Application of Plant-Microbe Interactions in Contaminated Agroecosystem Management

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Abstract

Agroecosystem is often confronted with a variety of pollutants. The application of plant-microbe interactions in remedying the ecosystem is called phytoremediation. Within the rhizosphere, plant roots interact with microorganisms and the soil, and plants usually secrete substances which affect microbial growth. Some plant-microbe relationships are beneficial to the plant while others are not. However, these interactions largely ensure a healthy plant growth while eliminating plant pathogens from the soil either by separate or combined activities of the plant exudates and beneficial microbes. The nature of microbes associated with each plant is apparently related to the exudates and signal molecules emanating from the plant and the interactive signals of the microbes. Sometimes, the soil is contaminated either deliberately or inadvertently by a variety of chemicals and heavy metals. To control or eliminate these contaminants, chemical and physical means have largely been applied. Unfortunately, some of these control measures introduce their own contaminants thereby causing secondary contamination. This necessitates the need and application of eco-friendly and sustainable solar-driven technology, viz., phytoremediation, to restitute the soils. Microbe-plant interactions sometimes improve the absorptive capacity of the plant for contaminants. Some microbes modify soil contaminants by using organic acids, redox reactions, producing siderophores, metal chelators, biosurfactants, causing bioleaching, biosorption, and bioexclusion. These microbes-contaminants interactions boost the reduction of toxicity and elimination of contaminants via various phytoremediation processes, viz., phytostimulation, phytodegradation, phytoextraction/phytoaccumulation,

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phytostabilization, phytovolatilization, and rhizofiltration. Nevertheless, phytoremediation faces certain major challenges as regards to its commercial-scale application in the field. To overcome these limitations, it is essential to have a better understanding of the relationships among plant microbes, soil types, chemicals, and heavy metal contaminants within an agroecosystem. Besides, it is important to develop phyto-hyper-accumulators and super microbial solubilizers, for various soil types.

4.1 Introduction

The agroecosystem is construed as a coherent functional unit of interactions that exist between living and nonliving components of the environment as well as their activities (Jalloh et al. 2012). The release of prevalent chemical contaminants into the environment due to increased anthropogenic activities has been on elevated levels. Chemical contaminants, such as polycyclic aromatic hydrocarbons (PAHs), petroleum hydrocarbons (PHCs), pesticides, halogenated hydrocarbons, metals, salts, and solvents, have been prompting stress on the ecosystem and human health (Gerhardt et al. 2009; Meagher 2000). The continuous discharge of pollutants into the environment poses a great threat to the microbiota, to flora and fauna, and also to human and animal health, as these chemicals are transferred down the food chain in the ecosystem (Esedafe et al. 2015). The pressure on production and application of agrochemicals either for yield improvement or insect and weed control has also caused perpetual stress and distortions in the ecosystems (Singh 2015; Vimal et al. 2017). The turnover of chemical contaminants in the ecosystem is a function of the viability and coherence of the functional interactions of the participating organisms in that environment. In-depth understanding of the processes involved in plant-microbe interactions will make the management of contaminated agroecosystems quite efficient (Fester et al. 2014). Some of these contaminants are recalcitrant and can persist for longer periods in the environment. Traditional methods of remediation employ the chemical or physical approaches which involve extraction of the contaminants onsite or removal of the contaminated soil. However, beneficial microbes and plants with tendencies for hyper-accumulation of metals have been identified as a promising approach for the cleanup of contaminants in the environment through phytovolatilization, phytostabilization, or phytoextraction processes (Glick 2010; Lebeau et al. 2008) (see Fig. 4.1).

Naturally, plants depend on soil, air, and water as essential ingredients for growth and development. They also interact with myriads of unicellular and multicellular organisms in mutualistic, pathogenic, or parasitic relationships (Ahmad et al. 2008; Lau and Lennon 2011; Siebers et al. 2016), which are triggered by exchange of molecular information when a microbial invader comes into contact with a host plant (Siebers et al. 2016). Microbes interacting with plant hosts can be found in the rhizosphere, root tissues, rhizoplane, and root nodules of leguminous plants (Antoun

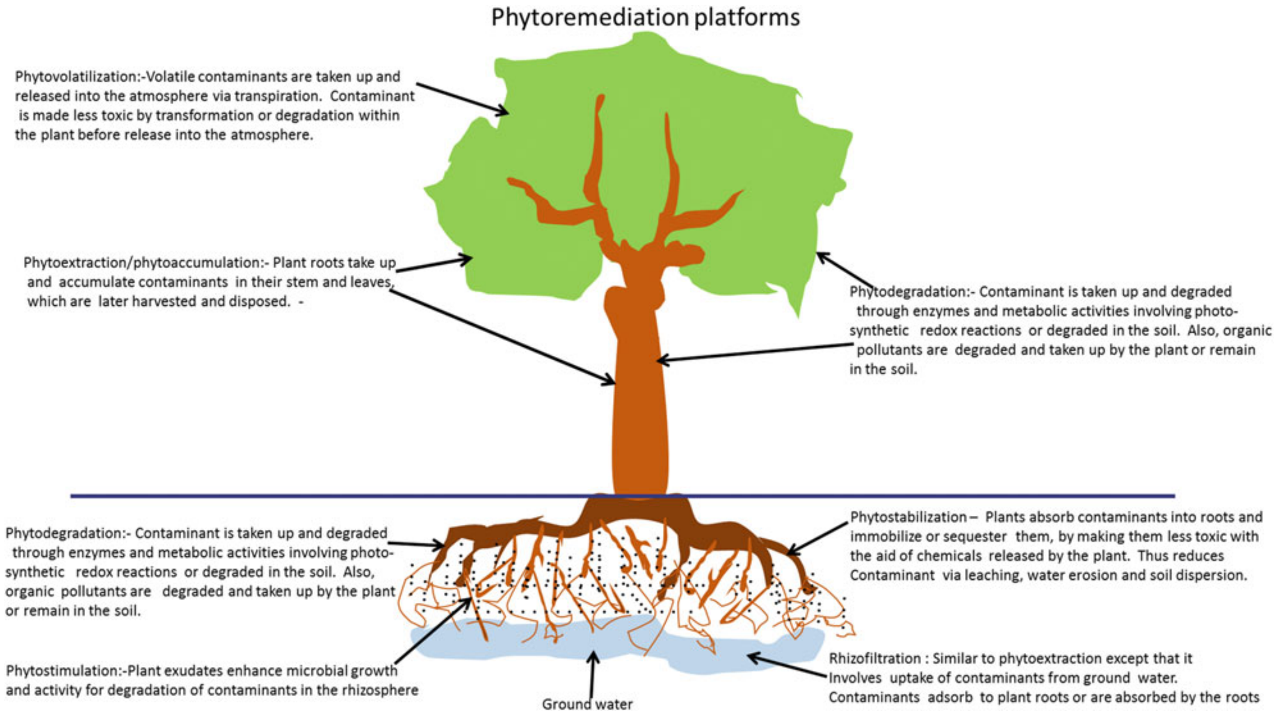

Fig. 4.1 Illustration of various phytoremediation processes involved in the removal of contaminants in an ecosystem

and Prévost 2005). Microbes such as fungi, bacteria, actinomycetes, algae, and protozoa have been identified in close interactions with plants roots and demonstrated proven characteristics of enhancing growth and development of plant (Bhattacharyya and Jha 2012; Hayat et al. 2010; Saharan and Nehra 2011). The plant growth-promoting rhizobacteria (PGPR), including members of the genera *Bacillus*, *Enterobacter*, *Pseudomonas*, *Klebsiella*, *Azospirillum*, *Variovorax*, *Burkholderia*, *Azotobacter*, *Alcaligenes*, *Rhizobium*, *Xanthomonas*, *Proteus*, *Flavobacterium*, *Erwinia*, *Arthrobacter*, and *Serratia*, constitute the rhizosphere microbiota producing noticeable impacts on host plants (Kaymak 2010; Nadeem et al. 2014; Prasad et al. 2015). Other than bacterial species abundance, fungi also constitute a large proportion of the rhizosphere microflora valuable for enhanced plant growth. Fungal symbiotic mycorrhizae are fundamental at increasing the surface area of the root, which invariably results in more effective water and nutrient uptake from the soil (Prasad et al. 2017). Ecto- and endo-mycorrhizae are known to associate with a host of plant species. Other than facilitating water and mineral uptake, mycorrhizae also provide the host plant with protection from certain abiotic stress factors (Miransari 2010).

In their coevolutionary history, plants and microbes interact in either beneficial or detrimental manner for survival, a relationship that is inevitable for their individual existence. Exudates produced from these interactions greatly enhance movements of nutrients and metals by (1) enzymatic transfer of electrons in the rhizosphere, (2) acidification and formation of complexes due to released proton (H^+) molecule, and (3) indirect enhancement of microbial activity in the rhizosphere, resulting in effective phytoremediation (Pérez-Esteban et al. 2013; Sessitsch et al. 2013). Phytoremediation of heavy metal-contaminated soil is a promising relatively new technology that is eco-friendly, solar-driven, and potentially cost-effective. The technology aims at managing the agroecosystems by exploiting the healthy interaction between soil, plant roots, and microbes in the rhizosphere to rid the soil of heavy metals. The effectiveness of phytoremediation depends on soil temperature, moisture, nutrients, microorganisms, and herbivory as well as contaminant distribution, soil type, soil pH, soil texture, variety of plant roots, and metal uptake capacity (Vangronsveld et al. 2009).

4.2 Beneficial Plant-Microbe Interactions

In nature, the interactions between plants and microbes are diverse and dynamic due to their coevolutionary pressures (Chaparro et al. 2013). Beneficial plant-microbe interactions in the environment have been severally reported as one of the major drivers of a functional ecosystem (Nadeem et al. 2014; Rashid et al. 2016; Singh et al. 2016). These interactions significantly alter the microbiological, biochemical, and physicochemical parameters of the rhizosphere as it is evident that the microbial population in the root environment is usually more enriched than the surrounding environment. The beneficial plant-microbe relationship is a critical factor that helps to determine and improve plant health and fertility of the soil (Hayat et al. 2010) and root growth and development (Gamalero et al. 2004) and promote resistance to environmental stress factors (Glick 2004). Plants are naturally capable of determining their root microbiota from the soil environment, and the microbiota species abundance is typical of each plant species (Hartmann et al. 2009), a feature that can be attributed to the composition of the root exudates and the characteristics of the rhizosphere soil (Chaparro et al. 2013; Ma et al. 2016). Some of these organic chemicals released from the plant roots function as effective signaling molecules that foster effective communications between the plant and its microbial associates (Bulgarelli et al. 2013; Doornbos et al. 2012; Drogue et al. 2012). It may also dictate the order of interactions among the participating microbial partners in the rhizosphere. Signaling molecules in plant-microbe interactions show reciprocal effects on the partners involved. The plant signals are perceived by the microbial partners, while the microbial signal molecules affect the plant physiology (Nadeem et al. 2014).

The root exudates of plants are composed of diverse organic compounds which have been classified into three major classes: (1) high molecular weight compounds, (2) low molecular weight compounds, and (3) volatile organic compounds (VOCs). The bulk of the root exudates are the low molecular weight compounds which contain organic acids, sugars, phenolics, vitamins, amino acids, and certain secondary metabolite compounds. Compounds such as aldehydes, alcohols, carbon dioxide, mucilage and proteins, and various secondary metabolites constitute the high molecular weight compounds (Badri and Vivanco 2009; Schulz and Dickschat 2007). Cultivated plants on phosphate-deficient soil or polluted soil with high aluminum concentration often demonstrate increased exudation of certain organic acids such as malic acid, citric acid, and oxalic acids (Lopez-Bucio et al. 2000; Neumann and Römheld 1999). These exudate organic molecules may function as chemical attractants to microbes and also as carbon source for enhanced microbial proliferations in the rhizosphere (Ortíz-Castro et al. 2009). The rhizosphere is a dynamic component of plant-microbe interactions that promotes plants growth and productivity. The ecological, physical, and biochemical features of the rhizosphere remain a function of the type and nature of exudates released and the timing for the release. About 20–40% of fixed carbon has been estimated to be released back into the rhizosphere. These events make the rhizosphere a significant integral component for enhanced processes such as water and nutrient uptake and promotion of beneficial microbial interactions (Badri and Vivanco 2009; Bais et al. 2004). Malic acid exuded from the root attracts the beneficial soil bacteria, *B. subtilis*, in an interaction that confers protection against *Pseudomonas syringae*, the foliar pathogen (Rudrappa et al. 2008). As well, root colonization by rhizobacteria and mycorrhizal fungi was increased in alfalfa and tobacco plants genetically manipulated to overproduce malic acid. Invariably, malic acid plays a significant role in plant-microbe interaction, and root exudates of plant contribute in determining the rhizosphere structure and composition of the soil. This presents a great potential to be exploited for biotechnological advancement of the rhizosphere and its application in agricultural productions.

Interactions between plant and arbuscular mycorrhizal fungi (AMF) help to confer resistance to the plant against biotic and abiotic factors, resulting in improved plant health (Nadeem et al. 2014). The water relations of plants can be affected by AMF through mechanisms such as regulation of host stomatal organelle, increase in absorption of water by extending hyphae, enhanced phosphorus uptake, and antioxidant enzyme activity (Birhane et al. 2012; Habibzadeh et al. 2013; Younesi et al. 2013). The activity of antioxidant enzymes (peroxidase and catalase) was found to increase compared to uninoculated plants in a study on wheat-AMF interactions under stressed environment (Khalafallah and Abo-Ghalia 2008; Nadeem et al. 2014). However, other than enhancing phosphorus uptake, AMF facilitate the availability of micro- and macronutrients such as Zn, Cu, N, Mg, and K in absorbable forms from the soil (Meding and Zasoski 2008). In addition, the AMF functions to maintain the stability of the soil structure and also the performance of the plant under environmental stress conditions (Smith et al. 2010).

Plant-microbe interactions can be beneficial to all participating partners of the association. The mutualism can occur between plant-microbe and microbe-microbe with effects on both partners involved. These synergies generate positive impacts and beneficial coexistence toward promoting each other's proliferation (Nadeem et al. 2014; Richardson et al. 2009). For example, *Pseudomonas* spp. produced certain antifungal secondary metabolite which was nontoxic to its fungal counterpart, *Glomus mosseae*; however when applied in combination with the fungus, the bacteria enhanced the fungal hyphae to colonize the roots (Barea et al. 1998). The exopolysaccharides produced by the PGPR are important at facilitating effective attachment of bacterial cells to mycorrhizal roots of plants (Bianciotto et al. 2009). Furthermore, while mycorrhizae facilitate nitrogen fixation and improved phosphorus solubilization (Linderman 1992), the bacteria promote fungal hyphal proliferation by enabling plant root permeability for ease of fungal hyphal penetration (Jeffries et al. 2003). For PGPMs, fungi offer better comparative advantage over bacteria by being capable of extending their mycelia to spread long distances in the soil and rhizosphere environments. Usually, plant growth promotion by fungi is achieved through mechanisms such as antibiotic production, competition with invading fungal pathogens, and invocation of host defense reactions. Additionally, certain beneficial fungi possess the ability to successfully parasitize the conidia, hyphae, or sclerotia of phytopathogens thereby enabling biocontrol of pathogens. Mycoparasitism is preceded by the fungal ability to sense a suitable host, toward which the hyphae grow. This is followed by the ability of the fungi to recognize, penetrate, and degrade the encountered host. Degradative enzymes such as the proteinases, chitinases, and glucanases are important integral components of the biocontrol activity (Harman et al. 2004).

Trichoderma species are beneficial fungi which are found as free-living soil inhabitants or in association with plant roots in the rhizosphere. Although they are known mycoparasites in nature, many strains are capable of colonizing plant roots for improved growth and development. Plant-*Trichoderma* interactions are usually beneficial with no harmful effects (Harman et al. 2004). Colonization by the fungus results in induced localized and systemic resistance due to the secretion of a protein elicitor called *small protein 1* (*Sm1*). *Sm1* is nontoxic to plants and microbes. The native purified form is able to stimulate the production of reactive oxygen species

(ROS) in cotton and rice seedlings and trigger both localized and systemic defense-like gene expression (Djonović et al. 2006; Ortíz-Castro et al. 2009). However, for plant growth enhancement, *Trichoderma* species including *T. atroviride* and *T. virens* employ mechanisms such as the production of indole-3-acetic acid (IAA) and some forms of auxin-like compounds (Contreras-Cornejo et al. 2009).

4.3 Harmful Plant-Microbe Interactions

Despite the myriad growth-promoting advantages conferred by the PGPR, there also exist harmful effects of these interactions in the ecosystem (Saharan and Nehra 2011). These harmful effects may be attributed to certain unique conditions and some specifically endowed traits (Nadeem et al. 2014). For example, cyanide produced by some *Pseudomonas* species plays dual role of plant growth promotion as well as a growth inhibition. Though the cyanide produced plays the role of biological control of certain phytopathogens for enhanced plant growth (Martínez-Viveros et al. 2010), it has been reported to demonstrate some harmful effects on plant growth (Bakker and Schippers 1987). The production of auxin, a plant hormone, by PGPR can impact negatively on plant growth (Vacheron et al. 2013), depending on its concentration. Auxins at low concentrations promote plant growth (Patten and Glick 2002), but at a much higher concentrations, and affect root growth (Xie et al. 1996). Similarly, *Bradyrhizobium elkanii* produces a secondary metabolite called rhizobitoxine, which plays dual role: inhibits ethylene production in order to reduce the effect on nodulation in legumes (Vijayan et al. 2013) or functions as a plant toxin that stimulates chlorosis in soybeans (Xiong and Fuhrmann 1996). In another perspective, it was observed that, though the PGPR are nonpathogenic, their combined application with fungi can trigger pathogenicity among partners (Dewey et al. 1999). This may be attributed to horizontal gene transfers within the gene pool of the rhizosphere. This could be possible due to the continuous microbial activity around the plant root environment under optimum conditions.

4.4 The Role of Plant Signal Molecules in Plant-Microbe Interactions

Cuticular waxes formed due to plant-microbe interactions create a physical bridge on epidermal cell layers, regulate host-microbe communications, function as signaling molecules and affect pathogen proliferation, or modulate the recognition of pathogen invasion by elicitor molecules. Elicitors serve as signal-inducing molecules and also as recognized components of the innate immune defense system of the host. They can be produced by both beneficial and pathogenic microorganisms. Usually, elicitor molecules such as microbe-associated molecular patterns (MAMPs), derived from beneficial microbes, or pathogen-associated molecular patterns (PAMPs), derived from pathogenic microbes in interactions with host plant, can elicit the immune reaction of the host. The recognition of these elicitor molecules is mediated by the transmembrane pattern-recognition receptors (PRRs), and pathogens can only proliferate inside the host when these responses are suppressed (Jones and Dangl 2006; Siebers et al. 2016). Basically, plant-stimulated roots exude different varieties of organic compounds than non-stimulated ones. For example, when defense signaling molecules (DSM) such as methyl, jasmonate, salicylic acid, and nitric oxide were exogenously applied on plants, the formation of diverse secondary metabolites such as phytoalexins, alkamides, and indole glucosinolates was induced which is critical in enhancing effective microbial communications (Zhao et al. 2005). Thus, the role of plant metabolites in determining the microbial structure of the rhizosphere is based on the ability of the host to selectively secrete organic compounds that signal the presence of either bacteria or fungi (Ortíz-Castro et al. 2009).

Flavonoids exuded from plant roots are vital signaling molecules in different plant-microbe interactions such as the legume-rhizobia symbiotic interactions and mycorrhiza formation (Steinkellner et al. 2007). Flavonoids stimulate the proliferation of host-specific rhizobacteria and also act as chemoattractants which can regulate the *nod* gene to stimulate nodule formation during synthesis of the Nod factor (lipochitin oligosaccharide) signaling molecule (Ma et al. 2016; Mandal et al. 2010). Exuded flavonoids from plant roots can be recognized by the transcriptional regulator molecules, the *nodD* proteins which are fundamental at determining the synthesis and transport of the *nod* gene. Other than inducing the expression of *nod* genes, flavonoids greatly impact on bacterial chemotaxis and multiplication (Bais et al. 2006), a characteristic that pairs rhizobia to root hairs of their ideal plant hosts. Isoflavonoids and plant flavone are effective inducers of *nod* gene expression in rhizobia (Zhang et al. 2007). In plant-AMF interactions, flavonoids play key role as effective activators of conidial germination, growth of hyphae, plant root colonization, and sporulation (Mandal et al. 2010). However, the role of flavonoids on AMF growth is significantly relative as it can be of negative or neutral effect depending on the fungal species involved in the symbiotic mycorrhizal interactions (Scervino et al. 2005).

4.5 Role of Microbial Signal Molecules in Plant-Microbe Interactions

During plant-microbe interactions, communications between interspecies and intraspecies can occur within the rhizosphere either through direct cell-cell interactions or via chemical signaling molecules (Badri et al. 2009). In nature, microbes involved in interactions with plants are capable of transforming the chemical composition of plant root exudates to alter its physiology by way of secretion of certain signal molecules such as the Nod factors, Myc factors, volatile organic compounds (VOCs), exopolysaccharides, and microbe-assisted molecular patterns (MAMPs) (Goh et al. 2014; Ma et al. 2016). VOCs are defined as organic compounds of high vapor pressure and can vaporize into the atmosphere under certain conditions. They are low molecular weight (usually ⍰300 g/mol^{-1}) compounds such as aldehydes, alcohols, ketones, and hydrocarbons (Ortíz-Castro et al. 2009). VOCs of bacterial origin such as 2,3-butanediol and acetoin can stimulate host defense and enhance growth of host plant through a mechanism that enables the plant to thrive on soil depleted of essential nutrients like sulfur and iron (Bailly and Weisskopf 2012). VOCs produced and secreted by PGPMs can function as (1) phytostimulators, stimulate the various hormonal networks required for signals to any given stimulus; (2) bioprotectants, provoke induced systemic resistance in plants (ISR); and (3) biopesticides, kill plant vectors (Ma et al. 2016). The positive effects of VOCs can enhance plant growth promotion for effective phytoremediation. For example, the VOCs produced by *Bacillus* B55 improved sulfur uptake by *Nicotiana attenuata* (Hofmann 2013). VOCs produced and secreted by *Bacillus amyloliquefaciens* and *B. subtilis* activated the ISR of *Arabidopsis* seedlings compromised by the phytopathogen, *Erwinia carotovora* (Ryu et al. 2004). As well, other bacterial VOCs such as hydrogen cyanide, ammonia, phenazine-1-carboxylic acid, butyrolactones, and certain alcohols affect fungal conidial sporulation and mycelial mat formations (Kai et al. 2009). This implies that VOCs can function as an effective signaling molecule between the prokaryotes and the eukaryotes colonizing the plant roots (Ma et al. 2016). Furthermore, the AM fungus *Glomus intraradices* is able to produce a variety of lipochito-oligosaccharides (LCOs) containing both sulfated and non-sulfated derivatives (Myc factors), signaling molecules similar to the Nod factors of rhizobia. The Myc factor and the Nod factor signaling molecules are important in determining plant root organization such as development of lateral roots and stimulation of organogenesis (Maillet et al. 2011; Oláh et al. 2005). Plants have developed mechanisms to initiate non-specific immunity against phytopathogens via the activity of elicitor molecules such as the MAMPs (Newman et al. 2013). Novel MAMPs, rhamnolipids produced by *Pseudomonas aeruginosa*, have been shown to effectively confer resistance to grapevine plant against the phytopathogen, *Botrytis cinerea* (Varnier et al. 2009). In addition, MAMPs isolated from three PGPBs including *P. fluorescens*, *Chryseobacterium balustinum*, and *Stenotrophomonas maltophilia* were found to stimulate germination in *Papaver somniferum* (Bonilla et al. 2014).

4.6 Bacterial Quorum-Sensing Signals

Quorum sensing (QS) is a genetic mechanism that regulates the functioning and structure of a bacterial community (Bhattacharyya and Jha 2012). It is a communication process that occurs during bacterial cell to cell interactions, thereby monitoring population growth and density, while signaling molecules produced by individual cells control the expression and alteration of genes in the community (Daniels et al. 2004; Ma et al. 2016). The discovery and understanding of the role of bacterial signaling molecules have enabled the identification of two principal mechanisms of interference in microbial QS signaling, the enzymatic and the nonenzymatic microbial signal interferences which possess the ability of regulating QS signaling (Zhang and Dong 2004) and preventing microbial biofilm formation (Ren et al. 2001). Individual cell to cell QS communication signals are usually activated by certain autoinducer molecules that regulate bacterial actions. The N-acyl homoserine lactones (AHLs) are the most reported signaling autoinducers (von Bodman et al. 2003). AHLs possess the ability to promote or inhibit various phenotypes of either pathogenic or beneficial bacteria (Ortíz-Castro et al. 2009). The production of AHL signaling molecule is sacrosanct for the establishment of quorum sensing among Gram-negative bacteria such as *Pseudomonas aeruginosa*, *Erwinia carotovora*, and *Rhizobium radiobacter*. Production of AHLs signaling has been observed among PGPBs including *Gluconacetobacter diazotrophicus* and *Burkholderia graminis* (Cha et al. 1998) and also among strains of *Agrobacterium*, *Pectobacterium*, and *Chromobacterium* (Chernin et al. 2011). It has been observed recently that AHLs of bacterial origin can be well recognized by plants, to regulate gene expression in tissues, host defenses, and homeostatic balance (Daniels et al. 2004). It was recently shown that related types of AHLs (including *N*-octanoyl homoserine lactone, the 3-oxo and 3-hydroxy derivatives) secreted by members of the *Rhizobia*, *R. sullae*, *R. rhizobium*, and *Sinorhizobium fredii* mediated effective interactions with their legume host plant (Pérez-Montaño et al. 2011). Interaction between *Arabidopsis thaliana* root and *N*-hexanoyl-DL-homoserine-lactone (C6-HSL) resulted in obvious transcriptional alterations in roots and shoots systems (von Rad et al. 2008). However, higher plants possess the ability to produce certain AHLs mimic compounds which play critical role in the structure composition of the microbe community population density. For example, mimic compounds such as furanones secreted by plants such as soybean, barrel clover, and rice are able to interfere with or manipulate bacterial QS behaviors (Pérez-Montaño et al. 2013). The AHL mimic molecules can interfere structure-wise with the bacterial AHLs by binding to bacterial AHL receptors to antagonize its signaling (Bauer and Mathesius 2004). In addition, the flavonoids and genistein components of plant root exudates play critical role in QS communication among bacteria, considering their ability to act as chemoattractants of rhizobia to colonize and regulate the expression of genes responsible for nodulation in legumes (Loh et al. 2002). However, in spite of the biological significance of QS, bacterial VOCs are known to exhibit quorum-quenching effect on bacterial cell to cell communications during QS network (Chernin et al. 2011; Dong et al. 2001).

4.7 Management of Contaminants in Agroecosystem

Under the stress of an agroecosystem contamination, growth-enhancing nutrients become a limiting factor to plant. Essential nutrients like phosphorus may be lacking either due to total absence from the soil or due to the antagonistic effect of other nutrients (Nadeem et al. 2014). However, the inoculation of microbial consortia into contaminated environments is capable of restoring deficient nutrients for enhanced plant growth. For example, a saline-stressed environment was restored via the application of PGPR and AMF. The application of a combination of PGPR and AMF significantly elevated uptake of essential nutrients by sunflower (*Helianthus annuus* L.) (Shirmardi et al. 2010). Also, the interactions between the PGPR and

AMF significantly improved nutrient and water absorption by the roots of barley plant (Najafi et al. 2012). These interactions aided better colonization of barley plant roots and increased grain yields. Both traditional and conventional bioremediation techniques are essential requirements in the management of contaminated agroecosystem. The emerging technology of phytoremediation by using heavy metals hyper-accumulating or genetically modified plants is also an immense palliative toward agroecosystem restitution.

4.8 Advances in Microbial Bioremediation

Bioremediation is the technology that harnesses the natural ability of living organisms to breakdown toxic chemical materials in the environment. Traditionally, the remediation of pollutant-contaminated soils was done by excavating and transporting the contaminated soil off-site for treatments such as thermal alkaline dechlorination, incineration, solvent extraction, or landfilling (Campanella et al. 2002). But because of the possible damages, cost implications, and the extent of contaminations in the environment, the method is considered cumbersome, rather cost-effective approaches based on plants and microbes are being developed (McCutcheon et al. 1995). Living organisms are constantly faced with the challenges of toxic chemical contamination from allelochemicals (natural toxic chemicals) or xenobiotics (man-made toxic chemicals) (see Tables 4.1 and 4.2), leading to supposedly avoidable environmental deterioration. These contaminations could sometimes result from intentional disposal or unintentional discharge due to the pressures of expanding societal development (Srivastava et al. 2014; Van Aken et al. 2010). The bioaccumulation of heavy metals and its toxicity on animals, humans, plants, and microbes constitute a global concern for the health and safety of the

Table 4.1 Ranking of substances that pose significant threat to human health due to their toxicity and threat of exposure according to the US Department of Health and Human Services (2015)

Rank	Substance
1	Arsenic
2	Lead
3	Mercury
4	Vinyl chloride
5	Polychlorinated
6	Benzene
7	Cadmium
8	Benzo(a)pyrene
9	Polycyclic Aromatic Hydrocarbons (PAHs)
10	Benzo(b)fluoranthene
11	Chloroform
12	Aroclor 1260
13	DDT, P,P
14	Aroclor 1254
15	Dibenzo(a,h)anthracene

Table 4.2 List of common environmental contaminants

Type of contaminant	Example
Metals and metalloids	Cr, Ni, Cd, Hg, Pb, Mn, etc.
Petroleum hydrocarbons	Benzene, toluene, hexane, naphthalene, xylenes, etc.
Organic pollutants	Dioxins, aldrin, chlordane, dieldrin, heptachlor, endosulfans, toxaphene, chlordecone, mirex, PCB, HCB, DDT, PCDF, etc.
Organophosphate insecticides	Dimethoate, parathion, chlorpyrifos, dichlorvos, phenthoate, parathion-methyl, phorate, etc.
Herbicides	Atrazine, 2,4-D, glyphosate, simazine, etc.
Carbamate insecticides	Carbofuran, aldicarb, carbaryl, aminocarb, methomyl, fenoxycarb, methiocarb, etc.
Radionuclides	Uranium, plutonium, thorium, cesium, strontium, etc.
Nanoparticles	Carbon nanotubes, metal phosphates, TiO_2, SiO_2, aluminosilicates, fullerenes, ZnO nanoparticles, silver nanoparticles, etc.
New and emerging pollutants	Antibiotics, anti-inflammatories, antiepileptics, analgesics, lipid regulators, psychostimulants, diuretics, beta-blockers, cosmetics, disinfectants, plasticizers and phthalates, antidepressants, paint additives, wood preservatives, etc.

environment (Mani and Kumar 2014). Bioremediation is the widely practiced approach for the natural attenuation of chemical contaminants of human and environmental health concerns (Abhilash et al. 2012; Fester et al. 2014); and the methods often focus on the use of either single microbial species, single microbial gene, microbial consortia, or interactions such as in phytoremediation (Fester et al. 2014).

The biodegradation of these pollutant materials in the soil is well enhanced in the rhizosphere. Root exudates are released to encourage the rapid proliferation of microbial biomass which in turn affects the growth of the plant (Kloepper et al. 1989). The consequence of the nutrients released as exudates from the plant root is the elevation in microbial concentration in the root environment compared to the nearby vicinity. For bacteria, the population in the rhizosphere is often 10- to 1000-fold higher compared to the population in the soil vicinity. The degradative potential of some rhizosphere microbes enables them to degrade (rhizodegradation or phytodegradation) organic or inorganic pollutants in the vicinity (Kuiper et al. 2004). In dealing with contaminants in the environment, microorganisms utilize them as sources of carbon and energy via co-metabolism with any suitable substrates. For example, the carbon material exuded from the plant root plays a significant role in the co-metabolism of certain pollutant materials. Under this condition, certain electron-donating contaminants get oxidized under both aerobic and anoxic conditions. Additionally, halogen-containing (halogenated) organic compounds can function as terminal electron acceptors to support de-halorespiration in microbes, or they are de-halogenated for lack of enzyme specificity during the co-metabolism processes. However, these organic contaminants (growth-supporting and co-metabolized) can be broken down to yield carbon dioxide and water (Fester et al. 2014). Table 4.2 shows the common environmental contaminants, which includes inorganic as well as organic sources.

Fungi are endowed with the capacity to break down environmental organic pollutants in order to alleviate the environment from the risks commonly associated with these chemical contaminants either through structural modifications or facilitating their bioavailability for degradation (Harms et al. 2011). During plant-fungal symbiotic interactions, ectomycorrhizae (ECM) are known to demonstrate high levels of efficiency in the degradation of chemical contaminants. For example, chemicals such as the explosive, 2, 4, 6-tinitrotoluene (TNT), polycyclic aromatic hydrocarbon (PAH), and certain chloro-aromatics have been reported to be successfully degraded by axenic cultures of ECM. However, AMF, though are less studied for bioremediation purposes, possess the ability to scale up the dissipation of atrazine and PAH in soils (Harms et al. 2011). A few investigations have shown the ability of AMF to colonize plant roots and elevate PAH uptake by a plant via its roots (Gao et al. 2010; Sun et al. 2012). Nevertheless, not all mycorrhizal interactions are capable of enhancing pollutants degradation during phytoremediation (Joner et al. 2006). However, endophytic fungi have also been implicated as beneficial agents of pollutants degradation, through efficient removal of chemical contaminants in soils (Cruz-Hernández et al. 2013). During phytoremediation, endophytic fungi also metabolize and detoxify plant defense materials secreted around the root environment, as well as express enzymes with efficient specificity for contaminants degradation (Zikmundova et al. 2002).

Microbial biodegradation has mostly been practiced as an effective biotechnological approach for environmental restitution (Biswas et al. 2015; Srivastava et al. 2014). The application of microbes for the degradation of environmental contaminants was due to the ability of microbes to acclimatize and proliferate at environmental extremes. However, these adaptations should not be seen only at the level of the microbial cells but also at the level of enzymes secreted and the metabolites released in these extreme environments (Srivastava et al. 2014).

Remarkable advances have been made in biotechnological techniques for bioremediation of contaminated ecosystems. Approaches like the use of renewable plant, live and dead microbial biomass, immobilization in the roots of plants (phytostabilization), synthesis of certain minerals by biological systems (bio-mineralization), uptake, translocation and concentration of metals or organic pollutants on plant tissues (hyper-accumulation), stimulation for increase in microbial population (bio-stimulation), stimulation of algal bloom (cyano-remediation), cultivation of crops in contaminated ecosystems (dendro-remediation), stimulation of fungal proliferation (myco-remediation), and stimulation of gene expression for remediation of contaminants (geno-remediation) (Mani and Kumar 2014). Concerted integration of these advances with the existing traditional approaches will greatly enhance effective ecosystem restitution.

4.9 Advances in Phytoremediation

The technology that employs plants and their microbial symbionts for the treatment and restoration of groundwater and contaminated soils is referred to as phytoremediation. This technology relies heavily on the performance and contributions of plant-associated microbes to achieving desired results (Van Aken et al. 2010). The idea of applying phytoremediation technology for environmental restitution was conceived some decades ago when plants were found to possess the ability to metabolize certain toxic pollutants such as benzopyrene and 1,1,1-trichloro-2,2-*bis*-(4′-chlorophenyl) ethane (DDT) (Castelfranco et al. 1961). The ability of plants to metabolize toxic chemical contaminants has been likened to the capability of the mammalian liver to metabolize and detoxify injurious chemicals, a phenomenon referred to as “green liver” for plants (Coleman et al. 1997; Sandermann 1994; Van Aken 2008). Although phytoremediation is considered as an efficient technology for the degradation of chemical contaminants, the difficulty surrounding its extensive large-scale applications for the restitution of contaminated fields negates its known significance (Eapen et al. 2007).

Plants determine to a large extent the diversity of a microbial community of highly contaminated soil. They possess elaborate enzyme systems that enable them to degrade contaminating organic pollutants. However, the driving force behind phytoremediation of organic contaminants may largely be the symbiotic microbes with which they coexist (Fester et al. 2014; van Loon 2016). On the contrary, plants lack the required catabolic machineries for total metabolism of organic pollutants of high recalcitrance (Eapen et al. 2007); nevertheless, the degradation of chemical pollutants around the root environment may be by enzymes secreted as natural defense mechanisms against allelochemicals (Gerhardt et al. 2009). Plant roots produce certain substance generally referred to as root exudates; and the phytoremediation of organic compounds occurs around the root environment because of the high turnover rate (Gerhardt et al. 2009). These are organic metabolite substances released by plant roots as critical metabolic components during the developmental stages of the plant. These organic chemicals play some critical roles in phytoremediation by enhancing the adjustment and survival of plants under stressed conditions by way of allelopathy or detoxification. The organic acid components of root exudates are good sorption vehicles of metals for enhanced solubility, bioavailability, and mobility in the soil (Luo et al. 2014a, b; Ma et al. 2016). Oxalic and citric acid components of root exudates of *Echinochloa crus-galli* can function as effective chelating agents which promote effective translocation and bioavailability of heavy metals (Pb, Cu, and Cd), signifying their importance in phytoextraction (Kim et al. 2010). The formation of metal complexes was observed during the release of oxalate (a low molecular weight organic acid) by mycorrhizal interactions with Scots pine seedlings which facilitated metal immobilization (Johansson et al. 2008). However, not all organic chemicals of the plant root exudates exert effects on the bioavailability or translocation of metals within the rhizosphere (Zhao et al. 2001).

Some endophytes are heavy metal resistant and effective degraders of contaminants. The use of endophyte-facilitated phytoremediation has long been reported as a viable technology for in situ restoration of contaminated soils. The effectiveness of the endophytes in aiding phytoremediation is attributed to their resistance to heavy metal toxicity, their ability to alter metal uptake and accumulation, and also their growth-promoting capability (Li et al. 2012). Organic pollutants such as the TNT explosives are successfully degraded by naturally occurring bacterial endophytes (Van Aken et al. 2004). For example, a genetic construct of an endophytic strain of *Burkholderia cepacia* bearing the plasmid pTOM from a strain of the same species, known for colonizing plant roots, was able to successfully degrade toluene. The genetically modified endophyte neutralized toluene phytotoxicity with less amount evatranspirated (Barac et al. 2004). Similarly, mineralization of toluene occurred when *Populus trichocarpa* and *Populus deltoides* were treated with separate toluene-degrading strains of *B. cepacia* (Taghavi et al. 2005). Phytoremediation has been applied in constructed wetlands (water-logged soils in basins) for the management of organic contaminants (Vymazal 2011), as well as for the elimination of pollutants from groundwater (Seeger et al. 2011). Phytoremediation in comparison with other remediation approaches confers advantages such as low cost of establishment and maintenance and less or no negative impact on the environment, enabling carbon sequestration and its utilization for biofuel production as well as providing the ecstatic beauty of green technology (Gerhardt et al. 2009; Van Aken 2008). However, the technology is faced with drawbacks such as the slow rate of degradation and the inability of plants to achieve complete metabolism for lack of established biochemical machineries required for mineralization of pollutants (McCutcheon et al. 1995). Because plants are autotrophic in nature, phytoremediation is capable of ensuring the return of accumulated chemical contaminants into the ecosystem upon death of the plant that can be evaporated into the atmosphere or be transferred down the food chain putting stress on the health of man and the ecosystem (Arthur et al. 2005; Eapen et al. 2007; Pilon-Smits 2005). The time length required for a plant to attain maturity also forms an important drawback to the phytoremediation technology (McCutcheon et al. 1995).

4.10 Relevance of Plant-Microbe Interactions to Agroecosystem

Plant growth-promoting microorganisms (PGPMs) confer better advantages over chemical conditioning for phytoremediation. This is because the metabolites they produce are easily biodegradable and of less toxicity (Rajkumar et al. 2012). Metal-resistant PGPMs have been evaluated for tendencies toward enhanced plant growth and development, reduced metal toxicity, as well as immobilization, mobilization, and transformation of metal contaminants in the soil (Rajkumar et al. 2012). Arbuscular mycorrhizal fungi (AMF) occurring in a heavy metal-contaminated environment have demonstrated the ability to enhance plant growth (Orłowska et al. 2013) and modification of the soil pH to affect metal availability (Rajkumar et al. 2012), improve nutrient and mineral uptake (Guo et al. 2013), influence metal translocation (Jianfeng et al. 2009), and affect induced metal toxicity (Meier et al. 2011). The AMF are important ecological organisms found in obligate symbiotic interactions with the roots of plants in the terrestrial ecosystems. During interactions, plant supplies the needed carbon for fungal cell development as well as benefit from enhanced nutrient uptake and resistance to abiotic stress factors and phytopathogens (Smith and Read 2010). AMF possess the ability to influence ecological community processes and plant community dynamics through the distribution of essential resources such as carbon (C), nitrogen (N), and phosphorus (P) required for effective interactions (Rashid et al. 2016; Smith et al. 2011). In P-deficient soils, AMF are able to facilitate a large supply of P for uptake by the plant roots (Cavagnaro et al. 2015) and liberate other essential (macro and micro) nutrients such as N, magnesium (Mg), potassium (K), zinc (Zn), and copper (Cu) from the ores or less soluble forms (Smith and Read 2010). AMF external hyphae have also been shown to liberate about 10% of K, 25% of N and Zn, and 60% of Cu (Hodge and Storer, 2015). Certain AMF members such as *Glomus mosseae*, *G. caledonium*, and *G. intraradices* enhance the performance of plant under drought and salt conditions (Hashem et al. 2015; Ortiz et al. 2015) and help to remedy heavy metal-induced stress (Zhipeng et al. 2016; Zong et al. 2015).

Plant growth-promoting rhizobacteria (PGPR) and mycorrhizal fungi are effective at promoting plant growth and development even in stressed environments (Bach et al. 2016; Nadeem et al. 2014; Singh 2015; Prasad et al. 2015). During interactions with their plant counterparts, the PGPR play three fundamental roles: (1) synthesizing essential compounds, (2) enhancing plant nutrient uptake, and (3) promoting plant defense against disease and its etiological agents (Hayat et al. 2010). The growth promotion and development of plants can occur through direct or indirect mechanisms based on the interactions involved. PGPR can also initiate indirect inhibition against phytopathogens by producing cell wall-degrading enzymes (β-1,3-glucanases and chitinases) that act against fungi and can also produce hydrogen cyanide for toxicity against intruding pathogens. The direct plant growth promotion mechanisms can be mediated by plant-associated PGPR via the production of plant growth hormones (such as gibberellins, auxins, cytokinins, abscisic acid, and ethylene), indole-3-acetic acids (IAA), or indole-3-ethanol. Some PGPR are able to hydrolyze the ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) into ammonia and α-ketoglutarate which enhance root development by regulating the concentration of ethylene in the rhizosphere. They can also facilitate organic phosphates and nutrient mineralization, improve soil aggregation and structure, and elevate the organic matter content of the soil (Bhattacharyya and Jha 2012; Hayat et al. 2010; Kurepin et al. 2015; Ma et al. 2016; Nadeem et al. 2014). The soil aggregation and structure are also improved by AMF due to the production of glomalin, an insoluble glycoprotein (Gadkar and Rillig 2006) which functions to stabilize the soil (Rillig et al. 2003; Sharma et al. 2017).

4.11 Plant-Microbe Interactions in Management of Phytopathogens

Plants basically defend themselves from pathogen invasion through the production of antimicrobials, phytoalexins, hydrolytic enzymes, hypersensitive reactions, and defense barriers such as lignin and suberin polymers (González-Teuber et al. 2010). Other defense mechanisms against pathogens include production of certain defense proteins and secondary metabolites (Ashry and Mohamed 2012; Castro and Fontes 2005). The phytohormone auxin apparently plays an important role in defense against phytopathogenic bacteria (Spaepen and Vanderleyden 2011). In the event of attack by phytopathogens, the plant immune system is elicited by pathogen-derived molecules produced by certain functional membrane receptors. Immune response can also be elicited through direct or indirect pathogen effector protein molecules when they interact with the nucleotide oligomerization domain (NOD)-like cytoplasmic receptors of a plant host. Similarly, the reorganization of the host skeleton and secretory functions is another principal approach to plant immune response (Spanu and Panstruga 2017). The microbial partners of the association are also vital at ensuring plant health and viability. Other than promoting plant growth through phosphate solubilization, nitrogen fixation, and production of ACC deaminase and phytohormones, the microbial partners facilitate antagonistic response through the production of substances such as siderophores, hydrolytic enzymes, and a spectrum of antibiotics (Bach et al. 2016; da Costa et al. 2014), outcompeting the phytopathogen or its physical displacement (Glick and Bashan 1997). The bacterial species such as *Paenibacillus riograndensis*, *Bacillus cepacia*, and *B. mycoides* extensively demonstrate defining biocontrol features such as motility, root colonization, production of biosurfactants, antifungal metabolites, and hydrolytic enzymes (which degrade cell walls of invading phytopathogens) (Bach et al. 2016). For the management of phytopathogens, mycorrhizal fungi play principal role in maintaining ecological balance for improved ecosystem viability. Plant-AMF interactions have been beneficial in the reduction of soil-borne phytopathogens. The AMF, *G. intraradices* and *G. mosseae*, enhanced nutrient uptake in wheat plant, resulting in improved tolerance against pathogens (Bach et al. 2016). Besides, the high presence of fungal biomass colonizing plant roots is highly beneficial in the aspect of competition with phytopathogens. These interactions have been perceived as the mechanism by which phytopathogens abundance is abated by AMF in the rhizosphere (Vimal et al. 2017).

Plant growth hormones are essential ingredients of plant-microbe interactions toward pathogen management (Chagnon and Bradley 2015). The organic compounds exuded from the rhizosphere of tomato AMF (involving *G. intraradices* and *G. mosseae*) were reported to be possibly modified by AMF to inhibit the phytopathogen, *Phytophthora nicotianae* (Lioussanne et al. 2009). The application of the AMF, *G. mosseae*, for biocontrol activity against nematodes has been reported (Vos et al. 2012). The fungus demonstrated systemic resistance to two nematode species *Pratylenchus penetrans* and *Meloidogyne incognita* which were found in association with the tomato *Lycopersicon esculentum* (Table 4.3). The

Table 4.3 Studies on plant-microbe interaction for the management of phytopathogens

Microbe	Plant host	Pathogen	Effect	Reference
G. mosseae, *G. intraradices*	*Lycopersicon esculentum*	*Phytophthora nicotianae*	Enhanced plant resistance via modification of exuded root substances	Lioussanne et al. (2009)
T. harzianum, *G. mosseae*	*Nicotiana tabacum*	*R. solanacearum*	Improved systemic resistance, nutrient uptake, and biomass	Saifei Yuan et al. 2016
G. mosseae	*Lycopersicon esculentum*	*Pratylenchus penetrans*, *Meloidogyne incognita*	Inhibited phytopathogenic nematodes infection	Vos et al. (2012)
G. mosseae, *G. intraradices*, *G. clarum*, *Gigaspora gigantea*, *G. margarita*	*Phaseolus vulgaris*	*Fusarium solani*	Enhanced nutrients uptake, phenolic content, and activities of defense-related enzymes resulting in decreased	Al-Askar and Rashad (2010)
G. mosseae, *G. intraradices*, *G. claroideum*, *G. geosporum*, *G. etunicatum*	*Senecio vernalis*, *Senecio inaequidens*, *Inula conyza*, *Conyza Canadensis*, *Solidago virgaurea*, *Solidago gigantea*	*Pythium ultimum*	Promotion of plant growth and pathogens inhibition	Del Fabbro and Prati (2014)
G. clarum, *T. harzianum*	*Helianthus tuberosus*	*Sclerotium rolfsii*	Reduced incidence of the disease, southern stem rot	Sennoi et al. (2013)
G. mosseae	*Hordeum vulgare*	*Gaeumannomyces graminis*	Formation of high mycorrhizal colonization network that inhibited root infection	Khaosaad et al. (2007)
G. monosporus, *G. clarum*, *G. deserticola*	*Phoenix dactylifera*	*Fusarium oxysporum*	Reduced incidence of disease, improved plant growth, and alters defense-related enzymes activity	Jaiti et al. (2007)

resistance induced by the mycorrhizal fungus was determined by the significant depreciation of the nematode species around the roots, 45% in the case of *Meloidogyne incognita* and 87% for *Pratylenchus penetrans* (Vos et al. 2012). Similarly, when *T. harzianum*-amended bioorganic fertilizer (BOF) or the AMF *G. mosseae* were separately applied in the rhizosphere of the plant, remarkable decrease occurred in the incidence of tobacco bacterial wilt (TBW) caused by *Ralstonia solanacearum* (Saifei Yuan et al. 2016). However, combined application of the mycorrhiza gave the highest inhibition of the pathogen. This could infer that the greater the mycorrhizal complexity, the more robust the benefits derived by the plant host in terms of systemic resistance, improved nutrient, and biomass yield. See Table 4.3 for some other important reports on the impact of plant-fungal association against phytopathogens.

4.12 Plant-Microbe Interactions for Enhanced Phytoremediation of Contaminants

Over the years, soil pollution by heavy metals has been tremendously amplified through increased anthropogenic activities such as urbanization, industrialization, and exploration. These activities are often characterized by inadequate waste disposals resulting in heavy metal pollution of agriculture soils and distortion in the functioning of the ecosystem and its food chain, effects on human and animal health through possible bio-magnification (McMichael et al. 2015; Zhipeng et al. 2016). Plants which grow in soil with high levels of metal contamination are naturally endowed with diverse microbial partners that tolerate metal contamination and also remedy the soil environment for plant growth (Rajkumar et al. 2012). Most vascular plants enter into a beneficial mutual relationship with mycorrhizal fungi for increased nutrient yield and its uptake (Hashem et al. 2015), a relationship which benefits the agroecosystem in the following ways: (1) enhanced nitrogen fixation in the rhizosphere (Krapp 2015), (2) osmoregulation of the rhizosphere environment for improved productivity, (3) production of bioactive secondary metabolites (Goicoechea et al. 1997), (4) increased phosphatase enzyme activity (Liu et al. 2015a, b), (5) enhanced photosynthesis (Hashem et al. 2015; Ruíz-Sánchez et al., 2011), (6) elevated resistance against stress factors (biotic and abiotic) (Del Fabbro and Prati 2014; Saifei Yuan et al. 2016), and (7) an improved metal detoxification (Amir et al. 2013; Nadeem et al. 2014; Zong et al. 2015). However, the effectiveness of these mechanisms remains a function of plant-AMF interactions and the plant and soil factors (Nadeem et al. 2014). Mycorrhizae-assisted phytoremediation has been applied for the restitution of contaminated soils for agriculture production purposes. Hyper-accumulating plant AMF-assisted phytoremediation via phytodegradation, phytoextraction, phytostabilization, phytovolatilization, and rhizofiltration (see Fig. 4.1) has been employed for efficient restoration of contaminated soils based on their unique abilities (Mohammad Miransari 2011). Fungal cell wall consists of certain free radicals, amino acids, and other functional groups with free binding sites to adsorb certain trace elements. The microbe-metal interaction enables the plant host to survive metal-contaminated soils (Vimal et al. 2017; Zhipeng et al. 2016). Liu et al. (2015a, b) observed an increased P uptake and growth in the cadmium (Cd) hyper-accumulator, *Solanum nigrum*, even under high Cd concentrations when *G. versiforme* was inoculated, suggesting AMF enhancement of plant growth, resistance to heavy metal toxicity, metal bioavailability, and uptake by plants. Moreover, *G. claroideum* obtained from Cu-contaminated soil has been suggested for the remediation of contaminated soils due to its ability to alleviate Cu toxicity (Meier et al. 2012a, b). For ECM, the formation of fungal mantle and Hartig net is essential for interaction with plant. The mycelia of the ECM fungus, *Tricholoma vaccinum*, form a structure called the Hartig net on the root apoplast of the host, *Picea abies*, which serves as the interface for the exchange of nutrients between the plant and the fungus (Henke et al. 2015). Nutrients for uptake are transported via the Hartig net and translocated unto the roots where they are released for uptake through the aid of plant metal transporters (Luo et al. 2014a, b). ECMs play critical role in the sequestration and detoxification of heavy metals from contaminated soils (Henke et al. 2015), as well as the organic compounds exuded from plant roots (Meier et al. 2012a, b). Similarly, the growth and performance of the Japanese red pine, *Pinus densiflora*, and the oak, *Quercus variabilis*, on copper mine tailings were attributed to effective nutrient uptake when inoculated with ECM fungi, *Pisolithus* spp. and *Cenococcum geophilum* (Zong et al. 2015). Thus, plant-microbe interactions are essential for the biogeochemical cycling of metal contaminants and can be applied in phytoremediation (Ma et al. 2016). Metal-stressed agricultural plants are capable of producing certain compounds, LMWOAs such as malic, succinic, citric, and oxalic acids which are essential at neutralizing metal phytotoxicity (Meier et al. 2012a, b; Songhu Yuan et al. 2007). In the ecosystem, plants strive for adaptation, uptake of nutrients, and growth when confronted with the challenge of pollution. The myriads of organic compounds produced in interactions serve as essential drivers for enhanced tolerance and resistance to metals or organic pollutants in agroecosystems. Some of these organic compounds that can be harnessed and applied to sustain a balance in the rhizosphere environment include organic acids, siderophores, metal chelators, and bacterial biosurfactants.

4.12.1 Organic Acids

Organic acids are carbohydrate-based natural compounds which are usually identified by the presence of carboxyl groups (Jones and Edwards 1998). Organic acids form complexes with metal ions in the soil in order to make them bioavailable for uptake by plants. The endophytic diazotroph *Gluconacetobacter diazotrophicus* produced 5-ketogluconic acid, a gluconic acid derivative which enhanced effective solubility of zinc compounds [ZnO, $ZnCO_3$, and $Zn_3(PO_4)_2$] (Saravanan et al. 2007). Similarly, airborne bacteria isolated from the tannery surrounding air, such as a strain of *P. aeruginosa*, effectively solubilized both zinc oxide (ZnO) and zinc phosphate [$Zn_3(PO_4)_2$] in the presence of glucose carbon source. The solubilization of zinc compound by the bacterium was attributed to its ability to produce

Table 4.4 Microbial metabolites and their significance on heavy metals activity in contaminated ecosystem

Metabolites of microbial origin	Microbe	Effects on metal transformation/ assimilation by plant	References
Organic acids			
2-Ketogluconic acid	*P. aeruginosa*	Enhanced solubility of ZnO and $Zn_3(PO_4)_2$	Fasim et al. (2002)
5-Ketogluconic acid	*G. diazotrophicus*	Solubilize zinc compounds ZnO, $ZnCO_3$ and $Zn_3(PO_4)_2$	Saravanan et al. (2007)
Gluconic acids and exopolymeric compounds	*B. caribensis*	Phosphorus mobilization	Delvasto et al. (2009)
Malic and citric acids	*O. maius*	Solubilize zinc compounds [ZnO, $ZnCO_3$ and $Zn_3(PO_4)_2$]	Martino et al. (2003)
Oxalic	*B. bassiana*	Solubilize $Zn_3(PO_4)_2$	Fomina et al. (2004)
Biosurfactants			
Lipopeptide	*Bacillus* spp.	Elevated uptake of Cd into above ground plant tissues	Sheng et al. (2008)
Rhamnolipids	*P. aeruginosa*	Mobilization of Cu for uptake by plants	Venkatesh and Vedaraman (2012)
Siderophore			
Pyochelin and pyoverdine	*P. aeruginosa*	Enhanced Pb and Cr bioavailability and assimilation	Braud et al. (2009)
Catecholate	*S. luteus*, *R. luteolus*, and *S. verrucosm*	Production of various forms of metal chelators for enhanced metal bioavailability	Machuca et al. (2007)
Desferrioxamine B and C and coelichelin	*S. tendae* F4	Facilitated increased Cu uptake	Dimkpa et al. (2009a, b)

2-ketogluconic acid (Fasim et al. 2002). Delvasto et al. (2009) observed that *Burkholderia caribensis* isolated from high-phosphorus iron ore demonstrated high level of phosphate mobilization from the phosphate-rich ores. The mobilization of phosphate by *B. caribensis* was possible due to its formation of dense biofilm and production of gluconic acid and exopolymeric compounds (Table 4.4). Similarly, rhizobacteria obtained from the rhizosphere of *Sedum alfredii*, a Cd/Zn hyper-accumulator, were able to solubilize Zn and Cd. The mobilization of these metals showed positive correlations with the production of organic acids such as tartaric acid, formic acid, oxalic acid, acetic acid, and succinic acids (Li et al. 2010). Mycorrhizal fungi are also able to secrete organic metal chelators into the rhizosphere for enhanced metal mobilization (Martino et al. 2003). The mycorrhizal strains of *Oidiodendron maius* were able to solubilize zinc compounds via the production of malic and citric acids. Similarly, the soilborne entomopathogen, *Beauveria bassiana*, produced oxalic acid molecules which enhanced the dissolution of pyromorphite and $Zn_3(PO_4)_2$ during acidolysis (Fomina et al. 2004). In addition, the fungus, *A. brasiliensis*, effectively mobilized large volumes of lead (Pb) and P from pyromorphite due to its elaborate production of organic acids, making these metals bioavailable for plant uptake. This feature substantiates the potential for the application of *A. brasiliensis* in phytoextraction for ecosystem restitution. Also, plant-associated microbes are known to secrete essential organic acids which promote plant root absorption of metal ions including Zn and Cd (Li et al. 2010; Rajkumar et al. 2013), Cu (Chen et al. 2005), and Pb (Sheng et al. 2008).

Nevertheless, organic acids can either be neutral or negative in effects against the mobilization of metals in contaminated environments (Rajkumar et al. 2012). For instance, no significant mobilization of metals (including Cu and Pb) occurred in a contaminated agricultural soil bio-augmented with the efficient organic acid-producing strain of *B. subtilis* (Braud et al. 2006). As well, LMWOAs (tartaric, oxalic, and citric acids) failed to facilitate the phytoextraction of Pb from contaminated soil even when applied in high amounts (Evangelou et al. 2006). The high rate of its biodegradation vis-à-vis the low mobility and bioavailability of Pb may explain its failure.

Most plant-associated microbes produce siderophores, the iron chelator molecules secreted in response to stress factors encountered in the rhizosphere (Das et al. 2007). Iron is an essential nutrient required in almost all forms of life. Other than few species of lactobacilli, all other microbes require iron as an essential nutrient for growth activity (Neilands 1995). Iron basically occurs as Fe^{3+} under aerobic conditions and as such can easily form insoluble hydroxides and oxyhydroxides, making it less accessible to both microbes and plants (Rajkumar et al. 2010). Bacteria secrete siderophores chelators which possess high affinity constants for complexing iron molecules. Other than iron, siderophores are capable of forming stable complexes with other heavy metals such as Cd, Al, Ga, In, Zn, and Pb and also with radionuclides including Np and U (Kiss and Farkas 1998; Neubauer et al. 2000). Siderophores have been classified based on solubility in water and functional groups. Based on solubility in water, siderophores are classed into extracellular and intracellular siderophores (Khan et al. 2009). As regards functional groups, siderophores are classified into three groups, namely, the hydroxamates (e.g., desferrioxamine B and C, ferrichrome, ornibactin, rhodoturolic acid, etc.), catecholates (e.g., enterobactin, bacillibactin, and vibriobactin), and (α-hydroxy) carboxylate (e.g., aerobactin) (Dimkpa et al. 2009a, b; Rajkumar et al. 2010). In both Gram-positive and Gram-negative bacteria, the iron (Fe^{3+}) component of Fe^{3+} siderophore complexed on the membrane is reduced to Fe^{2+} for onward delivery into the cell through a gating mechanism that connects both the outer and inner membranes. The reduction process can result in the siderophore being destroyed or recycled (Ahemad and Kibret 2014; Rajkumar et al. 2010). Because siderophores possess the ability to enhance metal solubility from their ores, microbes inhabiting the rhizosphere are believed to impact greatly on the phytoextraction of heavy metals (Rajkumar et al. 2010). The siderophores, pyochelin and pyoverdine, produced by *P. aeruginosa* enhanced the bioavailability of Pb and Cr in the rhizosphere for easy uptake by maize plant (Braud et al. 2009), while siderophores from a strain of

Streptomyces tendae F4 significantly elevated the uptake of Cd by the sunflower plant (Table 4.4) (Dimkpa et al. 2009a, b). This implies that bacterial siderophores are essential organic substances that are capable of alleviating stress factors including heavy metals from contaminated soils (Ahemad and Kibret 2014). Siderophores have also been produced by mycorrhizal fungi (Goodell et al. 1997; Machuca et al. 2007). For example, hydroxamate and catecholate siderophores were produced by the ECM fungi *Suillus luteus*, *Rhizopogon luteolus*, and *Scleroderma verrucosum* isolated from *Pinus radiata* fruiting bodies (Machuca et al. 2007).

However, plants utilize different mechanisms for the assimilation of microbial siderophores. These mechanisms include the direct uptake of siderophore-Fe complexes, chelate and release of iron, or ligand exchange reaction (Ahemad and Kibret 2014; Schmidt 1999; Das et al. 2007). For instance, Crowley and Kraemer (2007) described an iron transport process in oats that is siderophore mediated and deduced that siderophores originating from rhizospheric microbes effectively deliver iron to oats, which possess the mechanisms for Fe-siderophore complex utilization in iron-deficient soil conditions. Additionally, the formation of Fe-pyoverdine complex by *P. fluorescens* strain C7 was successfully assimilated by *A. thaliana* resulting in elevated iron accumulation in the plant tissues and growth (Vansuyt et al. 2007). Furthermore, Sharma et al. (2003) assessed the role of siderophores produced by *Pseudomonas* strain GRP$_3$ on the nutrition of *Vigna radiata* and observed a reduced chlorotic symptoms and an elevated level of chlorophyll in the plant after 45 days. However, chlorophyll a, chlorophyll b, and total chlorophyll content increased significantly compared to the control. Nevertheless, there are emerging arguments that the mobilization and uptake of metals in the rhizosphere are reduced by the presence of siderophore-producing microbes (Rajkumar et al. 2012). For example, Sinha and Mukherjee (2008) reported that the efficient siderophore-producing *P. aeruginosa* strain KUCd1 caused a reduction in Cd assimilation in the tissues of *Brassica juncea* and *Cucurbita pepo*. Moreover, Tank and Saraf (2009) observed a reduced Ni uptake when a species of a Ni-resistant siderophore-producing species of *Pseudomonas* was applied on chickpea plants. In addition, it has been observed that siderophore-producing microbes do not facilitate any increased assimilation of heavy metals by plants (Kuffner et al. 2010; Kuffner et al. 2008). The existing contrasts on the role of siderophores on metal uptake by plants may be attributed to variation in plants' ability to effectively assimilate heavy metals, which indirectly depends on the bioavailability of the metal, the plant type, and the system of heavy metal transport to their tissues (Dakora and Phillips 2002; Jones et al. 2003).

4.12.2 Biosurfactants

Biosurfactants are amphiphilic molecules containing a hydrophilic head and a hydrophobic tail. The hydrophilic moiety consists of mono-, oligo-, or polysaccharides, peptides, or proteins, whereas the hydrophobic group consists of saturated, unsaturated, and hydroxylated fatty alcohols or fatty acids (Rajkumar et al. 2012). Microbial biosurfactants can undergo complexation with heavy metals and their ions on the surface of the soil. The formed complex enables metal desorption from the soil matrix into readily soluble and bioavailable forms for plant uptake. Evidence shows that biosurfactant-producing microbes are capable of elevating metal mobilization in contaminated soils (Juwarkar and Jambhulkar 2008; Sheng et al. 2008). Biosurfactant rhamnolipids from *P. aeruginosa* have been shown to efficiently remove 71% and 74% of Cu from contaminated soil with initial Cu concentration of 474 and 4484 mg kg^{-1}, respectively, when applied at 2% (Venkatesh and Vedaraman 2012). Thus, biosurfactants can be applied as a cost-effective, environment-friendly, and specific metal bioremediation alternative to conventional chemicals. Also, live cells of biosurfactant-producing strain of *Bacillus* sp. significantly enhanced the mobilization and uptake of Cd from the contaminated soil compared to the control soil with dead bacterial cells (Sheng et al. 2008). Although existing studies reveal the significance of microbial biosurfactants on metal bioremediation and uptake by plants, a more elaborate understanding of the chemistry between plants and their biosurfactant-producing microbial partners is desirable.

The application of plant-microbe interactions for ecosystem management is a complex phenomenon. Both partners in the relationship employ diverse mechanisms for adaptation, resistance, and persistence in the face of stress factors. Plants are known to demonstrate resistance to metal contamination in agroecosystems through various mechanisms, such as (1) active efflux pump system, (2) metal sequestration, (3) biosorption and precipitation of metals, (4) metal chelate exclusion, and (5) enzyme-catalyzed redox reaction (Ma et al. 2016). Other ways by which plant-microbe interactions can be applied for the management of contaminated agroecosystems include bioaccumulation/biosorption, bioexclusion, and bioleaching.

4.12.3 Bioaccumulation/Biosorption

The role of the microbial partner in the plant-microbe interactions is enormous. Bioaccumulation refers to the phenomenon of intracellular accumulation of metals (Ma et al. 2016), whereas biosorption is defined as the adsorption of metals by microbial cells through passive, metabolism-independent and active metabolic processes (Ma et al. 2011). The bioaccumulation of metals is one significant way by which associated microbes contribute to metal resistance. Two major mechanisms through which these occur include biosorption (toxic metals being concentrated in the biomass of nonliving microbial cell) and bioaccumulation (concentration of poisonous compounds in the living microbial cell) (Ma et al. 2011; Rajkumar et al. 2012). The process of bioaccumulation involves two principal stages, viz., metabolism-dependent biosorption (e.g., metal ion exchange, physical and chemical adsorption, surface complexation, chelation, coordination, and micro-precipitation) and metabolism-dependent active bioaccumulation (e.g., endocytosis, carrier-dependent ion pumps, and metal assimilation and complex permeation) (Chojnacka 2010). Bioaccumulation processes in various microbes have been shown to reduce metal uptake and toxicity on their plant partners (Ma et al. 2011; Mishra and Malik 2013). More complex processes are required in bioaccumulation than in biosorption. These involve metabolic processes of living cells such as extracellular precipitation, intracellular sequestration, metal accumulation, and formation of complexes (Gadd 2004). Biosorption and bioaccumulation of heavy metals (Fe, As, Cr, Co, and Hg) by living cells of *B. sphaericus* and biosorption by dead cells of the bacterium showed that the living cells had higher degrees of biosorption and accumulation of these metals than the dead cells (Velásquez and Dussan 2009). The disparity in the biosorption and bioaccumulation levels of these metals was attributed to the lack of active metabolic machineries in the dead cells. It has been shown that biosorption of metals by microbial cells reduced uptake in plant. For example, inoculation of *Burkholderia* sp. and *Magnaporthe oryzae* caused a reduction in the accumulation of Cd and Ni in tomato plant (Madhaiyan et al. 2007). Similarly, reduction of Zn accumulation occurred when a strain of *Brevibacillus* sp. was introduced in *Trifolium repens*. The reduction in Zn concentration in the plant was traced to the biosorption capability of the bacterium (Vivas et al. 2006).

Recently, Ma et al. (2015) reported that the *Bacillus* sp. strain SC2b demonstrated extensive resistance to heavy metals such as cadmium (Cd), zinc (Zn), and lead (Pb) by mobilizing high concentration of the metals from the soil through different biosorption processes. Other than mobilization and biosorption of heavy metals, the strain expressed some PGP features such as P solubilization, production of siderophore and IAA, and utilization of 1-aminocyclopropane-1-carboxylate. However, no specific correlations exist between tolerance and biosorption of the metals, chromium (Cr) and Cd, among the filamentous fungi, *Rhizopus* and *Aspergillus*, isolates from metal-contaminated soil (Zafar et al. 2007). The mycelial network of mycorrhizae can function to effectively inhibit heavy metal translocation to plant tissues. A marked reduction has been observed in the translocation of Zn, Cd, and Pb by the mycelia of the ECMF, *Lactarius rufus*, *Amanita muscaria*, and *Scleroderma citrinum* with pine seedlings (Krupa and Kozdrój 2007). Metal biosorption by the fungal mycelia was reflected in the reduction of metal concentrations. Although plants and their associated microbial symbionts may vary in their tendencies to enhance metal bioavailability and uptake, the proliferation, survival, and colonization of the rhizosphere greatly affect the abundance of heavy metals in an environment and its accumulation in plants growing on such a soil. This is because biological processes in the rhizosphere are capable of causing such alterations (Rajkumar et al. 2012).

4.12.4 Bioexclusion

Bioexclusion mechanisms in microbes include the efflux pump system and active transport process. The efflux pump system and the active transport mechanisms responsible for ejecting toxic materials from microbial cytoplasmic enclosures are critical components of resistance to metals (Ma et al. 2016). The exclusion of inorganic metal ions through the microbial efflux pump system is a function of certain membrane proteins and the activity of ATPases, whereas ATPase efflux system forms an essential component of active transport of some required metal ions (Bruins et al. 2000).

4.12.5 Bioleaching

The solubilization of metals from ores in acid environments by certain group of microorganisms is termed bioleaching. Acidophilic microbes are mainly responsible for the bioleaching of metals from their ores most often resulting in acid mine drainage (AMD) which causes severe negative environmental effects. Usually, trapping of metal ions by metal chaperones and the efflux pump system are recognized mechanisms employed by bacteria to resist high levels of metals in contaminated environments (Navarro et al. 2013). Microbes, such as the iron-oxidizing bacteria (*Acidithiobacillus ferrooxidans* and *Leptospirillum*) and sulfur-oxidizing bacteria (*A. thiooxidans*, *A. albertis*, and *A. caldus*) (Wong et al. 2004), thermophiles (e.g., *Sulfobacillus thermosulfooxidans*, *Archaeans* sp., *S. brierleyi*, *S. ambivalens*, and *Thiobacter subterraneus*) (Kletzin 2007), heterotrophs (*Arthrobacter*, *Acetobacter*, *Pseudomonas*, and *Acidophilum*), as well as fungi (*Fusarium*, *Aspergillus*, *Trichoderma*, and *Penicillium*) (Mulligan and Galvez-Cloutier 2003), are capable of bioleaching metals from their ores in sediments, soils, and sludge. These microorganisms neutralize the ore’s phytotoxic effects on plants through direct or indirect metabolic processes such as complexation, oxidation, adsorption, dissolution, and reduction, respectively (Pathak et al. 2009). The endowed potential of microbes to bioleach heavy metals is species dependent. However, acidophiles are more efficient at bioleaching of metals from their ores than their neutrophilic counterparts (Navarro et al. 2013). Heavy metals such as Cd, Cu, Fe, Cr, Zn, and Pb were successfully bioleached by the acidophilic bacteria, *A. thiooxidans*, under acidic conditions (Kumar and Nagendran 2009).

4.12.6 Oxidation and Reduction of Metals

The redox reaction pathway has been successfully exploited by some microbial symbionts of plant to influence the bioavailability and mobility of heavy metals in agricultural fields. The phytoextraction of metals from contaminated rhizosphere is often a function of microbial metal oxidation. For example, sulfur-oxidizing bacteria in the rhizosphere enable the mobilization of Cu and its uptake by the plant tissues from a contaminated soil (Shi et al. 2011). This reflects the ability of the bacteria to reduce the ambient pH within the rhizosphere by way of converting the reduced sulfur into sulfate, to make the Cu ions bioavailable for uptake by plants (Rajkumar et al. 2012). One other mechanism adopted by microbial plant symbionts is to immobilize metals in the rhizosphere through reduction process (Rajkumar et al. 2012). For instance, metal-resistant strain of *Cellulosimicrobium cellulans* isolated from a waste canal harboring industrial effluents exhibited remarkable reduction of

Cr under aerobic conditions. The bacterial strain reduced greatly the uptake of this heavy metal by the chili test plant, through reducing the phytotoxic Cr (VI) to a nontoxic Cr (III) within the rhizosphere (Chatterjee et al. 2009). Similarly, selenite-resistant bacterium, *Stenotrophomonas maltophilia*, from the selenium hyper-accumulator legume, *Astragalus bisulcatus*, efficiently reduced the toxic selenite (IV) into the nontoxic elemental form Se (0) (Di Gregorio et al. 2005). These features explain the processes utilized by microbes in the rhizosphere to either mobilize, immobilize, or make bioavailable heavy metals that ordinarily could be of high phytotoxicity. In addition, microbes in synergistic interactions have been jointly applied to ameliorate heavy metal-contaminated agro-soils. The utilization of Fe-reducing and Fe-/S-oxidizing bacterial consortia enhanced greater heavy metal solubility than when separately applied for the same metal treatment (Beolchini et al. 2009).

4.13 Conclusion

Chemical contamination of soils and water is a serious environmental problem. The application of physical and chemical remedial methods is limited by their high cost, damages to microflora and microfauna in the soil, and potential creation of secondary pollution in the ecosystem. Thus, the need to consider solar-driven, eco-friendly phytoremediation technology derives from the interaction of plant roots and microbes to remedy hazardous chemical contaminations in agroecosystem. Bacterial roots and symbiotic mycorrhizal interactions modify soil pH; affect metal availability; improve nutrient and mineral uptake within the rhizosphere and plant growth-promoting microorganisms (PGPMs), particularly metal-resistant PGPMs; and produce easily biodegradable metabolites important for nutrient and mineral uptake that supports plant growth. Also, microbes contribute remarkably to phytoextraction of metals from contaminated rhizosphere through microbial metal oxidation and extraction of heavy metals, removing and detoxifying the contaminants in the soil. As well, biosurfactant-producing microbes and bacteria-secreting siderophore chelators are particularly involved in bioleaching, redox reaction and solubilization, bioavailability, and heavy metal mobility.

Plant exudates enhance root-microbes association and contribute to pathogen management. Besides, the association of plant and arbuscular mycorrhizal fungi boosts plant growth, resistance to heavy metal toxicity, and metal bioavailability and uptake by plants as well as encourages soil phytoremediation via phytostimulation, phytodegradation, phytoextraction, phytostabilization, phytovolatilization, and rhizofiltration. Although phytoremediation is considered a relatively cheap, eco-friendly technology for the restitution of contaminated fields, it is still challenged by the difficulty surrounding its extensive large-scale applications. Hence, further work is required for better understanding of the relationships among plant root microbes, soil types, chemicals, and heavy metal contaminants within the rhizosphere, so as to fully exploit the potential in phytoremediation of agroecosystems. Therefore, it is important to develop phyto-hyper-accumulators and super microbial solubilizers for various soil types either by conventional breeding techniques, other methods of hybridization (e.g., spheroplast fusion), or genetic modifications (transgenic plants), to improve on desirable plant traits (such as appropriate root exudates, efficient metal uptake, translocation, sequestration, and high tolerance) and enhance their soil remedying capabilities.

References

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

Ahemad M, Kibret M (2014) Mechanisms and applications of plant growth promoting rhizobacteria: current perspective. J King Saud Univ Sci 26(1):1–20

Ahmad F, Ahmad I, Khan M (2008) Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities. Microbiol Res 163(2):173–181

Al-Askar A, Rashad Y (2010) Arbuscular mycorrhizal fungi: a biocontrol agent against common bean fusarium root rot disease. Plant Pathol J 9(1):31–38

Amir H, Lagrange A, Hassaïne N, Cavaloc Y (2013) Arbuscular mycorrhizal fungi from New Caledonian ultramafic soils improve tolerance to nickel of endemic plant species. Mycorrhiza 23 (7):585–595

Antoun H, Prévost D (2005) Ecology of plant growth promoting rhizobacteria PGPR: biocontrol and biofertilization. Springer, Dordrecht, pp 1–38

Arthur EL, Rice PJ, Rice PJ, Anderson TA, Baladi SM, Henderson KL, Coats JR (2005) Phytoremediation—an overview. Crit Rev Plant Sci 24(2):109–122

Ashry NA, Mohamed HI (2012) Impact of secondary metabolites and related enzymes in flax resistance and/or susceptibility to powdery mildew. Afr J Biotechnol 11(5):1073–1077

Bach E, dos Santos Seger GD, de Carvalho Fernandes G, Lisboa BB, Passaglia LMP (2016) Evaluation of biological control and rhizosphere competence of plant growth promoting bacteria. Appl Soil Ecol 99:141–149

Badri DV, Vivanco JM (2009) Regulation and function of root exudates. Plant Cell Environ 32 (6):666–681

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

Bais HP, Park SW, Weir TL, Callaway RM, Vivanco JM (2004) How plants communicate using the underground information superhighway. Trend Plant Sci 9:26–32

Bais HP, Weir TL, Perry LG, Gilroy S, Vivancohe JM (2006) The role of root exudates in Rhizosphere interactions with plants and other organisms. Ann Rev Plant Biol 57:233–266

Bakker AW, Schippers B (1987) Microbial cyanide production in the rhizosphere in relation to potato yield reduction and *Pseudomonas* spp-mediated plant growth-stimulation. Soil Biol Biochem 19(4):451–457

Barac T, Taghavi S, Borremans B, Provoost A, Oeyen L, Colpaert JV et al (2004) Engineered endophytic bacteria improve phytoremediation of water-soluble, volatile, organic pollutants. Nat Biotechnol 22(5):583–588

Barea J, Andrade G, Bianciotto V, Dowling D, Lohrke S, Bonfante P et al (1998) Impact on arbuscular mycorrhiza formation of pseudomonas strains used as inoculants for biocontrol of soil-borne fungal plant pathogens. Appl Environ Microbiol 64(6):2304–2307

Bauer WD, Mathesius U (2004) Plant responses to bacterial quorum sensing signals. Curr Opin Plant Biol 7(4):429–433

Beolchini F, Dell'Anno A, De Propris L, Ubaldini S, Cerrone F, Danovaro R (2009) Auto-and heterotrophic acidophilic bacteria enhance the bioremediation efficiency of sediments contaminated by heavy metals. Chemosphere 74(10):1321–1326

Bhattacharyya P, Jha D (2012) Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. World J Microbiol Biotechnol 28(4):1327–1350

Bianciotto V, Andreotti S, Balestrini R, Bonfante P, Perotto S (2009) Extracellular polysaccharides are involved in the attachment of *Azospirillum brasilense* and *Rhizobium leguminosarum* to arbuscular mycorrhizal structures. Eur J Histochem 45(1):39–50

Birhane E, Sterck FJ, Fetene M, Bongers F, Kuyper TW (2012) Arbuscular mycorrhizal fungi enhance photosynthesis, water use efficiency, and growth of frankincense seedlings under pulsed water availability conditions. Oecologia 169(4):895–904

Biswas B, Sarkar B, Rusmin R, Naidu R (2015) Bioremediation of PAHs and VOCs: advances in clay mineral-microbial interaction. Environ Int 85:168–181

Bonilla A, Sarria A, Algar E, Ledesma FM, Solano BR, Fernandes J, 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

Braud A, Jézéquel K, Vieille E, Tritter A, Lebeau T (2006) Changes in extractability of Cr and Pb in a polycontaminated soil after bioaugmentation with microbial producers of biosurfactants, organic acids and siderophores. Water Air Soil Pollut: Focus 6(3):261–279

Braud A, Jézéquel K, Bazot S, Lebeau T (2009) Enhanced phytoextraction of an agricultural Cr-and Pb-contaminated soil by bioaugmentation with siderophore-producing bacteria. Chemosphere 74(2):280–286

Bruins MR, Kapil S, Oehme FW (2000) Microbial resistance to metals in the environment. Ecotoxicol Environ Saf 45(3):198–207

Bulgarelli D, Schlaeppi K, Spaepen S, van Themaat EVL, Schulze-Lefert P (2013) Structure and functions of the bacterial microbiota of plants. Annu Rev Plant Biol 64:807–838

Campanella BF, Bock C, Schröder P (2002) Phytoremediation to increase the degradation of PCBs and PCDD/Fs. Environ Sci Pollut Res 9(1):73–85

Castelfranco P, Foy CL, Deutsch DB (1961) Non-enzymatic detoxification of 2-chloro-4, 6-bis (ethylamino)-s-triazine (simazine) by extracts of Zea mays. Weeds 9:580–591

Castro MS, Fontes W (2005) Plant defense and antimicrobial peptides. Protein Pept Lett 12 (1):11–16

Cavagnaro TR, Bender SF, Asghari HR, van der Heijden MG (2015) The role of arbuscular mycorrhizas in reducing soil nutrient loss. Trends Plant Sci 20(5):283–290

Cha, C., Gao, P., Chen, Y.-C., and Shaw, P. D. (1998). Farrand SK 1998. Production of acyl-homoserine lactone quorum-sensing signals by Gram-negative plant-associated bacteria. Mol Plant-Microbe Interact, 11, 1119–1129

Chagnon P-L, Bradley RL (2015) The relative importance of host vigor and hormonal response to pathogens in controlling the development of arbuscular mycorrhizal fungi. Soil Biol Biochem 83:40–42

Chaparro JM, Badri DV, Bakker MG, Sugiyama A, Manter DK, Vivanco JM (2013) Root exudation of phytochemicals in Arabidopsis follows specific patterns that are developmentally programmed and correlate with soil microbial functions. PLoS One 8(2):e55731

Chatterjee S, Sau GB, Mukherjee SK (2009) Plant growth promotion by a hexavalent chromium reducing bacterial strain, Cellulosimicrobium cellulans KUCr3. World J Microbiol Biotechnol 25(10):1829–1836

Chen YX, Wang YP, Lin Q, Luo YM (2005) Effect of copper-tolerant rhizosphere bacteria on mobility of copper in soil and copper accumulation by Elsholtzia splendens. Environ Int 31 (6):861–866

Chernin L, Toklikishvili N, Ovadis M, Kim S, Ben-Ari J, Khmel I, Vainstein A (2011) Quorum-sensing quenching by rhizobacterial volatiles. Environ Microbiol Rep 3(6):698–704

Chojnacka K (2010) Biosorption and bioaccumulation–the prospects for practical applications. Environ Int 36(3):299–307

Coleman J, Blake-Kalff M, Davies E (1997) Detoxification of xenobiotics by plants: chemical modification and vacuolar compartmentation. Trends Plant Sci 2(4):144–151

Contreras-Cornejo HA, Macías-Rodríguez L, Cortés-Penagos C, López-Bucio J (2009) Trichoderma virens, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in Arabidopsis. Plant Physiol 149 (3):1579–1592

Crowley DE, Kraemer SM (2007) Function of siderophores in the plant rhizosphere. In: Pinton R, Varanini Z, Nannipieri P (eds) The rhizosphere: biochemistry and organic substances at the soil-plant interface, 2nd edn. CRC Press, Boca Raton, pp 173–200

Cruz-Hernández A, Tomasini-Campocosio A, Pérez-Flores L, Fernández-Perrino F, Gutiérrez-Rojas M (2013) Inoculation of seed-borne fungus in the rhizosphere of *Festuca arundinacea* promotes hydrocarbon removal and pyrene accumulation in roots. Plant Soil 362(1–2):261–270

da Costa PB, Granada CE, Ambrosini A, Moreira F, de Souza R, dos Passos JFM et al (2014) A model to explain plant growth promotion traits: a multivariate analysis of 2,211 bacterial isolates. PloS One 9(12):e116020

Dakora FD, Phillips DA (2002) Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil 245(1):35–47

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

Das A, Prasad R, Srivastava A, Giang PH, Bhatnagar K, Varma A (2007) Fungal siderophores: structure, functions and regulations. In: Varma A, Chincholkar SB (eds) Microbial Siderophores, vol 12. Springer-Verlag, Berlin Heidelberg, pp 1–42

Del Fabbro C, Prati D (2014) Early responses of wild plant seedlings to arbuscular mycorrhizal fungi and pathogens. Basic Appl Ecol 15(6):534–542

Delvasto P, Ballester A, Muñoz J, González F, Blázquez M, Igual J et al (2009) Mobilization of phosphorus from iron ore by the bacterium Burkholderia caribensis FeGL03. Miner Eng 22 (1):1–9

Dewey F, Wong YL, Seery R, Hollins T, Gurr S (1999) Bacteria associated with *Stagonospora* (Septoria) *nodorum* increase pathogenicity of the fungus. New Phytol 144(3):489–497

Di Gregorio S, Lampis S, Vallini G (2005) Selenite precipitation by a rhizospheric strain of *Stenotrophomonas* sp. isolated from the root system of *Astragalus bisulcatus*: a biotechnological perspective. Environ Int 31(2):233–241

Dimkpa C, Merten D, Svatoš A, Büchel G, Kothe E (2009a) Siderophores mediate reduced and increased uptake of cadmium by *Streptomyces tendae* F4 and sunflower (*Helianthus annuus*), respectively. J Appl Microbiol 107(5):1687–1696

Dimkpa CO, Merten D, Svatoš A, Büchel G, Kothe E (2009b) Metal-induced oxidative stress impacting plant growth in contaminated soil is alleviated by microbial siderophores. Soil Biol Biochem 41(1):154–162

Djonović S, Pozo MJ, Dangott LJ, Howell CR, Kenerley CM (2006) Sm1, a proteinaceous elicitor secreted by the biocontrol fungus *Trichoderma virens* induces plant defense responses and systemic resistance. Mol Plant-Microbe Interact 19(8):838–853

Dong Y-H, Wang L-H, Xu J-L, Zhang H-B, Zhang X-F, Zhang L-H (2001) Quenching quorum-sensing-dependent bacterial infection by an N-acyl homoserine lactonase. Nature 411 (6839):813–817

Doornbos RF, van Loon LC, Bakker PA (2012) Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere. A review. Agron Sustain Dev 32(1):227–243

Drogue B, Doré H, Borland S, Wisniewski-Dyé F, Prigent-Combaret C (2012) Which specificity in cooperation between phytostimulating rhizobacteria and plants? Res Microbiol 163(8):500–510

Eapen S, Singh S, D'souza S (2007) Advances in development of transgenic plants for remediation of xenobiotic pollutants. Biotechnol Adv 25(5):442–451

Esedafe WK, Fagade EO, Umaru FF, Akinwotu O (2015) Bacterial degradation of the polycyclic aromatic hydrocarbon (PAH) -fraction of refinery effluent. Int J Environ Bioremediation Biodegradation 3(1):23–27

Evangelou MW, Ebel M, Schaeffer A (2006) Evaluation of the effect of small organic acids on phytoextraction of Cu and Pb from soil with tobacco *Nicotiana tabacum*. Chemosphere 63 (6):996–1004

Fasim F, Ahmed N, Parsons R, Gadd GM (2002) Solubilization of zinc salts by a bacterium isolated from the air environment of a tannery. FEMS Microbiol Lett 213(1):1–6

Fester T, Giebler J, Wick LY, Schlosser D, Kästner M (2014) Plant–microbe interactions as drivers of ecosystem functions relevant for the biodegradation of organic contaminants. Curr Opin Biotechnol 27:168–175

Fomina M, Alexander I, Hillier S, Gadd G (2004) Zinc phosphate and pyromorphite solubilization by soil plant-symbiotic fungi. Geomicrobiol J 21(5):351–366

Gadd GM (2004) Microbial influence on metal mobility and application for bioremediation. Geoderma 122(2):109–119

Gadkar V, Rillig MC (2006) The arbuscular mycorrhizal fungal protein glomalin is a putative homolog of heat shock protein 60. FEMS Microbiol Lett 263(1):93–101

Gamalero E, Trotta A, Massa N, Copetta A, Martinotti MG, Berta G (2004) Impact of two fluorescent pseudomonads and an arbuscular mycorrhizal fungus on tomato plant growth, root architecture and P acquisition. Mycorrhiza 14(3):185–192

Gao Y, Cheng Z, Ling W, Huang J (2010) Arbuscular mycorrhizal fungal hyphae contribute to the uptake of polycyclic aromatic hydrocarbons by plant roots. Bioresour Technol 101 (18):6895–6901

Gerhardt KE, Huang X-D, Glick BR, Greenberg BM (2009) Phytoremediation and rhizoremediation of organic soil contaminants: potential and challenges. Plant Sci 176 (1):20–30

Glick BR (2004) Bacterial ACC deaminase and the alleviation of plant stress. Adv Appl Microbiol 56:291–312

Glick BR (2010) Using soil bacteria to facilitate phytoremediation. Biotechnol Adv 28(3):367–374

Glick BR, Bashan Y (1997) Genetic manipulation of plant growth-promoting bacteria to enhance biocontrol of phytopathogens. Biotechnol Adv 15(2):353–378

Goh H-H, Sloan J, Malinowski R, Fleming A (2014) Variable expansin expression in Arabidopsis leads to different growth responses. J Plant Physiol 171(3):329–339

Goicoechea N, Antolin M, Sánchez-Díaz M (1997) Gas exchange is related to the hormone balance in mycorrhizal or nitrogen-fixing alfalfa subjected to drought. Physiol Plant 100 (4):989–997

González-Teuber M, Pozo MJ, Muck A, Svatos A, Adame-Alvarez RM, Heil M (2010) Glucanases and chitinases as causal agents in the protection of *Acacia extrafloral* nectar from infestation by phytopathogens. Plant Physiol 152(3):1705–1715

Goodell B, Jellison J, Liu J, Daniel G, Paszczynski A, Fekete F et al (1997) Low molecular weight chelators and phenolic compounds isolated from wood decay fungi and their role in the fungal biodegradation of wood. J Biotechnol 53(2):133–162

Guo W, Zhao R, Zhao W, Fu R, Guo J, Bi N, Zhang J (2013) Effects of arbuscular mycorrhizal fungi on maize (Zea mays L.) and sorghum (*Sorghum bicolor* L. Moench) grown in rare earth elements of mine tailings. Appl Soil Ecol 72:85–92

Habibzadeh Y, Pirzad A, Zardashti MR, Jalilian J, Eini O (2013) Effects of arbuscular mycorrhizal fungi on seed and protein yield under water-deficit stress in mung bean. Agron J 105(1):79–84

Harman GE, Howell CR, Viterbo A, Chet I, Lorito M (2004) *Trichoderma* species—opportunistic, avirulent plant symbionts. Nat Rev Microbiol 2(1):43–56

Harms H, Schlosser D, Wick LY (2011) Untapped potential: exploiting fungi in bioremediation of hazardous chemicals. Nat Rev Microbiol 9(3):177–192

Hartmann A, Schmid M, Van Tuinen D, Berg G (2009) Plant-driven selection of microbes. Plant Soil 321(1–2):235–257

Hashem A, Abd_Allah EF, Alqarawi AA, Aldubise A, Egamberdieva D (2015) Arbuscular mycorrhizal fungi enhances salinity tolerance of *Panicum turgidum* Forssk by altering photosynthetic and antioxidant pathways. J Plant Interact 10(1):230–242

Hayat R, Ali S, Amara U, Khalid R, Ahmed I (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol 60(4):579–598

Henke C, Jung E-M, Kothe E (2015) Hartig' net formation of *Tricholoma vaccinum-spruce* ectomycorrhiza in hydroponic cultures. Environ Sci Pollut Res 22(24):19394–19399

Hodge A, Storer K (2015) Arbuscular mycorrhiza and nitrogen: implications for individual plants through to ecosystems. Plant Soil 386(1–2):1–19

Hofmann NR (2013) Volatile organic compounds: a bacterial contribution to plant sulfur nutrition. Am Soc Plant Biologist 25:2381

Jaiti F, Meddich A, El Hadrami I (2007) Effectiveness of arbuscular mycorrhizal fungi in the protection of date palm (*Phoenix dactylifera* L.) against bayoud disease. Physiol Mol Plant Pathol 71 (4):166–173

Jalloh A, Roy-Macauley H, Sereme P (2012) Major agro-ecosystems of West and Central Africa: brief description, species richness, management, environmental limitations and concerns. Agric Ecosyst Environ 157:5–16

Jeffries P, Gianinazzi S, Perotto S, Turnau K, Barea J-M (2003) The contribution of arbuscular mycorrhizal fungi in sustainable maintenance of plant health and soil fertility. Biol Fertil Soils 37(1):1–16

Jianfeng H, Xiangui L, Rui Y, Jiang Q, Yufang S (2009) Effects of arbuscular mycorrhizal fungi inoculation on arsenic accumulation by tobacco (*Nicotiana tabacum* L.). J Environ Sci 21 (9):1214–1220

Johansson EM, Fransson PM, Finlay RD, van Hees PA (2008) Quantitative analysis of exudates from soil-living basidiomycetes in pure culture as a response to lead, cadmium and arsenic stress. Soil Biol Biochem 40(9):2225–2236

Joner EJ, Leyval C, Colpaert JV (2006) Ectomycorrhizas impede phytoremediation of polycyclic aromatic hydrocarbons (PAHs) both within and beyond the rhizosphere. Environ Pollut 142 (1):34–38

Jones JDG, Dangl JL (2006) The plant immune system. Nature 444(7117):323–329

Jones D, Edwards A (1998) Influence of sorption on the biological utilization of two simple carbon substrates. Soil Biol Biochem 30(14):1895–1902

Jones D, Dennis P, Owen A, Van Hees P (2003) Organic acid behavior in soils–misconceptions and knowledge gaps. Plant Soil 248(1–2):31–41

Juwarkar AA, Jambhulkar HP (2008) Phytoremediation of coal mine spoil dump through integrated biotechnological approach. Bioresour Technol 99(11):4732–4741

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

Kaymak HC (2010) Potential of PGPR in agricultural innovations. In: Maheshwari DK (ed) Plant growth and health promoting bacteria, Springer, Berlin, pp 45–79

Khalafallah AA, Abo-Ghalia HH (2008) Effect of arbuscular mycorrhizal fungi on the metabolic products and activity of antioxidant system in wheat plants subjected to short-term water stress, followed by recovery at different growth stages. J Appl Sci Res 4(5):559–569

Khan MS, Zaidi A, Wani PA, Oves M (2009) Role of plant growth promoting rhizobacteria in the remediation of metal contaminated soils. Environ Chem Lett 7(1):1–19

Khaosaad T, Garcia-Garrido J, Steinkellner S, Vierheilig H (2007) Take-all disease is systemically reduced in roots of mycorrhizal barley plants. Soil Biol Biochem 39(3):727–734

Kim S, Lim H, Lee I (2010) Enhanced heavy metal phytoextraction by Echinochloa crus-galli using root exudates. J Biosci Bioeng 109(1):47–50

Kiss T, Farkas E (1998) Metal-binding ability of desferrioxamine B. J Incl Phenom Mol Recognit Chem 32(2–3):385–403

Kletzin A (2007) Metabolism of inorganic sulfur compounds in archaea. In: Archaea: evolution, physiology, and molecular biology, pp 261–274

Kloepper JW, Lifshitz R, Zablotowicz RM (1989) Free-living bacterial inocula for enhancing crop productivity. Trends Biotechnol 7(2):39–44

Krapp A (2015) Plant nitrogen assimilation and its regulation: a complex puzzle with missing pieces. Curr Opin Plant Biol 25:115–122

Krupa P, Kozdrój J (2007) Ectomycorrhizal fungi and associated bacteria provide protection against heavy metals in inoculated pine (*Pinus sylvestris* L.) seedlings. Water Air Soil Pollut 182 (1–4):83–90

Kuffner M, Puschenreiter M, Wieshammer G, Gorfer M, Sessitsch A (2008) Rhizosphere bacteria affect growth and metal uptake of heavy metal accumulating willows. Plant Soil 304 (1–2):35–44

Kuffner, M., De Maria, S., Puschenreiter, M., Fallmann, K., Wieshammer, G., Gorfer, M., Sessitsch, A. (2010). Culturable bacteria from Zn-and Cd-accumulating *Salix caprea* with differential effects on plant growth and heavy metal availability. J Appl Microbiol*,* 108(4), 1471–1484

Kuiper I, Lagendijk EL, Bloemberg GV, Lugtenberg BJ (2004) Rhizoremediation: a beneficial plant-microbe interaction. Mol Plant-Microbe Interact 17(1):6–15

Kumar RN, Nagendran R (2009) Fractionation behavior of heavy metals in soil during bioleaching with *Acidithiobacillus thiooxidans*. J Hazard Mater 169(1):1119–1126

Kurepin LV, Park JM, Lazarovits G, Bernards MA (2015) *Burkholderia phytofirmans*-induced shoot and root growth promotion is associated with endogenous changes in plant growth hormone levels. Plant Growth Regul 75(1):199–207

Lau JA, Lennon JT (2011) Evolutionary ecology of plant–microbe interactions: soil microbial structure alters selection on plant traits. New Phytol 192(1):215–224

Lebeau T, Braud A, Jézéquel K (2008) Performance of bioaugmentation-assisted phytoextraction applied to metal contaminated soils: a review. Environ Pollut 153(3):497–522

Li W, Ye Z, Wong M (2010) Metal mobilization and production of short-chain organic acids by rhizosphere bacteria associated with a Cd/Zn hyperaccumulating plant, *Sedum alfredii*. Plant Soil 326(1–2):453–467

Li H-Y, Wei D-Q, Shen M, Zhou Z-P (2012) Endophytes and their role in phytoremediation. Fungal Divers 54(1):11–18. https://doi.org/10.1007/s13225-012-0165-x

Linderman RG (1992) Vesicular-arbuscular mycorrhizae and soil microbial interactions. In: Mycorrhizae in sustainable agriculture (mycorrhizaeinsu). American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America, Madison, pp 45–70

Lioussanne L, Jolicoeur M, St-Arnaud M (2009) Role of the modification in root exudation induced by arbuscular mycorrhizal colonization on the intraradical growth of *Phytophthora nicotianae* in tomato. Mycorrhiza 19(6):443–448

Liu D, Li S, Islam E, Chen JR, Wu JS, Ye ZQ et al (2015a) Lead accumulation and tolerance of Moso bamboo (*Phyllostachys pubescens*) seedlings: applications of phytoremediation. J Zhejiang Univ Sci B 16(2):123–130

Liu H, Yuan M, Tan S, Yang X, Lan Z, Jiang Q et al (2015b) Enhancement of arbuscular mycorrhizal fungus (Glomus versiforme) on the growth and Cd uptake by Cd-hyperaccumulator Solanum nigrum. Appl Soil Ecol 89:44–49

Loh J, Carlson RW, York WS, Stacey G (2002) Bradyoxetin, a unique chemical signal involved in symbiotic gene regulation. Proc Natl Acad Sci 99(22):14446–14451

Lopez-Bucio J, Nieto-Jacobo MF, Ramırez-Rodrıguez V, Herrera-Estrella L (2000) Organic acid metabolism in plants: from adaptive physiology to transgenic varieties for cultivation in extreme soils. Plant Sci 160(1):1–13

Luo Q, Sun L, Hu X, Zhou R (2014a) The variation of root exudates from the hyperaccumulator *Sedum alfredii* under cadmium stress: metabonomics analysis. PLoS One 9(12):e115581

Luo Z-B, Wu C, Zhang C, Li H, Lipka U, Polle A (2014b) The role of ectomycorrhizas in heavy metal stress tolerance of host plants. Environ Exp Bot 108:47–62

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

Ma Y, Oliveira RS, Wu L, Luo Y, Rajkumar M, Rocha I, Freitas H (2015) Inoculation with metal-mobilizing plant-growth-promoting rhizobacterium *Bacillus* sp. SC2b and its role in rhizoremediation. J Toxic Environ Health A 78(13–14):931–944

Ma Y, Oliveira RS, Freitas H, Zhang C (2016) Biochemical and molecular mechanisms of plant-microbe-metal interactions: relevance for phytoremediation. Front Plant Sci 7:19

Machuca A, Pereira G, Aguiar A, Milagres A (2007) Metal-chelating compounds produced by ectomycorrhizal fungi collected from pine plantations. Lett Appl Microbiol 44(1):7–12

Madhaiyan M, Poonguzhali S, Sa T (2007) Metal tolerating methylotrophic bacteria reduces nickel and cadmium toxicity and promotes plant growth of tomato (*Lycopersicon esculentum* L.). Chemosphere 69(2):220–228

Maillet F, Poinsot V, Andre O, Puech-Pagès V, Haouy A, Gueunier M et al (2011) Fungal lipochitooligosaccharide symbiotic signals in arbuscular mycorrhiza. Nature 469 (7328):58–63

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

Mani D, Kumar C (2014) Biotechnological advances in bioremediation of heavy metals contaminated ecosystems: an overview with special reference to phytoremediation. Int J Environ Sci Technol 11(3):843–872

Martínez-Viveros O, Jorquera MA, Crowley DE, Gajardo G, Mora ML (2010) Mechanisms and practical considerations involved in plant growth promotion by rhizobacteria. J Soil Sci Plant Nutr 10(3):293–319

Martino E, Perotto S, Parsons R, Gadd GM (2003) Solubilization of insoluble inorganic zinc compounds by ericoid mycorrhizal fungi derived from heavy metal polluted sites. Soil Biol Biochem 35(1):133–141

McCutcheon S, Schnoor J, Wolfe N, Carreira L (1995) Phytoremediation of organic and nutrient contaminants. Environ Sci Technol 29(7):318A–323A

McMichael A, Butler C, Dixon J (2015) Climate change, food systems and population health risks in their eco-social context. Public Health 129(10):1361–1368

Meagher RB (2000) Phytoremediation of toxic elemental and organic pollutants. Curr Opin Plant Biol 3(2):153–162

Meding SM, Zasoski RJ (2008) Hyphal-mediated transfer of nitrate, arsenic, cesium, rubidium, and strontium between arbuscular mycorrhizal forbs and grasses from a California oak woodland. Soil Biol Biochem 40(1):126–134

Meier S, Azcón R, Cartes P, Borie F, Cornejo P (2011) Alleviation of Cu toxicity in Oenothera picensis by copper-adapted arbuscular mycorrhizal fungi and treated agrowaste residue. Appl Soil Ecol 48(2):117–124

Meier S, Alvear M, Borie F, Aguilera P, Ginocchio R, Cornejo P (2012a) Influence of copper on root exudate patterns in some metallophytes and agricultural plants. Ecotoxicol Environ Saf 75:8–15

Meier S, Borie F, Bolan N, Cornejo P (2012b) Phytoremediation of metal-polluted soils by arbuscular mycorrhizal fungi. Crit Rev Environ Sci Technol 42(7):741–775

Miransari M (2010) Contribution of arbuscular mycorrhizal symbiosis to plant growth under different types of soil stress. Plant Biol 12(4):563–569

Miransari M (2011) Hyperaccumulators, arbuscular mycorrhizal fungi and stress of heavy metals. Biotechnol Adv 29(6):645–653

Mishra A, Malik A (2013) Recent advances in microbial metal bioaccumulation. Crit Rev Environ Sci Technol 43(11):1162–1222

Mulligan CN, Galvez-Cloutier R (2003) Bioremediation of metal contamination. Environ Monit Assess 84(1–2):45–60

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

Najafi A, Ardakani MR, Rejali F, Sajedi N (2012) Response of winter barley to co-inoculation with *Azotobacter* and Mycorrhiza fungi influenced by plant growth promoting rhizobacteria. Ann Biol Res 3:4002–4006

Navarro CA, von Bernath D, Jerez CA (2013) Heavy metal resistance strategies of acidophilic bacteria and their acquisition: importance for biomining and bioremediation. Biol Res 46(4):363–371

Neilands J (1995) Siderophores: structure and function of microbial iron transport compounds. J Biol Chem 270(45):26723–26726

Neubauer U, Furrer G, Kayser A, Schulin R (2000) Siderophores, NTA, and citrate: potential soil amendments to enhance heavy metal mobility in phytoremediation. Int J Phytoremediation 2 (4):353–368

Neumann G, Römheld V (1999) Root excretion of carboxylic acids and protons in phosphorus-deficient plants. Plant Soil 211(1):121–130

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

Oláh B, Brière C, Bécard G, Dénarié J, Gough C (2005) Nod factors and a diffusible factor from arbuscular mycorrhizal fungi stimulate lateral root formation in *Medicago truncatula* via the DMI1/DMI2 signalling pathway. Plant J 44(2):195–207

Orłowska E, Przybyłowicz W, Orlowski D, Mongwaketsi NP, Turnau K, Mesjasz-Przybyłowicz J (2013) Mycorrhizal colonization affects the elemental distribution in roots of Ni-hyperaccumulator Berkheya coddii Roessler. Environ Pollut 175:100–109

Ortiz N, Armada E, Duque E, Roldán A, Azcón R (2015) Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: effectiveness of autochthonous or allochthonous strains. J Plant Physiol 174:87–96

Ortíz-Castro R, Contreras-Cornejo HA, Macías-Rodríguez L, López-Bucio J (2009) The role of microbial signals in plant growth and development. Plant Signal Behav 4(8):701–712

Pathak A, Dastidar M, Sreekrishnan T (2009) Bioleaching of heavy metals from sewage sludge: a review. J Environ Manag 90(8):2343–2353

Patten CL, Glick BR (2002) Role of *Pseudomonas putida* indoleacetic acid in development of the host plant root system. Appl Environ Microbiol 68(8):3795–3801

Pérez-Esteban J, Escolástico C, Moliner A, Masaguer A (2013) Chemical speciation and mobilization of copper and zinc in naturally contaminated mine soils with citric and tartaric acids. Chemosphere 90(2):276–283

Pérez-Montaño F, Guasch-Vidal B, González-Barroso S, López-Baena FJ, Cubo T, Ollero FJ et al (2011) Nodulation-gene-inducing flavonoids increase overall production of autoinducers and expression of N-acyl homoserine lactone synthesis genes in rhizobia. Res Microbiol 162 (7):715–723

Pérez-Montaño F, Jiménez-Guerrero I, Sánchez-Matamoros RC, López-Baena FJ, Ollero FJ, Rodríguez-Carvajal MA et al (2013) Rice and bean AHL-mimic quorum-sensing signals specifically interfere with the capacity to form biofilms by plant-associated bacteria. Res Microbiol 164(7):749–760

Pilon-Smits E (2005) Phytoremediation. Annu Rev Plant Biol 56:15–39

Prasad R, Kumar M, Varma A (2015) Role of PGPR in soil fertility and plant health. In: Egamberdieva D, Shrivastava S, Varma A (eds) Plant Growth-Promoting Rhizobacteria (PGPR) and medicinal plants. Springer International Publishing, Switzerland, pp 247–260

Prasad R, Bhola D, Akdi K, Cruz C, Sairam KVSS, Tuteja N, Varma A (2017) Introduction to mycorrhiza: historical development. In: Varma A, Prasad R, Tuteja N (eds) Mycorrhiza. Springer International Publishing AG, pp 1–7

Rajkumar M, Ae N, Prasad MNV, Freitas H (2010) Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. Trends Biotechnol 28(3):142–149

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

Rajkumar M, Prasad MNV, Swaminathan S, Freitas H (2013) Climate change driven plant–metal–microbe interactions. Environ Int 53:74–86

Rashid MI, Mujawar LH, Shahzad T, Almeelbi T, Ismail IM, Oves M (2016) Bacteria and fungi can contribute to nutrients bioavailability and aggregate formation in degraded soils. Microbiol Res 183:26–41

Ren D, Sims JJ, Wood TK (2001) Inhibition of biofilm formation and swarming of Escherichia coli by (5Z)-4-bromo-5-(bromomethylene)-3-butyl-2 (5H)-furanone. Environ Microbiol 3(11):731–736

Richardson AE, Barea J-M, McNeill AM, Prigent-Combaret C (2009) Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. Plant Soil 321 (1–2):305–339

Rillig MC, Maestre FT, Lamit LJ (2003) Microsite differences in fungal hyphal length, glomalin, and soil aggregate stability in semiarid Mediterranean steppes. Soil Biol Biochem 35(9):1257–1260

Rudrappa T, Czymmek KJ, Paré PW, Bais HP (2008) Root-secreted malic acid recruits beneficial soil bacteria. Plant Physiol 148(3):1547–1556

Ruíz-Sánchez M, Armada E, Muñoz Y, de Salamone IEG, Aroca R, Ruíz-Lozano JM, Azcón R (2011) *Azospirillum* and arbuscular mycorrhizal colonization enhance rice growth and physiological traits under well-watered and drought conditions. J Plant Physiol 168 (10):1031–1037

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

Saharan B, Nehra V (2011) Plant growth promoting rhizobacteria: a critical review. Life Sci Med Res 21(1):30

Sandermann H Jr (1994) Higher plant metabolism of xenobiotics: the 'green liver'concept. Pharmacogenet Genomics 4(5):225–241

Saravanan V, Madhaiyan M, Thangaraju M (2007) Solubilization of zinc compounds by the diazotrophic, plant growth promoting bacterium *Gluconacetobacter diazotrophicus*. Chemosphere 66(9):1794–1798

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

Schmidt W (1999) Mechanisms and regulation of reduction-based iron uptake in plants. New Phytol 141(1):1–26

Schulz S, Dickschat JS (2007) Bacterial volatiles: the smell of small organisms. Nat Prod Rep 24 (4):814–842

Seeger EM, Reiche N, Kuschk P, Borsdorf H, Kaestner M (2011) Performance evaluation using a three compartment mass balance for the removal of volatile organic compounds in pilot scale constructed wetlands. Environ Sci Technol 45(19):8467–8474

Sennoi R, Singkham N, Jogloy S, Boonlue S, Saksirirat W, Kesmala T, Patanothai A (2013) Biological control of southern stem rot caused by *Sclerotium rolfsii* using *Trichoderma harzianum* and arbuscular mycorrhizal fungi on Jerusalem artichoke (*Helianthus tuberosus* L.). Crop Prot 54:148–153

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

Sharma A, Johri B, Sharma A, Glick B (2003) Plant growth-promoting bacterium Pseudomonas sp. strain GRP 3 influences iron acquisition in mung bean (*Vigna radiata* L. Wilczek). Soil Biol Biochem 35(7):887–894

Sharma S, Prasad R, Varma A, Sharma AK (2017) Glycoprotein associated with *Funneliformis coronatum*, *Gigaspora margarita* and *Acaulospora scrobiculata* suppress the plant pathogens in vitro. Asian J Plant Pathol. https://doi.org/10.3923/ajppaj.2017

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(1):17–22

Shi J-Y, Lin H-R, Yuan X-F, Chen X-C, Shen C-F, Chen Y-X (2011) Enhancement of copper availability and microbial community changes in rice rhizospheres affected by sulfur. Molecules 16(2):1409–1417

Shirmardi M, Savaghebi GR, Khavazi K, Akbarzadeh A, Farahbakhsh M, Rejali F, Sadat A (2010) Effect of microbial inoculants on uptake of nutrient elements in two cultivars of sunflower (*Helianthus annuus* L.) in saline soils. Notulae Sci Biol 2(3):57

Siebers M, Brands M, Wewer V, Duan Y, Hölzl G, Dörmann P (2016) Lipids in plant–microbe interactions. Biochim Biophys Acta (BBA) – Mol Cell Biol Lipids 1861(9 Part B):1379–1395

Singh JS (2015) Microbes: the chief ecological engineers in reinstating equilibrium in degraded ecosystems. Agric Ecosyst Environ 203:80–82

Singh JS, Abhilash P, Gupta VK (2016) Agriculturally important microbes in sustainable food production. Trends Biotechnol 34(10):773

Sinha S, Mukherjee SK (2008) Cadmium–induced siderophore production by a high Cd-resistant bacterial strain relieved Cd toxicity in plants through root colonization. Curr Microbiol 56 (1):55–60

Smith SE, Read DJ (2010) Mycorrhizal symbiosis. Academic, Oxford

Smith SE, Facelli E, Pope S, Smith FA (2010) Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas. Plant Soil 326(1–2):3–20

Smith SE, Jakobsen I, Grønlund M, Smith FA (2011) Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. Plant Physiol 156(3):1050–1057

Spaepen S, Vanderleyden J (2011) Auxin and plant-microbe interactions. Cold Spring Harb Perspect Biol 3(4):a001438

Spanu PD, Panstruga R (2017) Editorial: biotrophic plant-microbe interactions. Front Plant Sci 8:4

Srivastava J, Naraian R, Kalra SJS, Chandra H (2014) Advances in microbial bioremediation and the factors influencing the process. Int J Environ Sci Technol 11(6):1787–1800

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

Sun Y, Ling W, Liu J, Zong J (2012) Effects of arbuscular mycorrhizal fungi on the uptake of phenanthrene and pyrene by Alfalfa. J Agro-Environ Sci 31(10):1920–1926

Taghavi S, Barac T, Greenberg B, Borremans B, Vangronsveld J, van der Lelie D (2005) Horizontal gene transfer to endogenous endophytic bacteria from poplar improves phytoremediation of toluene. Appl Environ Microbiol 71(12):8500–8505

Tank N, Saraf M (2009) Enhancement of plant growth and decontamination of nickel-spiked soil using PGPR. J Basic Microbiol 49(2):195–204

U.S. Department of Health and Human Services, A. f. T. S. a. D. R. A (2015) ATSDR's substance priority list. Retrieved 5/05/2017 http://www.atsdr.cdc.gov/cercla/07list.html

Vacheron J, Desbrosses G, Bouffaud M-L, Touraine B, Prigent-Combaret C (2013) Plant growth-promoting rhizobacteria and root system functioning. Front Plant Sci 4:356

Van Aken B (2008) Transgenic plants for phytoremediation: helping nature to clean up environmental pollution. Trends Biotechnol 26(5):225–227

Van Aken B, Yoon JM, Schnoor JL (2004) Biodegradation of nitro-substituted explosives 2, 4, 6-trinitrotoluene, hexahydro-1, 3, 5-trinitro-1, 3, 5-triazine, and octahydro-1, 3, 5, 7-tetranitro-1, 3, 5-tetrazocine by a phytosymbiotic *Methylobacterium* sp. associated with poplar tissues (Populus deltoides× nigra DN34). Appl Environ Microbiol 70 (1):508–517

Van Aken B, Correa PA, Schnoor JL (2010) Phytoremediation of polychlorinated biphenyls: new trends and promises. Environ Sci Technol 44(8):2767

van Loon LC (2016) The intelligent behavior of plants. Trends Plant Sci 21(4):286–294

Vangronsveld J, Herzig R, Weyens N, Boulet J, Adriaensen K, Ruttens A, Thewys T, Vassilev A, Meers E, Nehnevajova E, Van der Lelie D, Mench M (2009) Phyto-remediation of contaminated soils and groundwater: lessons from the field. Environ Sci Pollut Res 16:765–794

Vansuyt G, Robin A, Briat J-F, Curie C, Lemanceau P (2007) Iron acquisition from Fe-pyoverdine by *Arabidopsis thaliana*. Mol Plant-Microbe Interact 20(4):441–447

Varnier AL, Sanchez L, Vatsa P, Boudesocque L, Garcia-Brugger A, Rabenoelina F et al (2009) Bacterial rhamnolipids are novel MAMPs conferring resistance to *Botrytis cinerea* in grapevine. Plant Cell Environ 32(2):178–193

Velásquez L, Dussan J (2009) Biosorption and bioaccumulation of heavy metals on dead and living biomass of *Bacillus sphaericus*. J Hazard Mater 167(1):713–716

Venkatesh NM, Vedaraman N (2012) Remediation of soil contaminated with copper using rhamnolipids produced from *Pseudomonas aeruginosa* MTCC 2297 using waste frying rice bran oil. Ann Microbiol 62(1):85–91

Vijayan R, Palaniappan P, Tongmin S, Elavarasi P, Manoharan N (2013) Rhizobitoxine enhances nodulation by inhibiting ethylene synthesis of *Bradyrhizobium elkanii* from *Lespedeza* species: validation by homology modeling and molecular docking study. World J Pharm Pharm Sci 2:4079–4094

Vimal SR, Singh JS, Arora NK, Singh S (2017) Soil-plant-microbe interactions in stressed agriculture management: a review. Pedosphere 27(2):177–192

Vivas A, Biro B, Ruiz-Lozano J, Barea J, Azcon R (2006) Two bacterial strains isolated from a Zn-polluted soil enhance plant growth and mycorrhizal efficiency under Zn-toxicity. Chemosphere 62(9):1523–1533

von Bodman SB, Bauer WD, Coplin DL (2003) Quorum sensing in plant-pathogenic bacteria. Annu Rev Phytopathol 41(1):455–482

von Rad U, Klein I, Dobrev PI, Kottova J, Zazimalova E, Fekete A et al (2008) Response of Arabidopsis thaliana to N-hexanoyl-DL-homoserine-lactone, a bacterial quorum sensing molecule produced in the rhizosphere. Planta 229(1):73–85

Vos C, Tesfahun A, Panis B, De Waele D, Elsen A (2012) Arbuscular mycorrhizal fungi induce systemic resistance in tomato against the sedentary nematode *Meloidogyne incognita* and the migratory nematode *Pratylenchus penetrans*. Appl Soil Ecol 61:1–6

Vymazal J (2011) Plants used in constructed wetlands with horizontal subsurface flow: a review. Hydrobiologia 674(1):133–156

Wong J, Xiang L, Gu X, Zhou L (2004) Bioleaching of heavy metals from anaerobically digested sewage sludge using FeS 2 as an energy source. Chemosphere 55(1):101–107

Xie H, Pasternak J, Glick BR (1996) Isolation and characterization of mutants of the plant growth-promoting rhizobacterium *Pseudomonas putida* GR12-2 that overproduce indoleacetic acid. Curr Microbiol 32(2):67–71

Xiong K, Fuhrmann J (1996) Comparison of rhizobitoxine-induced inhibition of β-cystathionase from different bradyrhizobia and soybean genotypes. Plant Soil 186(1):53–61

Younesi O, Moradi A, Namdari A (2013) Influence of arbuscular mycorrhiza on osmotic adjustment compounds and antioxidant enzyme activity in nodules of salt-stressed soybean (*Glycine max*). Acta Agric Slov 101(2):219

Yuan S, Xi Z, Jiang Y, Wan J, Wu C, Zheng Z, Lu X (2007) Desorption of copper and cadmium from soils enhanced by organic acids. Chemosphere 68(7):1289–1297

Yuan S, Li M, Fang Z, Liu Y, Shi W, Pan B et al (2016) Biological control of tobacco bacterial wilt using Trichoderma harzianum amended bioorganic fertilizer and the arbuscular mycorrhizal fungi Glomus mosseae. Biol Control 92:164–171

Zafar S, Aqil F, Ahmad I (2007) Metal tolerance and biosorption potential of filamentous fungi isolated from metal contaminated agricultural soil. Bioresour Technol 98(13):2557–2561

Zhang LH, Dong YH (2004) Quorum sensing and signal interference: diverse implications. Mol Microbiol 53(6):1563–1571

Zhang J, Subramanian S, Zhang Y, Yu O (2007) Flavone synthases from Medicago truncatula are flavanone-2-hydroxylases and are important for nodulation. Plant Physiol 144(2):741–751

Zhao F, Hamon R, McLaughlin MJ (2001) Root exudates of the hyperaccumulator Thlaspi caerulescens do not enhance metal mobilization. New Phytol 151(3):613–620

Zhao J, Davis LC, Verpoorte R (2005) Elicitor signal transduction leading to production of plant secondary metabolites. Biotechnol Adv 23(4):283–333

Zhipeng W, Weidong W, Shenglu Z, Shaohua W (2016) Mycorrhizal inoculation affects Pb and Cd accumulation and translocation in Pakchoi (*Brassica chinensis* L.). Pedosphere 26(1):13–26

Zikmundova M, Drandarov K, Bigler L, Hesse M, Werner C (2002) Biotransformation of 2-benzoxazolinone and 2-hydroxy-1, 4-benzoxazin-3-one by endophytic fungi isolated from *Aphelandra tetragona*. Appl Environ Microbiol 68(10):4863–4870

Zong K, Huang J, Nara K, Chen Y, Shen Z, Lian C (2015) Inoculation of ectomycorrhizal fungi contributes to the survival of tree seedlings in a copper mine tailing. J For Res 20(6):493–500