

Plants have well developed root and shoot system for uptake of nutrients, water, minerals etc. HMs can be accumulated in tissues through foliar transfer, xylem and phloem transportation (Schreck et al. 2012; Ngugi et al. 2022). Atmospheric particles gets deposited on leaf surface which then gets adsorbed and enter through cuticle followed by penetration through stomatal pores. Entry through the cuticle of leaf depends upon the particle size of HM and suggested to follow two distinct pathways. Lipohilic particles diffuse easily through cuticle (Larue et al. 2014a, b), whereas hydrophilic enter through stomatal and aqueous pores (Schreiber and Schonherr 2009). The small sized particles can penetrate through stomata as well as through cuticle (Xiong et al. 2014; Pasricha and Mathur 2021). Cuticle of sub-stomatal cells is comparatively thinner which makes entry through stomatal pathway easy (Roth-Nebelsick 2007). Metals like Co, Mn, and Cu can easily penetrate through the aerial parts of the plant (Ward 1990; Shahid et al. 2017; Ngugi et al. 2022). After entering through leaf surface, HMs undergo long distance transport via phloem toward other parts of the plant. Translocation inside the plant depends upon the HMs deposits onto epidermis, plant age, cuticle composition, and plant metabolism (Fig. 2).

HM-uptake have been predominantly reported via root system of the plants in contrast to foliar penetration. Plants raised under HM-contaminated soils or irrigated with polluted water exhibited higher accumulation (Enya et al. 2019; Ngugi et al. 2022) which also shows significant correlation with HM concentration in water and in plant tissues. HMs transportation through soil matrix toward roots depend upon pH, organic matter, particle size, chemical nature of metal, cation-exchange capacity, micro flora etc. which varies with

environmental conditions (Edelstein and Ben-Hur 2018). HM-ions are insoluble, unable to move by their own toward the vascular system of plants, so they form complexes for their free movement. Metal ions present in soil solution first gets adsorb onto root surface, followed by interaction with polysaccharides or carboxyl groups of root cells and mucilage uronic acids (Seregin and Ivanov 2001). Due to electrochemical gradient, plasma membrane (high negative potential) facilitates intake of metal ions. Heavy metal then follows two pathways in root cells, i.e., apoplastic and symplastic pathways via xylem loading (Kumar et al. 2022a, b, c; Ngugi et al. 2022; Pasricha et al. 2021; Pathak and Bhattacharya 2021). Various metal transporters, membrane transport proteins, chelators have been recognized which play significant role in transportation of metals toward aerial parts (Kaur et al. 2018; Khanna et al. 2019).

Plants are sensitive to deficiency as well as the excessive availability of essential trace elements. Higher concentration of metals like Hg, Pb, Cd, Cr, and As proves fatal for the normal metabolic activities of a plant (Shahid et al. 2020). HM-polluted soils have become a global issue due to their chronic effects on plant growth and development. Bioaccumulation of these metals in plants contaminates the whole ecosystem with their presence. Fruits, vegetables, cereals, nuts, and pluses all were documented to have high As, Pb, Ni, and Cd accumulation which proves fatal for humans (Hussain et al. 2019). Many studies have been carried out globally to understand the detrimental effects of HM on plants. Phytotoxicity of Cd, Pb, Zn, Hg, As, Cr, Ni was signified by downregulation of plant development and decreased productivity, hampered metabolic activities as well as oxidative damage (Ogunkunle et al. 2020; Zhao et al. 2020; Jung et al. 2019; Ribeiro et al. 2020). Ni toxicity reduced the germination potential of



**Fig. 2** Uptake and transportation of heavy metals in plants
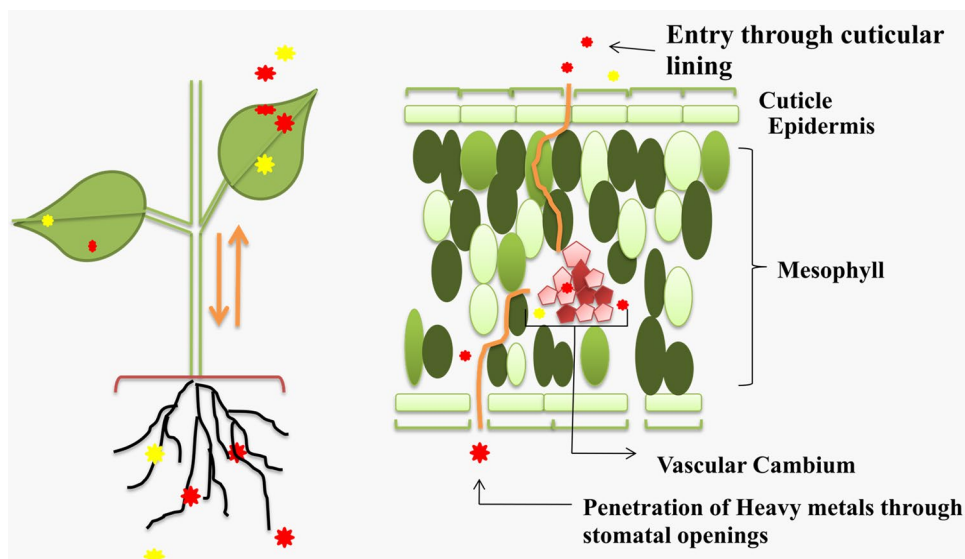
seeds, plant growth, and productivity. Moreover, it also causes necrosis, chlorosis, altered the photosynthesis, transpiration process, and oxidative stress in plants (Hassan et al. 2019). Toxic concentration of Hg can decrease the protein pool (Shahid et al. 2020), generation of ROS, altered photosynthesis (Nagajyoti et al. 2010), stomatal conductance, transpiration rate (Guo et al. 2015). Cr stress also induced visible damaged in plants which includes altered physiological processes like disrupted chlorophyll biosynthesis, inhibit photosynthesis by targeting PSII, oxidative burst, enzymes activies (Sharma et al. 2020). Mn stress leads to chlorosis, inhibited the uptake of other elements, ROS generation (Faria et al. 2020). High As levels induce wilting of leaves, necrosis, chlorosis of shoots, lipid peroxidation, chloroplast membrane damage, altered cellular biomolecules, decreased shoot and root growth (Bhadauria 2019). Symptoms of Pb phytotoxicity involve abnormal plant growth, ROS generation, DNA and cellular proteins, altered membrane integrity (Fig. 3) (Kohli et al. 2020).

## Phytoremediation of Heavy Metals

Phytoremediation is defined as green, clean, aesthetic, cost effective, and eco-friendly technology that utilizes the ability of plant species and associated microorganisms to remove toxic contaminants from the environment (Thakur et al. 2019; Laghlimi et al. 2015; Singh et al. 2022). As the name indicates, phytoremediation makes use of green plants to clean up the pollutants from the environment. This technology can be used for a broad range of organic and inorganic pollutants (Gupta et al. 2016). Plant roots release exudates in the rhizosphere and enhance the growth of soil microbes that are involved in the detoxification and degradation of contaminants (Saxena et al. 2020; Feng 2022).

The process of phytoremediation are most efficient where the concentration of contaminants range between low to medium levels, as high levels of contaminants hinder the growth of plant and microbes and reduce their activity (Malik et al. 2017; Anum et al. 2022). HMs are taken up by the plants by the same mechanism involved for the uptake,
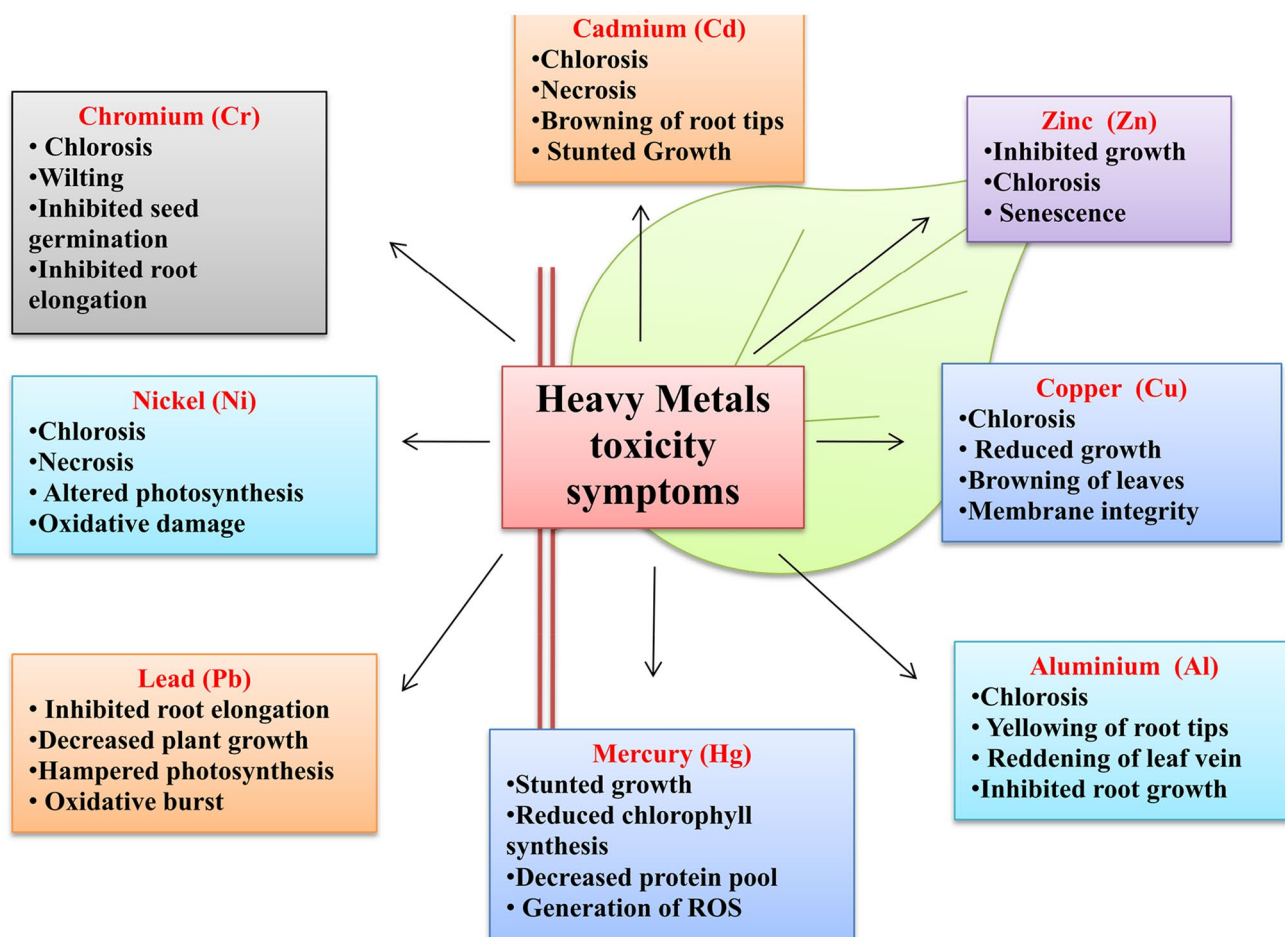


**Fig. 3** Phytotoxic symptoms of heavy metals

translocation, and storage of micronutrients (Subhashine et al. 2013; Ngugi et al. 2022). Plants used for phytoremediation process are the hyperaccumulators having high HM accumulation potential (Abbaszadeh-Dahaji et al. 2016; Kumar et al. 2022a, b, c). Hyperaccumulators are special plant species that are capable of accumulating large concentrations of HMs in them and tolerate extreme metal toxicity as compared to non hyperaccumulators (Sharma et al. 2016; Ojuederie and Babalola 2017; Yang et al. 2022). Hyperaccumulators store toxic pollutants store in their vegetative and reproductive parts. Also, plants with rapid growth, high biomass, extensive root system and high tolerance to pollutants are preferred (Manoj et al. 2020). As many as 45 families and 500 plant species have been identified which come under the category of metal hyperaccumulators (Jaffre et al. 2013; Ullah et al. 2015). It, therefore, is a promising green technology that has proven to be effective for both organic and inorganic pollutants and has been successfully applied to polluted soils and waters (Kumar et al. 2017; Ratna et al. 2021). Plants used for environmental clean-up also aid in keeping the soils intact and biologically productive and hence, it offers to be a non-destructive remedial measure against the pollutants. Apart from being one of the most environment friendly alternative for reclamation, it is also a cost-effective method wherein it requires little input in terms of nutrients and is easy to manage (Manoj et al. 2020; Agarwal et al. 2020). Although, it has been tested against both organic and inorganic pollutants, this technology has been widely applied in remediation of metal polluted soils. The technique has either been used solely with hyperaccumulator plants which comes under the category of direct phytoremediation or with plants supported by symbiotic microorganisms residing in soils in association with the roots and is known as indirect phytoremediation. Phytoremediation of HM-contaminated sites can be achieved via different strategies. These strategies include phytoextraction, rhizodegradation, phytostabilization, and phytovolatilization (Ma et al. 2016a, 2016b; Malik et al. 2017; Kumar et al. 2022a, b, c; Breton-Deval et al. 2022).

In case of phytoextraction plants remove heavy metals by absorbing them from the contaminated sites (soil and water) along with water and essential micronutrients and accumulate them in their harvestable parts (Muthusaravanan et al. 2018; Pathak and Bhattacharya 2021). *Alternanthera bettzickiana* was reported to be efficient in enduring Pb and Cd induced toxicity by changing the physiological attributes. *A. bettzickiana* was successful in accumulating higher concentrations of both metals in shoots (Tauqeer et al. 2016). Plant growth promoting bacteria are reported to improve the plant growth and also enhance metal uptake. Wang et al. (2019) reported that inoculation of *Brassica juncea* with *Burkholdria* SaMR10 and *Sphingomonas* SaMR12 promoted plant growth and enhanced phytoremediation

efficiency of Cd contaminated soils. Moreover, phytostabilization involves immobilization of the contaminants by adsorption, accumulation by roots, metal valence reduction, complexation, and precipitation in rhizosphere. This process reduces the bioavailability of contaminants by confining their movement and prevents their entry into food chain (Adiloğlu 2017; Muthusaravanan et al. 2018). *Miscanthus × giganteus* (M × G), is an important energy crop, that has the potential for the stabilization of Hg and Cd due to their less accumulation in aboveground biomass (Zgorelec et al. 2020). Ornamental flowers are proved to be the potential candidate for the phytostabilzation of Cd polluted soils. Zeng et al. (2018) documented that five ornamental plants *Osmanthus fragrans*, *Ligustrum vicaryi* L, *Cinnamomum camphora*, *Loropetalum chinense* var. rubrum, and *Euonymus japonicas* cv. Aureo-mar showed normal growth in soils having Cd concentration less than 24.6 mg·kg$^{-1}$. The plants accumulated high Cd concentration in roots as compared to shoots which indicates reduced translocation of Cd to other parts of the plant.

In addition, rhizodegradation involves the use of microorganisms (bacteria, fungi, and yeasts) for degradation of organic pollutants (Ely and Smets 2017; Anum et al. 2022). Microbes within rhizosphere degrade the pollutants as their metabolic activities are enhanced by the secretion of root exudates comprising of amino acids, carbohydrates, and flavonoids. The nutrients in the root exudates provides nitrogen and carbon to the soil microorganisms. And plants also liberate some enzymes which degrades organic contaminants in soils (Ali et al. 2013; Awa et al. 2020). Alongside, in phytovolatilization the plants are used for uptake/transformation of pollutants into less toxic and volatile forms which are subsequently released into the atmosphere through their foliage. It can be used for remediation of organic pollutants and HMs like Se and Hg (Chibuike and Obiora 2014; Ali et al. 2013; Liu and Tran 2021). Guarino et al. (2020) studied the potential of *Arundo donax* L. to endure and remediate water contaminated with very high concentrations of As. It was reported that the plant supplemented with *Stenotrophomonas maltophilia* sp. and *Agrobacterium* sp did not show any toxicity symptoms. As accumulation in plant biomass was comparatively low as most of it was efficiently volatilized by the plant.

## Plant–Microbe Reciprocity During Abiotic Stress Management

Plants and microbes co-occur or compete for endurance and their unified relations play an important role in changing the bioavailability of metals and nutrients. Root exudates of plant provide nutrients and energy to soil microbes which in turn stimulate the secretion of root exudates from plant roots.

Root exudates are good source of amino acids, organic acids, and phytochelatins (PC) which act as binding compounds for heavy metals (Mishra et al. 2017). PGPM like bacteria and fungi, may reduce metal phytotoxicity and stimulate the growth of plant by enhancing the solubilization of mineral nutrients like phosphate, nitrogen, iron, potassium and production of phytohormones(Ma et al. 2016a, 2016b; Bhanse et al. 2022). The synergistic association between plants and their associated rhizospheric microbes enhance the phytoremediation process in different ways (Rabani et al. 2022). Microbes impede plant growth, enhance plant biomass, metal solubility, modulate the soil structure by the production of plant growth promoting chemicals, organic acids, and polysaccharides (Ashraf et al. 2017; Wang et al. 2017). Microbes can assist phytoremediation by increasing (phytoextraction) or decreasing (phytostabilization) metal availability in soil, they also assist in translocation of metal from soil to roots (bioaccumulation) or from root to shoots (translocation) (Kumar et al. 2017; Pathak and Bhattacharya 2021). Inoculation of plants with microbes has shown amplified positive results on phytoremediation of heavy metals which are mentioned in the Table 2.

## Mechanisms of PGPR Governing Abiotic Stresses

Plants, as sedentary organisms, have to face a range of environmental adversities which inadvertently affect their normal growth and development by changes in morphology, physiology and molecular and cellular biology. Mostly, all abiotic stresses are associated with the excessive production and accumulation of ROS, which causes the alterations at physiological and biochemical levels (Paul et al. 2017; Khalid et al. 2021). Such an imbalance of ions results in damage to vital biomolecules such as proteins, carbohydrates, lipids and nucleic acids, thereby leading to altered metabolic processes which ultimately affect the overall growth and development of plants (Paul et al. 2017).Although, there is an internal defence mechanism that aids in plant protection, the role of communities of microflora and microfauna residing in the rhizosphere cannot be ignored which according to recent studies, have a significant contribution in inducing resistance against various abiotic stresses (Goswami and Deka 2020; Paul et al. 2017; Gavrilescu 2022). In this regard, plant growth promoting rhizobacteria (PGPR) have garnered much interest, and their variety of roles, not only in abiotic stress management, but also in crop protection and productivity are put into application. These are a group of bacteria which are explored for their diverse biological functions. The rhizosphere of higher plants, which is enriched with root exudates, is the nutrient enriched microhabitat which has a direct influence on the type of microbial species

flourishing it. Under the conditions of abiotic stress, through direct or indirect mechanisms, the PGPR are found to have an imperative role in regulating growth and development (Goswami and Deka 2020; Breton-Deval et al. 2022).

The PGPR have been explored for their ability to produce several phytohormones to combat stress in plants. Most common phytohormone produced by these microorganisms is auxin, typically indole-3- acetic acid (IAA), and at least 80% of rhizospheric bacteria synthesize it (Ahemad and Kibret 2014; Gavrilescu 2022). Rhizobacteria follow multiple pathways for IAA synthesis, and out of those, one is the making use of tryptophan released in the form of exudates by the plant roots and converting it into IAA (Ilangumaran and Smith 2017). This exogenous IAA is absorbed by plant roots and along with the endogenous IAA pool starts auxin signaling cascade (Ilangumaran and Smith 2017; Khalid et al. 2021). However, the working of rhizobacterial auxin is dependent on endogenous levels of auxins. It affects the plant growth and development by influencing cell division and elongation, seed germination, enhanced root development, increased rate of xylem formation, regulation of phototactic responses, biosynthesis of photosynthetic pigments, and several other metabolites. In case of salinity and drought stress, it has been established by Verbon and Liberman (2016) that production of IAA causes significant modifications in root structure and help in stress alleviation. The roots, under the influence of auxins, gain high biomass, surface area, and volume. This increases the capacity of roots to take up more water as well as mineral nutrients, and thus makes the plant capable to overcome water scarcity (Mantelin and Touraine, 2004; Egamberdieva and Kucharova 2009; Yang et al. 2020). Conversely, the rhizobacterial IAA also aids in loosening of the cell walls of roots which in turn enhances the root exudation, thereby promoting the rhizobacterial growth (Ahemad and Kibret 2014).

Ethylene is a plant hormone that has inhibitory effect on plant growth and development and it is known to expedite leaf senescence thereby leady to poor crop performance. Elevation in endogenous ethylene levels are seen in both biotic and abiotic stress (Ahemad and Kibret 2014). Such response is attributed to its repressive effects on auxin response factors (Ilangumaran and Smith 2017; Agarwal et al. 2020). PGPR, on the other hand, are known to possess an enzyme called 1-aminocyclopropane-1-carboxylase (ACC) deaminase which aids in restricting the biosynthesis of ethylene in plants. This enzyme acts on ethylene precursor ACC and metabolizes it into ammonia and α-ketobutyrate. Such activity lowers the levels of ethylene in the plants and consequently its inhibitory effects are also reduced (Paul et al. 2017; Ratna et al. 2021). The bacteria producing ACC deaminase are known to commonly reside on root surfaces and regulate root and leaf growth by influencing ethylene signaling (Bashan and Holguin

**Table 2** Microbial-assisted phytoremediation of different heavy metals

| S. No | Heavy metal (Conc.) | Micro-organisms | Plant species | Role of micro-organisms in phytore-mediation | References |
|---|---|---|---|---|---|
| 1 | As (150, 300 mg kg$^{-1}$) | Agrobacterium radiobacter | Populus deltoides | Enhanced growth, uptake and trans-location of As | Wang et al. (2011) |
| 2 | Cd (5, 10, 25, 50, 100 ppm) | Arbuscular mycorrhizal fungi | Ipomoea aquatica | Improved biomass, Cd-accumulation in plant roots as compared to shoots | Bhaduri et al. (2019) |
| 3 | As (83.60 mg kg$^{-1}$) | Rhodococcus sp.TS1, Delftia sp.TS33, Comamonas sp.TS37, Delftia sp.TS41, and Streptomyces lividans sp. PSQ22 | Pteris vittata | Improved plant growth, accumula-tion of As in plant tissues | Yang et al. (2012) |
| 4 | Cr (1977.8 mg kg$^{-1}$) | Bacillus licheniformis | Brassica alba | Higher accumulation of Cr in shoots | Brunetti et al. (2012) |
| 5 | Ni (100, 250, 500, 1000 ppm) | Bacillus licheniformis NCCP-59 | Oryza sativa L | Improved plant growth, chlorophyll, carotenoids, total protein and nitrogen | Jamil et al. (2014) |
| 6 | Ni (6 mM) | Arthrobacter sp, Microbacterium oxydans | Noccaea caerulescens | Improved plant growth, biomass of shoot and enhanced uptake of Ni | Visioli et al. (2014) |
| 7 | Ni (100 mg kg$^{-1}$), Cd (100 mg kg$^{-1}$),Cr (150 mg kg$^{-1}$) | Pseudomonas aeruginosa KP717554, Alcaligenes feacalis KP717561, and Bacillus subtilis KP717559 | Brassica juncea | Enhanced root and shoot length, fresh and dry weight, translocation of metals from roots to shoots | Kamran et al. (2016) |
| 8 | Ni (150, 250,5000 ug g$^{-1}$) | Pseudomonas putida | Eruca sativa | Increased root and shoot length, biomass, chlorophyll, proline and nickel uptake | Kamran et al. (2016) |
| 9 | Cu(400 mg kg$^{-1}$), Zn (500 mg kg$^{-1}$) | Pseudomonas libanensis TR1 and Pseudomonas reactans Ph3R3 | Brassica oxyrrhina | Improved plant growth, relative water of leaf and chlorophyll. Enhanced organ metal content, translocation of Cu and Zn | Ma et al. (2016a, 2016b) |
| 10 | Ni (200 mg kg$^{-1}$) | Bacillus thuringiensis 002, Bacillus fortis 162, Bacillus subtilis 174, and Bacillus farraginis 354 | Althea rosea | Improved biomass and enhanced uptake of nickel in plants | Khan et al. (2017) |
| 11 | Cd 100 μM | Enterobacter sp. | Hibiscus cannabinus | Better plant growth, enhanced uptake of Fe and immobilization of Cd$^{2+}$, with reduced accumula-tion of Cd | Chen et al. (2017) |
| 12 | Cr (40, 80, and 120 (mg L$^{-1}$) | Bacillus cereus T1B3 | Vetiveria zizanoides | Increased root, shoot length, fresh and dry weight, Cr accumulation, chlorophyll and protein content with altered enzymatic antioxidant activities | Nayak et al. (2018) |
| 13 | Cu | Pseudomonas fluorescens | Suaeda vera | Enhanced Cu-accumulation in roots and shoots of plant | Gómez-Garrido et al. (2018) |

**Table 2** (continued)

| S. No | Heavy metal (Conc.) | Micro-organisms | Plant species | Role of micro-organisms in phytoremediation | References |
|---|---|---|---|---|---|
| 14 | Cu | Paenibacillus mucilaginosus and Sinorhizobium meliloti | Medicago sativa | Increased activities of antioxidant enzymes along with translocation of Cu in plant tissues | Ju et al. (2019) |
| 15 | Cd(2 μM) | Burkholderia SaMR10 and Sphingomonas SaMR12 | Brassica juncea L. Var. Xikouhuazi | Increased shoot and root length with Cd accumulation in shoots and roots | Wang et al. (2019) |
| 16 | Ni (450 mg kg$^{-1}$) | Pseudomonas libanensis TR1 and Claroideoglomus claroideum BEG210 | Helianthus annuus | Improved plant growth, altered electrolyte leakage, and enhanced chlorophyll, proline and Ni accumulation | Ma et al. (2019) |
| 17 | Cr (10, 25 mg/L) | Bacillus sp. MH778713 | Prosopis laevigata | Inoculated plant showed increased plant weight, length of leaves and stems | Ramírez et al. (2019) |
| 18 | Ni (30 mg kg$^{-1}$), Pb (16 mg kg$^{-1}$) | Trichoderma harzianum | Arundo donax | Improved plant growth, enhanced bioaccumulation and translocation of metals | Cristaldi et al. (2020) |
| 19 | Cd (1 mg kg$^{-1}$) | Penicillium janthinellum | Cynodon dactylon | Higher capacity for Cd$^{2+}$ absorption, enhanced indole-3-acid (IAA), and plant growth, Cd uptake in the stem and roots | Xie et al. (2021) |
| 20 | Pb (600 mg kg$^{-1}$) | Rhizobacteria | Sonchus asper | Enhanced sequestration and phytoremediation potential | Mei et al. (2022) |
| 21 | Ni (15 mM) Pb (9 mM), As (8 mM) Cd (2 mM) | Rossellomorea vietnamensis | Arthrocnemum macrostachyum | IAA and siderophore biosynthesis and upregulation of transporters genes and genes related to HM resistance | Navarro-Tore et al. (2021) |
| 22 | Pb (1.5 mg/L) | Bacillus cereus | Pistia stratiotes, Eichhornia crassipes | Pb removal done via rhizofiltration mechanism | Zahari et al. (2021) |
| 23 | Cd (20 mg/kg), Cr (20 mg/kg), Pb (100 mg/kg) | Pseudomonas putida | Trifolium repens | improved soil fertility phytoremediation | Liu et al. (2021) |
| 24 | Cu, Pb | Bacillus cereus, Paenibacillus alvei, Aeromonas caviae, Paenibacillus taiwanensis, and Achromobacter spanius | Eichhornia crassipes | Higher and effective phytoremediation potential | Kabeer et al. (2022) |
| 25 | As, Pb, and Zn | Bacillus simplex and Bacillus atrophaeus, AM fungi | Lygeum spartum | Enhanced Bioaccumulation factor, translocation factor, and the mobility ratio with lowered lipid peroxidation, free proline, non-protein thiols, and reduced glutathione | Terwayet Bayouli et al. (2022) |

| S. No | Heavy metal (Conc.) | Micro-organisms | Plant species | Role of micro-organisms in phytoremediation | References |
|---|---|---|---|---|---|
| 26 | Fe, Mn, Pb, Cd, Cr, Cu, Zn, Ni, As, and Hg | *Brevundimonas* sp. | *Saccharum munja* L. | Enhanced ligninolytic enzymes, hydrolytic enzymes, IAA, and siderophores | Sharma et al. (2022a, b) |

**Table 2** (continued)

1998; Paul et al. 2017). Abscisic acid (ABA) is another stress hormone which shows accumulation chiefly during water and salt stress (Paul et al. 2017). It has a vital role in regulation of rate of transpiration through stomatal movement. During stress conditions, its accumulation leads to stomatal closure, thereby leading to reduced transpiration rate and hence, enhanced tolerance to stress. Studies have demonstrated that PGPR that produce ABA, increase the tolerance of plants toward stress (Paul et al. 2017; Ratna et al. 2021).

PGPR are also reported to be actively involved in maintaining the osmotic balance of the stressed host plants, in particular subjected to water or salt stress. Release of osmolytes or compatible solutes is a common mechanism of stressed plants to overcome water deficit conditions which helps in restoring the osmotic potential. Rhizobacteria that encounter osmotic fluctuations in their environment have been observed to synthesize and accumulate compatible solutes in their cytoplasm (Kempf and Bremer 1998; Ilangumaran and Smith 2017; Feng 2022). Also, it has been established that rhizobacteria can quickly synthesize osmolytes such as proline, glycine betaine, and trehalose in comparison to their host plants and the same get exuded into the rhizosphere (Ilangumaran and Smith 2017; Kumar et al. 2022a, b, c). These rhizobacterial osmolytes get absorbed by plant root, act synergistically with endogenous osmolytes and help in osmoregulation, thereby improving the survival of the stressed plants (Ilangumaran and Smith 2017; Paul et al. 2017; Kumari et al. 2022). Other than osmotic balance, PGPR are also actively involved in maintaining ionic balance of stressed plants. Mainly during high salinity conditions, the rhizobacteria curtail the salt uptake by roots through regulation of ion affinity transporters, causing alterations in the external toot structure or trapping the harmful cations in exopolysaccharide matrix (Ilangumaran and Smith 2017). It has been established that rhizobacteria can enhance the nutrient availability to plants through inducing the changes in pH by release of organic acids, enhancing chelation of metal ions through siderophores and increased mineralization (Lugtenberg et al. 2013). The increased macro and micro mineral nutrient exchange in turn restricts the influx of sodium ($Na^+$) and chloride ($Cl^-$) ions (Ilangumaran and Smith 2017; Feng 2022). Also, PGPR maintain ion homeostasis and ameliorate stress by inducing exclusion of $Na^+$ ions from roots, activating $K^+$ transporters and reducing the accumulation of $Na^+$ and $Cl^-$ in leaves (Ilangumaran and Smith 2017). They aid in amelioration of abiotic stress via growth promotion during unfavorable conditions as the healthier plant is better able to cope with stress; secondly, by complementing the plant stress tolerance mechanisms. PGPR-elicited tolerance against several abiotic stresses is often referred to as induced systemic tolerance (Ratna et al. 2021).

## PGPR in Plant Growth and Development

The PGPR competitively colonizing in the rhizosphere can promote plant growth through several direct and/or indirect mechanisms, which depend upon both the plant species and the bacterial strain (Tiwari and Lata 2018; Kumari et al. 2022; Singh et al. 2022; Breton-Deval et al. 2022). Particularly, the direct actions include their ability to regulate phytohormones levels and facilitate plant nutrient (N, P, K, and Fe) acquisition, while indirect mechanism mainly comprises their biocontrol potential (Ratna et al. 2021).

### Nutrient Acquisition

As nutrients are indispensable for proper growth and functioning of plants, therefore, nutritional deficiencies often lead to stunted growth, chlorosis, development of purplish-red colouration, or necrosis in plants (Fan et al. 2018). Predominantly, the nutrients are organically bound in the soil and consequently, they are stable and have limited bioavailability. Having excellent metabolic machinery to mineralize and depolymerize organically bound nutrients, soil microorganisms actively assimilate these nutrients, which are subsequently available for plant nutrition upon microbial turnover (Liu and Tran 2021). PGPR can enhance not only the nutrient bioavailability but also nutrient uptake in plants (Fan et al. 2018). Some rhizobacteria elevate nutrient acquisition by modulating root morphology while others may stimulate root's nutrient transporter genes (Yang et al. 2020). Hence, plants rely upon soil microbes for mineral nutrition.

Even though Earth's atmosphere constitutes 78% of $N_2$, still N is one of the major growth limiting factors for plants because they cannot directly utilize molecular nitrogen for their nutritional requirements. Processes like biological nitrogen fixation (BNF), atmospheric lightning, and industrial fixation (Haber–Bosch process) transforms the atmospheric $N_2$ to plant usable forms such as $NH_3$ and $NO_3$. BNF is carried out by biological nitrogen-fixing microbes in symbiotic or non-symbiotic association contributes to about two-thirds of total nitrogen fixed globally (Yang et al. 2020). The nitrogen-fixing bacteria known as diazotrophs contain the nitrogenase enzyme complex, which is responsible for catalytic reduction of $N_2$ to $NH_3$ (Ratna et al. 2021). The diazotrophs have either symbiotic or non-symbiotic interaction with their host. The symbionts usually form root nodules on either on legumes (e.g., rhizobia) or non-legumes (e.g., *Frankia*), while the non-symbionts (e.g., *Azotobacter*, *Anabaena*, *Azospirillum*, *Azoarcus*, *Herbaspirillum*, *Azoarcus*, and *Gluconoacetobacter diazotrophicus*) may be free living, associated or endophytic (Ahemad and Kibret 2014; Yang et al. 2022). Moreover, plants readily absorb P as monobasic ($H_2PO_4^-$) and dibasic ($HPO_4^{2-}$) phosphate forms; however, P is mainly present as insoluble inorganic/organic forms in

natural ecosystems. PGPR can solubilize or mineralizes the insoluble forms, particularly, inorganic forms by secreting mineral dissolving substances such as organic acids, protons, and siderophores while, organic forms by releasing alkaline/acidic phosphatises and phytases (Agarwal et al. 2020). Predominantly, organic acids enhance solubility of inorganic P through acidification, chelation of cations bound to P or competition with P for soil adsorption sites. Although gluconic and 2-ketogluconic acids are the most commonly reported organic acids secreted by phosphate solubilizing rhizobacteria, other acids reported are tartaric, formic, acetic, oxalic, lactic, malic, citric, succinic, and propinoic acid (Rai et al. 2020; Feng 2022). Bacteria belonging to genera *Pseudomonas*, *Rhizobium*, and *Bacillus* are the most powerful inorganic P solubilizing rhizobacteria. Additionally, *Achromobacter*, *Agrobacterium*, *Aereobacter*, *Burkholderia*, *Erwinia*, *Flavobacterium*, and *Microccocus* genre also exhibit ability to solubilize inorganic phosphate factions, for example, $Ca_3(PO_4)_2$, $CaHPO_4$, and hydroxyapatite. On the other hand, phosphatases such as phytase hydrolyze the organic phosphate mainly originating from plant and animal remains into inorganic P for plant assimilation, and this process play a significant role in P cycling (Singh and Satyanarayana 2011; Khalid et al. 2021).

Although K is a 7th most abundant element in the Earth's crust, majority (99–98%) of it is bound with other minerals making it unavailable for plants absorption. Several bacteria species such as *Acidithiobacillus ferrooxidans*, *Burkholderia*, *B. mucilaginosus*, *B. edaphicus*, *B. circulans* and *Paenibacillus* (Liu et al. 2021), *Agrobacterium tumefaciens*, *Rhizobium pusense* (Meena et al. 2016), *Bacillus licheniformis*, *Pseudomonas azotoformans* (Saha et al. 2016), *Pantoea ananatis*, *Rahnella aquatilis*, and *Enterobacter* sp. are reported to liberate K from insoluble minerals and stimulate plant growth. Moreover, P solubilizing bacteria can also improve K bioavailability in the rhizosphere and K uptake in the plant tissues since these bacteria employ similar mechanisms for K solubilization such as proton extrusion and organic acid synthesis (Bakhshandeh et al. 2017).

Iron is indispensable for proper growth and development of all organisms owing to its participation various primary metabolic processes such as photosynthesis, respiration and reduction of $N_2$ and ribonucleotides; however, Fe acquisition is a big challenge for both the plants and microbes (Arantza et al. 2022). Fe bioavailability in the soil is principally, regulated by soil pH and redox potential. For instance, if the soil pH is low, Fe exist as $Fe^{2+}$ (soluble form) that is available for root uptake, whereas at physiological pH (7.35–7.40) or under aerobic conditions $Fe^{2+}$ gets oxidized and mainly exists as insoluble $Fe^{3+}$ oxides or hydroxides (Saha et al. 2016; Kumari et al. 2022). In order to meet its Fe demand under Fe limiting circumstances, microorganisms synthesize low molecular weight iron-chelating compounds known as

siderophores, which regulate and augment Fe bioavailability in the rhizosphere. In bacteria, transport systems that transport the siderophore-$Fe^{3+}$ complex into cell vary in gram negative and positive bacteria, detail reviewed by Ahmed and Holmström (2014). However, once the complex reaches inside the cytosol, $Fe^{3+}$ions are reduced back to $Fe^{2+}$ and the freed siderophore molecules are either degraded or effluxed out for recycling (Saha et al. 2016; Bhanse et al. 2022). On the other hand, bacterial siderophores improve Fe acquisition in plants that are capable of recognizing siderophore-$Fe^{3+}$ complex (Ratna et al. 2021). Additionally, *Paenibacillus polymyxa* is reported to stimulate Fe acquisition by secretion of IAA and phenolic compounds, which improves plant root architecture and Fe mobilization in calcareous or alkaline soils, respectively. Moreover, *P. polymyxa* also simulated Fe-deficiency-induced transcription factor 1, which lead to up-regulation of Fe uptake genes, particularly ferric chelate reductase (FRO2) and membrane localized divalent metal transporter, Iron-Regulated Transporter 1 (IRT1) revealing the potential of rhizobacteria to trigger plant's Fe uptake machinery. Similarly, PGPR *Azospirillum brasilense-can* improved Fe acquisition in plants by regulating both the Fe availability in the rhizosphere and plant's Fe acquisition mechanism. Furthermore, rhizobacteria can also impact Fe nutrition in plant roots and leaves by releasing organic acids in addition to its availability in soil (Singh et al. 2022). Siderophores are proficient in not only solubilizing Fe but also large array of metals and radionucleotides (Rajkumar et al. 2012).Thus, siderophore secreting PGPR execute a momentous role in phytoremediation of heavy metal contaminated sites by stimulating metal availability and plant growth (Ma et al. 2016a, 2016b; Feng 2022).

## Modulation of Phytohormone Levels

Since phytohormones control diverse growth and developmental processes as well as stress responses in plants, the tendency of PGPR to secret phytohormones is also implicated in plant growth promotion and stress tolerance (Mashabela et al. 2022). Several PGPR are capable of inducing changes in root system architecture and root structure, which are linked to their ability to modulate phytohormones homeostasis involved in root development, particularly, auxin to cytokinin ratio (Bhat et al. 2022). Predominantly, PGPR colonization restricts elongation of primary root instead promotes development of lateral roots and root hairs by altering cell differentiation and division, which leads to improved shoot growth (Verbon and Liberman 2016). These changes ultimately influence root functioning plant's nutritional status (Choudhury et al. 2022).

Auxins are group of plant growth promoting hormones that controls almost every aspect of plant growth and development such as seed germination, vegetative growth, embryogenesis, fruit ripening, shaping plant architecture, photosynthesis, responses to light and gravity, cell division, expansion and differentiation, biosynthesis of metabolites and stress tolerance (Bhat et al. 2022). IAA is a predominant naturally occurring auxin in plants and acts as a signaling molecule in plant–microbe interactions. At a particular site, response of auxin is usually concentration dependent. The higher exogenous auxin concentration may even have inhibitory effect and therefore plants possess various mechanisms for maintenance of auxin homeostasis (Choudhury et al. 2022). However, PGPR modulate various plant developmental processes by altering plant's endogenous IAA levels by exogenously supplying IAA (Ahemad and Kibret 2014; Zeng et al. 2022). Exogenously applied IAA has concentration dependent effects on plant root architecture, for example, at low concentrations it promotes primary root development, whereas at high concentrations stimulates proliferation of lateral roots. PGPR can regulate root architecture by either directly providing IAA to the plant or modulating plant IAA levels by regulating auxin-responsive genes (Mashabela et al. 2022).

Although ethylene regulates plant growth, development, and senescence, it promotes or inhibits these physiological processes depends upon its concentration and plant species. Ethylene concentration generally elevates in response to environmental stress conditions and beyond the threshold level, ethylene inhibits plant growth (Singh et al. 2011; Choudhury et al. 2022). Several PGPR bacteria possess ACC (1-aminocyclopropane-1-carboxylate) deaminase enzyme that enables bacteria to utilize plant ACC as a nitrogen and carbon source. ACC is a precursor of ethylene biosynthesis, thereby its hydrolysis into α-ketobutyrate and ammonia lowers plant's ethylene levels. Therefore, ACC deaminase producing rhizobacteria are an eco-friendly solution to cope with diverse environmental stresses by normalizing stress ethylene levels and restoring plant growth and development (Bhattacharyya et al. 2022; Singh et al. 2022; Mashabela et al. 2022).

Cytokinins producing bacteria can manipulate host's growth and endogenous hormone levels and help host plant to cope drought stress by alleviating water stress induced shoot growth inhibition (Zeng et al. 2022). Additionally, these bacteria also modify root exudations to promote rhizobacterial colonization on the plant root surfaces and confer resistance against pathogenic microbes (Vocciante et al. 2022). Thus, bacterial cytokinins have not only role in bio-stimulation but also in protection against pathogens. However, both beneficial and pathogenic microorganisms produce cytokinins, they have antagonistic effects on plants, and this warrants further elucidation of exact mode of action of these microbial synthesized cytokinins (Vocciante et al. 2022). Similarly, gibberellin synthesizing bacteria,

for example, *Bacillus cereus, B. macroides*, *B. pumilus*, *B. amyloliquefaciens* (Shahzad et al. 2016), *Acinetobacter calcoaceticus* (Kang et al. 2007), and *Promicromonospora* sp. (Kang et al. 2007) are also reported to improve plant growth by influencing plant's endogenous hormone levels.

### Biocontrol Potential

Antagonistic action of PGPR against phytopathogens is generally attributed to their capability to synthesize antibiotic or other metabolites and induce plant systemic resistance against diverse plant pathogens (Bhat et al. 2022). In addition, PGPR's ability to compete for nutrients and niches with pathogenic microorganisms are also responsible for suppression of these plant pathogens. For example, siderophores synthesized by PGPR such as *Azotobacter*, *Bacillus*, *Enterobacter*, *Pseudomonas*, and *Serratia* can subdue the proliferation of plant pathogens by limiting the availability of $Fe^{3+}$ for them (Ali et al. 2020; Della Monica et al. 2022).

### Direct Mechanism of Phytoremediation

Plants, when exposed to metal contaminated soils, adopt various phytoremedial techniques and aid in cleaning up the soils and waters such as phytostabilization, phytoextraction, phytovolatilization, and phytofiltration (Fig. 4).

### Phytostabilization

It is the technique in which plants are used to reduce the bioavailability of HMs in the contaminated soils (Yan et al. 2020; Yang et al. 2022). It is chiefly employed on soils which are highly contaminated with HMs and these can become the sources of metal dispersion in the environment (Sabir et al. 2015; Liu and Tran 2021). HMs are stabilized in the soil with the help of phytostabilizing plants which keep the metals in below ground parts by immobilizing them (Marques et al. 2009; Sabir et al. 2015; Ratna et al. 2021). These plants regulate soil erosion, prevent leaching, and release organic compounds that bind to the metal ions in the soil and this
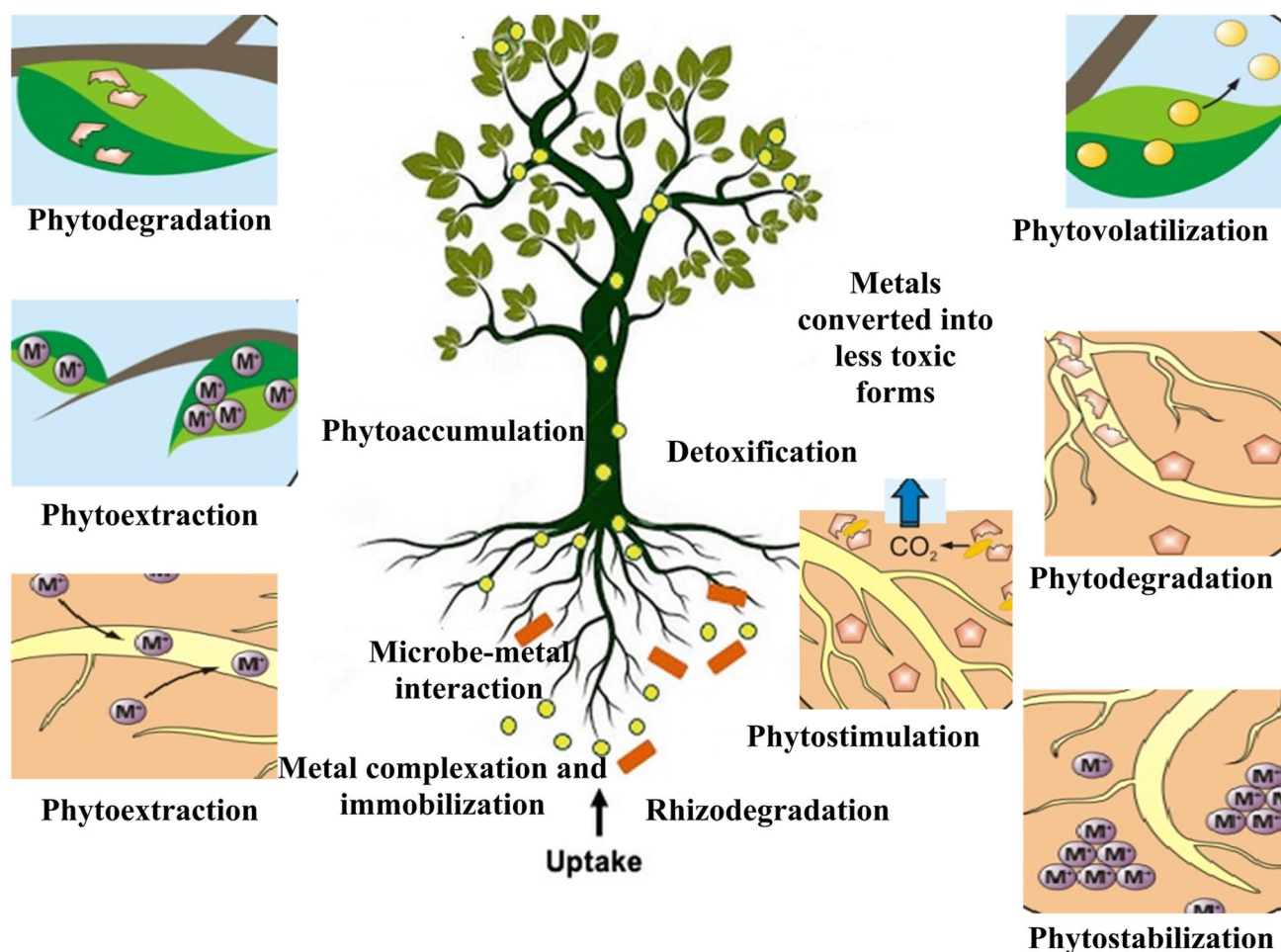


**Fig. 4** Schematic presentation of Direct Mechanism of Phytoremediation process

helps in immobilizing the metals in the rhizosphere thereby restricting their bioavailability. Such immobilization also restricts their translocation to above ground plants parts and binding makes them less toxic for both plants and animals (Sabir et al. 2015; Anjum et al. 2022). Metal sequestration by plants usually occurs by adsorption on the surface of roots, precipitation into carbonates and sulfides of metals which are less soluble, formation of complexes by organic compounds released by plant roots and accumulation of metals ions in the root tissues (Wong 2003). Apart from these, organic acids released in the rhizosphere also reduce the availability of metal ions in the soil (Sabir et al. 2015; Kumari et al. 2022). Also, it has been reported that metal ions can bind to the pectins present in the cell walls of the roots which restricts the mobility of these ions. Similarly, the negatively charged surfaces of the membranes can arrest the ionic movement by binding to them due to their electrochemical potential (Sabir et al. 2015; Anjum et al. 2022). Another way that the phytostabilizing plants detoxify substratum from metal ions is by the release of redox enzymes which reduce their valency thereby converting them into less toxic form (Ali et al. 2013).

## Phytoextraction

Phytoremediating plants take up contaminants and store them in their above ground parts, then the technique is known as phytoextraction. This technique has attracted a lot of attention recently and has become one of the most followed methods for reclamation of polluted sites as it offers a permanent solution to the problem. (Ali et al. 2013; Sarwar et al. 2017; Choudhury et al. 2022). For phytoextraction to be effective, the primary requirement is the mobility of heavy metals in the soils as plant roots are unable to take up immobile metal derivatives from the rhizosphere. Therefore, mobility of metal ions also becomes the first step of phytoextraction which is followed by their uptake by the roots of phytoremediating plants (Yan et al. 2020; Yang et al. 2022). Once the metal ions enter the root system, they now are translocated to the upper or aerial parts of the plants through xylem (Sabir et al. 2015; Yan et al. 2020; Ratna et al. 2021). In the aerial parts, the metal ions are sequestered and compartmentalized in plant tissues. The common sites include epidermis, trichomes, and cuticle (Rascio and Navari-Izzo 2011; Pasricha et al. 2021). Apart from these, leaf vacuoles have also been found to be the sites of metal sequestration as tonoplast of these vacuoles have shown enhanced metal transport (Sabir et al. 2015; Kumar et al. 2022a, b, c). The processes of metal sequestration and detoxification are under genetic control as metal ion exclusion and transfer across membranes is regulated by specific proteins (Sabir et al. 2015; Singh et al. 2022).

The major factor for efficient phytoextraction is the selection of the plant species. They should be highly tolerant to the toxic concentrations of heavy metals. Also, the phytoextracting plants should have the ability to accumulate high concentrations of metal ions in their above ground parts. In addition, it is highly preferable that these plants have high biomass, abundant shoots, and quick growth which will enable them to store high levels of metal ions. For supporting all these attributes, it also becomes imperative that these plants should have an extensive and well growing root system. As polluted sites have poor environment and adverse growth conditions, the phytoextracting plants should have the ability to adapt themselves to grow in these surroundings. Furthermore, to prevent HMs from entering the food chain, the phytoextracting plants should preferably be resistant to pathogens, pests, and herbivores (Seth 2012; Ali et al. 2013; Yan et al. 2020; Pathak and Bhattacharya 2021). Once the choice of plant is made, then the key drivers of phytoextraction efficacy are type of soil, bioavailability of heavy metals, and properties of rhizosphere (Yan et al. 2020). Apart from all these, bioconcentration factor, which is the ratio of concentration of metal in shoots to metal concentration in soil, is an important parameter widely used to gauge the efficiency of uptake and translocation by the plant (Sabir et al. 2015; Rai et al. 2020). The values of bioconcentration factor help determining the plants suitable for phytoextraction. The plants having the values more than 1 are put under the category of hyperaccumulators and can be recommended for phytoextraction (Sabir et al. 2015). It has also been suggested in a study on Zn phytoremediation that its hyperaccumulation and tolerance are controlled by separate genes (Macnair et al. 1999). Moreover, hyperaccumulation can only be achieved if plants have high tolerance toward toxic levels of metals and there is efficient transfer from roots to shoots (Sabir et al. 2015; Sharma et al. 2022a, b).

At cellular level, detoxification of metals in tissues during phytoextraction occurs chiefly by their chelation by ligands. When the metal ions enter the cytosol, the organic molecules bind to these ions and prevent them from harming the active sites in the cells. These ligands can be several organic acids, amino acids, and peptides (Cobbett and Goldsbrough 2002; Feng 2022). Also, phytochelatins and metallothioneins are two chief, and one of the most effective polypeptides that are widely involved in metal detoxification through chelation (Sabir et al. 2015). Other thiol group containing biomolecule is glutathione that participates actively in metal detoxification. Its high potential against the metal ions can be attributed firstly to its ability to form mercaptide bonds with metals, and secondly to its presence in almost all cellular compartments like chloroplast, mitochondria, endoplasmic reticulum, and cytoplasm (Mullineaux and Rausch 2005; Rausch et al. 2007; Yadav 2010; Khursheed et al. 2022). Glutathione is a multifaceted biomolecule which is

also involved in ascorbic-glutathione pathway where it participates in scavenging of reactive oxygen species produced as a result of oxidative stress caused by metals. It also has the ability to form conjugates with metals and other xenobiotics through glutathione -S- transferase which are then transported to the vacuole (Yazaki 2006; Sabir et al. 2015; Khalid et al. 2021).

## Phytovolatilization

Volatilization of soil contaminants with the help of plants and their diffusion into the air is termed as phytovolatilization. This mechanism is chiefly used for organic contaminants, however, certain metals such as mercury, arsenic, and selenium are also known to be converted to their volatile derivatives by plants (Sabir et al. 2015; Limmer and Burken 2016; Yan et al. 2020). The major concern with this technique is the risk of pollutants being still present in the atmosphere as they are simply transferred from soil to air and these can enter the soil again with precipitation (Yan et al. 2020; Della Monica et al. 2022). Therefore, it is usually suggested to conduct a risk assessment before applying this technique in the field. However, some researchers also argue that ambient air will be less contaminated even if pollutants are released as they get dispersed, diluted, and undergo photochemical decay in the atmosphere (Sabir et al. 2015; Limmer and Burken 2016). Still, in urban areas which are assumed to have poor air quality, the risk assessment is recommended (Limmer and Burken 2016; Pasricha et al. 2021).

The process of phytovolatilization has been described to exist in two distinct forms. The first being direct phytovolatilization process which requires the contaminants to be taken up by the plants, translocated to upper parts through stem/trunk, and released from foliage after conversion to volatile forms. Earlier it was thought that the contaminants were released through the process of transpiration, but later, the studies indicated the hydrophobic nature of the volatile compounds (Limmer and Burken 2016; Mansoor et al. 2022). These hydrophobic compounds get diffused through the hydrophobic barriers of the plants such as cutin and suberin (Limmer and Burken 2016). The second mechanism is indirect phytovolatilization in which volatilization of pollutants occurs from subsurface of the soil and the process is aided by root activities (Limmer and Burken 2016; Kumari et al. 2022). Plant roots, due to their ability to move soil water and their enhanced reach in the soils, largely affect the fate and transport of the chemicals present in the soil. They enhance the flux of the contaminants chiefly by lowering the water table, enhancing the soil permeability, use of hydraulic redistribution in transport of the chemicals and advection with water and gas fluxes (Limmer and Burken 2016; Bhanse etal. 2022).

## Phytofiltration

When treatment of surface waters or waste waters is done using plant roots, shoots, or seedlings, the technique is known as phytofiltration (Mesjasz-Przybyłowicz et al. 2004). Rhizofiltration or phytofiltration with roots is most commonly used wherein contaminants are either adsorbed or absorbed by the roots (Yan et al. 2020; Yang et al. 2022). The plants chosen for the process of rhizofiltration are firstly raised hydroponically so as to develop abundant root system. Both terrestrial and aquatic plants have been successfully used for this process. Then these plants are subjected to contaminated waters so that they can acclimatize to adverse environment. Once the process of acclimatization is complete, these are transferred to the polluted sites for remediation. The plants are allowed to grow and when the roots become saturated with contaminants, they are harvested and disposed (Wuana and Okieimen 2011; Arantza et al. 2022). Contaminants, chiefly heavy metals, present in the polluted waters respond to the pH changes caused by the activity of root exudates which further makes them precipitate on the surface of the roots and restricts their movement to underground water (Javedet al. 2019; Yan et al. 2020).

## Indirect Mechanism of Phytoremediation

Environmental clean-up by plants, when aided by symbiotic or root associated microorganisms, is often categorized under indirect method of phytoremediation. Chiefly, PGPR are regarded as vital components in assisting phytoremediation and this technique is used to enhance the performance of plants (Jing et al. 2007; Kumar et al. 2017; Kumar et al. 2022a, b, c). The studies conducted on indirect phytoremediation have been mainly focused on the environmental reclamation of HM pollution and thus, the mechanisms pertaining to those will be discussed further. It is commonly known that rhizosphere, in comparison to the bulk soil, has high metabolic activity due the presence of a wide array of microorganisms. These microbes and their activities directly affect the mobility and further bioavailability of HMs and this ability is used for bioremediation (Jing et al. 2007; Ma et al. 2016a, 2016b; Yang et al. 2022). The microbial communities residing in the rhizosphere themselves are affected by metal toxicity but their properties of bioaccumulation, bioleaching, and bioexclusion impart them the ability to adapt, resist or tolerate heavy metal rich environment (Ma et al. 2016a, 2016b). This is commonly accomplished by mechanisms involving either mobilization or immobilization of HM ions. Mobilization usually occurs by acidification, chelation or protonation, while immobilization is caused by precipitation, alkalinization, or complexation of heavy metal ions and these processes ultimately lead to alteration in the nature of the HMs (Ma et al. 2016a, 2016b; Manoj et al. 2020).

Enhanced metal mobility is directly related to enhanced phytoremediation ability of plants. The pH of the soil is one of the key factors that alters the mobility of metal ions. The rhizospheric pH is highly influenced both by plant root exudates and PGPR which have the ability to release hydrogen ions. These hydrogen ions can displace the metal ions present on the soil particles and this process further causes acidification of rhizosphere thereby leading to both enhanced metal mobility and bioavailability (Ma et al. 2016a, 2016b; Anum et al. 2022). The PGPR can also cause acidification of rhizosphere through protonation in which protons are exported to replace metal cations adsorbed on the soil particles (Breton-Deval et al. 2022). Metal ions are also scavenged from the adsorption sites of soil particles through chelation. Both plants roots and PGPR release chelators that prevent the resorption of metal ions (Ma et al. 2016a, 2016b). Several metabolic compounds such as organic acids, biosurfactants, siderophores, and exopolysaccharides are reported to be released by PGPR that aid in achieving metal chelation in the rhizospheric environment (Manoj et al. 2020). Organic acids, in particular, are widely known for their properties of complexation that dissolve metals from solid phase thereby increasing their bioavailability for uptake (Ma et al. 2016a, 2016b; Yang et al. 2022). Similarly, microbial siderophores and biosurfactants also play key roles in altering the solubility and mobility of the HMs. Siderophores from PGPR have been found to have more affinity for metals than siderophores from plants and hence facilitating efficient uptake because of increased solubility. Likewise, biosurfactant producing microbial strains have also been proven highly beneficial for metal mobility and thus bioavailability. These compounds are amphiphilic in nature and possess both hydrophilic and hydrophobic moieties. The amphiphilic structure provides them the ability to form complexes with metal ions at soil interface and move them from soil matrix to soil solution (Sheng et al. 2008; Agarwal et al. 2020).These mechanisms have been successfully applied for microbial assisted phytoextraction and enhancing the phytoremedial abilities of plant species.

## Transgenic Strategies to Boost Bioremediation in Plants

The potential employment of bioenergy and biofuel plants has been suggested from long time as a source of maximal economic and phytoremedial returns, still there are wide-array of concerns related to utilization of harvested plants and the upshot of hazardous toxic wastes in the plant parts (Banwart 2011; Ma et al. 2011; Rai et al. 2020). Recent progress in understanding of omic approaches has provided the scientist with prospects to explore varied techniques viz. proteomics, genomics, metabolomic, and transcriptomic strategies in order to alter the endurance, sequestration, and

degradation potency of plants and microbes to combat ill-effects of various inorganic and organic pollutants. Plants transgenic can be extensively exploited for augmenting detoxification potential of plants (Maestri and Marmiroli 2011; Mansoor et al. 2022). Plethora of experimental evidences suggests symbiotic association between genetically engineered micro-organisms and plants and their utilization for in situ phytoremediation of wide array of organic pollutants. Few reports also reveal bioremediation of HM contaminants employing these types of symbiotic associations (Villacieros et al. 2005; Ratna et al. 2021; Kumari et al. 2022). For remediation of HMs the genetically modified PGP aided remediation is considered as a novel phytobacterial tool. In the genetically modified bacteria one or more genes are popped in for augmenting the remediation process, such as certain genes encoding biodegradative enzymes, metal chelators and transporters, metal uptake modulators and risk alleviation (Singh et al. 2011, 2022). One such experimental evidence was provided by Yong et al. (2014), who cloned phytochelatin synthase (*PCS*) gene isolated from *Schizosaccharomyces pombe* which were expressed in *Pseudomonas putida* KT2440. Phytochelatins (PCs) are cysteine rich biomolecules which have a very high binding kinship with the toxic metal ions. The recombinant mutant of *Pseudomonas putida* KT2440 showed elevated endurance to Hg, Ag, Cd and augment in efficacy of phytoremediation. Moreover, the engineered bacteria showed an imperative enhancement in seed germination and growth of wheat plants. Another observation by Wu et al. (2006) affirmed that the expression of EC20 a metal binding peptide as influenced by recombinant *P. putida* was up-regulated and improved the binding of Cd ions and lowered its toxicity. They further suggested that, inoculation of *Helianthus annuus* roots with *P. putida* 06909 also resulted in reduction in Cd toxicity. The symbiotic relationship markedly replenished the phytoextraction ability and augmented growth in plants.

Sriprang et al. (2002), engineered a phytobacterial system for bioremediation of HMs. They expressed tetrameric human metallothionein (MTL4) in *Mesorhizobium huakuii* sub sp. *rengei* B3 and as a result observed enhancement in production of metallothioneins (MTs) and consequently led to 1.7–2 folds augment in Cd sequestration. In another experiment conducted by Sriprang et al. (2003), he expressed *Arabidopsis thaliana AtPCS* gene in *M. huakuii* sub sp. *rengei* B3. The elevated expression resulted in up-regulation in the accumulation of PCs and binding affinity of Cd ions by 9–19 folds. Furthermore, Ike et al. (2007) inserted *AtMTL4* and *ATPCS* genes in *M. huakuii* sub sp. *rengei* B3. The developed recombinant strains showed 25 folds elevation in Cd accumulation with over expressed *AtMTL4* genes and 12 folds elevation in Cd-accumulation with over expressed *ATPCS* genes, respectively. Moreover, the iron regulated transporter 1 gene isolated from

*A. thaliana* (*ATIRT1*) was inserted in *AtMTL4* or *ATPCS*-recombinant strain B3 mentioned earlier. Resultant strains showed further elevation in accumulation of copper (Cu) and arsenic (As) in the nodules than Cd and Zinc (Zn). Poplar plant with elevated expression of microbial mercuric reductase genes showed augmented endurance to Hg stress. Similarly, another report of elevation in detoxification of Cu and Cd toxicity in polar plants was reported in response to insertion of g-glutamylcysteine synthetase gene from *Escherichia coli* (Van Dillewijn et al. 2008; Doty et al. 2007). Due to outstanding catabolic potency of the inserted gene, the biomass produced showed negligible accumulation of metal ions and they further suggested that the harvested biomass can be employed for energy production. Kang et al. (2007), reported similar observation in recombinant *E. coli* which led to augment in Cd accumulation in 25 folds when compared to the control strain. Patel et al. (2010) revealed that the recombinant bacterial strain, i.e., *Caulobacter crescentus* JS4022/p723-6H which expressed RsaA-6His fusion protein had the potential to eliminate 99.9% of Cd when compared to control bacterium which had the potency to eliminate 37% of Cd. Another observation made by Freeman et al. (2005), showed elevated Ni endurance in *Thlaspi goesingense* plants with recombinant *E. coli* introduced with serine acetyltransferase gene. The future manipulations of plants with desired genes (multiple) should assist in degradation of pollutants to guarantee complete usage of the harvested biomass for additional reimbursement (Abhilash et al. 2012). Table 3 enlists various reports on genetically engineered plants and their role in phytoremediation.

## Signaling Molecules and Their Role in Phytoremediation

Ecology of plant and microbial association is extremely complicated and interweaved network. It is significant to understand the homeostasis and amalgamation of wide array of signals produced in response to microbial interaction with plants for crop improvement. A plant has to survive under several abiotic and biotic environmental cues. Plethora of stress factors generate composite defense signaling cascades in plants and the fate of plant-microbial association can be decided by triage of physiological phenomena's in plants (Schenk et al. 2012; Sharma et al. 2022a, b). The association of plants and microbes triggers multifarious responses in confined or distal plant organs at multiple levels including physio-biochemical and molecular. For dissecting the mechanism, multi-omic strategies can be employed to tackle the exigent risk in deciphering the alterations in plants at gene, protein and metabolite levels. The understanding of these omics approaches advances our knowledge about composition of microbial population and their functional

conduct under varied environments such as rhizosphere, where the plant–microbe interaction directs multifaceted plant responses (de Castro et al. 2013; Anjum et al. 2022). Flavonoids as a root exude is an imperative signaling component in numerous plant and microbial association's viz. mycorrhiza formation and organization of plant and rhizobia symbiosis (Steinkellner et al. 2007; Khalid et al. 2021). Wide array of experimental evidences affirm important role of AMF spore formation and its germination, hyphal growth and development, colonization of root AMF etc. (Mandal et al. 2010; Khalid et al. 2021). Once the plants are properly colonized with AMF, the flavoinoid composition is drastically altered and this alteration plays a significant role in modulating the plant and AMF association (Badri et al. 2009; Kumar et al. 2022a, b, c). The triggering impact of flavonoid on plant–microbe interaction might be neutralized, because flavoinoid in excess can also have a negative influence on specific fungi due to certain explicitness involved in symbiotic association (Scervino et al. 2005; Khalid et al. 2021). Flavonoids also have ability to endorse growth of host- precise rhizobia by performing the role of chemo-attractant and stimulator of nodulation (*nod*) genes. The *nod* genes are involved in the production of lipochitin-oligosaccharides signaling constituents, i.e., the Nod factor (Mandal et al. 2010). Flavonoids exuded from the plant roots are identified by the rhizobial *nod* proteins which are transcriptional modulators that bind to signaling molecules having the ability to synthesize and elevate the expression of *nod* genes. Augment in the *nod* gene expression leads to stimulation of root hair cell infection as well as nodule formation (Bakker et al. 2012). This explicitness enables the microbial community to identify the specific host plant and get associated to its roots.

The free-living microbial communities such as PGPB, fungi, and rhizobia have the capability to change the chemical symphony of root exuded biochemicals and physiology of plants via release of varied signaling components including Nod factor, Myc factor, volatile organic components (VOCs), exopolysaccharides, and microbes associated molecular patterns (MAMPs) (Mansoor et al. 2022). Varied bacterial VOCs have the ability to interact with plants and stimulate plants defense responses and growth mechanism by enhancing the synthesis of plant–microbe colonization nutrient such as sulfurandiron (Bailly and Weisskopf 2012; Khursheed et al. 2022). More recently, Hofmann (2013) revealed that VOCs are also produced by *Bacillus* B55 and significantly alters sulfur levels in *Nicotiana attenuate* plants. The VOCs synthesis has a vital effect on most of the PGPMs of the PGPB by serving as: (i) bio-protectants by stimulating ISR (Induced systemic resistance), (ii) phyto-stimulator by stimulating hormonal signaling cascades, and (iii) bio-pesticide by antibiotic functions (Ryu et al. 2004; Zhang et al. 2008; Trivedi and Pandey 2008). Furthermore,

**Table 3** Genetically modified plants and their role in phytoremediation

| Heavy metal | Origin of genes | Gene | Genetically modified plant species | Role in phytoremediation | References |
|---|---|---|---|---|---|
| Cd (13, 32, 76 μM) | – | PPH6HIS | Nicotiana tabacum | Metal binding peptide enhanced accumulation potential | Vershinina et al. (2022) |
| Cd (0.5, 1 mM) | – | HIPP24 | Beta vulgaris | Induced detoxification mechanism and antioxidative potential | Liu et al. (2022a, b) |
| Cd (30 mg/L) | Klebsiella sp. | HMA2, HMA3, HMA4 | Solanum nigrum | Improved plant growth and phytoremediation potential | Ullah et al. (2022) |
| As (0.5 μM) | Pteris vittata | ACR3;2, ACR3;3 | Nicotiana tabacum | Improved translocation and sequestration in plants | Chen et al. (2021) |
| Zn (0.7 μM) | Saccharomyces cerevisiae | ZRC1 | Poplus alba | Enhanced Zn accumulation and antioxidant activities | DalCorso et al. (2021) |
| Cd (5, 2, 10 μM) | Agrobacterium tumefaciens | MT1e | Oryza sativa | Overexpression of metallothioneins and enhanced phytoremediation | Rono et al. (2021) |
| As (200 μM) | Arabidopsis thaliana | AtACR2 | Nicotiana tabacum | Significant augment in accumulation metal in root of plant Reduce arsenic content of the soil | Nahar et al. (2017) |
| As, Cd, Cu, Pb and Zn (contaminated mine site soils) | Pseudomonas koreensis | AGB-1 | Miscanthus sinensis | Increased plant biomass, chlorophyll, protein content, superoxide dismutase and catalase activities, and metal uptake; however decreased malondialdehyde content in plants | Babu et al. (2015) |
| Cd Zn and Cu (50 μM) | Streptococcus thermophilus | StGCS-GS | Beta vulgaris | Increased expression of StGCS-GS and consequent overproduction of both GSH (glutathione) and PC (phytochelatin) | Liu et al. (2015) |
| Cr (tannery sludge soil) | Pseudomonas monteilii and Pseudomonas plecoglossicida | 16S rRNA gene sequence | Pelargonium graveolens | Increased plant dry biomass, essential oil yield and chlorophyll, helped Cr(VI) sequester in roots | Dharmi et al. (2014) |
| Methyl-Hg and Hg (0.3 μM and 10 μM) | E. coli XL1-Blue | MerE | Arabidopsis thaliana | Significantly more methylmercury and mercuric ions into plants than the wild-type Arabidopsis Expression of the bacterial mercury transporter MerE promoted the transport and accumulation of methylmercury in the transgenic plants | Sone et al. (2013) |

**Table 3** (continued)

| Heavy metal | Origin of genes | Gene | Genetically modified plant species | Role in phytoremediation | References |
|---|---|---|---|---|---|
| Hg and Trichloroethane | Homo sapiens | CYP2E1 and GST | Homo sapiens Alfalfa (Medicago sativa) | Improved resistance and accumulation to heavy metal–organic complex contaminants pKHCG transgenic plants were more resistant to Hg/TCE complex pollutants and many folds higher in Hg/TCE-accumulation than the non-transgenic control plants | Zhang et al. (2013) |
| Cd, Zn and Pb (contaminated soil) | Streptococcus cerevisiae | ScYCF1 | Populus alba | Enhanced growth, reduced toxicity symptoms, and increased Cd content in the aerial tissue. Plants accumulated increased amounts of Cd, Zn, and Pb in the root, because they could establish an extensive root system | Shim et al. (2013) |
| As, Cu, Cd, Ni, Pb and Zn (contaminated mine trailing sites) | Bacillus thuringiensis | GDB-1 based on 16S ribosomal DNA sequencing | Alnus firma | Production of Indole 3-Acetic Acid, siderophores and solubilization of Phosphorus Bioremoval of Pb, Zn, As, Cd, Cu and Ni in metal amended and mine tailing extract medium; Increased biomass, chlorophyll content, nodule number and metal (As, Cu, Pb, Ni, and Zn) accumulation | Babu et al. (2013) |
| Cd (0.1 mM) and Pb (3 mM) | Streptococcus cerevisiae | YCF1 | Brassica juncea | Transgenic B. juncea seedlings showed 1.3- to 1.6-fold enhanced tolerance to Cd stress and 1.2- to 1.4-fold elevated tolerance to Pb stress compared to wild type (WT) plants | Babu et al. (2013) |
| Cu and Zn (contaminated soil) | Neurospora crassa | tcu1 | Nicotiana tabacum | Plants showed higher acquisition of Cu (up to 3.1 times) compared with control plants | Singh et al. (2011) |
| Cd, Fe, Ni, Cu, Mn and Pb (contaminated soil) | Neurospora crassa | tzn1 | Nicotiana tabacum | Improved Zn uptake, without co-transport of Cd and may have implications in Zn phytofortification and phytoremediation | Dixit et al. (2010) |

As, Arsenic; AtACR2, Arabidopsis thaliana arsenic reductase 2; Cd, Cadmium; Cu, Copper; Pb, Lead; Zn, Zinc; AGB-1, Arabidopsis Gβ-Protein 1; StGCS-GS, Streptococcus thermophiles based γ-glutamylcysteine synthetase- gluthathione synthetase; GSH, Glutahione; PC, Phytochelatins; Cr, Chromium; rRNA, Ribosomal RNA; Methyl-Hg, Methylmercury; Hg, Mercury; MerE, Mercury Metabolizing Gene E; CYP2E1, Cytochrome P450 2E1; GST, Glutathione-S-transferase; pKHCG, Transgenic alfalfa plant; Hg/TCE, Mercury/Trichloroethane; ScYCF1, Saccharomyces cerevisiae Yeast Cadmium Factor 1; Ni, Nickel; GDB-1, Bacillus thurigiensis starin; YCF-1, Yeast Cadmium Factor; tcu1, Transporter Copper Gene 1; tzn1, Transporter Zinc Gene 1

certain bioactive VOCs such as ammonia, hydrogen cyanide, butyrolactones, and phenazine-1-carboxylic acid have the ability to impact the hyphal growth and sporulation in varied fungal species (Kai et al. 2009). Moreover, the signaling components released by AMF include Myc factors and those released by rhizobia include (Nod factors) are able to alter lateral root growth, formation of novel parts, and nodulation (Maillet et al. 2011). Myc factor also have an imperative impact on Nod factor signaling cascade which eventually aids in AMF formation (Maillet et al. 2011; Khalid et al. 2021). The identification of a plant pathogen can be accomplished via MAMPs which are also termed as biotic stimulators of explicit immune response in plants (Newman et al. 2013). An observation by Varnier et al. (2009) revealed release of a new MAMPs, i.e., rhamnolipids from *Pseudomona saeruginosa* which aids in providing protection to grape vine plants against the pathogen infestation. More recently, MAMPs were also reported to be released from three PGPB, i.e., *Stenotrophomonas maltophilia*, *Pseudomonas fluorescens*, and *Chryseobacterium balustinum*

were able to stimulate growth and metabolism of *Papaver somniferum* (Bonilla et al. 2014). Figure 5 demonstrates root exudates induced signaling components and their impact on plant–microbe interaction.

Quorum sensing is a bacterial cell to cell signaling phenomena's whereby it harmonizes population response viz. population density monitoring and modification in bacterial gene expression is regulated by signaling components generated by individual bacterial cells (Daniels et al. 2004). Quorum sensing has the ability to stimulate sporulation, bioflim, and antibiotic synthesis in response to plant-microbial association (Williams and Camara, 2009). Certain quantum sensing signals such as *N*-acyl-L-homoserine lactones (AHLs) are imperative constituent of specifically this signaling network. AHL signals can augment or decrease the diverse phenotypes of bacteria affecting its beneficial or pathogenic traits. Bacterial AHLs can be identified by plants resulting in alteration of tissue specific gene expression, plant growth homeostasis and defense retaliations (Daniels et al. 2004).
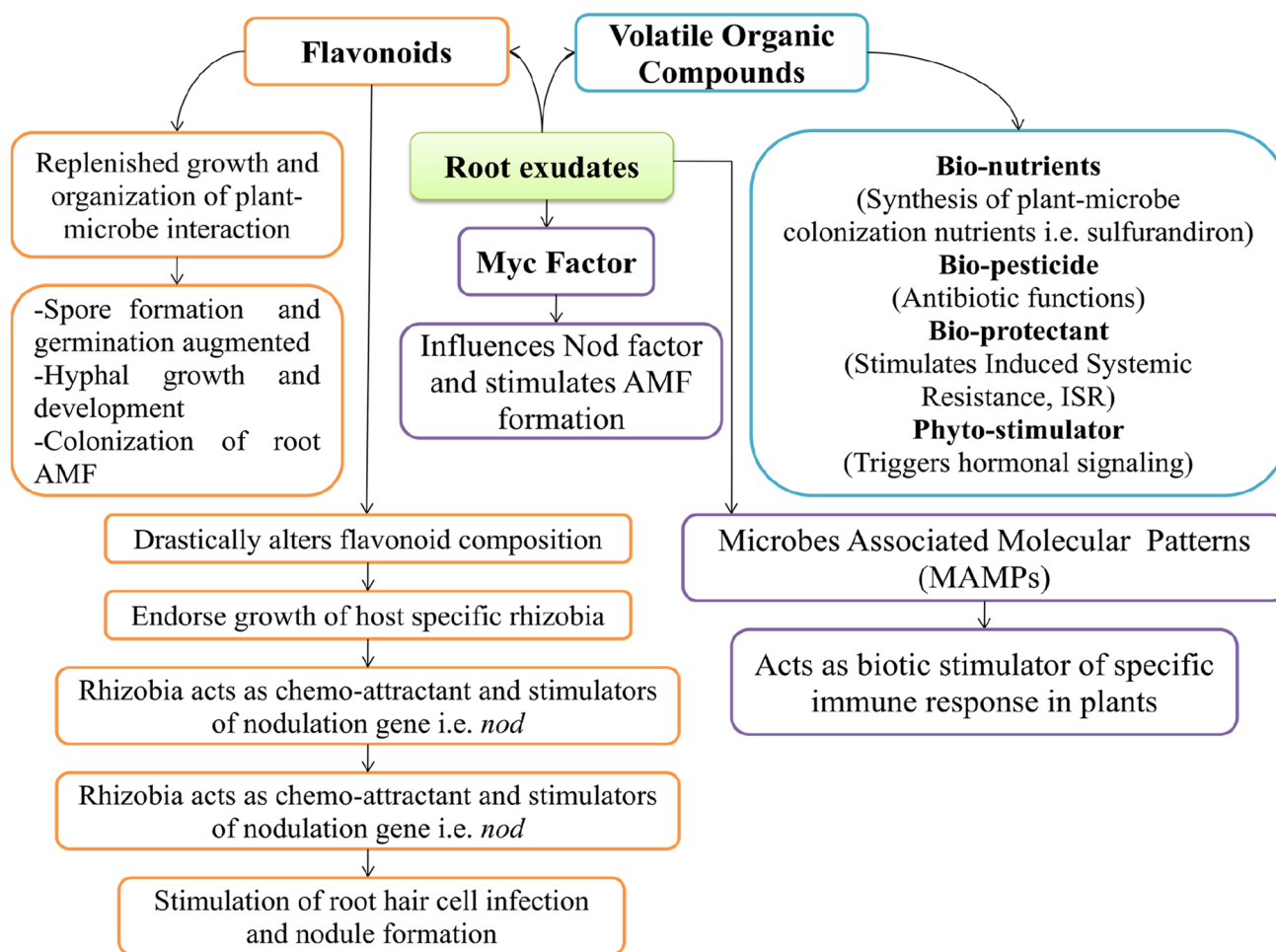


**Fig. 5** Root exudates induced signaling components and their impact on plant–microbe interaction

# Flourishing High-Throughput Sequencing and Other Strategies for Phytoremediation Effectiveness

Phytoremediation is a most propitious technique that is still on the conduit of achieving utmost potential of success. One of the most commonly observed obstacle in its accomplishment is ambiguity of its effectiveness (Linacre et al. 2005). However, the utilization of transgenic plants with specific traits of induced uptake, resistance toward metal ions, excessive hyperaccumulation and biomass provides us with the feasibility of phytoremediation with success. In essence, the well adaptability and effective understanding of molecular based phytoremediation is extremely important. Transcriptomics with the aid of high-throughput sequencing has dispensed the leaps for acquiring the process of phytoremediation at genetic level (Bhattacharya et al. 2022). Transcriptome involve complete set of transcripts within a cell or at specific site of cell stages like developmental stage or any physiological state (Wang et al. 2009). Moreover, the transcriptomic profiling with RNA-sequencing is an advanced technology for evaluating précised gene-expression levels. Also, they have been getting impetus in gene expression related studies, owing to their ability to identify novel transcripts, splice junctions where no hybridization related studies or genome sequence biasness is essential.

Nevertheless, the next-generation sequencing (NGS) technique is known since decades due to its enormous contribution in various sectors. Moreover, it has gained much more importance from last few years because of its economic friendly nature with massive environmental benefits with respect to control hazardous wastes or contaminants. For instance, high-throughput sequencing has been known to control As toxicity and hyperaccumulation in different plants (Kumar et al. 2022a, b, c). It is a holistic technique that works in a sequential manner from, comparing the plants growing in absence or presence of contaminants on the basis of transcriptomes using high-throughput sequencing followed by the identification of genes involved in stress perception and tolerance, transcription factors, transporters, and gene oncology. All these steps result in the generation of plants with phytoremediation potential using transgenic approaches (Thakur et al. 2019). A study conducted with the help of RNA sequencing enabled the identification of almost 1720 differentially expressed genes encoding hormone synthesis, As hyperaccumulation, transcripts (HSF and MYB) and oxidative stress linked proteins in As contaminated *Panax notoginseng* respectively (Liu et al. 2016). Likewise, the phytoremediation potential of *Salix purpurea* was analyzed through gene expression profiling by RNA-sequencing and transporters (PHO1, NIP1) (Yanitch et al. 2017). Alongside, illumina sequencing method was used for

transcriptomic profiling during metal stressed conditions, where genes encoding phytohormones and lipid metabolism were recognized (Yu et al. 2012). According to their research, nearly 350 gene-toolbox along with 580 differentially expressed genes encoding membrane transporter proteins were identified in *Brassica juncea* affected with As through transcriptomics. ABC transporters along with antioxidants such as glutathione function in As sequestration. Moreover, Ca-signaling pathway and MAPK pathway also participated in As perception.

In the forging arguments, it was found that miRNAs were principal components during biotic and abiotic stress responses, flowering, cell proliferation and maturation (Khraiwesh et al. 2012). miRNAs are crucial during stress management and by using RNA-sequencing the identification of stress responsive miRNAs encoding various metabolic as well as cellular processes were recognized in *Oryza sativa* (Liu and Zhang 2012). Similarly, 70 miRNA involved in the plant developmental processes, hormonal biosynthesis, sulfur metabolism were identified in *B. juncea* under As stress (Srivastava et al. 2013). Moreover, differential gene expression in *Zea mays* revealed the upregulation of 22 and downregulation of 35 miRNAs that influenced As resistance mechanisms, plant developmental processes and hormonal signaling (Ghosh et al. 2017). Another technique, Clustered Regularly Interspaced Palindromic Repeats (CRISPER) is widely known genetic tool that can boost the efficacy of phytoremediation (Basharat et al. 2018). It is basically RNA-regulated CRISPER/Cas9 toolkit, easily designable, specific, and most suitable for high-throughput gene editing (Ma et al. 2015). Genome editing for fine tuning the hyperaccumulator plants for effective phytoremediation can be attained via CRISPER/Cas9 toolbox (Basharat et al. 2018). For augmentation of this system, the genes encoding metal uptake are targeted for gene editing. Interestingly, there are many microbial species that function in metal detoxification with the aid of possessing metal resistance operon systems to provide the resistance (Rosen 1999). Further, the overexpression of stress responsive proteins also induce accumulation. Meanwhile, all these genes with excellent traits of metal uptake and resistance can be transferred from microbes to plants through CRISPER/Ca9 tools or synthetic genes. Synthetic genes are substantial where the role of nature gene transfer is negligible or complete failure (Kunjapur et al. 2018). For instance, synthetic gene triphenylmethane reductase carried by *Citrobacter* sp. when transferred to *Arabidopsis* showcased enhanced resistance against recalcitrant compounds (Fu et al. 2013). Henceforth, the synthetic genes from various microbes can be easily transferred to plants to enhance their phytoremediation abilities.

# Conclusion and Future Prospects

Heavy metals have led to grim environmental situation and to find an economical, eco-friendly, and efficient technique to deal with is situation is primarily important. The exploration of plant–microbe synergism for land restoration and toxicity management is a promising method but at benign level. The beneficial aspects of HM-PGPM are immensely studied due to their multifarious nature in promoting soil quality, plant growth promotion, metal detoxification, chelation, bioaccumulation, and remediation of HM from the soils. There is a need of vast research for developing bio-formulations using microbes for promoting phytoremediation. We have discussed various aspects of plants and microbes and their interactions underlying phytoremediation mechanisms. For instance, a depth insight on biochemical and molecular basis of plant–microbe interactions has been provided that could provide an evolution in studying the microbial dynamics. Moreover, our aim has always been inclined toward the efficacy of the microbes to perform their best and devote best toward stressed conditions for conferring metal resistant or bio-protectants. All these aspects enhance our understanding about the perspective of microbe-assisted phytoremediation in promoting ecosystem diversity by acting as biofertilizers. Henceforth, various mechanisms elucidating a cooperative association among plants and microbes include metal detoxification, remediation, mobilization, chelation, immobilization, transformation, complexation, accumulation, and translocation. These mechanisms hold a strong layout toward an effective phytoremediation strategies. Further, the genetic engineering has opened as many new opportunities for improving plant growth as well as phytoremediation practice. Many other studies like illumina sequencing, RNA sequencing, high throughput sequencing have shown their biotechnological role in improving the phytoremediation technique. In addition, this technique is more sustainable, eco-friendly, cost-effective and by far the best with respect to regulatory concerns. Therefore, the advancement in technology provides us with a ray of hope and studies should be broadened on these aspects to provide a theoretical and practical implementation of microbial phytoremediation on large scale.

## Declarations

**Conflict of interest** The authors declare that they have no competing interests.

**Ethical Approval** Not applicable.

**Consent to Participate** Not applicable.

**Consent for Publication** Not applicable.

## References

Abbaszadeh-Dahaji P, Omidvari M, Ghorbanpour M (2016) Increasing phytoremediation efficiency of heavy metal-contaminated soil using PGPR for sustainable agriculture. Plant-microbe interaction: an approach to sustainable agriculture. Springer, Singapore, pp 187–204

Abhilash PC, Powell JR, Singh HB, Singh BK (2012) Plant–microbe interactions: novel applications for exploitation in multipurpose remediation technologies. Trends Biotechnol 30(8):416–420

Adiloğlu S (2017) Heavy metal removal with phytoremediation. In: Shiomi N (ed) Advances in bioremediation and phytoremediation. IntechOpen, London

Agarwal P, Giri BS, Rani R (2020) Unravelling the role of rhizospheric plant-microbe synergy in phytoremediation: a genomic perspective. Curr Gen 21(5):334–342

Ahmad N (2014) Konseling Agama: Terapi Terhadap Pengidap Penyakit Manusia Modern. Konseling Religi 5(1):1–20

Ali H, Khan E, Sajad MA (2013) Phytoremediation of heavy metals: concepts and applications. Chemosphere 91(7):869–881

Ambrosini A, de Souza R, Passaglia LM (2016) Ecological role of bacterial inoculants and their potential impact on soil microbial diversity. Plant Soil 400(1–2):193–207

Anjum S, Yousuf S, Mirza U (2022) Recent trends in transgenic plants for enhanced phytoremediation. Bioremediation and phytoremediation technologies in sustainable soil management. Apple Academic Press, Boca Raton, pp 241–261

Anum W, Riaz U, Murtaza G, Raza MU (2022) Sustainable agroecosystems: recent trends and approaches in phytoremediation and rhizoremediation. Bioremediat Phytoremediat Technol Sustain Soil Manag 2022:185–204

Arantza SJ, Hiram MR, Erika K, Chávez-Avilés MN, Valiente-Banuet JI, Fierros-Romero G (2022) Bio-and phytoremediation: plants and microbes to the rescue of heavy metal polluted soils. SN Appl Sci 4(2):1–14

Ashraf MA, Hussain I, Rasheed R, Iqbal M, Riaz M, Arif MS (2017) Advances in microbe-assisted reclamation of heavy metal contaminated soils over the last decade: a review. J Environ Manag 198:132–143

Awa SH, Hadibarata T (2020) Removal of heavy metals in contaminated soil by phytoremediation mechanism: a review. Water Air Soil Pollut 231(2):47

Babu AG, Kim JD, Oh BT (2013) Enhancement of heavy metal phytoremediation by *Alnus firma* with endophytic *Bacillus thuringiensis* GDB-1. J Hazard Mater 250:477–483

Babu AG, Shea PJ, Sudhakar D, Jung IB, Oh BT (2015) Potential use of *Pseudomonas koreensis* AGB-1 in association with *Miscanthus sinensis* to remediate heavy metal (loid)-contaminated mining site soil. J Environ Manag 151:160–166

Badri DV, Weir TL, Van der Lelie D, Vivanco JM (2009) Rhizosphere chemical dialogues: plant–microbe interactions. Curr Opin Biotechnol 20(6):642–650

Bailly A, Weisskopf L (2012) The modulating effect of bacterial volatiles on plant growth: current knowledge and future challenges. Plant Signal Behav 7(1):79–85

Bakhshandeh E, Pirdashti H, Lendeh KS (2017) Phosphate and potassium-solubilizing bacteria effect on the growth of rice. Ecol Eng 103:164–169

Bakker MG, Manter DK, Sheflin AM, Weir TL, Vivanco JM (2012) Harnessing the rhizosphere microbiome through plant breeding and agricultural management. Plant Soil 360(1):1–13

Banwart S (2011) Save our soils. Nature 474(7350):151–152

Bashan Y, Holguin G (1998) Proposal for the division of plant growth-promoting rhizobacteria into two classifications: biocontrol-PGPB (Plant Growth-Promoting Bacteria) and PGPB. Soil Biol Biochem 30(8–9):1225–1228

Basharat Z, Novo LA, Yasmin A (2018) Genome editing weds CRISPR: what is in it for phytoremediation? Plants 7(3):51

Bhadauria R (2019) Arsenic toxicity: an overview. Horticult Int J 3(1):20–22

Bhanse P, Kumar M, Singh L, Awasthi MK, Qureshi A (2022) Role of plant growth-promoting rhizobacteria in boosting the phytoremediation of stressed soils: opportunities, challenges, and prospects. Chemosphere 303:134954

Bhat BA, Tariq L, Nissar S, Islam ST, Islam SU, Mangral Z, Ilyas N, Sayyed RZ, Muthusamy G, Kim W, Dar TUH (2022) Unraveling the role of plant-associated rhizobacteria in plant growth, biocontrol, and abiotic stress management. J Appl Microbiol. https://doi.org/10.1111/jam.15796

Bhattacharyya N, Anand U, Kumar R, Ghorai M, Aftab T, Jha NK, Rajapaksha AU, Bundschuh J, Bontempi E, Dey A (2022) Phytoremediation and sequestration of soil metals using the CRISPR/Cas9 technology to modify plants: a review. Environ Chem Lett. https://doi.org/10.1007/s10311-022-01474-1

Bonilla A, Sarria ALF, Algar E, Ledesma FM, Solano BR, Fernandes JB, Mañero FG (2014) Microbe associated molecular patterns from rhizosphere bacteria trigger germination and *Papaver somniferum* metabolism under greenhouse conditions. Plant Physiol Biochem 74:133–140

Breton-Deval L, Guevara-García A, Juarez K, Lara P, Rubio-Noguez D, Tovar-Sanchez E (2022) Role of rhizosphere microbiome during phytoremediation of heavy metals. Microbial biodegradation and bioremediation. Elsevier, Amsterdam, pp 263–291

Brunetti G, Farrag K, Soler-Rovira P, Ferrara M, Nigro F, Senesi N (2012) The effect of compost and *Bacillus licheniformis* on the phytoextraction of Cr, Cu, Pb and Zn by three brassicaceae species from contaminated soils in the Apulia region, Southern Italy. Geoderma 170:322–330

Burdman S, Jurkevitch E, Okon Y (2000) Recent advances in the use of plant growth promoting rhizobacteria (PGPR) in agriculture. In: Subba-Rao NS, Dommergues YR (eds) Microbial interactions in agriculture and forestry (Volume II). Science Publishers Inc, New York, pp 229–250

Chen Y, Yang W, Chao Y, Wang S, Tang YT, Qiu RL (2017) Metal-tolerant *Enterobacter* sp. strain EG16 enhanced phytoremediation using *Hibiscus cannabinus* via siderophore-mediated plant growth promotion under metal contamination. Plant Soil 413(1–2):203–216

Chen JX, Cao Y, Yan X, Chen Y, Ma LQ (2021) Novel PvACR3; 2 and PvACR3; 3 genes from arsenic-hyperaccumulator *Pteris vittata* and their roles in manipulating plant arsenic accumulation. J Hazard Mater 415:125647

Cheng Z, Chen LJ, Li HH, Lin JQ, Yang ZB, Yang YX, Zhu XM (2018) Characteristics and health risk assessment of heavy metals exposure via household dust from urban area in Chengdu, China. Sci Totl Environ 619:621–629

Chibuike GU, Obiora SC (2014) Heavy metal polluted soils: effect on plants and bioremediation methods. Appl Environ Soil Sci. https://doi.org/10.1155/2014/752708

Choudhury D, Tarafdar S, Dutta S (2022) Plant growth promoting rhizobacteria (PGPR) and their eco-friendly strategies for plant growth regulation: a review. Plant Sci Today 9(3):524–537

Clemens S, Ma JF (2016) Toxic heavy metal and metalloid accumulation in crop plants and foods. Ann Rev Plant Biol 67:489–512

Cobbett C, Goldsbrough P (2002) Phytochelatins and metallothioneins: roles in heavy metal detoxification and homeostasis. Ann Rev Plant Biol 53(1):159–182

Cristaldi A, Conti GO, Cosentino SL, Mauromicale G, Copat C, Grasso A, Ferrante M (2020) Phytoremediation potential of *Arundo donax* (Giant Reed) in contaminated soil by heavy metals. Environ Res 185:109427

DalCorso G, Martini F, Fasani E, Manara A, Visioli G, Furini A (2021) Enhancement of Zn tolerance and accumulation in plants mediated by the expression of *Saccharomyces cerevisiae* vacuolar transporter ZRC1. Planta 253(6):1–17

Daniels R, Vanderleyden J, Michiels J (2004) Quorum sensing and swarming migration in bacteria. FEMS Microbiol Rev 28(3):261–289

de Castro AP, Sartori da Silva MR, Quirino BF, Kruger RH (2013) Combining" omics" strategies to analyze the biotechnological potential of complex microbial environments. Curr Protein Peptide Sci 14(6):447–458

Della Mónica IF, Wong Villarreal A, Stefanoni Rubio PJ, Vaca-Paulín R, Yañez-Ocampo G (2022) Exploring plant growth-promoting rhizobacteria as stress alleviators: a methodological insight. Arch Microbiol 204(6):1–20

Dharni S, Srivastava AK, Samad A, Patra DD (2014) Impact of plant growth promoting *Pseudomonas monteilii* PsF84 and *Pseudomonas plecoglossicida* PsF610 on metal uptake and production of secondary metabolite (monoterpenes) by rose-scented geranium (*Pelargonium graveolens* cv. bourbon) grown on tannery sludge amended soil. Chemosphere 117:433–439

Dixit P, Singh S, Vancheeswaran R, Patnala K, Eapen S (2010) Expression of a *Neurospora crassa* zinc transporter gene in transgenic *Nicotiana tabacum* enhances plant zinc accumulation without co-transport of cadmium. Plant Cell Environ 33(10):1697–1707

Edelstein M, Ben-Hur M (2018) Heavy metals and metalloids: sources, risks and strategies to reduce their accumulation in horticultural crops. Sci Horticul 234:431–444

Egamberdieva D, Kucharova Z (2009) Selection for root colonising bacteria stimulating wheat growth in saline soils. Biol Fertil Soils 45(6):563–571

Ely CS, Smets BF (2017) Bacteria from wheat and cucurbit plant roots metabolize PAHs and aromatic root exudates: implications for rhizodegradation. Int J Phytorem 19(10):877–883

Enya O, Lin C, Qin J (2019) Heavy metal contamination status in soil-plant system in the Upper Mersey Estuarine Floodplain, Northwest England. Mar Pollut Bull 146:292–304

Fan M, Xiao X, Guo Y, Zhang J, Wang E, Chen W, Lin YG (2018) Enhanced phytoremdiation of *Robinia pseudoacacia* in heavy metal-contaminated soils with rhizobia and the associated bacterial community structure and function. Chemosphere 197:729–740

Faria JM, Teixeira DM, Pinto AP, Brito I, Barrulas P, Alho L, Carvalho M (2020) Toxic levels of manganese in an acidic Cambisol alters antioxidant enzymes activity, element uptake and subcellular distribution in *Triticum aestivum*. Ecotoxicol Environ Saf 193:110355

Faust K, Raes J (2016) CoNet app: inference of biological association networks using Cytoscape. F1000Res 5:1519

Feng Y (2022) Interactions among rhizosphere microorganisms, mechanisms and potential application in phytoremediation. SHS Web Conf 144:01003

Freeman JL, Persans MW, Nieman K, Salt DE (2005) Nickel and cobalt resistance engineered in *Escherichia coli* by overexpression of serine acetyltransferase from the nickel hyperaccumulator plant *Thlaspi goesingense*. Appl Environ Microbiol 71(12):8627–8633

Fu XY, Zhao W, Xiong AS, Tian YS, Zhu B, Peng RH, Yao QH (2013) Phytoremediation of triphenylmethane dyes by overexpressing a *Citrobacter* sp. triphenylmethane reductase in transgenic *Arabidopsis*. Appl Environ Microbiol 97(4):1799–1806

Gavrilescu M (2022) Enhancing phytoremediation of soils polluted with heavy metals. Curr Opi Biotechnol 74:21–31

Ghosh S, Singh K, Shaw AK, Azahar I, Adhikari S, Ghosh U, Basu U, Roy S, Saha S, Sherpa AR, Hossain Z (2017) Insights into the miRNA-mediated response of maize leaf to arsenate stress. Environ Exp Bot 137:96–109

Gjorgieva Ackova D (2018) Heavy metals and their general toxicity on plants. Plant Sci Today 5(1):15–19

Gómez-Garrido M, Mora Navarro J, Murcia Navarro FJ, Faz Cano Á (2018) The chelating effect of citric acid, oxalic acid, amino acids and *Pseudomonas fluorescens* bacteria on phytoremediation of Cu, Zn, and Cr from soil using *Suaeda vera*. Int J Phytorem 20(10):1033–1042

Goswami M, Deka S (2020) Plant growth-promoting rhizobacteria—alleviators of abiotic stresses in soil: a review. Pedosphere 30(1):40–61

Guarino F, Miranda A, Cicatelli A, Castiglione S (2020) Arsenic phytovolatilization and epigenetic modifications in *Arundo donax* L. assisted by a PGPR consortium. Chemosphere 251:126310

Guo YC, Liu YY, Wang RY, Wang S, Lu XP, Wang B (2015) Effect of mercury stress on photosynthetic characteristics of two kinds of warm season turf grass. Int J Environ Monit Anal 3:293–297

Gupta N, Khan DK, Santra SC (2010) Determination of public health hazard potential of wastewater reuse in crop production. World Rev Sci Technol Sustain Dev 7(4):328–340

Gupta A, Joia J, Sood A, Sood R, Sidhu C, Kaur G (2016) Microbes as potential tool for remediation of heavy metals: a review. J Microb Biochem Technol 8(4):364–372

Hassan MU, Chattha MU, Khan I, Chattha MB, Aamer M, Nawaz M, Khan TA (2019) Nickel toxicity in plants: reasons, toxic effects, tolerance mechanisms, and remediation possibilities: a review. Environ Sci Pollut Res 26(13):12673–12688

Hussain S, Rengel Z, Qaswar M, Amir M, Zafar-ul-Hye M (2019) Arsenic and heavy metal (cadmium, lead, mercury and nickel) contamination in plant-based foods. Plant and human health, vol 2. Springer, Cham, pp 447–490

Ike A, Sriprang R, Ono H, Murooka Y, Yamashita M (2007) Bioremediation of cadmium contaminated soil using symbiosis between leguminous plant and recombinant rhizobia with the MTL4 and the PCS genes. Chemosphere 66(9):1670–1676

Ilangumaran G, Smith DL (2017) Plant growth promoting rhizobacteria in amelioration of salinity stress: a systems biology perspective. Front Plant Sci 8:1768

Jaffre T, Pillon Y, Thomine S, Merlot S (2013) The metal hyperaccumulators from New Caledonia can broaden our understanding of nickel accumulation in plants. Front Plant Sci 4:279

Jamil M, Zeb S, Anees M, Roohi A, Ahmed I, ur-Rehman S, Rha ES (2014) Role of *Bacillus licheniformis* in phytoremediation of nickel contaminated soil cultivated with rice. Int J Phytoremediat 16(6):554–571

Javed MT, Tanwir K, Akram MS, Shahid M, Niazi NK, Lindberg S (2019) Phytoremediation of cadmium-polluted water/sedimentby aquatic macrophytes: role of plant-induced pH changes. In: Hasanuzzaman M, Prasad MNV, Fujita M (eds) Cadmium toxicity and tolerance in plants. Academic Press, London, pp 495–529

Jiang Y, Chao S, Liu J, Yang Y, Chen Y, Zhang A, Cao H (2017) Source apportionment and health risk assessment of heavy metals in soil for a township in Jiangsu Province, China. Chemosphere 168:1658–1668

Jing YD, He ZL, Yang XE (2007) Role of soil rhizobacteria in phytoremediation of heavy metal contaminated soils. J Zhejiang Univ Sci B 8(3):192–207

Ju W, Liu L, Fang L, Cui Y, Duan C, Wu H (2019) Impact of co-inoculation with plant-growth-promoting rhizobacteria and rhizobium on the biochemical responses of alfalfa-soil system in copper contaminated soil. Ecotoxicol Environ Saf 167:218–226

Jung HI, Kong MS, Lee BR, Kim TH, Chae MJ, Lee EJ, Kim YH (2019) Exogenous glutathione increases arsenic translocation into shoots and alleviates arsenic-induced oxidative stress by sustaining ascorbate-glutathione homeostasis in rice seedlings. Front Plant Sci. https://doi.org/10.3389/fpls.2019.01089

Kabeer R, PrveenKumar CS, Thomas AP, Radhakrishnan EK, Baiju KR (2022) Role of heavy metal tolerant rhizosphere bacteria in the phytoremediation of Cu and Pb using *Eichhornia crassipes* (Mart.) Solms. Int J Phytorem 24(11):1120–1132

Kai M, Haustein M, Molina F, Petri A, Scholz B, Piechulla B (2009) Bacterial volatiles and their action potential. Appl Microbiol Biotechnol 81(6):1001–1012

Kamran MA, Eqani SAMAS, Bibi S, Xu RK, Monis MFH, Katsoyiannis A, Chaudhary HJ (2016) Bioaccumulation of nickel by *E. sativa* and role of plant growth promoting rhizobacteria (PGPR) under nickel stress. Ecotoxicol Environ Saf 126:256–263

Kang SH, Singh S, Kim JY, Lee W, Mulchandani A, Chen W (2007) Bacteria metabolically engineered for enhanced phytochelatin production and cadmium accumulation. Appl Microbiol Biotechnol 73(19):6317–6320

Kaur R, Yadav P, Thukral AK, Sharma A, Bhardwaj R, Alyemeni MN, Ahmad P (2018) Castasterone and citric acid supplementation alleviates cadmium toxicity by modifying antioxidants and organic acids in *Brassica juncea*. J Plant Growth Regul 37(1):286–299

Kempf B, Bremer E (1998) Uptake and synthesis of compatible solutes as microbial stress responses to high-osmolality environments. Arch Microbiol 170(5):319–330

Khalid M, Saeed UR, Hassani D, Hayat K, Pei Z, Nan H (2021) Advances in fungal-assisted phytoremediation of heavy metals: a review. Pedosphere 31(3):475–495

Khan WU, Yasin NA, Ahmad SR, Ali A, Ahmed S, Ahmad A (2017) Role of Ni-tolerant Bacillus spp. and *Althea rosea* L. in the phytoremediation of Ni-contaminated soils. Int J Phytoremediat 19(5):470–477

Khanna K, Jamwal VL, Gandhi SG, Ohri P, Bhardwaj R (2019) Metal resistant PGPR lowered Cd uptake and expression of metal transporter genes with improved growth and photosynthetic pigments in *Lycopersicon esculentum* under metal toxicity. Sci Rep 9(1):1–14

Khraiwesh B, Zhu JK, Zhu J (2012) Role of miRNAs and siRNAs in biotic and abiotic stress responses of plants. Biochim Biophys Acta (BBA) 2:137–148

Khursheed M, Wani KA, Rehman S, Manzoor J (2022) Omics and phytoremediation. phytoremediation. Academic Press, Cambridge, pp 179–194

Kidd KA, Muir DC, Evans MS, Wang X, Whittle M, Swanson HK, Johnston T, Guildford S (2012) Biomagnification of mercury through lake trout (*Salvelinus namaycush*) food webs of lakes with different physical, chemical and biological characteristics. Sci Total Environ 438:135–143

Klonowska A, Moulin L, Ardley JK, Braun F, Gollagher MM, Zandberg JD, Woyke T (2020) Novel heavy metal resistance gene

clusters are present in the genome of *Cupriavidus neocaledonicus* STM 6070, a new species of *Mimosa pudica* microsymbiont isolated from heavy-metal-rich mining site soil. BMC Genom 21(1):1–18

Kohli SK, Handa N, Bali S, Khanna K, Arora S, Sharma A, Bhardwaj R (2020) Current scenario of Pb toxicity in plants: unraveling plethora of physiological responses. Rev Environ Contam Toxicol 249:153–197

Kong Z, Wu Z, Glick BR, He S, Huang C, Wu L (2019) Co-occurrence patterns of microbial communities affected by inoculants of plant growth-promoting bacteria during phytoremediation of heavy metal-contaminated soils. Ecotoxicol Environ Saf 183:109504

Kumar B, Smita K, Flores LC (2017) Plant mediated detoxification of mercury and lead. Arab J Chem 10:S2335–S2342

Kumar K, Shinde A, Aeron V, Verma A, Arif NS (2022a) Genetic engineering of plants for phytoremediation: advances and challenges. J Plant Biochem Biotechnol 2022:1–19. https://doi.org/10.1007/s13562-022-00776-3

Kumar R, Ivy N, Bhattacharya S, Dey A, Sharma P (2022b) Coupled effects of microplastics and heavy metals on plants: Uptake, bioaccumulation, and environmental health perspectives. Sci Total Environ 836:155619

Kumar S, Thakur N, Singh AK, Gudade BA, Ghimire D, Das S (2022c) Microbes-assisted phytoremediation of contaminated environment: global status, progress, challenges, and future prospects. Phytoremediation technology for the removal of heavy metals and other contaminants from soil and water. Elsevier, Amsterdam, pp 555–570

Kumari K, Cherian S, Bauddh K (2022) Microbial augmented phytoremediation with improved ecosystems services. Advances in microbe-assisted phytoremediation of polluted sites. Elsevier, Amsterdam, pp 27–62

Kunjapur AM, Pfingstag P, Thompson NC (2018) Gene synthesis allows biologists to source genes from farther away in the tree of life. Nat Commun 9(1):1–11

Laghlimi M, Baghdad B, Hadi HE, Bouabdli A (2015) Phytoremediation mechanisms of heavy metal contaminated soils: a review. Open J Ecol 5:375–388

Lamine S, Petropoulos GP, Brewer PA, Bachari NEI, Srivastava PK, Manevski K, Macklin MG (2019) Heavy metal soil contamination detection using combined geochemistry and field spectroradiometry in the United Kingdom. Sensors 19(4):762

Larue C, Castillo-Michel H, Sobanska S, Cécillon L, Bureau S, Barthès V, Sarret G (2014a) Foliar exposure of the crop *Lactuca sativa* to silver nanoparticles: evidence for internalization and changes in Ag speciation. J Hazard Mater 264:98–106

Larue C, Castillo-Michel H, Sobanska S, Trcera N, Sorieul S, Cécillon L, Sarret G (2014b) Fate of pristine $TiO_2$ nanoparticles and aged paint-containing $TiO_2$ nanoparticles in lettuce crop after foliar exposure. J Hazard Mater 273:17–26

Liang J, Feng C, Zeng G, Gao X, Zhong M, Li X, Fang Y (2017) Spatial distribution and source identification of heavy metals in surface soils in a typical coal mine city, Lianyuan, China. Environ Pollut 225:681–690

Limmer M, Burken J (2016) Phytovolatilization of organic contaminants. Environ Sci Technol 50(13):6632–6643

Linacre NA, Whiting SN, Angle JS (2005) The impact of uncertainty on phytoremediation project costs. Int J Phytoremediat 7(4):259–269

Liu Z, Tran KQ (2021) A review on disposal and utilization of phytoremediation plants containing heavy metals. Ecotoxicol Environ Saf 226:112821

Liu Q, Zhang H (2012) Molecular identification and analysis of arsenite stress-responsive miRNAs in rice. J Agric Food Chem 60(26):6524–6536

Liu D, An Z, Mao Z, Ma L, Lu Z (2015) Enhanced heavy metal tolerance and accumulation by transgenic sugar beets expressing *Streptococcus thermophilus* StGCS-GS in the presence of Cd, Zn and Cu alone or in combination. PLoS ONE 10(6):e0128824

Liu Y, Mi Y, Zhang J, Li Q, Chen L (2016) Illumina-based transcriptomic profiling of Panax notoginseng in response to arsenic stress. Bot Stud 57(1):1–11

Liu C, Lin H, Li B, Dong Y, Menzembere ERGY (2021) Endophyte *Pseudomonas putida* enhanced *Trifolium repens* L. growth and heavy metal uptake: a promising in-situ non-soil cover phytoremediation method of nonferrous metallic tailing. Chemosphere 272:129816

Liu C, Li B, Dong Y, Lin H (2022a) Endophyte colonization enhanced cadmium phytoremediation by improving endosphere and rhizosphere microecology characteristics. J Hazard Mater 434:128829

Liu D, Gao Z, Li J, Yao Q, Tan W, Xing W, Lu Z (2022b) Effects of cadmium stress on the morphology, physiology, cellular ultrastructure, and BvHIPP24 gene expression of sugar beet (*Beta vulgaris* L.). Int J Phytorem 2022:1–11. https://doi.org/10.1080/15226514.2022.2090496

Lugtenberg BJ, Malfanova N, Kamilova F, Berg G (2013) Plant growth promotion by microbes. Mol Microbial Ecol Rhizosphere 2:561–573

Ma Y, Prasad MNV, Rajkumar M, Freitas H (2011) Plant growth promoting rhizobacteria and endophytes accelerate phytoremediation of metalliferous soils. Biotechnol Adv 29(2):248–258

Ma Y, Rajkumar M, Luo Y, Freitas H (2013) Phytoextraction of heavy metal polluted soils using *Sedum plumbizincicola* inoculated with metal mobilizing *Phyllobacterium myrsinacearum* RC6b. Chemosphere 93(7):1386–1392

Ma Y, Oliveira RS, Nai F, Rajkumar M, Luo Y, Rocha I, Freitas H (2015) The hyperaccumulator *Sedum plumbizincicola* harbors metal-resistant endophytic bacteria that improve its phytoextraction capacity in multi-metal contaminated soil. J Environ Manag 156:62–69

Ma Y, Oliveira RS, Freitas H, Zhang C (2016a) Biochemical and molecular mechanisms of plant-microbe-metal interactions: relevance for phytoremediation. Front Plant Sci 7:918

Ma Y, Rajkumar M, Zhang C, Freitas H (2016cb) Inoculation of *Brassica oxyrrhina* with plant growth promoting bacteria for the improvement of heavy metal phytoremediation under drought conditions. J Hazard Mater 320:36–44

Ma Y, Rajkumar M, Oliveira RS, Zhang C, Freitas H (2019) Potential of plant beneficial bacteria and arbuscular mycorrhizal fungi in phytoremediation of metal-contaminated saline soils. J Hazard Mater 379:120813

Macnair MR, Bert V, Huitson SB, Saumitou-Laprade P, Petit D (1999) Zinc tolerance and hyperaccumulation are genetically independent characters. Proc R Soc Lond Ser B Biol Sci 266(1434):2175–2179

Maillet F, Poinsot V, André O, Puech-Pagès V, Haouy A, Gueunier M, Cromer L, Giraudet D, Formey D, Niebel A, Martinez EA (2011) Fungal lipochitooligosaccharide symbiotic signals in arbuscular mycorrhiza. Nature 469(7328):58–63

Malik ZH, Ravindran KC, Ganesan S (2017) Phytoremediation: a novel strategy and eco-friendly green technology for removal of toxic metals. Int J Agric Environ Res 3(1):1–18

Mandal SM, Chakraborty D, Dey S (2010) Phenolic acids act as signaling molecules in plant-microbe symbioses. Plant Signal Behav 5(4):359–368

Manoj SR, Karthik C, Kadirvelu K, Arulselvi PI, Shanmugasundaram T, Bruno B, Rajkumar M (2020) Understanding the molecular mechanisms for the enhanced phytoremediation of heavy metals through plant growth promoting rhizobacteria: a review. J Environ Manag 254:109779

Mansoor S, Khan NF, Farooq I, Kaur N, Manhas S, Raina S, Khan IF (2022) Phytoremediation at molecular level. Phytoremediation. Academic Press, Cambridge, pp 65–90

Mantelin S, Touraine B (2004) Plant growth-promoting bacteria and nitrate availability: impacts on root development and nitrate uptake. J Exp Bot 55(394):27–34

Marques AP, Rangel AO, Castro PM (2009) Remediation of heavy metal contaminated soils: phytoremediation as a potentially promising clean-up technology. Crit Rev Environ Sci Technol 39(8):622–654

Mashabela MD, Piater LA, Dubery IA, Tugizimana F, Mhlongo MI (2022) Rhizosphere tripartite interactions and PGPR-mediated metabolic reprogramming towards ISR and plant priming: a metabolomics review. Biology 11(3):346

Meena VS, Maurya BR, Verma JP, Meena RS (eds) (2016) Potassium solubilizing microorganisms for sustainable agriculture. Springer, New Delhi

Mei X, Wang Y, Li Z, Larousse M, Pere A, da Rocha M, Zhan F, He Y, Pu L, Panabières F, Zu Y (2022) Root-associated microbiota drive phytoremediation strategies to lead of *Sonchus Asper* (L.) Hill as revealed by intercropping-induced modifications of the rhizosphere microbiome. Environ Sci Pollut Res 29(16):23026–23040

Mesjasz-Przybyłowicz J, Nakonieczny M, Migula P, Augustyniak M, Tarnawska M, Reimold W, Koeberl C, Przybyłowicz W, Głowacka E (2004) Uptake of cadmium, lead nickel and zinc from soil and water solutions by the nickel hyperaccumulator *Berkheyacoddii*. Acta Biol Cracoviensia Ser Bot 46:75–85

Mishra J, Singh R, Arora NK (2017) Alleviation of heavy metal stress in plants and remediation of soil by rhizosphere microorganisms. Front Microbiol 8:1706

Mullineaux PM, Rausch T (2005) Glutathione, photosynthesis and the redox regulation of stress-responsive gene expression. Photosynth Res 86(3):459–474

Muthusaravanan S, Sivarajasekar N, Vivek JS, Paramasivan T, Naushad M, Prakashmaran J, Al-Duaij OK (2018) Phytoremediation of heavy metals: mechanisms, methods and enhancements. Environ Chem Lett 16(4):1339–1359

Nadeem SM, Ahmad M, Zahir ZA, Javaid A, Ashraf M (2014) The role of mycorrhizae and plant growth promoting rhizobacteria (PGPR) in improving crop productivity under stressful environments. Biotechnol Adv 32(2):429–448

Nagajyoti PC, Lee KD, Sreekanth TVM (2010) Heavy metals, occurrence and toxicity for plants: a review. Environ Chem Lett 8(3):199–216

Nahar N, Rahman A, Nawani NN, Ghosh S, Mandal A (2017) Phytoremediation of arsenic from the contaminated soil using transgenic tobacco plants expressing ACR2 gene of *Arabidopsis thaliana*. J Plant Physiol 218:121–126

Navarro-Torre S, Carro L, Igual JM, del Carmen M-CM (2021) *Rossellomorea arthrocnemi* sp. Nov., a novel plant growth-promoting bacterium used in heavy metal polluted soils as a phytoremediation tool. Int J Syst Evol Microbiol 71(10):752. https://doi.org/10.1099/ijsem.0.005015

Nayak AK, Panda SS, Basu A, Dhal NK (2018) Enhancement of toxic Cr (VI), Fe, and other heavy metals phytoremediation by the synergistic combination of native *Bacillus cereus* strain and *Vetiveria zizanioides* L. Int J Phytoremediat 20(7):682–691

Newman MA, Sundelin T, Nielsen JT, Erbs G (2013) MAMP (microbe-associated molecular pattern) triggered immunity in plants. Front Plant Sci 4:139

Ngugi MM, Gitari HI, Muui CW, Gweyi-Onyango JP (2022) Growth tolerance, concentration, and uptake of heavy metals as ameliorated by silicon application in vegetables. Int J Phytoremediat 2022:1–14

Ogunkunle CO, Odulaja DA, Akande FO, Varun M, Vishwakarma V, Fatoba PO (2020) Cadmium toxicity in cowpea plant: effect of foliar intervention of nano-TiO$_2$ on tissue Cd bioaccumulation, stress enzymes and potential dietary health risk. J Biotechnol 310:54–61

Ojuederie OB, Babalola OO (2017) Microbial and plant-assisted bioremediation of heavy metal polluted environments: a review. Int J Environ Res Public Health 14(12):1504

Pasricha S, Mathur V, Garg A, Lenka S, Verma K, Agarwal S (2021) Molecular mechanisms underlying heavy metal uptake, translocation and tolerance in hyperaccumulators-an analysis: heavy metal tolerance in hyperaccumulators. Environ Challenges 4:100197

Patel J, Zhang Q, McKay RML, Vincent R, Xu Z (2010) Genetic engineering of *Caulobacter crescentus* for removal of cadmium from water. Appl Biochem Biotechnol 160(1):232–243

Pathak P, Bhattacharya D (2021) Phytoextraction of heavy metals by weeds: physiological and molecular intervention. Handbook of bioremediation. Academic Press, Cambridge, pp 49–59

Paul S, Dukare AS, Manjunatha BS, Annapurna K (2017) Plant growth-promoting rhizobacteria for abiotic stress alleviation in crops. Advances in soil microbiology: recent trends and future prospects. Springer, Singapore, pp 57–79

Rabani MS, Hameed I, Mir TA, Gupta MK, Habib A, Jan M, Hussain H, Tripathi S, Pathak A, Ahad MB, Gupta C (2022) Microbial-assisted phytoremediation. phytoremediation. Academic Press, Cambridge, pp 91–114

Rai PK, Kim KH, Lee SS, Lee JH (2020) Molecular mechanisms in phytoremediation of environmental contaminants and prospects of engineered transgenic plants/microbes. Sci Totl Environ 705:135858

Rajkumar M, Sandhya S, Prasad MNV, Freitas H (2012) Perspectives of plant-associated microbes in heavy metal phytoremediation. Biotechnol Adv 30(6):1562–1574

Ramírez V, Baez A, López P, Bustillos MDR, Villalobos MA, Carreño R, Munive JA (2019) Chromium hyper-tolerant *Bacillus* sp. MH778713 assists phytoremediation of heavy metals by mesquite trees (*Prosopis laevigata*). Front Microbiol 10:1833

Rascio N, Navari-Izzo F (2011) Heavy metal hyperaccumulating plants: how and why do they do it? And what makes them so interesting? Plant Sci 180(2):169–181

Ratna S, Rastogi S, Kumar R (2021) Phytoremediation: a synergistic interaction between plants and microbes for removal of unwanted chemicals/contaminants. Microbes and signaling biomolecules against plant stress. Springer, Singapore, pp 199–222

Rausch T, Gromes R, Liedschulte V, Müller I, Bogs J, Galovic V, Wachter A (2007) Novel insight into the regulation of GSH biosynthesis in higher plants. Plant Biol 9(05):565–572

Ribeiro AT, de Oliveira VP, Junior UDOB, da Silva BRS, Batista BL, da Silva Lobato AK (2020) 24-Epibrassinolide mitigates nickel toxicity in young *Eucalyptus urophylla* ST Blake plants: nutritional, physiological, biochemical, anatomical and morphological responses. Ann for Sci 77(1):1–19

Rono JK, Le Wang L, Wu XC, Cao HW, Zhao YN, Khan IU, Yang ZM (2021) Identification of a new function of metallothionein-like gene OsMT1e for cadmium detoxification and potential phytoremediation. Chemosphere 265:129136

Rosen BP (1999) Families of arsenic transporters. Trends Microbiol 7(5):207–212

Roth-Nebelsick A (2007) Computer-based studies of diffusion through stomata of different architecture. Ann Bot 100(1):23–32

Ryu CM, Farag MA, Hu CH, Reddy MS, Kloepper JW, Paré PW (2004) Bacterial volatiles induce systemic resistance in *Arabidopsis*. Plant Physiol 134(3):1017–1026

Sabir M, Waraich EA, Hakeem KR, Öztürk M, Ahmad HR, Shahid M (2015) Phytoremediation: mechanisms and adaptations. Soil Remed Plants Prospects Challenges 85:85–105

Saha M, Sarkar S, Sarkar B, Sharma BK, Bhattacharjee S, Tribedi P (2016) Microbial siderophores and their potential applications: a review. Environ Sci Pollut Res 223(5):3984–3999

Sarwar N, Imran M, Shaheen MR, Ishaque W, Kamran MA, Matloob A, Rehim A, Hussain S (2017) Phytoremediation strategies for soils contaminated with heavy metals: modifications and future perspectives. Chemosphere 171:710–721

Saxena G, Kishor R, Saratale GD, Bharagava RN (2020) Genetically Modified Organisms (GMOs) and their potential in environmental management: constraints, prospects, and challenges. Bioremediation of industrial waste for environmental safety. Springer, Singapore, pp 1–19

Scervino JM, Ponce MA, Erra-Bassells R, Vierheilig H, Ocampo JA, Godeas A (2005) Flavonoids exhibit fungal species and genus specific effects on the presymbiotic growth of *Gigaspora* and *Glomus*. Mycol Res 109(7):789–794

Schenk PM, Carvalhais LC, Kazan K (2012) Unraveling plant–microbe interactions: can multi-species transcriptomics help? Trends Biotechnol 30(3):177–184

Schreck E, Foucault Y, Sarret G, Sobanska S, Cécillon L, Castrec-Rouelle M, Dumat C (2012) Metal and metalloid foliar uptake by various plant species exposed to atmospheric industrial fallout: mechanisms involved for lead. Sci Total Environ 427:253–262

Schreiber L, Schonherr J (2009) Water and solute permeability of plant cuticles. Springer, Berlin

Seregin IV, Ivanov VB (2001) Physiological aspects of cadmium and lead toxic effects on higher plants. Russ J Plant Physiol 48(4):523–544

Sessitsch A, Kuffner M, Kidd P, Vangronsveld J, Wenzel WW, Fallmann K, Puschenreiter M (2013) The role of plant-associated bacteria in the mobilization and phytoextraction of trace elements in contaminated soils. Soil Biol Biochem 60:182–194

Seth CS (2012) A review on mechanisms of plant tolerance and role of transgenic plants in environmental clean-up. Bot Rev 78(1):32–62

Shahid M, Dumat C, Khalid S, Schreck E, Xiong T, Niazi NK (2017) Foliar heavy metal uptake, toxicity and detoxification in plants: a comparison of foliar and root metal uptake. J Hazard Mater 325:36–58

Shahid M, Khalid S, Bibi I, Bundschuh J, Niazi NK, Dumat C (2020) A critical review of mercury speciation, bioavailability, toxicity and detoxification in soil-plant environment: ecotoxicology and health risk assessment. Sci Total Environ 711:134749

Shahzad R, Waqas M, Khan AL, Asaf S, Khan MA, Kang SM, Yun BW, Lee IJ (2016) Seed-borne endophytic *Bacillus amyloliquefaciens* RWL-1 produces gibberellins and regulates endogenous phytohormones of Oryza sativa. Plant Physiol Biochem 106:236–243

Sharma R, Bhardwaj R, Handa N, Gautam V, Kohli SK, Bali S, Vig AP (2016) Responses of phytochelatins and metallothioneins in alleviation of heavy metal stress in plants: an overview. Plant metal interaction. Elsevier, Amsterdam, pp 263–283

Sharma A, Kapoor D, Wang J, Shahzad B, Kumar V, Bali AS, Yan D (2020) Chromium bioaccumulation and its impacts on plants: an overview. Plants 9(1):100

Sharma P, Chaturvedi P, Chandra R, Kumar S (2022a) Identification of heavy metals tolerant *Brevundimonas* sp. from rhizospheric zone of *Saccharum munja* L. and their efficacy in in-situ phytoremediation. Chemosphere 295:133823

Sharma R, Kumar R, Hajam YA, Rani R (2022b) Role of biotechnology in phytoremediation. Phytoremediation. Academic Press, Cambridge, pp 437–454

Sheng X, He L, Wang Q, Ye H, Jiang C (2008) Effects of inoculation of biosurfactant-producing *Bacillus* sp. J119 on plant growth and cadmium uptake in a cadmium-amended soil. J Hazard Mater 155(12):17–22

Shim D, Kim S, Choi YI, Song WY, Park J, Youk ES, Jeong SC, Martinoia E, Noh EW, Lee Y (2013) Transgenic poplar trees expressing yeast cadmium factor 1 exhibit the characteristics necessary for the phytoremediation of mine tailing soil. Chemosphere 90(4):1478–1486

Singh JS, Abhilash PC, Singh HB, Singh RP, Singh DP (2011) Genetically engineered bacteria: an emerging tool for environmental remediation and future research perspectives. Gene 480(1–2):1–9

Singh G, Bhadange S, Bhawna F, Shewale P, Dahiya R, Aggarwal A, Manju F, Arya SK (2022) Phytoremediation of radioactive elements, possibilities and challenges: special focus on agricultural aspects. Int J Phytoremediat 2022:1–8. https://doi.org/10.1080/15226514.2022.2043239

Sone Y, Nakamura R, Pan-Hou H, Sato MH, Itoh T, Kiyono M (2013) Increase methylmercury accumulation in *Arabidopsis thaliana* expressing bacterial broad-spectrum mercury transporter MerE. AMB Express 3(1):1–8

Sriprang R, Hayashi M, Yamashita M, Ono H, Saeki K, Murooka Y (2002) A novel bioremediation system for heavy metals using the symbiosis between leguminous plant and genetically engineered rhizobia. J Biotechnol 99(3):279–293

Sriprang R, Hayashi M, Ono H, Takagi M, Hirata K, Murooka Y (2003) Enhanced accumulation of Cd2+ by a Mesorhizobium sp transformed with a gene from *Arabidopsis thaliana* coding for phytochelatin synthase. Appl Environ Microbiol 69(3):1791–1796

Srivastava S, Srivastava AK, Suprasanna P, D'souza SF (2013) Identification and profiling of arsenic stress-induced microRNAs in Brassica juncea. J Exp Bot 64(1):303–315

Steinkellner S, Lendzemo V, Langer I, Schweiger P, Khaosaad T, Toussaint JP, Vierheilig H (2007) Flavonoids and strigolactones in root exudates as signals in symbiotic and pathogenic plant-fungus interactions. Molecules 12(7):1290–1306

Subhashini V, Swamy AVVS (2013) Phytoremediation of Pb and Ni contaminated soils using *Catharanthus roseus* (L.). Univ J Environ Res Technol 3(4):2319

Sytar O, Kumar A, Latowski D, Kuczynska P, Strzałka K, Prasad MNV (2013) Heavy metal-induced oxidative damage, defense reactions, and detoxification mechanisms in plants. Acta Physiol Plant 35(4):985–999

Tauqeer HM, Ali S, Rizwan M, Ali Q, Saeed R, Iftikhar U, Abbasi GH (2016) Phytoremediation of heavy metals by *Alternanthera bettzickiana*: growth and physiological response. Ecotoxicol Environ Saf 126:138–146

Terwayet-Bayouli I, Robledo-Mahón T, Meers E, Calvo C, Aranda E (2022) Assessment of the antioxidative response and culturable micro-organisms of *Lygeum spartum* Loefl. ex L. for prospective phytoremediation applications. Int J Phytoremediat 2022:1–12. https://doi.org/10.1080/15226514.2022.2077694

Thakur S, Choudhary S, Majeed A, Singh A, Bhardwaj P (2019) Insights into the molecular mechanism of arsenic phytoremediation. J Plant Growth Regul 39:1–12

Thijs S, Sillen W, Rineau F, Weyens N, Vangronsveld J (2016) Towards an enhanced understanding of plant–microbiome interactions to improve phytoremediation: engineering the metaorganism. Front Microbiol 7:341

Tiwari S, Lata C (2018) Heavy metal stress, signaling, and tolerance due to plant-associated microbes: an overview. Front Plant Sci 9:452

Trivedi P, Pandey A (2008) Plant growth promotion abilities and formulation of *Bacillus megaterium* strain B 388 (MTCC6521)

isolated from a temperate Himalayan location. Indian J Microbiol 48(3):342–347

Ullah A, Heng S, Munis MFH, Fahad S, Yang X (2015) Phytoremediation of heavy metals assisted by plant growth promoting (PGP) bacteria: a review. Environ Exp Bot 117:28–40

Ullah I, Mateen A, Ahmad MA, Munir I, Iqbal A, Alghamdi KM, Al-Solami HM, Siddiqui MF (2022) Heavy metal ATPase genes (HMAs) expression induced by endophytic bacteria, "AI001, and AI002" mediate cadmium translocation and phytoremediation. Environ Pollut 293:118508

Van Dillewijn P, Couselo JL, Corredoira E, Delgado A, Wittich RM, Ballester A, Ramos JL (2008) Bioremediation of 2, 4, 6-trinitrotoluene by bacterial nitroreductase expressing transgenic aspen. Environ Sci Technol 42(19):7405–7410

Varnier AL, Sanchez L, Vatsa P, Boudesocque L, Angela GA, Rabenoelina F, Sorokin A, Renault JH, Kauffmann S, Pugin A, Clément C (2009) Bacterial rhamnolipids are novel MAMPs conferring resistance to *Botrytis cinerea* in grapevine. Plant Cell Environ 32(2):178–193

Verbon EH, Liberman LM (2016) Beneficial microbes affect endogenous mechanisms controlling root development. Trends Plant Sci 21(3):218–229

Verkleij JA, Golan-Goldhirsh A, Antosiewisz DM, Schwitzguébel JP, Schröder P (2009) Dualities in plant tolerance to pollutants and their uptake and translocation to the upper plant parts. Environ Exp Bot 67(1):10–22

Vershinina ZR, Maslennikova DR, Chubukova OV, Khakimova LR, Fedyaev VV (2022) Contribution of artificially synthetized phytochelatin encoded by the gene PPH6HIS to increase the phytoremediative qualities of tobacco plants. Russ J Plant Physiol 69(4):1–9

Villacieros M, Whelan C, Mackova M, Molgaard J, Sánchez-Contreras M, Lloret J, de Cárcer DA, Oruezábal RI, Bolanos L, Macek T, Karlson U (2005) Polychlorinated biphenyl rhizoremediation by *Pseudomonas fluorescens* F113 derivatives, using a *Sinorhizobium meliloti* nod system to drive *bph* gene expression. Appl Environ Microbiol 71(5):2687–2694

Visioli G, D'Egidio S, Vamerali T, Mattarozzi M, Sanangelantoni AM (2014) Culturable endophytic bacteria enhance Ni translocation in the hyperaccumulator *Noccaea caerulescens*. Chemosphere 117:538–544

Vocciante M, Grifoni M, Fusini D, Petruzzelli G, Franchi E (2022) The role of plant growth-promoting rhizobacteria (PGPR) in mitigating plant's environmental stresses. Appl Sci 12(3):1231

Vongdala N, Tran HD, Xuan TD, Teschke R, Khanh TD (2019) Heavy metal accumulation in water, soil, and plants of municipal solid waste landfill in Vientiane, Laos. Int J Environ Res Public Health 16(1):22

Wang Z, Gerstein M, Snyder M (2009) RNA-Seq: a revolutionary tool for transcriptomics. Nat Rev Gen 10(1):57–63

Wang Q, Xiong D, Zhao P, Yu X, Tu B, Wang G (2011) Effect of applying an arsenic-resistant and plant growth–promoting rhizobacterium to enhance soil arsenic phytoremediation by Populus deltoides LH05-17. J Appl Microbiol 111(5):1065–1074

Wang L, Ji B, Hu Y, Liu R, Sun W (2017) A review on in situ phytoremediation of mine tailings. Chemosphere 184:594–600

Wang Q, Ma L, Zhou Q, Chen B, Zhang X, Wu Y, Feng Y (2019) Inoculation of plant growth promoting bacteria from hyperaccumulator facilitated non-host root development and provided promising agents for elevated phytoremediation efficiency. Chemosphere 234:769–776

Ward NI (1990) Lead contamination of the London orbital (M25) motorway (since its opening in 1986). Sci Totl Environ 93:277–283

Wei Y, Hou H, ShangGuan Y, Li J, Li F (2014) Genetic diversity of endophytic bacteria of the manganese-hyperaccumulating plant *Phytolacca americana* growing at a manganese mine. Eur J Soil Biol 62:15–21

Wong MH (2003) Ecological restoration of mine degraded soils, with emphasis on metal contaminated soils. Chemosphere 50(6):775–780

Wu CH, Wood TK, Mulchandani A, Chen W (2006) Engineering plant-microbe symbiosis for rhizoremediation of heavy metals. Appl Environ Microbiol 72(2):1129–1134

Wu ML, Cheng H, Zhao H, Sun FL, Wang YT, Yin JP, Wang YS (2020) Distribution patterns and source identification for heavy metals in Mirs Bay of Hong Kong in China. Ecotoxicol (lond, Engl) 29:767–770

Wuana RA, Okieimen FE (2011) Heavy metals in contaminated soils: a review of sources, chemistry, risks and best available strategies for remediation. Int Schol Res Notices 2011:402647

Xia F, Qu L, Wang T, Luo L, Chen H, Dahlgren RA, Huang H (2018) Distribution and source analysis of heavy metal pollutants in sediments of a rapid developing urban river system. Chemosphere 207:218–228

Xie Y, Bu H, Feng Q, Wassie M, Amee M, Jiang Y, Bi Y, Hu L, Chen L (2021) Identification of Cd-resistant microorganisms from heavy metal-contaminated soil and its potential in promoting the growth and Cd accumulation of bermudagrass. Environ Res 200:111730

Xiong TT, Leveque T, Austruy A, Goix S, Schreck E, Dappe V, Dumat C (2014) Foliar uptake and metal (loid) bioaccessibility in vegetables exposed to particulate matter. Environ Geochem Health 36(5):897–909

Yadav SK (2010) Heavy metals toxicity in plants: an overview on the role of glutathione and phytochelatins in heavy metal stress tolerance of plants. S Afr J Bot 76(2):167–179

Yan A, Wang Y, Tan SN, Mohd Yusof ML, Ghosh S, Chen Z (2020) Phytoremediation: a promising approach for revegetation of heavy metal-polluted land. Front Plant Sci 11:359

Yang Q, Tu S, Wang G, Liao X, Yan X (2012) Effectiveness of applying arsenate reducing bacteria to enhance arsenic removal from polluted soils by *Pteris vittata* L. Int J Phytoremediat 14(1):89–99

Yang Y, Liu Y, Li Z, Wang Z, Li C, Wei H (2020) Significance of soil microbe in microbial-assisted phytoremediation: an effective way to enhance phytoremediation of contaminated soil. Int J Environ Sci Technol 17(4):2477–2484

Yang L, Wang J, Yang Y, Li S, Wang T, Oleksak P, Chrienova Z, Wu Q, Nepovimova E, Zhang X, Kuca K (2022) Phytoremediation of heavy metal pollution: Hotspots and future prospects. Ecotoxicol Environ Saf 234:113403

Yanitch A, Brereton NJ, Gonzalez E, Labrecque M, Joly S, Pitre FE (2017) Transcriptomic response of purple willow (*Salix purpurea*) to arsenic stress. Front Plant Sci 8:1115

Yazaki K (2006) ABC transporters involved in the transport of plant secondary metabolites. FEBS Lett 580(4):1183–1191

Yong X, Chen Y, Liu W, Xu L, Zhou J, Wang S, Chen P, Ouyang P, Zheng T (2014) Enhanced cadmium resistance and accumulation in *Pseudomonas putida* KT 2440 expressing the phytochelatin synthase gene of *S. chizosaccharomyces* pombe. Lett Appl Microbiol 58(3):255–261

Yu LJ, Luo YF, Liao B, Xie LJ, Chen L, Xiao S, Shu WS (2012) Comparative transcriptome analysis of transporters, phytohormone and lipid metabolism pathways in response to arsenic stress in rice (*Oryza sativa*). New Phytol 195(1):97–112

Zahari NZ, Tuah PM, Rahim SA (2021) Inoculation of Bacillus cereus enhance phytoremediation efficiency of *Pistia stratiotes* and *Eichhornia crassipes* in removing heavy metal Pb. IOP Conf Ser 847(1):012012

Zeng P, Guo Z, Cao X, Xiao X, Liu Y, Shi L (2018) Phytostabilization potential of ornamental plants grown in soil contaminated with cadmium. Int J Phytoremediat 20(4):311–320

Zeng Q, Ding X, Wang J, Han X, Iqbal H, Bilal M (2022) Insight into soil nitrogen and phosphorus availability and agricultural sustainability by plant growth-promoting rhizobacteria. Environ Sci Pollut Res 29:1–18

Zgorelec Z, Bilandzija N, Knez K, Galic M, Zuzul S (2020) Cadmium and Mercury phytostabilization from soil using *Miscanthus× giganteus*. Sci Rep 10(1):1–10

Zhang H, Xie X, Kim MS, Kornyeyev DA, Holaday S, Paré PW (2008) Soil bacteria augment *Arabidopsis* photosynthesis by decreasing glucose sensing and abscisic acid levels in planta. Plant J 56(2):264–273

Zhang Y, Liu J, Zhou Y, Gong T, Wang J, Ge Y (2013) Enhanced phytoremediation of mixed heavy metal (mercury)–organic pollutants (trichloroethylene) with transgenic alfalfa co-expressing glutathione S-transferase and human P450 2E1. J Hazard Mater 260:1100–1107

Zhao L, Meng B, Feng X (2020) Mercury methylation in rice paddy and accumulation in rice plant: a review. Ecotoxicol Environ Saf 195:110462

Zhuang P, Lu H, Li Z, Zou B, McBride MB (2014) Multiple exposure and effects assessment of heavy metals in the population near mining area in South China. PLoS ONE 9(4):e94484