Pedosphere **31**(3): 475–495, 2021
doi:10.1016/S1002-0160(20)60091-1
ISSN 1002-0160/CN 32-1315/P

Published by Elsevier B.V. and Science Press

PEDOSPHERE

www.elsevier.com/locate/pedosphere

Advances in fungal-assisted phytoremediation of heavy metals: A review

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(Received March 9, 2020; revised May 15, 2020)

ABSTRACT

Trace metals such as manganese (Mn), copper (Cu), zinc (Zn), and iron (Fe) are essential for many biological processes in plant life cycles. However, in excess, they can be toxic and disrupt plant growth processes, which is economically undesirable for crop production. For this reason, processes such as homeostasis and transport control of these trace metals are of constant interest to scientists studying heavily contaminated habitats. Phytoremediation is a promising cleanup technology for soils polluted with heavy metals. However, this technique has some disadvantages, such as the slow growth rate of metal-accumulating plant species, low bioavailability of heavy metals, and long duration of remediation. Microbial-assisted phytoremediation is a promising strategy for hyperaccumulating, detoxifying, or remediating soil contaminants. Arbuscular mycorrhizal fungi (AMF) are found in association with almost all plants, contributing to their healthy performance and providing resistance against environmental stresses. They colonize plant roots and extend their hyphae to the rhizosphere region, assisting in mineral nutrient uptake and regulation of heavy metal acquisition. Endophytic fungi exist in every healthy plant tissue and provide enormous services to their host plants, including growth enhancement by nutrient acquisition, detoxification of heavy metals, secondary metabolite regulation, and enhancement of abiotic/biotic stress tolerance. The aim of the present work is to review the recent literature regarding the role of AMF and endophytic fungi in plant heavy metal tolerance in terms of its regulation in highly contaminated conditions.

Key Words: arbuscular mycorrhizal fungi, bioremediation, endophytic fungi, environmental stress, metal tolerance, microbe, plant transporter, soil contaminant

Citation: Khalid M, Ur-Rahman S, Hassani D, Hayat K, Zhou P, Hui N. 2021. Advances in fungal-assisted phytoremediation of heavy metals: A review. *Pedosphere*. **31**(3): 475–495.

INTRODUCTION

Microbes are cosmopolitan in nature and even reside in habitats with extreme environmental conditions. Many of them can make biofilms for tolerating harsh environmental surroundings including arid conditions and high temperatures (Ma *et al*., 2016). The soil around plant roots is a natural habitat for different kinds of microorganisms including fungi, bacteria, protozoa, and algae. The microbes associated with plants are important for their hosts, greatly influencing their overall performance in different situations. At the root surface, they communicate through signal molecules to attain structural stability in an exopolysaccharide matrix; in this way, they perform a particular function *via* quorum sensing (Bais *et al*., 2004). The rhizospheric and endophytic microbiota contributes to plant protection, stability, productivity, growth, and phytoremediation. The use of metal resistance and plant growth-promoting features of rhizospheric or endophytic microorganisms is one of the most cost effective and ecologically friendly strategies (Rajkumar *et al*., 2010).

Due to the presence of a chelation system and metal sequestration abilities, fungi can alleviate heavy metal stress (Janoukov *et al*., 2006; Aly *et al*., 2011). Fungi develop a symbiotic relationship with most terrestrial plants and are an important component of an efficient ecosystem. Several studies have shown their beneficial interactions with different host plants (Smith and Read, 2008). To build symbiotic relationships, plants recruit different beneficial fungi through a communication process using signal molecules (Smith and Read, 2008). Such mutualistic symbionts include ectomycorrhizal fungi (EMF), arbuscular mycorrhizal fungi (AMF), and dark septate endophytes (DSEs). Plant associated AMF mainly belong to Zygomycota (150 species), and EMF mainly include basidiomycetes with a few zygomycetes and ascomycetes (600 species). Ectomycorrhizal fungi are mainly found in association with specific woody trees, while AMF have been reported in association with a variety of plants from herbs to woody species. Arbuscular mycorrhizal fungi colonize plant roots and proliferate in the rhizosphere region in the form of microscopic filaments, assisting in the translocation of nutrients to the host plant (Latef *et al*., 2016). It has been extensively reported that AMF develop symbiotic relationships with almost 90% of

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plants and provide multifaceted amenities such as enhanced metabolism and growth of the host plant under normal or abiotic/biotic stress conditions. Overall, AMF are immensely important in a well-developed ecosystem because of their capability to build mutualistic relationships with the majority of terrestrial plants, as well as some wetland plants (Latef *et al*., 2016). Some plant species are non-mycorrhizal, such as a few members of the Cruciferae and Amaranthaceae; however they have alternative substitute relationships with different endophytes (Usuki and Narisawa, 2007).

All plant species analyzed so far have their own endophytic microbial community. Endophytes are microbes that colonize the internal tissue of a host plant without causing any harm or infection. Over the last few decades, the attention of the scientific community towards endophytes and their bioactive compounds has increased, with a higher number of publications on the subject especially focusing on the study of *Epichloë*, *Frankia*, *Piriformospora*, and *Rhizobium* species (Chibucos and Tyler, 2009; Stadler, 2012). Endophytic fungi are extremely diverse, having broad (non-clavicipitaceous fungi) to narrow (clavicipitaceous mutualistic fungi) host ranges and asymptomatically localizing in internal plant tissues such as roots, stems, leaves, shoots, seeds, and even bark (Rodriguez *et al*., 2009). Some fungi have a higher level of adaptation to certain physiological conditions and usually colonize specific plant organs or tissues. It is quite interesting that after over 400 years of continuous evolution, there are plants that still rely on a symbiotic association with fungi to cope with stressful conditions and to maintain healthy growth (Aly *et al*., 2011). Fungi also participate and have a potential role in element cycling, transformation of rock and minerals, bioweathering, cycling of different elements, fungal-metal interactions, and transformation of organic and inorganic compounds (Gadd, 2007). Endophytes employ different metabolic pathways which are very important for the biotransformation of organic substances and different types of pollutant remediation (Stępniewska and Kuźniar, 2013). To date, many studies have reviewed bioremediation through bacterial strains, but the role of AMF and endophytic fungi in such studies has been mostly overlooked. The contribution of AMF and endophytic microbiota in plant protection, stability, productivity, growth, and phytoremediation is summarized in Fig. 1. The aim of the current review is to provide information regarding the role of AMF and endophytic fungi in phytoremediation and the benefits they provide to their host plants.

ARBUSCULAR MYCORRHIZA AND PLANT INTERACTIONS: METAL TOLERANCE

Generally, mycorrhizal fungi are associated with plant roots in the form of an internal or external network, thus increasing the surface area and absorption capacity of a plant's root system. Excessive uptake of essential or non-essential heavy metals from soil by plants can cause adverse effects. The AMF enhance plant resistance and heavy metal tolerance, but their influence on plants growing on contaminated medium largely depends on plant species, fungal species, and the type of associated heavy metal. Inducing resistance to heavy metals is not related to reduced heavy metal uptake; there are some reports which show hyperaccumulation by plants associated with AMF (Carvalho *et al*., 2006; de

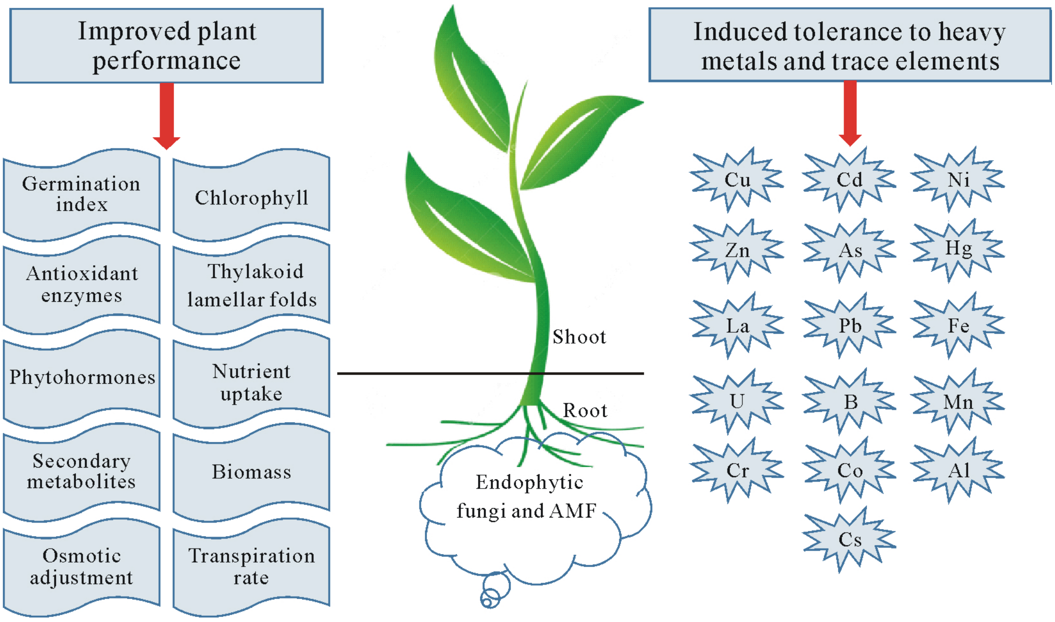

Fig. 1 Scheme showing the positive influences of endophytic fungi and arbuscular mycorrhizal fungi (AMF) on plant overall performance under stresses caused by heavy metals and trace elements. The heavy metals and trace elements include Cu, Cd, Ni, Zn, As, Hg, La, Pb, Fe, U, B, Mn, Cr, Co, Al, and Cs.

Andrade *et al*., 2008; de Souza *et al*., 2012). However, convincing evidence proves that AMF hinder heavy metal transport from root to shoot, thus regulating the partitioning of heavy metals (Christie *et al*., 2004; Wang *et al*., 2007; Wu *et al*., 2016). For example, *Diversispora spurcum* and *Funneliformis mosseae* cause retention of heavy metals in the underground part of plants and thus have been shown to reduce zinc (Zn), lead (Pb), and cadmium (Cd) contents in the shoot in comparison to the roots in maize plants (Zhan *et al*., 2018). In some cases, potentially toxic effects decreased because metal concentrations were reduced as a consequence of the improvement in phosphorus (P) nutrition and growth of the mycorrhizal plant (Chen *et al*., 2003). For instance, the mycorrhizal poplar has been shown to have lower stress symptoms even with higher concentrations of copper (Cu) and Zn in its tissues (Lingua *et al*., 2008). Some studies have shown that AMF alleviate heavy metal stress by hindering its uptake by the host plant. For example, AMF attenuated the heavy metal impact on *Calendula officinalis* development by reducing the uptake of heavy metals (Cd and Pb) and enhancing the beneficial secondary metabolites in comparison to non-mycorrhizal plants (Hristozkova *et al*., 2016). Similarly, reduced Zn uptake and concentration was observed in mycorrhizal tomato plants (Watts-Williams *et al*., 2013). Immobilization of heavy metals has also been attributed to the changes in biogeochemistry made by mycorrhizae in the rhizosphere region (Kangwankraiphaisan *et al*., 2013). This was found in indigenous plants growing at Zn smelting and disposal sites, which have a higher capacity for Zn accumulation and sediment emending ($72\,540 \pm 5\,092$ mg kg^{-1} dry weight) compared to the same plants treated with fungicide, halting AMF colonization. Likewise, Zn immobilization and prevention of arsenic (As) translocation have been shown by some studies (Chen *et al*., 2012; Chen X W *et al*., 2013). Heavy metals also cause a degree of damage to the fungal cells themselves. The propagules of AMF remain in soil as infectious units if a favorable environment and compatible host are not available. In pre-symbiotic states, the walls of the hyphae are thinner and highly exposed to the noxious heavy metals in soil. Spore counts are generally used to determine successful colonization rate, and usually spore count frequency is lower in heavy metal-contaminated areas (Lpez *et al*., 2000). Arbuscular mycorrhizal fungi propagate by producing mycelia or spores that separate through a fragmentation process and develop into new hyphae. However, these indigenous young propagules always persist in soil to some extent and are resistant to heavy metals, enhancing host plant heavy metal tolerance upon colonization. For instance, the isolate *Rhizophagus intraradices* Br1 from the heavy metal-resistant plant *Viola calaminaria* induces high resistance in maize, tomato, and *Medicago truncatula*, unlike the ecotypes belonging to the same species (Kaldorf *et al*., 1999). Some reports have shown the reduction of spore production by mycelia; however, this depends on the species, degree of tolerance, and even the type of metal (Klauberg-Filho *et al*., 2002). Studies regarding the contribution of AMF to heavy metal and trace element tolerance are listed in Table I.

ROLE OF AMF IN METAL UPTAKE AND DISTRIBUTION

A number of advanced techniques have been developed to investigate the uptake, translocation, and transformation of metals by AMF such as inductively coupled plasma-mass spectrometry (ICP-MS), scanning electron microscopy with energy dispersive spectroscopy (SEM-EDS), and transmission electron microscopy with energy dispersive spectroscopy (TEM-EDS). For example, the direct influences of AMF on chromium (Cr) translocation and transformation in the soil-plant continuum have been studied, showing that AMF can immobilize quantities of Cr *via* reduction of Cr(VI) to Cr(III), forming Cr(III)-phosphate analogues (Wu *et al*., 2015). Similarly, light microscopy (LS) and transmission (TEM) and scanning electron microscopy (SEM) studies showed that inoculation of *Leucaena leucocephala* with AMF resulted in better growth in soil with high As concentration, as well as significant As removal from the soil (Schneider *et al*., 2013a). The movement of essential metals through the mycorrhizal uptake pathway begins with their uptake through the plasma membrane of the extraradical mycelium (Fig. 2).

At a molecular level, the genome of *Rhizophagus irregularis* has been analyzed *in silico*, identifying several genes that code for proteins that mediate the transport of important metals such as iron (Fe), Zn, and Cu from the soil medium (Tisserant *et al*., 2013; Tamayo *et al*., 2014). Specifically, the Cu-ATPases, natural resistance-associated macrophage proteins (NRAMPs), vitamins, the influx mediator of Fe/Zn (*RiFTR1*, *RiZRT1*), and the vacuolar mobilizer of Cu/Zn (*RiCTR2*, *RiZRT3*) have been identified, but currently there is no evidence regarding their exact location and medium specificity. It is possible to speculate that these transporters are involved in homeostasis of metals, especially Zn, Cu, and Fe. Most of the metals taken up by the fungus may be used to maintain fungal functioning, while surplus metals are transferred to the plant. In contrast, for excess metal ions in the cytoplasm, organisms have developed a different mechanism through which heavy metals are modified to bounded form and sequestered. Vacuoles are usually considered as store houses and detoxification sites for extra metal concentrations, while later mobilization is induced by enzymes such as in the case of Fe permease/oxidase complex mediating its mobilization on nutritional demand (Hijikata *et al*., 2010). Similarly, SMF3 proteins have been shown to transport Zn

TABLE I

Studies regarding contribution of arbuscular mycorrhizal fungi (AMF) to phytoremediation of pollutions caused by heavy metals and trace elements

Study	AMF species	Host plant species	Experiment type(s)	Element(s)	Effect on plant
Abbaslou and Bakhtiari, 2017	*Glomus mosseae*	Eucalyptus grandis, Ailanthus altissima	Pot	Cu, Cd, Zn	Enhanced growth of *Ailanthus altissima* while no changes in the growth of *Eucalyptus grandis*
Wang S *et al*., 2018	*Glomus versiforme*	Trifolium repens L.	Pot	As	Enhanced dry biomass, antioxidants, and As extraction efficiency
Arora *et al*., 2016	*Glomus mosseae*, *Glomus fasciculatum*, *Gigaspora margarita*	*Panicum virgatum* (switchgrass)	Pot	Pb, Cd	Accumulation of high concentrations of Pb and Cd
Ma *et al*., 2019	*Claroideoglomus claroideum* (BEG210)	*Helianthus annuus*	Pot	Ni	Enhanced plant growth, altered physiological characteristics
Chen *et al*., 2019	*Funneliformis mosseae*	*Oryza sativa*	Pot	Cd	Reduced Cd uptake
Wang F Y *et al*., 2018	*Funneliformis caledonium*	*Sorghum bicolor*	Pot	Cd	Increased soil enzyme activities, phosphate nutrition, and overall plant growth
Debeljak *et al*., 2018	*Glomus* sp., fungi from Glomeromycota	*Zea mays*	Pot	Hg	Higher Hg concentration in central cylinder of the AMF-colonized plants, increased overall biomass
Chaturvedi *et al*., 2018a	No description	*Solanum melongena* L.	Earthen pot	Pb, Cd, As	Improved antioxidant defense system and biomass
Huang *et al*., 2018	*Rhizophagus irregularis*	*Phragmites australis* (Cav.) Trin. ex Steud.	Pot	Cd	Alleviated Cd toxicity in all organs
Lam and Lai, 2018	AMF No.1 (commercial)	*Ipomoea aquatica* Forsk	Pot	Cd, Ni	Improved growth, decreased accumulation of Ni
Chang *et al*., 2018	*Claroideoglomus etunicatum*	*Zea mays*	Pot	Cd, La	Alleviated phytotoxicity of La and Cd to maize seedlings
Liu *et al*., 2018	*Funneliformis mosseae*, *Claroideoglomus etunicatum*	*Puccinellia tenuiflora*	Pot	B	Alleviated B toxicity
Chaturvedi *et al*., 2018b	*Glomus mosseae*	*Solanum lycopersicum*	Pot	Cd, Pb	Improved growth performance and enzymatic defense system
Sut *et al*., 2016	Rhizophagus irregularis	*Lolium perenne* L.	Field, pot	Fe-CN	Increased CN accumulation in roots
Hristozkova *et al*., 2016	*Claroideoglomus claroideum*, *Funneliformis mosseae*	*Calendula officinalis* L.	Pot	Pb, Cd	Increased accumulation of secondary metabolites, decreased distribution of metals in aboveground parts
El Faiz *et al*., 2015	*Glomus* sp.	*Canna indica* L.	Pot	Zn, Cu, Cd	Increased accumulation of pollutants
Gunathilakae *et al*., 2018	Indigenous	*Eichhornia crassipes* (Mart.) Solms	Pot	Cd	Improved plant biomass, increased concentration of Cd in shoots and roots
Li J M *et al*., 2017	No description	*Elsholtzia splendens*	Plastic boxes	Cu	Increased germination index and rate and fresh weight of radical and hypocotyl
Zhang *et al*., 2018	*Funneliformis caledonium*, *Funneliformis mosseae*	*Helianthus annuus* L.	Pot	Cu, Pb, Cd, Zn, Ni, Cr	Enhanced P absorption and plant growth, decreased heavy metals in the shoots
Li *et al*., 2019	*Rhizophagus intraradices*	*Amaranthus hypochondriacus* L.	Pot	Cd, BDE-209	Increased BDE-209 level in roots and Cd content in shoots
Neagoe *et al*., 2017	*Rhizophagus irregularis*	*Nicotiana tabaccum* L. cv. Virginia gold	Pot	Cu, Zn, Pb	Improved phytoextraction, biomass, and biochemical variables
Firmin *et al*., 2015	Commercial	*Miscanthus* × *giganteus*	Pot	Cd, Zn, Pb	Increased fatty acid content, better protection from oxidative stress
Kafil *et al*., 2019	*Glomus mosseae*	*Vetiveria zizanioides*	Field	Fe, Cu, Cd, Pb, Zn	Enhanced biomass, reduced stress
Mani *et al*., 2015	*Pseudomonas putida*, *Glomus fasciculatum*	*Helianthus annuus* L.	Pot	Zn, Cd	Increased plant dry biomass, higher bioaccumulation of metals
Nafady and Elgharably, 2018	*Glomus aggregatum*, *Glomus intraradices*	*Zea mays* L.	Pot	Cd, Zn, Pb	Increased plant dry biomass and Cd and Pb in the shoots
Wężowicz *et al*., 2015	*Glomus aureum*, *Rhizophagus irregularis*, *Rhizophagus clarus*	*Iris pseudacorus*	Pot	Fe, Zn, Pb, Cd	Higher Cd accumulation
Singh *et al*., 2019	*Glomus aggregatum*, *Funneliformis mosseae*, *Rhizophagus intraradices*, *Rhizophagus fasciculatus*	*Zea mays* L.	Pot	Pb, Cr, Cd, Ni	Increased root and shoot length, chlorophyll content, and P

(to be continued)

TABLE I (continued)

Study	AMF species	Host plant species	Experiment type(s)	Element(s)	Effect on plant
de Ftima Pedroso *et al.*, 2018	*Glomus macrocarpum*, *Paraglomus occultum*, *Glomus* sp.	*Acacia mangium*, *Sorghum bicolor*, *Urochloa brizantha*	Pot	Cd, Pb, Cu, Zn	Larger chlorophyll content and root length
Chen *et al.*, 2015	*Funneliformis mosseae*	*Populus cathayana*	Pot	Pb	Increased uptake of P under stress conditions
de Andrade *et al.*, 2015	*Rhizophagus irregularis*	*Oryza sativa*	Pot	As(III), As(IV)	Higher biomass, chlorophyll content, and water use efficiency
Rollon *et al.*, 2017	*Gigaspora margarita*, *Glomus etunicatum*, *Glomus macrocarpum*	*Paraserianthes falcataria*	Pot	Cu	Improved dry matter content and alleviated Cu stress
Ren *et al.*, 2019	*Glomus etunicatum* (BGC NM03F)	*Sesbania rostrata*	Pot	U	Enhanced biomass and reclamation of U
Ferreira *et al.*, 2018	*Rhizophagus clarus*	*Crotalaria juncea*	Pot	Cu	Enhanced growth, decreased phytotoxicity
Rafique *et al.*, 2019	*Rhizophagus clarus*	*Zea mays*	Pot	Cd	Increased dry matter content
Chamba *et al.*, 2017	Rhizospheric	*Erato polymnioides*	Pot	Hg	Higher Hg accumulation
Rasouli-Sadaghiani *et al.*, 2019	*Glomus intraradices*, *Glomus mosseae*, *Glomus fasciculatum*	*Acroptilon repens* L.	Pot	Cd	Higher biomass under stress conditions
Setyaningsih *et al.*, 2017	*Glomus etunicatum* (NPI 126), *Acaulospora tuberculata* (INDO-2), *Gigaspora margarita*, *Glomus manihotis* (INDO-1)	*Anthocephalus cadamba*	Pot	Pb	Reduced Pb concentration in roots, stems, and leaves
Li *et al.*, 2018	*Rhizophagus intraradices*, *Funneliformis mosseae*	*Solanum nigrum*	Pot	Cd	Improved biomass and Cd uptake
Ahmed *et al.*, 2017	*Glomus mosseae*, *Glomus lamellosum*, *Gigaspora margarita*, *Acaulospora bireticulata*	*Daucus carota* L., *Corchorus olitorius* L.	Pot	Ni, Cd	Reduced metal accumulation, improved plant growth
Cozzolino *et al.*, 2016	*Funneliformis mosseae*, *Rhizophagus irregularis*	*Lactuca sativa* L.	Pot	Hg	Inhibited Hg translocation from roots to the shoot, enhanced nutrition, color, and texture
Li *et al.*, 2020	*Funneliformis mosseae*	*Lycopersicon esculentum* L.	Pot	Cd	Improved plant growth, hindered Cd distribution from root to shoot
Yang *et al.*, 2016	*Rhizophagus intraradices*	*Robinia pseudoacacia* (with red clover and alfalfa)	Pot	Pb	Enhanced plant growth , Pb uptake
Alvarado-Lpez *et al.*, 2019	*Glomus intraradices*	*Daucus carota* L.	Pot	Pb	Enhanced pollutant tolerance
Baghaie *et al.*, 2019	*Indigenous*	*Triticum aestivum*	Pot	Cd	Improved plant growth, reduced Cd uptake
Gu *et al.*, 2017	*Funneliformis mosseae*	*Lolium perenne*, *Festuca arundinacea*, *Hylotelephium spectabile*, *Tradescantia pallida*	Field	Cd, Cu, Pb, Zn	Improved plant biomass, higher concentrations of Cd, Pb, Cu, and Zn in roots than in shoots
Li *et al.*, 2016	*Funneliformis mosseae*, *Rhizophagus intraradices*	*Oryza sativa* L.	Hydroponic	Cd	Reduced Cd concentration in both shoots and roots
Ruscitti *et al.*, 2017	*Rhizophagus intraradices*, *Funneliformis mosseae*	*Capsicum annuum* L.	Pot	Cu	Higher leaf area and total dry weight
Sadaghiani *et al.*, 2016	*Glomus fasciculatum*, *Glomus mosseae*, *Glomus intraradices*	*Onopordum acanthium*	Pot	Cd	Improved plant performance, higher Cd accumulation
Sheikh-Assadi *et al.*, 2015	*Glomus intraradices*, *Glomus mosseae*	*Limonium sinuatum* Mill.	Pot	Pb, Cd	Higher metal accumulation in roots, less metal translocation to shoots
Zhang *et al.*, 2019	*Glomus aggregatum*, *Glomus versiforme*, *Glomus etunicatum*, *Glomus intraradices*	*Medicago sativa*	Pot	Cd	Increased N, P in shoots, reduced Cd in shoots
Wu *et al.*, 2020	*Rhizophagus irregularis*	*Phragmites australis* (Cav.) Trin ex Steud.	Pot	Cu	Enhanced photosynthesis, improved growth, development
Lermen *et al.*, 2015	*Rhizophagus clarus*	*Cymbopogon citratus*	Pot	Pb	Increased essential oil content and its constituents
Amna *et al.*, 2015	*Glomus intraradices*	*Linum usitatissimum*	Pot	Ni	Enhanced tolerance to Ni toxicity, higher uptake of Ni

to the cytosol from the vacuole and (in combination with CCC1) induce homeostasis inside the cell (Diffels *et al.*, 2006). Considering this, metals are essential micronutrients, and all organisms compete for them when in short supply, activating transport systems that enable the uptake of metals required for their development. In contrast, excess levels of these heavy metals are toxic, and therefore suitable transport systems exist in mycorrhizae. Their transport is thus probably

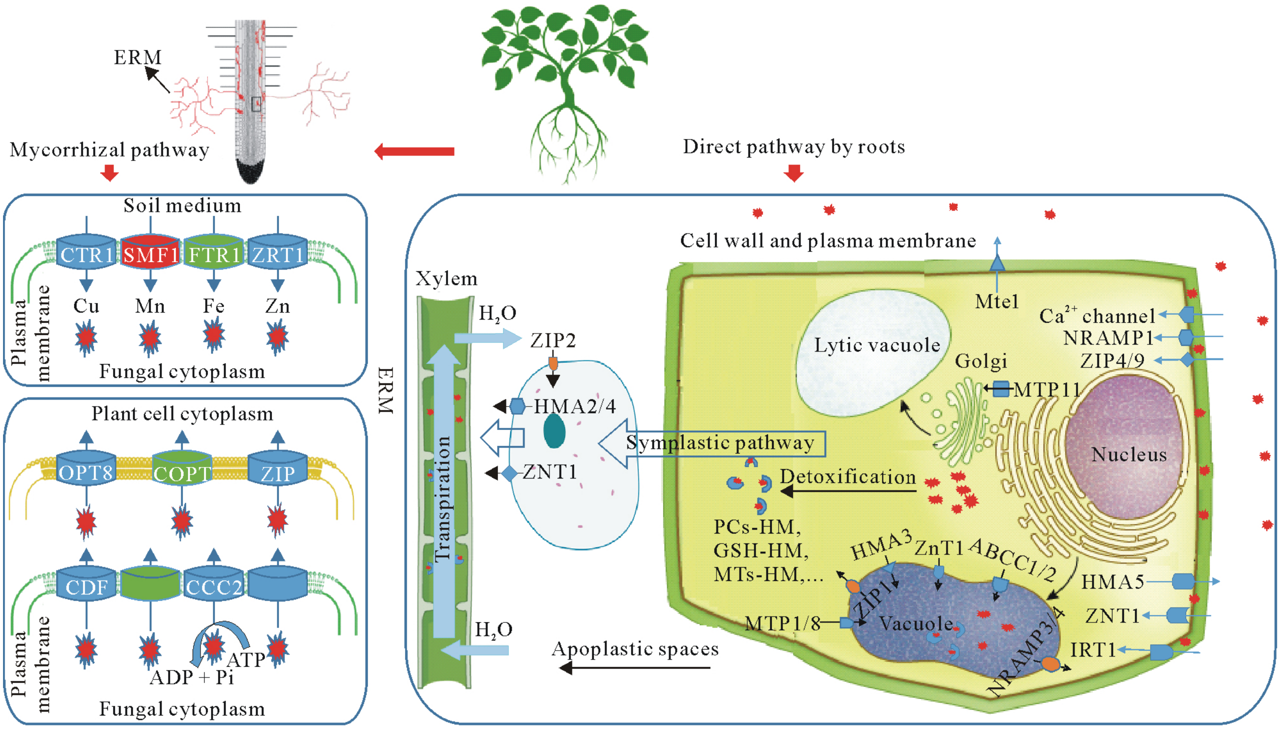

Fig. 2 Scheme showing plant heavy metal (HM, red star) distribution and acquisition (uptake, detoxification, translocation, and accumulation). Uptake of metals takes place through either the mycorrhizal or direct pathway. The extraradical mycelia (ERM) are in direct contact with HMs in the soil and possess high-affinity metal transporters that translocate HMs *via* dense hyphae to intracellular spaces, before finally delivering them to the roots at the symbiotic interface. Fungal and plant metal transporters include CCC2 (Cu-ATPase), CTR (fungal Cu transporter), COPT (plant Cu transporter), CDF (cation diffusion facilitator), ZRT1 (Zn transporter), FTR1 (Fe permease), ZIP (Zn-Fe permease), SMF1 (Mn transporter), and OPT (oligopeptide transporter). The metal transporters, which are located in both the epidermal cells and root hairs, are involved in the direct pathway of HM translocation. Once HMs are taken up by the roots, they are then sequestered, detoxified, or translocated along the apoplastic or symplastic pathways towards vascular tissues. Heavy metals enter the root cell *via* plasma membrane channels or transporters, including Ca^{2+} channels (implicated in Cd^{2+} uptake in endodermal cells), NRAMPs (natural resistance-associated macrophage proteins), ZIPs (Zn^{2+} transporters), ZNT1 (transporting apoplastic Zn^{2+} and Cd $^{2+}$ into the cytosol), IRT1 (transporting apoplastic Mn^{2+}, Fe^{2+}/Fe^{3+}, Zn^{2+}, and Cd^{2+} into the cytosol), Mte1 (exporting HM ions outside of the cell or transporting Cu $^{2+}$/Ni^{2+} into vacuoles), and HMA5 (translocation and detoxification of Cu). The detoxification of HMs in root cells is carried out by chelators such as glutathione (GSH), metallothioneins (MTs), and phytochelatins (PCs). Moreover, free and chelated HM ions are sequestered in cell vacuoles by HMA3 (transporting cytosolic Co^{2+}, Zn^{2+}, Cd^{2+}, and Pb^{2+} into vacuoles), MTP1/8 (mobilizing excessive Zn^{2+} from the cytosol into vacuoles), and ABCC1/2 (transporting cytosolic Cd-PCs and Hg-PCs to vacuoles). Such sequestering in Golgi bodies occurs *via* MTP11 (metal tolerance proteins) and ZnT1 (transporting excessive Zn^{2+} from the cytosol into vacuoles). Sequestered HMs inside the vacuole can also be excreted back to the cytoplasm through NRAMP3/4 (exporting vacuolar Fe^{2+}/Mn^{2+} into the cytosol) and ZIP1 (Zn^{2+} transport). Other putative proteins such as ZNT1 (transporting excessive Zn^{2+} from the cytosol into vacuoles) and HMA2/4 are mainly involved in the loading of HMs to the vascular tissues of plant roots.

accomplished by transport systems for the essential elements Cu, Zn, Fe, and manganese (Mn), or even through phosphate transporters, as has been shown for the uptake of the metalloid arsenate that occurs *via* the high affinity phosphate transporter GiPT (Gonzlez-Chvez *et al*., 2011).

ASSOCIATION OF AMF INTERFACES WITH PLANT TRANSPORTERS

Arbuscular mycorrhizae establish a direct link between soil and roots of the host plant, thus participating in the transport of materials, including metals, from soil to plant. Extraradical mycelium provides an uptake pathway for the different metals through its plasma membrane. An inducing effect on Cu and Zn genes has been observed in *M. truncatula* roots colonized by mycorrhizae (Kaldorf *et al*., 1999). Regulation of proteins related to Fe transport such as ferric chelate reductase and cell organelle-based Fe transporters, as well as Zn transporters, has been studied in *Sorghum bicolor* (Handa *et al*., 2015). The metallothionein family set of genes has also been reported extensively in a wide range of different organisms that express them differentially upon exposure to metals such as Zn, Cu, or Cd. Distinct regulation of a metallothionein gene (*BI451899*) in extraradical mycelium associated with *Glomus intraradices* has been studied in the presence of Zn, while its role in Cu detoxification has also been reported (Lanfranco *et al*., 2002). Genome-wide analysis of transcription patterns in laser-microdissected cortical cells colonized by arbuscules revealed that a Cu transporter was specifically expressed in arbuscule-containing cortical cells, suggesting that it may be involved in Cu acquisition by the periarbuscular membrane (Hogekamp *et al*., 2011; Gaude *et al*., 2012). However, some studies show that transport of metals is not restricted to arbuscule-colonized cortical cells. For example, the Zn and Mn transporter gene, *MtZIP7*, shows the same expression pattern in arbuscule-colonized and non-colonized cortical cells of plant roots. Another study revealed the genetic expression pattern of strategy II plants; AMF do not induce strategy II-related genes, but regulate other putative genes (*OPT8a* and *OPT8b*), performing a role in increasing Fe transport by more than 50-fold (Kobae *et al*., 2014). Nicotianamines are also important metal chelators and the main building blocks for phytosiderophores synthesis. Their functions have been characterized in many model plants such as rice, barley, and *Arabidopsis*. Studies have mainly identified their function in Fe transport at both intracellular and extracellular levels. Furthermore, it was suggested that they play a role in chelating the Fe supplied by mycorrhizae (Zhou *et al*., 2013). The study of expression patterns of 53 genes in the model plant *Arabidopsis* has shown that Zn^{2+} transporter (ZIP) genes, *ZIP2* and *ZIP4*, are prominently involved in Fe transport (Wintz *et al*., 2003). Along with stress augmentation and transportrelated gene expression, evidence increasingly shows that symbiotic fungi contribute to the modulation of various biochemicals (antioxidative system) in plants. The mycorrhizal-induced antioxidative system (enzymatic and non-enzymatic antioxidants) in host plants can scavenge excess reactive oxygen species (ROS) produced by heavy metal exposure (Gill and Tuteja, 2010; Emamverdian *et al*., 2015). There is overwhelming evidence that mycorrhizal association can augment antioxidant enzyme systems, including monodehydroascorbate reductase, dehydroascorbate reductase, and other enzymatic and non-enzymatic ROS scavenging systems (Vadassery *et al*., 2009; White and Torres, 2010). Recently, it has been shown that the activities of ascorbate peroxidases, glutathione peroxidase, and superoxide dismutase are elevated in arbuscular mycorrhizal *Robinia pseudoacacia* L., which probably contributes to the mitigation of Pb-induced toxicity (Yang *et al*., 2015). Similarly, modulation of stress-related enzymes in plants associated with AMF under As stress has been highlighted in *L. leucocephala*, emphasizing the potential of *L. leucocephala*-AMF symbiosis for As phytostabilization in moderately As-contaminated soils (Schneider *et al*., 2017). In addition, non-enzymatic antioxidants also play key roles in ROS homeostasis in mycorrhizal plants exposed to heavy metals (Coninx *et al*., 2017). For instance, under higher Cu and Zn concentrations, *Populus alba (*AL35) pre-inoculated with AMF showed an overall upregulation of metallothionein (MT) and foliar polyamine (PA) biosynthetic genes, together with increased PA levels (Cicatelli *et al*., 2014). Although the exact mechanisms are still unclear and need to be elucidated, these biochemicals may act as free radical scavengers, stabilize membranes, and retard senescence (Harada *et al*., 2010).

ARBUSCULAR MYCORRHIZAL FUNGI: INSIGHTS INTO DIVERSITY AT METAL-CONTAMINATED SITES

Associations of AMF with plant roots in heavy metal-contaminated soils have been widely recognized. In addition, they can play an important role in heavy metal tolerance, accumulation, and transportation from roots to aboveground plant parts (Karimi *et al*., 2011). Generally, plant roots (mostly from native species) at mine wastes are associated with AMF. For example, the evaluation of occurrence and diversity of AMF in areas with different As concentrations showed that the most frequent species occurring in all these areas were *Paraglomus occultum*, *Acaulospora morrowiae*, and *Glomus clarum*, indicating their high tolerance to excess As (Schneider *et al*., 2013b). Similarly, evaluation of the diversity of AMF and plant species, as well as their interactions, in soil contaminated with Pb found that *Acaulospora* and *Glomus* genera exhibited the highest occurrence in both bulk and rhizosphere soils (Schneider *et al*., 2016). In another study, AMF diversity varied in the roots of *Veronica rechingeri*, ranging from six to two types in unpolluted plots and plots with high heavy metal contamination, respectively (Zarei *et al*., 2008a). Diverse responses have been shown by AMF to heavy metals at the level of species, ecotype, or both. For instance, *Glomus mosseae* (isolated from heavy metal-contaminated soils) was found to be more tolerant to Cd stress than the same species isolated from uncontaminated substrate (Weissenhorn *et al*., 1994). Similarly, *Glomus etunicatum* is more sensitive to Pb, Cd, and Zn than *G. intraradices* (Pawlowska and Charvat, 2004). Furthermore, *Rhizophagus clarus* (average hyphal diameter of 4 μm) absorbs more Cd, Cu, and Pb than *Glomus gigantea* (average hyphal diameter of 13 μm), indicating that absorption potential varies among different species of AMF (Cabral *et al*., 2015). It is important to understand how the AMF community reacts to heavy metal-stress, which can play crucial role in phytoremediation or re-vegetation of heavy metal-contaminated regions (Hildebrandt *et al*., 2007). It has been found that several plant species, such as *Solidago giantea*, *Thlaspi praecox*, *V. rechingeri*, *Fragaria vesca*, *Thymus polytrichus*, and *V. calaminaria*, colonized by AMF grow well in metal-contaminated areas, while their AMF isolates positively regulate the resistance of plants to heavy metal stress (Zarei *et al*., 2008b). The mycorrhizal effect of two strains of the AMF *Claroideoglomus claroideum* (S1 and S2), isolated from heavy metal-polluted soils, was investigated (Hristozkova *et al*., 2015). The highest rate of colonization was shown by S1, while no significant differences were found between S2 and S3 (*F. mosseae*, another strain isolated from an industrial area). Interestingly, AMF can affect the transformation of metals (especially trace metals) in the rhizosphere using various approaches, such as modification of root exudates, acidification, chemical precipitation in soil, and immobilization of heavy metals (Upadhyaya *et al*., 2010). Heavy metal-contaminated soils can be restored and re-vegetated using AMF that affect the rate of phytostabilization and phytoextraction processes (Ghre and Paszkowski, 2006).

BENEFITS OF ENDOPHYTIC FUNGI IN PHYTOREMEDIATION

It has been reported that endophytes can play a significant role in host plant adaptation to different heavy metal-polluted environments. In addition, they can enhance phytoremediation by degrading, mobilizing, or immobilizing contaminants in soil, decreasing phytotoxicity, enhancing plant growth, and improving plants' metal tolerance (Zhang *et al*., 2011). Being suitable candidates for remediation, endophytic fungi can be useful in soils, used for long-term cropping. Besides promoting seedling growth, a significant increase in seed germination (69.8%) has been reported with application of endophytic fungi (Chen Y *et al*., 2013). Co-cultivation of watermelon seedlings with *Ceratobasidium stevensii* (an endophytic fungus) degrades phenolic compounds and significantly increases stems growth and leaf length compared to uninoculated (control) plants (Xiao *et al*., 2014). Similarly, in an aged petroleum-polluted soil, petroleum hydrocarbons were degraded by two grass species (*Festuca pratensis* and *F. arundinacea*) infected by endophytic fungi (Soleimani *et al*., 2010a). Furthermore, phytoremediation efficiency can be improved by adopting a number of strategies including the management of microbial consortia: managing the beneficial effects of microbes on phytoremediator plants and their metal-modifying capabilities, along with the selection of certain microbes and engineering for metal tolerance. Certain fungi can reduce metals and provide resistance to metals, resulting in accumulations of gold, platinum, and silver in the form of nanoparticles in their intracellular spaces, while periplasmic and cytoplasmic hydrogenases play a crucial role in the metal transformation. Plants depend on a pseudo-equilibrium between solid and aqueous soil phases for metal availability, but not on total metal content. The adsorption of metal to soil greatly restricts the metals available for plant uptake. Furthermore, soil components and their interactions with root exudates prevent or restrict the increase of water-soluble organometallic chelates in the rhizospheric region; consequently, the organic compounds (root exudates) can be rapidly sorbed to soil. The reduction in the labile pools of metals or water-soluble chelates is less than 10% of the total metal uptake by plants, suggesting that metals are generally acquired from less available pools (Durn *et al*., 2011). A number of transgenic species have also been used to enhance phytoextraction of metals, such as Cu, Cd, and Pb, and metalloids (selenium (Se), As) as they accumulate in the aerial parts of soil. Such approaches mainly involve the production of phytochelatins and metallothioneins (metal-detoxifying chelators), enhanced synthesis of enzymes involved in sulphur (S) metabolism, and implementation of metal transporters (Kotrba *et al*., 2009). An endophytic fungus, *Penicillium janthinellum* LK5, minimized Cd-induced oxidative stress and membrane injury by reducing lipid peroxidation and electrolytes as well as increasing catalase activity and glutathione content in comparison with experimental control plants (Khan *et al*., 2014). Therefore, endophytes are suggested to counteract metal stress, which has drastic effect on plant growth and development. However, heavy metal accumulation, absorption, or tolerance by endophytes and their effects on host plant growth are not associated with the origin of endophyte (Shen *et al*., 2013). Intriguingly, endophytic microbes are not only resistant to heavy metals, but they are also capable of degrading organic contaminants by producing specific enzymes. Thus, remediation through these microorganisms (endophyte-assisted phytoremediation) is a promising technology for *in-situ* remediation of multi-metal-polluted soils. Endophytes significantly enhance plant growth, enhance metabolism, and reduce phytotoxicity by augmenting metal translocation and accumulation during the phytoremediation process (Li *et al*., 2012b). They can interact efficiently with their host plants and more closely degrade heavy metals in contaminated soil than other microorganisms in the rhizosphere (Zhang *et al*., 2011). Host plant resistance to multi-metal contamination can be increased through endophytic fungi. For instance, *Aspergillus* G16 associated with *Brassica juncea* L. and *Trichoderma* H8 associated with *Acacia auriculiformis* improved plant growth (44% and 167%, respectively) in Cd- and nickel (Ni)-contaminated soils. Collectively, these two strains induced a greater plant yield (178%) compared to uninoculated plants in such contaminated soils (Jiang *et al*., 2008). Another Zn-, Cd-, and Pb-resistant endophytic fungus (*Lasiodiplodia* sp. MXSF31), isolated from the stem of *Portulaca oleracea*, increased the Cd extraction amount and enhanced canola biomass in soils contaminated with Pb and Cd (Deng *et al*., 2014b). It has also been reported that certain endophytic yeasts can confer host plant resistance to different metals. Inoculating *Brassica alboglabra* with *Cryptococcus* sp. CBSB78 increased the extraction amounts of different metals such as Zn, Pb, and Cd in multi-metal-contaminated soils (Deng *et al*., 2012). Studies showing contributions of endophytic fungi to the phytoremediation of different metals and trace elements are summarized in Table II.

ENDOPHYTIC FUNGI AND THEIR PHYSIOLOGICAL CHARACTERISTICS

Plant interactions with the microbial community are

TABLE II

Studies showing contribution of endophytic fungi (EF) to phytoremediation of pollutions caused by different metals and trace elements

Study	EF species	Host plant species	Experiment type(s)	Element(s)	Effect on plant
Li and Zhang, 2015	EF0801	*Oryza sativa* L.	Hydroponic	Pb	Increased resistance to Pb stress, enhanced photosynthesis
Li X M *et al*., 2012	EF0801	*Oryza sativa* L.	Hydroponic	Pb	Enhanced photosynthetic capacity
Monnet *et al*., 2001	*Neotyphodium lolii*	*Lolium perenne*	Hydroponic, pot	Zn	Induced tolerance to Zn stress
Zhang *et al*., 2010	*Neotyphodium gansuense*	*Achnatherum inebrians*	Field, pot	Cd	Improved Cd tolerance
Soleimani *et al*., 2010b	*Neotyphodium* sp.	*Festuca arundinacea*, *Festuca pratensis*	Field, pot	Cd	Increased resistance to Cd stress
Li *et al*., 2012a	*Alternaria* sp.	*Arabis hirsuta*	Field	Zn	Enhanced resistance to Zn stress
Wang *et al*., 2013	*Cryptococcus* sp. CBSB78	*Brassica chinensis*	Pot	Cd, Pb, Zn, Cu	Enhanced resistance to Cd, Pb, Zn, Cu
Babu *et al*., 2014b	*Penicillium aculeatum* PDR-4, *Trichoderma* sp. PDR-16	*Sorghum bicolor* × *sudanense*	Pot	Zn, Pb, As	Increased total biomass and chlorophyll content
Cao *et al*., 2008	*Trichoderma atroviride* F6	*Brassica juncea* (L.) Coss. var. *foliosa*	Pot	Cd, Ni	Alleviated cellular toxicity of Cd, Ni
Adams *et al*., 2007	*Trichoderma harzianum* T22	*Salix fragilis*	Hydroponic	Cd, Pd, Mn, Ni, Zn	Increased root, shoot biomass, enhanced resistance to multi-metals
Xiao *et al*., 2010	*Microsphaeropsis* sp. LSE10	*Solanum nigrum*	Field	Cd	Increased Cd biosorption capacity
Khan *et al*., 2014	*Penicillium janthinellum* LK5	Solanum lycopersicum (Sitiens and Rhe)	Pot	Cd	Reduced Cd toxicity
Jiang *et al*., 2008	*Trichoderma* H8, *Aspergillus* G16	*Brassica juncea* (L.) Coss. var. *foliosa*	Pot	Cd, Ni	Increased yield, enhanced efficiency of phytoextraction
Deng *et al*., 2014b	*Lasiodiplodia* sp. MXSF31	*Brassica napus* L.	Pot	Cd, Pb, Zn	Increased plant biomass, Cd extraction amount, and translocation factors
Deng *et al*., 2012	Cryptococcus sp. CBSB78	*Brassica alboglabra*	Field	Cd, Pb, Zn	Increased plant biomass, Cd, Pb, and Zn extraction amounts
Wang *et al*., 2013	*Rhodotorula* sp. CBSB79	*Brassica* sp.	Field	Cd, Pb, Zn, Cu	Improved efficacy of Cd, Pb, Zn, and Cu extraction
Shahabivand *et al*., 2018	*Piriformospora indica*	*Helianthus annuus*	Pot	Cd	Improved tolerance to Cd toxicity, reduced Cd accumulation and MDA content of leaves
Khan *et al*., 2017a	*Fusarium tricinctum* RSF-4L, *Alternaria alternata* RSF-6L	*Solanum nigrum* L.	Pot	Cd	Improved tolerance index, reduced Cd uptake
Hui *et al*., 2015	*Piriformospora indica*	*Nicotiana tabacum*	Hydroponic, pot, field	Cd	Increased Cd in roots, increased antioxidant enzymes, pigments, and proline content
Nanda and Agrawal, 2018	*Piriformospora indica*	*Cassia angustifolia* Vahl.	Medium	Cu	Reduced DNA damage, lipid peroxidation, hydrogen peroxide
Mohd *et al*., 2017	*Piriformospora indica*	*Oryza sativa* L. IR64	Hydroponic	As	Immobilized As contents, restricted As in colonized roots
Shahabivand *et al*., 2017	*Piriformospora indica*	*Helianthus annuus* cv. Zaria	Pot	Cd	Increased accumulation of Cd in roots, alleviated Cd toxicity
Arriagada *et al*., 2009	*Trichoderma harzianum*	*Eucalyptus globulus*	Pot	As	Increased root and shoot dry weight, chlorophyll content
Zhu *et al*., 2018	*Phialophora mustea* strains	*Lycopersicon esculentum* Miller	Pot	Zn, Cd	Enhanced metal tolerance, improved growth
Shi *et al*., 2017	*Fusarium* sp. CBRF44	*Brassica napus*	Pot	Cd, Pb	Improved phytoremediation efficacy
Berthelot *et al*., 2016	Dark septate endophyte (DSE) strains	*Populus* sp.	Field	Cd, Pb, Zn	Stimulated growth through the release of volatile organic compounds
Zahoor *et al*., 2017	*Mucor* sp. MHR-7	*Brassica campestris* L.	Pot	Cr, Zn, Mn, Cu, Co	Increased resistance to multi-metal contamination
Mohd *et al*., 2019	*Aspergillus flavus* MTCC 25041	*Oryza sativa* IR64	Hydroponic	As	Reduced As toxicity
Li X N *et al*., 2017	*Aspergillus aculeatus*	*Cynodon dactylon* (L.) Pers.	Pot	Cd	Increased relative growth rate and normalized relative transpiration rate
Sabra *et al*., 2018	*Serendipita indica*	*Ocimum basilicum*	Pot	Pb, Cu	Increased root and shoot dry weights, reduced metal contents in shoot
Shen *et al*., 2013	*Peyronellaea* sp.	*Zea mays* L.	*In vitro*, pot	Pb, Zn, Cd	Improved tolerance to heavy metals

(to be continued)

TABLE II (continued)

Study	EF species	Host plant species	Experiment type(s)	Element(s)	Effect on plant
Ren *et al*., 2011	*Neotyphodium coenophialum*	*Lolium arundinaceum*	Pot	Cd	Increased tiller number and biomass, enhanced Cd accumulation and transport from root to shoot
Li *et al*., 2011	*Exophiala pisciphila* H93	*Zea mays* L.	Pot	Zn, Pb, Cd	Increased growth, alleviated heavy metal toxicity
Waqas *et al*., 2014	*Galactomyces geotrichum* WLL1	*Glycine max* L. var. Hwangkeumkong	Pot	Zn	Improved growth
Shahabivand *et al*., 2012	*Piriformospora indica*	*Triticum aestivum* cv. Sardari39	Pot	Cd	Increased root and shoot Cd accumulation
Deng *et al*., 2013	*Mucor* sp. CBRF59	*Brassica napus*	Pot	Cd, Pb	Increased dry weight and metal translocation from root to shoot
Lacercat-Didier *et al*., 2016	*Serendipita vermifera* sp. P04	*Populus* clone INRA 717-1B4	*In vitro*	Cd, Zn, Pb, Cu	Increased root tip number and shoot biomass
Likar and Regvar, 2013	DSE strains	*Salix caprea* L.	Pot	Cd, Zn, Pb	Increased chlorophyll level and normal growth
Khan *et al*., 2015	*Penicillium janthinellum* LK5 (PjLK5)	*Solanum lycopersicum*	*In vitro*	Al	Increased morphological attributes and normal growth
Khan and Lee, 2013	*Penicillium funiculosum* LHL06	*Glycine max* L.	Pot	Cu	Increased biomass and nutrient uptake, better root physiology
Abou Alhamed and Shebany, 2012	*Chaetomium globosum*	*Zea mays*	Pot	Cu	Increased seedling dry weight, osmotic solute content, and antioxidant enzyme activity
Babu *et al*., 2014a	*Trichoderma* sp. PDR1-7	*Pinus sylvestris*	Pot	Pb	Increased nutrient availability, seedling growth, chlorophyll and protein contents, and antioxidative enzyme (superoxide dismutase) activity
Emamverdian *et al*., 2015	*Paraphaeosphaeria* sp. SR46	*Zea mays*	Pot	Cd	Enhanced resistance to Cd stress
Ban *et al*., 2017	*Gaeumannomyces cylindrosporus*	*Zea mays* L.	Pot	Pb	Improved efficiency of photosynthesis, enhanced resistance to Pb
Diene *et al*., 2014	*Pseudosigmoidea ibarakiensis* I.4-2-1, *etc*.	*Brassica* sp. cv. Musou, *Solanum lycopersicum* cv. Hausu Momotaro	Hydroponic	Cs	Higher Cs accumulation in the aboveground parts
Zamani *et al*., 2015	*Neotyphodium* sp.	*Festuca arundinacea*, *Lolium perenne*	Pot	Zn	Improved chlorophyll fluorescence, reduced Zn stress
Wang *et al*., 2016	*Exophiala pisciphila*	*Zea mays* L.	*In vitro*	Cd	Increased tolerance to Cd stress, decreased Cd toxicity
Gucwa-Przepira *et al*., 2013	*Glomus tenue*	*Deschampsia cespitosa*	Field	Cd, Pb, Zn	Enhanced tolerance to metal stress
Yamaji *et al*., 2016	*Phialocephala fortinii*, *etc*.	*Clethra barbinervis* Sieb. et Zucc.	*In vitro*	Cu, Zn, Ni, Pb	Enhanced growth, increased K uptake in shoots, reduced concentrations of Cu, Ni, Zn, Cd, Pb in roots
Jin *et al*., 2018	*Acrocalymma vagum*	*Nicotiana tabacum*	Pot	Cd, As, Pb	Decreased heavy metal contents in leaves
Sim *et al*., 2018	*Bipolaris* sp., *etc*.	*Phragmites* sp.	*In vitro*	Al, Cd, Cu, Pb, Zn	Enhanced resistance to multi-metal stress
Zhang *et al*., 2008	*Exophiala pisciphila* (H93)	*Arundinella bengalensis*	*In vitro*	Cd	Enhanced accumulation of Cd
Deng *et al*., 2014a	*Mucor* sp. CBRF59, *Fusarium* sp. CBRF14	*Brassica napus*	Pot	Cd, Pb, Zn	Promoted growth, increased metal concentrations, elevated extractable metal amount
Gong *et al*., 2017	*Purpureocillium* sp. A5	*Kandelia candel*	Pot	Cu	Reduction Cu content
Pietro-Souza *et al*., 2017	*Fusarium* sp., *etc*.	*Aeschynomene fluminensis*	Pot	Hg	Better growth
Ikram *et al*., 2018	*Penicillium roqueforti* Thom.	*Triticum aestivum* var. Bhakkar-2000 (KJ672075)	Pot	Ni, Cd, Cu, Zn, Pb	Enhanced resistance to heavy metals
Bibi *et al*., 2018	*Aspergillus fumigatus*, *etc*.	*Lactuca sativa* L	Pot	Cr	Reduced Cr toxicity
Mirzahosseini *et al*., 2014	*Neotyphodium coenophialum*	*Festuca arundinacea*	Field	Ni	Increased growth and Ni tolerance
Sun *et al*., 2017	*Mucor circinelloides*	*Solanum nigrum* L.	Pot	Pb	Enhanced Pb removal and growth
Ding *et al*., 2016	*Fusarium oxysporum*	*Oryza sativa* (Guangliangyou, 272)	*In vitro*	Cr, Cd	Increased resistance to high levels of both metals
He *et al*., 2017	*Exophiala pisciphila* ACCC32496	*Zea mays* L.	Pot	Cd	Increased growth, more Cd in roots, decreased Cd content in shoots

symbiotic relationships that play an important role in structuring different plant communities and ecosystems (Müller and Krauss, 2005). Root tissue transport systems of hyperaccumulator plants are correlated with excessive amounts of metalloid and metal accumulation. In addition, root exudates are thought to have an effect on the diversity of microbes (Weyens *et al.*, 2009). Attention has been given in the recent past to the capacity of endophytes to promote plant growth, as well as the relationship between endophytes and microbes living in the rhizosphere. After getting inside plants through the roots (main site of endophytic colonization) and establishing themselves, endophytes confer resistance to insects and pathogens. Besides inducing heavy metal resistance in plant (Khan and Doty, 2011), endophytes can also promote plant growth in different ways, such as producing growth-regulating substances (cytokinins and indole acetic acid) and metabolizing the ethylene precursor 1-aminocyclopropane-1-carboxylic acid produced under stress (Glick, 2003). The *Cryptococcus* species CBSB78 (endophytic yeast) possesses low 1-aminocyclopropane-1-carboxylic acid deaminase activity and is a low indole-3-acetic acid producer (Deng *et al.*, 2012). Furthermore, endophytic fungi boost plant fitness and other competitive abilities by enhancing growth rate and germination or by increasing the plants' absorption capacity for nutritional elements (Aly *et al.*, 2011). Possession of a metal sequestration or chelation system and suitable degradation pathways by fungal endophytes increases host plant tolerance to heavy metal stress and assists the plants to survive in metal-contaminated soils (Aly *et al.*, 2011). The fungal interaction of *Trichoderma atroviride* F6 with *B. juncea* L. significantly increases resistance to Ni^{2+} and Cd^{2+} and alleviates cellular toxicity. Additionally, plants inoculated with this F6 strain results in 170%, 40%, and 110% increases in fresh weight in Cd-Ni-, Ni-, and Cd-polluted soils, respectively (Cao *et al.*, 2008). Some yeasts, such as *Rhodotorula mucilaginosa*, have been reported to promote plant growth by producing indole-3-pyruvic acid and indole-3-acetic acid. However, such effects have been scarcely reported in soils contaminated with metals (Xin *et al.*, 2009). The tolerance mechanisms of endophytic fungi in toxic environments includes compartmentation, intracellular sequestration and complexation, extracellular metal precipitation and sequestration, volatilization, and binding of metal to the fungal cell walls (Fomina *et al.*, 2005).

MECHANISMS BEHIND FUNGAL ENDOPHYTE-DERIVED BENEFITS UNDER HEAVY METAL STRESS

Different molecular and cellular systems have been adopted by fungi living in metal-contaminated soils to cope and survive in such environments (Chiapello *et al.*, 2015). Detoxification mechanisms can be intracellular, such as binding to non-protein thiols and transporting into intracellular compartments (to reduce metal burden in the cytosol), or extracellular, such as avoidance of excessive metal entry, chelation, and cell wall binding (Ruytinx *et al.*, 2013). All such processes contribute to the protection of fungal species from metal toxicity. Among these mechanisms, metal transporters are thought to be the most important contributors. They maintain suitable concentrations of metal ions in the cellular compartments in two ways: by allowing metal sequestration into intracellular compartments and by extruding toxic metal ions on inherent metal-tolerant ions from the cytosol to the outside of cell (Park *et al.*, 2012). Various members of the *Nramp* family have been reported to play a major role in homeostatic mechanisms, thereby preventing toxicity of metal ions in living cells (Ehrnstorfer *et al.*, 2014). Sub-cellular sequestration of various metal ions is mediated by diverse metal transporters, which not only control metal partitioning, but also contribute to cellular metal tolerance, especially when the rates of metal influx into organisms are high. A metal transporter gene, homologous to the natural resistance associated macrophage protein (*Nramp*), was cloned from *Exophiala pisciphila* (DSE metal-tolerant fungi) and analyzed for functional characterization. The gene (*Nramp*, 1716 bp) encodes a polypeptide of 571 amino acid residues. In addition, green fluorescence protein assay of EpNramp revealed it to be a plasma membrane metal transporter; this was confirmed by bioinformatics analysis with 11 transmembrane domains. Further experiments with yeast functional complementation showed that the growth defect of the Fe-uptake yeast mutant could be complemented by mediating the transport of Fe^{2+}. Furthermore, Cd^{2+} accumulation and sensitivity increased with the expression of *EpNramp*. Expression of *EpNramp* was significantly downregulated with elevated Cd^{2+} exposure, as revealed by quantitative polymerase chain reaction (qPCR) studies (Wei *et al.*, 2016). Glutathione (GSH) and GSH-related tolerance are also one of the metal tolerance mechanisms in fungi, induced in response to various environmental factors (Na and Salt, 2011). Endophytic fungi are capable of accumulating high quantities of toxic metals in their mycelia. However, the mechanisms of metal transport, sequestration, and detoxification are not well documented (Zahoor *et al.*, 2017). Transcriptome analysis of *E. pisciphila* (growing in the presence of Cd) using RNA sequencing (RNA-Seq) revealed that several genes associated with ROS, S assimilation, redox homeostasis maintenance, and metal binding, transport, and detoxification were upregulated. The researchers suggested that various molecules including MTs, GHS, and phytochelatins could increase under Cd stress (Na and Salt, 2011). Another tripeptide GHS (γ-glu-cys-gly) frequently found in cell compartments has been shown to sequester metals and also acts as a potent antioxidant under oxidative stress (Freeman *et al.*, 2004). A transient increase in GSH content after Pb treatment was recorded in *Gaeumannomyces cylindrosporus* that enhanced tolerance to Pb (Ban *et al.*, 2017). To date, there are no reports showing that endophytic fungi may affect metal translocation by interfering with the expression of metal transporters. However, an increased expression level of *pcr2* (encoding plant cadmium resistance 2) results in higher metal accumulation in the shoots of inoculated plants (Rozpądek *et al.*, 2018). In another study, an unspecified *zip* gene was inhibited with endophytic fungus inoculation, which coincided with the decreased uptake of Cd. Furthermore, *mpt1* (encoding metal transporter protein 1) expression was also upregulated in a group inoculated with endophytic fungi under Cd stress (Wang *et al.*, 2016). In addition, several genes including *zif1* (encoding zinc-induced facilitator 1), *hma3* (encoding heavy metal-associated 3), *cax2* (encoding cation exchanger 2), and *mtp1* that encode tonoplast-bound vacuole carrier protein were upregulated in *Arabidopsis arenosa* subjected to metal stress. The authors suggested that these genes are involved in the reduction of metal accumulation, distribution, exclusion, sequestration in the vacuole and ROS scavenging (Rozpądek *et al.*, 2018). The overexpression or complementation of these genes improves resistance to various metal stresses in yeast and plants (Morel *et al.*, 2009).

ASSOCIATION OF ENDOPHYTIC FUNGI WITH PLANTS UNDER CONDITIONS OF METAL STRESS

The diversity of endophytic fungi is thought to be abundant, especially in tropical forests. However, their diversity in hyperaccumulators has not yet been well documented. It has been reported that endophytic fungi of plants at Pb-Zn sites, especially mine wastelands, harbor fewer endophytic fungi in their leaves than in their stems. For instance, *Alternaria*, *Phoma*, and *Peyronellaea* were the dominant genera among twenty identified fungal taxa, some of which showed marked adaptation to Zn^{2+} and Pb^{2+} (Li *et al.*, 2012a). In addition, *Rhodotorula* sp. CBSB79 and *Cryptococcus* sp. CBSB78 (endophytic yeasts) have been found in the roots of *Brassica chinensis* in soils contaminated with Pb, Cu, Cd, and Zn. These species have shown resistance to various metals in multi-metal-contaminated soils (Wang *et al.*, 2013). Various endophytic species in genera such as *Aspergillus*, *Trichoderma*, *Penicillium*, *Fusarium*, *Cladosporium*, *Lasiodiplodia*, and *Paecilomyces* are harbored in *Portulaca* spp., multiple heavy metal-hyperaccumulating plants (Deng *et al.*, 2014b). Similarly, *A. auriculiformis* contains fungi *Penicillium*, *Aspergillus*, *Alternaria*, *Fusarium*, *Trichoderma*, and *Mycelia sterilia* (Cao *et al.*, 2008). *Trichoderma* spp. and *Penicillium* spp. are famous and frequently isolated species that can resist heavy metal stress (Babu *et al.*, 2014b; Khan *et al.*, 2014). Conventional culture methods are not enough to isolate all fungi; however, the bias towards fast-growing ubiquitous species is the prominent shortcoming of cultivation-dependent studies for unraveling endophyte diversity. Consequently, rare species with more specialized requirements and minor competitive strengths may remain undiscovered. Methods that have been used for bacterial isolation do not favor fungal growth and other fungal colonizers in the same samples. Besides culture studies, advanced techniques such as barcoded amplicon pyrosequencing and next-generation sequencing can be utilized to analyze endophytic flora where diverse fungal species would be found in hyperaccumulator plants (Deng and Cao, 2017). Heavy metal-resistant endophytes in contaminated areas have attributes that decrease metal phytotoxicity, enhance plant growth, and affect metal accumulation and translocation in plants (Li *et al.*, 2012b). Different sensitivities to metals have been shown by endophytes isolated from different plant species or even from different tissues of the same plant. This suggests that isolates are different in metal tolerance due to long-term adaptation in plant tissues with different concentrations of heavy metals (Li *et al.*, 2012a). Intriguingly, many metal-resistant endophytes have not only been isolated from hyperaccumulating plants such as *Alnus firma*, *Nicotiana tabacum*, *Solanum nigrum*, *Thlaspi caerulescens*, *Brassica napus*, *Alyssum bertolonii*, and *Thlaspi goesingense*, but also from non-hyperaccumulating plants such as *Acacia decurrens*, *Symplocos paniculata*, and *Arabis hirsuta*. These isolates from non-metal-polluted plants were also found to be resistant to heavy metals (Moore *et al.*, 2006). Another root-colonizing endophytic fungus with a wide number of hosts, *Piriformospora indica*, can colonize the roots of a number of plants growing on metal-contaminated soils and confer resistance against Cd, Cu, As, Zn, and Pb (Mohd *et al.*, 2017). In addition, DSEs have been isolated from the roots of *Erica herbacea* grown on Cd-, Pb-, and Zn-polluted soils (Čevnik *et al.*, 2000). In another study, fungal endophyte communities of *Salix caprea* in locations highly enriched with Cd and Pb contained species belonging to the genera *Leptodontidium*, *Phialophora*, and *Phialocephala*. Furthermore, root colonization of *Salix caprea* and the resulting frequency of the sequences have an affinity towards *Phialophora*, showing correlation with available phosphate concentration and soil Pb and Cd, probably indicating that these endophytes confer tolerance to heavy metal contamination (Likar and Regvar, 2009). Furthermore, the interactions of endophytic fungi with a number of *Salix* species in heavy metal-polluted areas are well documented (Baum *et al.*, 2006).

ECOLOGICAL AND ENVIRONMENTAL CONDITIONS AND THEIR EFFECTS ON POPULATION STRUCTURE OF ENDOPHYTIC FUNGI

Different environmental or ecological conditions such as humidity, temperature, and different levels of soil nutrition are amongst the significant factors that determine the amounts and types of secondary metabolites from endophytic fungi and host plants, which indirectly affect the population structure of endophytic fungi. If the environmental conditions comprise a high mean annual humidity with a low mean annual sunshine hours, host plants may produce an abundance of nutrients that might be suitable for reproduction, colonization, and dissemination of the endophytic fungi (Wu *et al.*, 2013). In contrast, only a few types of host plants can grow successfully if environmental conditions are cold with unsuitable pH value, oxygen concentration, and respiration rate. Consequently, certain endophytic fungi (in a limited number) can form symbiotic relationships with corresponding host species, indicating a definite degree of regional specificity on the population structure of endophytic fungi (Jiang *et al.*, 2010). Generally, the population structures of endophytic fungi and their related host plants (usually the same species from different climatic regions) have shown a very low degree of similarity (Jiang *et al.*, 2010). However, a high degree of similarity has been shown in terms of endophytic fungus species taxonomy in the same regions, indicating a certain degree of regional specificity (D'Amico *et al.*, 2008).

PHYTOREMEDIATION

Some plants have the capability to retain high concentrations of heavy metals, while their normal development remains unaffected; using such plants for the remediation of heavy metals is known as phytoremediation. Phytoremediation is the most feasible option to decontaminate the serious pollution areas, especially when the harvested biomass is valorized to produce bioenergy, as in the production of biodiesel. Such plants can maintain homeostasis while growing in highly polluted soil medium and can be used to degrade, transfer, or remove heavy metal contaminants (Wong, 2003). A significant number of plants have been reported for their capability to hyperaccumulate metals in their tissues. Approximately 500 plant species, belonging to 45 families, have been extensively reported on and recognized as having high potential for metal-accumulating capabilities. Among these plants, members of Euphorbiaceae, Fabaceae, Lamiaceae, Brassicaceae, Scrophulariaceae, and Asteraceae are the most prominent (Ghosh and Singh, 2005; Jaffr *et al.*, 2013). *Eleocharis acicularis*, *A. bertolonii*, and *T. caerulescens* are some of the highly effective examples studied for their accumulation of Ni, Cd, and Zn (Lasat, 2002; Assuno *et al.*, 2003; Glick, 2010), and *T. caerulescens* has been shown to accumulate Cd of 0.3–1 020 mg kg^{-1} and Zn of 500–52 000 mg kg^{-1} (Zhao *et al.*, 2003).

Phytoremediation approaches involve various plant-based strategies with different mechanisms and actions, the most common of which are phytostabilization, phytofiltration, phytoextraction, and phytodegradation or phytotransformation. Phytostabilization is the reduction of heavy metal bioavailability in soil by plants (Salt *et al.*, 1995). Some plants gain metal resistance capabilities through gradual evolution or get them inherently (Wu, 1990). Plants used for phytostabilization are selected based on their resistance to certain contaminants, along with their capability of holding the contaminant in roots and hampering its distribution towards the upper parts, avoiding its entrance to the food chain (Padmavathiamma and Li, 2007). Recently, *Agrostis castellana* has been reported to be a good candidate for accumulating high concentrations of pollutant elements including Zn, Cu, Pb, Cd, and As. Analysis of its below- and above-ground biomass have shown that it accumulates most of the pollutant elements in the roots, proving that this plant is a good phytostabilizer (Pastor *et al.*, 2015). In another study, the phytostabilization potential of *Gentiana pennelliana* has been shown at Zn-, Cu-, and Pb-contaminated sites (Yoon *et al.*, 2006).

Phytofiltration implies the removal of contaminants from water sources (wastewater) by utilizing different plants to purify the aquatic ecosystem (Mesjasz-Przybyłowicz *et al.*, 2004). For example, removal of Cr, Cd, Ni, and Cu has been reported in the wetland plant *Eichhornia crassipes*, showing that it is a promising candidate for cleaning polluted wastewater. However, in rhizofiltration, terrestrial plants are preferred because of their extensive root system, which provides a wide surface area. Another reason for this preference might be the high water storage contents of aquatic plants, making later composting, drying, and incineration difficult. *Ricinus communis* L. has been shown to accumulate higher Cd in its root system compared to shoots and leaves grown in hydroponic solution (Hadi *et al.*, 2015). Similarly, *B. juncea* has shown maximum accumulation of Cr, Cu, Zn, Cd, Ni, and Pb from hydroponic solution (Dushenkov *et al.*, 1997).

Phytoextraction, phytoaccumulation, and phytoabsorption are the most highly used techniques for the uptake of heavy metals in vast quantities by plants and shifting them to their harvestable parts or components (Ma *et al.*, 2011; Kamran *et al.*, 2014). After harvesting, the metal-hyperaccumulated harvested biomass of plants can be processed to extract and recover the possible pollutant or contaminant (Ha *et al.*, 2011). Phytomining technology employs hyperaccumulator plants to take up metal in harvestable plant biomass. Harvesting, drying, and incineration of the biomass generate a high-grade bio-ore. Thus, "agromining" (a variant of phytomining) could provide local communities with an alternative type of agriculture on degraded lands: farming not for food crops, but for metals. However, phytoextraction of some elements to remediate soils results in recovered biomass with little economic value (for example Cd and As), and disposal of the biomass would be costly. A few elements such as Ni, cobalt (Co), and uranium (Au) may have sufficient economic values for phytomining biomass to support commercialization. The development of phytomining requires: i) selection of high-biomass hyperaccumulator plant species, ii) evaluation of genetic diversity and breeding of improved strains with higher yields of the phytoextracted element, iii) development of agronomic practices to maximize economic return, and iv) development of methods to recover the phytomined element from the plant biomass. Full commercial phytomining of Ni is commencing in Albania using *Alyssum murale*, while major trials in Malaysia are underway using *Phyllanthus securinegioides*. The variable prices of commodity metals add confusion to the development of commercial phytomining (van der Ent *et al*., 2015).

Many flowering plants (500 species) have been reported with the potential to accumulate various metals (Cd, Co, Cu, As, Ni, Mn, stibium (Sb), Pb, thallium (Tl), Zn, and Se), and scientists are still in search of new plant species with hyperaccumulation capabilities (Padmavathiamma and Li, 2007; Rascio and Navari-Izzo, 2011; Jaffr *et al*., 2013). Some recent examples include *T. goesingense*, *Sedum alfredii*, and *Arabidopsis halleri*, which are hyperaccumulators of Zn. *Nicotiana tabacum* L. has been shown to have potential for Cd hyperaccumulation, while *S. alfredii*, *T. caerulescens*, *Thymus praecox*, and *A. halleri* have been shown to have both Zn and Cd hyperaccumulation potential (Rascio and Navari-Izzo, 2011; Yang *et al*., 2017). Another common mechanism is phytodegradation or phytotransformation involving the external degradation of pollutant *via* excreted metabolic compounds or breaking down the pollutant after being taken in by plant tissues through various metabolic processes (Tangahu *et al*., 2011). The endophytic or rhizospheric microbes in association with plants have also been extensively reported to assisting in the biodegradation of contaminants (Tangahu *et al*., 2011; Bibi *et al*., 2018). For instance, the endophytic strains *Aspergillus fumigatus* ML43 and *Penicillium radicum* PL17 have been shown to biotransform Cr from its hexavalent form to its trivalent form (less toxic), while maintaining healthy growth and development of the host plant *Lactuca sativa* (Bibi *et al*., 2018). Similarly, *Microbacterium* sp. G16 and *Pseudomonas fluorescens* G10 have been reported to produce organic acids and increase the accumulation of Pb in rape plants (Sheng *et al*., 2008).

CONCLUSIONS AND FUTURE PROSPECTS

Soils contaminated with toxic heavy metals not only have drastic effects on the diversity and composition of microbial communities, which play a significant role in the reduction of important microbial species, but also result in the enrichment of metal-tolerant or resistant microbial strains. Interestingly, these microbial strains (fungi, bacteria, algae, and other microorganisms) are not only metal tolerant, but also promote plant growth on soils contaminated with the toxic metals. In the recent past, the mycorrhizal effects on plants growing under metal stress conditions and plant adaptations to these metals have been extensively studied. Based on the recent research articles discussed here, fungal-assisted (particularly AMF and endophytic fungi) phytoremediation is the most suitable and ecofriendly technology for the remediation of soils polluted with heavy metals. Fungal interactions with plants at metal-contaminated sites can enhance plant growth, mobilize heavy metals, degrade organic contaminants, improve nutrient uptake, promote seed germination, significantly affect contaminant accumulation, and decrease phytotoxicity. Besides other important factors, this review article highlights fungal-plant interactions, particularly in metal-polluted soils, as well as the benefits that these fungi provide to their host plants. Although worldwide attention has been given to the removal of heavy metals and pollutants from the environment (water, soil, and sediment), there are many areas which remain poorly understood and require additional research. For example, much of the reported work is confined to experimental studies; more effort should be made into field trials. Additionally, fungal-plant interaction mechanisms have not been clearly explained. Besides a bioengineering system to understand antagonistic or mutualistic symbiosis of fungi with their host plants, a rapid screening guide is necessary for beneficial fungi rather than isolating the whole microflora uncritically. Being a dynamically growing area of green biotechnology, bioremediation (despite a few disadvantages) is a cost-effective and environmentally friendly (without any hazardous effects) technology; however, the various pending questions should be addressed. For instance, how much the analogous impacts of mycorrhizal fungi differ from the influences of endophytes on plant toxic metal tolerance? Do fungi adapted to heavy metal stress directly affect specific metal tolerance mechanisms, or is this a result of indirect action such as improving the uptake of water and nutrients from the soil and conferring plant fitness? Thus, a greater understanding of the mechanisms behind metal tolerance in beneficial fungi will provide essential tools for their efficient use in phytoremediation practices. Additional studies regarding the role of fungal symbionts in plant responses to toxic metals should be carried out to answer these and other important questions.

ACKNOWLEDGEMENTS

This work was supported by the National Key Research and Development Program of China (No. 2016YFD-0800807), the National Nature Science Foundation of China (Nos. 31702003 and 31902105), the Young Elite Scientists Sponsorship Program of China Association for Science and Technology (CAST) (No. 2017QNRC001), the China Postdoctoral Science Foundation (No. 2019 M651505), the "Chenguang Program" of the Shanghai Education Development Foundation and Shanghai Municipal Education Commission, China (No. 17CG07), and the Shanghai Agriculture Science and Technology Development Project, China (No. 2018-4-13).

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