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The Role of the Rhizosphere and Microbes Associated with Hyperaccumulator Plants in Metal Accumulation

Emile Benizri and Petra S. Kidd

Abstract

Phytomining can be limited by low biomass productivity by plants or limited availability of soil metals. Ongoing research attempts to overcome these potential constraints and to make phytomining a successful commercial technique in the recovery of metals from polluted or naturally metal-rich soil by (hyper)accumulating plants. Recently, the benefits of combining phytoremediation with bioremediation, which consists in the use of beneficial microorganisms such as endophytes or rhizosphere bacteria and fungi, for metal removal from soils have been demonstrated. Metal-resistant microorganisms play an important role in enhancing plant survival and growth in these soils by alleviating metal toxicity and supplying nutrients. Furthermore, these beneficial microorganisms are able to enhance the metal bioavailability in the rhizosphere of plants. An increase in plant growth and metal uptake increases the effectiveness of phytoremediation processes coupled with bioremediation. Herein, we highlight the specificity of the rhizosphere and the critical roles in soil nutrient cycling and provision of ecosystem services that can be brought by rhizosphere microorganisms. We discuss how abiotic factors, such as the presence of metals in polluted sites or in naturally rich (ultramafic) soils modulate activities of soil microbial communities. Then we introduce the concept of microbe-assisted phytomining, and underline the role of plant-associated microorganisms in metal bioavailability and uptake by host plants that has attracted a growing interest over the last decade. Finally, we present various techniques, including phenotypic, genotypic, and metagenomic approaches, which allow for characterising soil microbial community structure and diversity in polluted or naturally metal-rich soils.

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B. napus	Pseudomonas fluorescens G10, Microbacterium sp. G16	IAA; Siderophore; ACCD; PO ₄	Pb	↑ plant biomass (root elongation) ↑ Pb uptake (shoot)	Sheng et al. (2008a)
B. napus	Pseudomonas putida UW4	ACCD	Ni	↑shoot biomass ↑ Ni tolerance	Farwell et al. 2007
B. napus	Pseudomonas putida UW4, Pseudomonas putida HS2	ACCD High Ni-tolerance (<i>P</i> . <i>p</i> HS2)	ïZ	↑ plant growth ↑ Ni yield	Farwell et al. (2006)
B. napus	Not determined	Cd-resistant	Cd	↑ [Cd] shoot	Sheng and Xia (2006)
B. napus, L. esculentum, Z. mays, Sorghum sudanense	Bacillus sp. J119	Metal-resistance; Antibiotic resistance; Biosurfactant; IAA; Siderophore	Cd	↑ shoot/root biomass of <i>L. esculentum</i> ; ↑ [Cd] shoot (<i>B. napus</i> , <i>L. esculentum</i>); ↑ [Cd] root (<i>B. napus</i> , <i>L. esculentum</i> , <i>Z.mays</i>)	Sheng et al. (2008b)
Heliathnus annuus	Bacillus weihenstephanensis SM3	IAA; PO ₄ ; Cu, Ni, Zn mobilization	Cu, Ni, Zn	↑ plant biomass ↑ Cu, Zn uptake	Rajkumar et al. (2008)
H. annuas	Pseudomonas fluorescens	IAA, Siderophore	As	↑ shoot biomass; ↑ [As] shoot; ↑ phloem fluxes	Shilev et al. (2006)
Lycopersicon esculentum	Pseudomonas sp. RJ10, Bacillus sp. RJ16	IAA; Siderophore; ACCD; Cd, Pb mobilization	Cd, Pb	↑ plant biomass and root length ↑ Cd, Pb uptake	He et al. (2009)
Medicago sativa	Pseudomonas fluorescens (strains Avm, U), Rhizobium leguminosarum bv phaseoli (strains CPMex44, CPMex46), Azospirillum lipopherum (strains UAP40, UAP154)	Siderophore Growth promotion	Cu	↑ Cu, Fe root-shoot translocation (<i>CPMex46</i> , <i>Avm</i>)	Carrillo- Castañeda et al. (2002)
Nicotiana tabacum	Sanguibacter sp., Enterobacter sp., Pseudomonas sp.	pu	Cd	↑ plant biomass (Sanguibacter sp. S-d2 and consortia) ↑ Cd translocation ↑ Cd, Fe uptake	Mastretta et al. (2009)
					(continued)

Table 4 (continued)					
Plant species	Bacterial strain	Characteristics	Metal	Effect	Reference
Orychophragmus violaceus	Bacillus subtilis, B. cereus, Flavobacterium sp., Pseudomonas aeruginosa	Zn-tolerance	Zn	↑ plant biomass and root length ↑ Zn solubilization and uptake	He et al. (2010b)
Pteris vittata	Rhodococcus sp. TS1, Delffia sp. TS33, Comamonas sp. TS37, Delffia sp. TS41 Streptomyces lividans sp. PSQ22	As-reducing	As	↑ plant biomass ↑ As uptake ↑ As solubilization ↓ As leaching	Yang et al. (2012)
Populus deltoides	Agrobacterium radiobacter	As-tolerance IAA; Siderophore	As	↑ plant biomass ↑ chlorophyll, enzymatic activity ↑ [As] root, stem, leaf ↑ As uptake and translocation	Wang et al. (2011)
Ricinus communis	Pseudomonas sp. PsM6, P. jessenii PjM15	IAA; Siderophore; ACCD; Cu, Ni, Zn mobilization	Cu, Ni, Zn	↑ plant biomass ↑ Zn translocation and uptake	Rajkumar and Freitas (2008a)
Salix caprea	Agromyces sp. AR33, Streptomyces sp. AR17	1	Cd, Zn	↑ soil extractable-Cd/ Zn; ↑ plant growth ↑ Cd/Zn uptake	Kuffner et al. (2008)
Salix viminalis and S. alba x alba	Rahnella sp., Sphingobacterium sp., Caulobacter sp., Curtobacterium sp., Pseudomonas sp.	Acid: IAA, ACCD	Cd, Zn	↑ Twig biomass, ↑ Cd/Zn extraction potential (with <i>Rahnella</i> sp.)	Janssen et al. (2015)
Sedum alfredii	Burkholderia sp. D54	IAA; Siderophore; ACCD; PO ₄	Cd, Pb, Zn	↑ plant biomass; ↑ [Cd] shoot and root; ↑Cd, Pb, Zn uptake	Guo et al. (2011)
S. alfredii	5 bacterial strains (unidentified)	pu	Cd, Cu, Pb, Zn	↑ plant biomass ↑chlorophyll and nutrient content ↓ Cd, Cu, Pb, Zn toxicity ↑ Cd, Cu, Pb, Zn uptake from contaminated water	Xiong et al. (2008)

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S. alfredii	Burkholderia cepacia	1	Cd, Zn	↑ plant biomass; ↑ [Cd/Zn] shoot; ↑ metal tolerance; ↑ [Cd/Zn] _{root} ratio	Li et al. (2007)
Sedum plumbizincicola	Phyllobacterium myrsinacearum RC6b	Metal-resistance; Metal mobilization; IAA; Siderophore; ACCD; PO ₄	Cd, Pb, Zn	↑ plant biomass ↑ [Cd, Zn] root and shoot	Ma et al. (2013)
Sorghum bicolor, Z. mays	Bacillus subrilis, B. pumilus, Pseudomonas pseudoalcaligenes, Brevibacterium halotolerans	1	Pb, Zn Pb, Zn	\uparrow plant biomass (with inoculum mixture); \uparrow shoot biomass (<i>Br</i> . <i>h</i> , <i>P</i> . <i>p</i>); \uparrow solubility Cr, Cu (<i>B</i> . <i>s</i> , <i>B</i> . <i>p</i>); \uparrow [Cu, Cr, Pb, Zn] shoot on Cu-rich soil; \uparrow [Cr] shoot on Cr-rich soil	Abou-Shanab et al. (2007)
S. bicolor	Pseudomonas monteillii	nd	Cd	↑ plant biomass ↑ Cd uptake	Duponnois et al. (2006)
Thlaspi caerulescens	Mixed inoculum (<i>Microbacterium saperdae</i> , <i>Pseudomonas monteilii</i> , <i>Enterobacter cancerogenes</i>)	I	Zn	↑ [Zn] water-soluble; ↑ [Zn] shoot	Whiting et al. (2001)
Thlaspi caerulescens	Mixed inoculum: <i>Bacillus pumilus</i> and <i>Micrococcus</i> sp.	Ni-resistant	Ņ	↓[Ni] _{water-soluble} ; ↑plant biomass; ↑Ni yield	Aboudrar et al. (2013)
Trifolium repens Linn.	Bacterial strain mix (Bacillus cereus)	Metal-tolerance; IAA	Cd	↑ plant biomass and phytoextraction	Azcón et al. (2009)
Trifolium hybridum, Alopecurus pratensis, Poa pratensis, Hordeum violaceum, Ranunculus kotschyi, Cerastium sp.	Bacillus megaterium var. phosphaticum	Nutrient-solubilization; Pathogens control	B, Ni, Mn, Pb, Zn	↑ Ni, Pb, Fe, Zn, Na, B desorption from the soil ↑ Pb, Ni, B, Mn, Zn uptake	Gullap et al. (2014)
Zea mays	Pseudomonas aeruginosa, Pseudomonas fluorescens, Ralstonia metalidurans	Siderophore	Cr, Pb	↑ Cr. Pb exchangeable fraction in the soil (<i>P. aeruginosa</i>) ↑ [Cr, Pb] shoot	Braud et al. (2009)

Durand et al. 2016; Álvarez-López et al. 2016a). Schlegel et al. (1991) found that bacterial strains isolated from serpentine soils tolerated up to 10-20 mM Ni (in the culture medium), whereas strains from other soil types tolerated only 1 mM Ni. Turgay et al. (2012) reported that bacterial strains, isolated from Turkish serpentine soils, could tolerate up to 34 mM Ni in the growth medium. Furthermore, as described above, the rhizosphere bacterial communities associated with Ni-hyperaccumulating plants have been shown to differ from those of non-accumulating plants growing at the same site or of non-vegetated soil, but are also known to host a higher number of Ni-tolerant bacteria (Schlegel et al. 1991; Mengoni et al. 2001; Abou-Shanab et al. 2003b; Becerra-Castro et al. 2009; Álvarez-López et al. 2016a). Schlegel et al. (1991) reported a higher occurrence of Ni-resistant bacteria in soil samples collected with increasing proximity to the Ni-hyperaccumulating tree Sebertia (= Pycnandra) acuminata. Mengoni et al. (2001) also found a higher proportion of Ni-resistant cfu in proximity to the Ni-hyperaccumulator A. bertolonii in than non-vegetated soil. These authors observed simultaneous resistance to a set of metals and highest resistance from isolates of the rhizosphere. Becerra-Castro et al. (2009) found higher proportions of Ni-tolerant bacteria in the rhizosphere of A. serpyllifolium ssp. lusitanicum. This selective enrichment of Ni-tolerant bacteria in the rhizosphere was correlated with an increase in soil Ni availability (Becerra-Castro et al. 2009). Alvarez-López et al. (2016a) confirmed higher densities of Ni-tolerant bacteria associated with the Ni-hyperaccumulators A. serpyllifolium ssp. lusitanicum and Α. serpyllifolium ssp. malacitanum, but observed significant differences in this selective enrichment amongst different plant populations across the Iberian Peninsula.

The screening of bacterial isolates associated with metal (hyper)accumulating plants has led to the identification of candidate inoculants for application in phytomining. Bacterial strains are commonly characterized for the presence of PGP traits such as the capacity to produce phytohormones (IAA), to solubilize inorganic P or K, to fix atmospheric N_2 , to release siderophores, or for their ACC activity. Most bioaugmentation studies have evaluated the effects of re-inoculating host plants with their associated isolates (Abou-Shanab et al. 2003a; Abou-Shanab et al. 2006; Li et al. 2007; Cabello-Conejo et al. 2014). However, the specificity of these plant-bacterial combinations is not always clear, and some inoculants have been shown to have beneficial effects on a wide range of plant hosts (Grandlic et al. 2008; Ma et al. 2011; Becerra-Castro et al. 2012). The main objective of these studies has been to improve metal yields during phytoextraction. In this technique, a simple improvement in biomass can result in an increase in overall trace element removal (Sessitsch et al. 2013). In a metaanalysis carried out by Sessitsch et al. (2013), including results from more than 70 publications and 738 individual cases, the authors found that bacterial inoculation was generally more successful in promoting plant growth and biomass production (60% of total cases analyzed) than in influencing shoot trace elements accumulation (only 30% of cases showed a significant increase in shoot trace elements concentration, and 16% a decrease in trace elements concentration).

Ma et al. (2009a, b) found that inoculation with PGP rhizobacteria (Psychrobacter SRA1, Bacillus cereus SRA10 sp. and Achromobacter xylosoxidans strain Ax10) improved the growth of Brassica juncea and B. oxyrrhina, enhanced soil Ni availability, and increased Ni accumulation in both species. Similarly, Rajkumar and Freitas (2008b) observed that inoculation with the PGP rhizobacterial strains Pseudomonas sp. PsM6 and P. jessenii PjM15 isolated from a serpentine soil in R. communis caused an increase in above-ground biomass, mainly due to IAA production and phosphate solubilization, and consequently enhanced phytoextraction efficiency. Zaidi et al. (2006) demonstrated that inoculation with Bacillus subtilis strain SJ-101 not only stimulated the growth of, and Ni accumulation in, Brassica juncea, but also protected the plant from Ni toxicity. Various authors also reported increases in Ni uptake by В. juncea and other non-hyperaccumulating plant species (B. napus, Ricinus communis, Poa pratensis, etc.) after bacterial inoculation (Rajkumar and Freitas 2008a, b; Kumar et al. 2009; Gullap et al. 2014). With regard to Ni-hyperaccumulating species, Abou-Shanab et al. (2003b) showed that the strain Microbacterium arabinogalacta*nolyticum* isolated from the rhizosphere of A. murale significantly increased availability of Ni in the soil and enhanced Ni accumulation by A. murale. In agreement with these results, a posterior study with A. murale grown in artificially Ni-polluted soils demonstrated that inoculation with selected rhizobacteria strains increased Ni extraction from the soil and Ni uptake by A. murale (Abou-Shanab et al. 2006). These authors considered the presence of such rhizobacteria to be an important factor that influenced metal hyperaccumulation. Becerra-Castro et al. (2013) used two strains of Arthrobacter (SBA82 and LA44) harbouring several plant growth-promoting characteristics are able to mobilize Ni from serpentine rock, as an inoculum for A. serpyllifolium ssp. malacitanum grown in ultramafic soil, and observed an increase in plant biomass and shoot Ni concentrations. Durand et al. (2016) isolated plant growth-promoting rhizobacteria from the rhizosphere soil of two hyperaccumulator plant associations: B. tymphaea-N. tymphaea (NB) and B. tymphaea-A. murale (AB), both being characteristic of a serpentine outcrop in Greece. The screening of the isolates revealed two PGPR strains (AB30 and NB24) that were affiliated to Variovorax paradoxus and that were used to inoculate the same plant associations growing in mesocosms. Biomass (root and shoot), shoot Ni uptake, and Ni removal by the B. tymphaea-N. tymphaea plant association inoculated with strain NB24 was significantly higher than that of the respective non-inoculated association.

Benefits to plants of mycorrhizal inoculation in highly stressed and nutrient-poor environments are well documented. Inoculation with arbuscular mycorrhizae in trace elementspolluted mine tailings has proven particularly effective in enhancing plant survival and performance during restoration (Orłowska et al. 2011; Kohler et al. 2015; Maltz and Treseder 2015). However, fewer studies have found inoculating with mycorrhizal fungi species or strains to enhance metal uptake and accumulation. In fact, until the early 2000s, hyperaccumulating plants were generally considered non-mycorrhizal (Gonçalves et al. 1997; Leyval et al. 1997; Pawlowska et al. 2000). Since then, several studies have found that hyperaccumulators can form symbioses with arbuscular mycorrhizal fungi (AMF). Pteris vitatta, an As-hyperaccumulating fern, tended to show higher mycorrhizal colonization on As-polluted soil. Leung et al. (2007) suggested that enhanced P uptake could be linked to increased As absorption and transport. Mycorrhizal colonisation has been observed in Thlaspi *praecox*, a Cd- and Zn-hyperaccumulator of the Brassicaceae family (generally considered to be non-mycorrhizal) growing on metal-polluted soil in Slovenia (Vogel-Mikus et al. 2005). Berkheya coddii was the first Ni-hyperaccumulating plant in which the presence of arbuscular mycorrhizal (AM) symbiosis was reported (Turnau and Mesjasz-Przybylowicz 2003). Arbuscular mycorrhizal fungi (AMF) isolated from serpentine soil significantly enhanced growth and survival of the Ni-hyperaccumulator B. coddii when growing in the same soil (Orłowska et al. 2011). AMF inoculation reduced shoot and root Ni concentrations, however, and owing to the higher biomass the total Ni yield was up to 20 times greater in mycorrhizal plants compared to the non-mycorrhizal ones. The authors proposed that AMF enhancement of Ni uptake may help to improve Ni phytomining techniques.

5 Improving Soil Metal Removal Using Metal-Mobilizing Microbial Strains

Metal-hyperaccumulating plant species have an extraordinary capacity for trace metal accumulation. Many authors have considered the possibility that such species actively mobilize trace elements from non-labile soil metal pools, as a means of increasing the labile concentrations and consequently plant uptake and accumulation. In accordance, several studies have shown a higher labile fraction of hyperaccumulated metals, such as Ni, at the rhizosphere of these plants compared to those of non-accumulating plant species or the surrounding non-vegetated soil (Puschenreiter et al. 2005). However, most authors have concluded that this effect is not a result of specific metal-mobilizing mechanisms employed by hyperaccumulators. It seems more likely, therefore, that the pronounced depletion of trace elements in the rhizosphere, caused by the high rate of uptake of the element from the soil solution, induces their replenishment from the lessmobile fraction to the mobile pools, and maintains a sustained high metal concentration in the soil solution. Root activity of N. goesingensis has been proposed to participate in an enhanced dissolution of Ni-bearing minerals, contributing to higher Ni uptake (Puschenreiter et al. 2005). Similarly, mineralogical studies have shown the presence of smectite in the rhizosphere of A. serpyllifolium ssp. lusitanicum, which was related to a more intense weathering of Ni-rich ferromagnesium minerals (chlorite, serpentine) and an increase in labile Ni (Kidd et al. 2009). Chardot-Jacques et al. (2013) found that growth of the Ni-hyperaccumulator L. emarginata increased the dissolution of chrysotile (a silicate mineral of the serpentine group with low Ni solubility). These authors suggested that the high Ni uptake by the plant causes a decrease in water-soluble Ni, which in turn induces chrysotile dissolution. However, whether this phenomenon is plant- or microbially-induced, or the result of complex plant-microbial interactions, is unknown. It is well established that microbial transformation of soil minerals leads to the solubilization of metals together with essential nutrients, and to the modification of their form and distribution in the solid phase (Quantin et al. 2002). Soil metal availability greatly influences the success of phytomining and its long-term sustainability, and bioaugmentation with metal-mobilizing,

plant-associated bacteria could enhance the viability of this technique (Kidd et al. 2009).

Microbes are intimately associated with the biogeochemical cycling of metals. Microbial activity can result in metal mobilization or immobilization depending on the mechanism involved and the microenvironment where the organism(s) are located (Violante et al. 2008; Ehrlich and Newman 2009; Gadd 2010) (Fig. 2). Some metal-tolerant bacterial strains associated with (hyper)accumulating plants have been shown to mobilize metals in soils, and consequently increase the phytoavailable metal fraction in the soil, as well as plant uptake and accumulation. Muehe et al. (2015) found Arabidopsis halleri accumulated 100% more Cd and 15% more Zn when grown on natural Cd-polluted soil than on the same soil that had undergone gamma-irradiation. Gamma irradiation affected neither plant growth nor soil metal availability, but strongly altered the composition and density of the soil microbial community. Bacteria can modify trace elements mobility and bioavailability through several mechanisms: the release of chelating agents (such as organic acids, phenolic compounds, and siderophores), and acidification or redox changes in the rhizosphere (Lloyd 2003; Glick 2010). Sessitsch et al. (2013) reviewed potential mechanisms for microbial effects on bioavailability in the rhizosphere environment. Sorbed, precipitated, and occluded trace elements can be solubilized by acidification, chelation, and ligand-induced dissolution. To date, two groups of bacterially produced natural chelators are known: organic acids and siderophores. Low-molecular mass carboxylic acids can play an important role in chemical attack of minerals, providing protons as well as a metal-chelating anion (Jacobs et al. 2002; Huang et al. 2004; Lian et al. 2008).

Oxalic acid can leach metals such as Al and Fe that form soluble oxalate complexes (Strasser et al. 1994). Bacteria that produce trace elementchelating organic acids, such as citric, oxalic, or acetic acid, have been shown to mobilize various trace elements in soil (Becerra-Castro et al. 2013). As mentioned above, siderophores form



Fig. 2 Interactions between metals and bacteria (adapted from Ledin 2000). S corresponds to the reactive groups present on the bacterial cell wall. Me^{2+} represents a cation metallic. Org corresponds to an organic compound

high-affinity complexes with Fe(III), but can also form complexes of lower stability with other trace elements (Al, Cd, Cu, Ga, In, Ni, Pb and Zn), thus affecting their bioavailability (Schalk et al. 2011; Rajkumar et al. 2012; Sessitsch et al. 2013). Plants can then take up metals from siderophores via various mechanisms, such as chelate degradation, the direct uptake of siderophore-metal complexes, or by a ligand exchange reaction (Schmidt 1999). Braud et al. (2009) reported that inoculating soils with siderophore-producing P. aeruginosa significantly increased the concentrations of bioavailable Cr and Pb compared with non-inoculated controls. Enhanced heavy metal uptake was correlated with the increased production of siderophores. Siderophore-producing bacteria that are present in metal-polluted or metalenriched soil, and their interaction with

hyperaccumulators, could be used in MAP. Several siderophore-producing bacterial strains associated with plants, such as the non-hyperaccumulator Brassica juncea, and the hyperaccumulators Τ. goesingense, A. bertolonii, and A. murale, have been isolated and characterized from metal-rich soils. They belong to different genera, such as Staphylococcus sp., Microbacterium sp., Pseudomonas sp., Curtobacterium sp., Bacillus sp., Arthrobacter sp., Paenibacillus sp., Leifsonia *Methylobacterium* mesophilicum, sp. Methylobacterium extorquens, Methylobacterium sp., terricola, Okibacterium Burkholderia fritillariae, Rhodococcus fascians, Rhodococcus sp. (Idris et al. 2004; Barzanti et al. 2007). Becerra-Castro et al. (2013) evaluated the weathering capacities of, and Ni mobilization by, two rhizobacterial strains associated with the Ni-hyperaccumulator A. serpyllifolium ssp. lusitanicum and ssp. malacitanum. A minimal culture medium containing ground ultramafic rock was inoculated with either of two Arthrobacter strains: LA44 (indoleacetic acid [IAA] producer) or SBA82 (siderophore producer, PO₄ solubilizer, and IAA producer). Strain LA44 is a more efficient Ni mobilizer, apparently solubilizing Ni associated with Mn oxides, and this appeared to be related to the exudation of oxalate. On the other hand, strain SBA82 also led to the release of Ni and Mn, albeit to a much lower extent. In the latter case, the concurrent mobilization of Fe and Si reflects preferential weathering of Fe-oxides and serpentine minerals, possibly related to siderophore production capacity of the strain. However, some conflicting results showed that the presence of siderophore producers decreased the uptake of metals by plants. Siderophores produced by Pseudomonas sp., Serratia marcescens, and Streptomyces sp. had either no effect or negatively affected Zn and Cd uptake by Salix caprea (Kuffner et al. 2010). These contrasting effects suggest that the mechanisms underlying metal uptake are largely plant dependent, but that the efficiency of siderophore producers to either mobilize or immobilize heavy metals from soils is also dependent on several factors such as the binding form of the heavy metals present, the charge of the siderophores, and the pH of the soil and its mineral composition and organic content.

The influence of organic matter content in soil on metal availability and uptake by plants has been extensively studied. It was reported that metal adsorption onto soil constituents declined with decreasing organic matter content in soils (Zeng et al. 2011). Moreover, dissolved organic matter (DOC) in soils may increase the mobility and uptake of heavy metals by plant roots (Du Laing et al. 2008). In fact, organic matter decomposition appears to be one of the most important microbial activities in the rhizosphere, and it is well known that microbes, mainly bacteria and fungi, utilize a wide spectrum of organic compounds such as sugars, organic acids, and amino acids to more complex molecules such as cellulose, pectin, lignin, lignocellulose, chitin, and starch. Consequently, organic matter decomposition by soil microorganisms releases metals such as Fe, Mn, Zn, Cu, Mo, Ni, Co and Se, which are typically found in the tissues of organisms.

6 Final Remarks and Future Directions

It seems clear that the rhizosphere microbiome plays an important role in plant trace elements bioaccumulation, given experimental evidence suggesting that by reshaping this microbiome we can further enhance the efficiency of phytoextraction and phytomining. However, the efficacy of plant-associated bioinoculants is dependent on a complex array of interacting factors: plant-microbe specificity, soil type and properties, trace elements concentration and type (mono- or poly-metallic), proliferation and survival of the inoculant, etc. Moreover, from the literature it can be seen that inoculation methods differ greatly among studies (inoculation of seed/ plant/soil, frequency/timing of inoculation events, bacterial cellular densities, etc.), and these aspects are likely to influence whether or not a beneficial microbially induced effect is observed.

Bioaugmentation can be challenged by the strong competition encountered in the soil when a selected microbe is introduced. Also, the selected host plant species may not necessarily be compatible with the inoculated bacterial or fungal strain, since these are not naturally selected for by the host (Thijs et al. 2016). The importance of rhizosphere competence or effective root colonization in beneficial plant-microbe interactions is underlined by several studies as contributing to the success of bioaugmentation (Lugtenberg and Dekkers 1999). Moreover, inoculation methods should be optimised in orderoptimized to enhance the success of the introduced microorganisms (Álvarez-López et al. 2016b). Pereira et al. (2015) and Álvarez-López et al. (2016b) recently showed that the size of the inoculum applied in the soil rhizosphere, and the mode of application (seed or soil inoculation), are important factors that should be taken into account when planning MAP strategies. Endophytes do not have to compete with the large abundance and diversity of soil microorganisms, which may enhance their chances of establishing a stable and active population. To date, the field of MAP has focused on the use of individual bioinoculants. However, promising results have been found when using mixtures or consortia of different PGP-strains with complementary actions. Visioli et al. (2015)reported that co-inoculating the Ni-hyperaccumulator Noccaea caerulescens, when growing in serpentine soil with two root endophytes belonging to the Arthrobacter and Microbacterium genera, had a more positive effect on plant growth, soil Ni removal, and Ni translocation, than when inoculated individually. Both strains were strong IAA producers and presented ACC deaminase activity. Moreira et al. (2016) showed the benefits of combined inoculation of AMF and PGPR for the growth of maize as an 'energy-crop' in metal-polluted their potential application in soils and phytomanagement strategies.

Ultramafic rocks occupy <1% of Earth's land surface and these outcrops have the potential to provide multiple ecosystem services and contribute to producing renewable raw materials and energy (i.e. agromining). In the same way, polluted soils are an ever-increasing environmental concern due to increased industrialization. Phytoremediation coupled with bioaugmentation could be a solution towards the recovering soil quality, underlining the role of the rhizosphere and microbes associated with hyperaccumulator plants in metal accumulation.

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