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► To cite this version:

Louise Barberis, Serge Michalet, Florence Piola, Philippe Binet. Root fungal endophytes: Identity, phylogeny and roles in plant tolerance to metal stress. *Fungal Biology*, 2021, 125, pp.326-345. 10.1016/j.funbio.2020.11.011 . hal-03160127

HAL Id: hal-03160127

<https://hal.inrae.fr/hal-03160127>

Submitted on 24 Apr 2023

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1 Root fungal endophytes: identity, phylogeny and roles in plant tolerance to metal
2 stress

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Abstract

Metal trace elements accumulate in soils mainly because of anthropic activities, leading living organisms to develop strategies to handle metal toxicity. Plants often associate with root endophytic fungi, including nonmycorrhizal fungi, and some of these organisms are associated with metal tolerance. The lack of synthetic analyses of plant-endophyte-metal tripartite systems and the scant consideration for taxonomy led to this review aiming (1) to inventory non-mycorrhizal root fungal endophytes described with respect to their taxonomic diversity and (2) to determine the mutualistic roles of these plant-fungus associations under metal stress. More than 1500 species in 100 orders (mainly Hypocreales and Pleosporales) were reported from a wide variety of environments and hosts. Most reported endophytes had a positive effect on their host under metal stress, but with various effects on metal uptake or translocation and no clear taxonomic consistency. Future research considering the functional patterns and dynamics of these associations is thus encouraged.

Keywords: metallic trace element, fungal endophytes, taxonomy, accumulation, mutualism, plant-fungi interactions

31 Introduction

32 Metal accumulation in soils is a growing concern in developed and developing countries. Fertilizers and
33 pesticides rich in As, Pb, Cr, Cu and Zn, among others (Senesil et al., 1999), contribute directly to the deposition of
34 metal trace elements (MTEs) in soils. MTEs may also be emitted to the atmosphere by road traffic (Cu, Zn, Pb)
35 (Nikolaeva et al., 2019), industries (Bourennane et al., 2010), or coal combustion (Cd, Cu, Ni, Pb, Zn...) and may be
36 deposited on soil secondarily (Senesil et al., 1999). As metal ions are not biodegradable, they tend to accumulate and
37 persist in soil over more than two years (Senesil et al., 1999).

38 As primary producers, vascular plants are essential components of the terrestrial food chain. Thus, MTE
39 transfer and its biological effects on plants constitute crucial information for understanding the environmental fate of
40 these pollutants. Contaminated sites present toxicity for plants, leading to scarce vegetation and negatively affecting
41 agriculture and human health. For example, Zn and Cd are easily taken up by plants, causing chlorosis and stunted
42 growth and disturbing N metabolism (Påhlsson, 1989); Cr reduces germination, yield and plant height and leads to the
43 formation of thick roots (Shanker et al., 2005). MTEs in general induce oxidative stress and ionic homeostasis
44 disturbance in plants (Yadav, 2010). However, several plant species developed metal tolerance, either to one metal
45 (Zn for instance (Påhlsson, 1989)) or to several metals with a common mechanism (recapitulative figures in Domka et
46 al., 2019; Singh et al., 2016). Metabolomics, ionomics and proteomics have shown numerous modifications in plant
47 metabolism in the presence of heavy metals (Singh et al., 2016), such as phytochelatins and glutathione, which
48 increase on metal contamination (Seth et al., 2012). Amino acids, organic acids and phenols participate in the
49 chelation and transport of metals, whereas glutathione and alpha-tocopherol are involved in the scavenging of ROS
50 and lipid peroxides. Peptides such as phytochelatins and metallothioneins bind metal ions, and hormones such as
51 salicylic acid or abscisic acid participate in plant systemic responses to abiotic stress (Hu et al., 2020; Raza et al.,
52 2020; Saeed-Ur-Rahman et al., 2020; Singh et al., 2016). Metal ions bound to phytochelatins are transported from the
53 cytosol to the vacuolar compartment, thus detoxifying the cytosol and limiting oxidative stress (Yadav, 2010; Zenk,
54 1996).

55 The plant and fungal kingdoms are strongly linked, with more than 85% of vascular plants forming symbiotic
56 associations with mycorrhizal fungi (Brundrett & Tedersoo, 2018). Although seven categories of mycorrhizal
57 symbioses have been reported (Finlay, 2008), two types, namely, arbuscular mycorrhizal and ectomycorrhizal
58 symbioses, have been extensively studied for their role in plant-MTE interactions. Although the literature concerning

59 the role of ericoid mycorrhizal (ErM) fungi is not as extensive as that for arbuscular mycorrhizal fungi (AMF) and
60 ectomycorrhizal fungi (EMF), some data are also available for this group.

61 At metal-contaminated sites, AM fungi are found in more than 80% of plants across a wide diversity and have
62 been shown to promote plant growth (Wang, 2017), demonstrating that not only are fungi tolerant to metals, but they
63 may also help plants tolerate metals. Therefore, the role of AMFs and EMFs on plant tolerance to metal stress has
64 been widely studied (*e.g.*, Luo et al., 2014; Miransari, 2011; Shi et al., 2019, Zhan et al., 2019). AMFs increase plant
65 growth and alleviate metal stress, especially under high metal concentrations. Stress alleviation may come from
66 increased plant growth (metal dilution effect) and/or decreased concentrations of available metals in soil (Miransari,
67 2011, Khan, 2005) but also from participation and improvement of plant defences (Ferrol et al., 2016).
68 Ectomycorrhizae are present in approximately 2% of plant species, mainly trees (Brundrett, 2009; Brundrett &
69 Tedersoo 2018). Some EMFs immobilize metals in soil, whereas other EMFs promote metal uptake by the host plant.
70 Metal transporters produced by EMFs are important in mediating tolerance (Luo et al., 2014). Thus, in mycorrhizal
71 plants, both AMFs and EMFs can alleviate plant metal stress by sequestering metal ions, improving the nutritional
72 and antioxidative status of the plant and stimulating the expression of genes involved in metal accumulation in both
73 partners (Shi et al., 2019; Yu et al., 2020). Similarly, ErM favour plant growth under Cu and Zn contamination with
74 lower MTE concentrations in shoots but higher concentrations in roots, suggesting an adsorption mechanism (Bradley
75 et al., 1982), or with lower concentrations in roots, suggesting a filtering effect (Casrribia et al., 2020). The metal
76 tolerance of fungal partners may explain in some way their host plant metal tolerance (Bradley et al., 1982): in
77 particular, the involvement of several fungal genes coding for antioxidant enzymes, metal transporters, and DNA
78 damage repair proteins are under investigation (Daghino et al., 2016). Transporters and metallothioneins, which could
79 be involved in MTE sequestration in roots or MTE transport into plant tissues, have been identified in all three types
80 of mycorrhizae (Ruytinx et al., 2020) and seem to mitigate oxidative stress (Zou et al., 2020), but the precise
81 mechanism at the plant root-fungi interface remains unknown (Becquer et al., 2019).

82 In addition to mycorrhizae, other fungi associate with plant roots without forming an exchange structure.
83 Dark-septate endophytes (DSEs) belong to this category. Rather well studied, they are often named
84 “pseudomycorrhizae” (Jumpponen and Trappe, 1998) because of their specific association with plant roots and their
85 mutualistic effects on plants. A meta-analysis of inoculation experiments showed that DSEs have positive or neutral
86 effects on plant growth (Newsham, 2011). Keeping these four groups –AMF, EMF, ErM and DSE– aside, a high
87 diversity of fungi is still found in plants. Some are classified as parasitic despite harbouring non-pathogenic

88 interactions with some plants, while others are not truly studied. *Olpidium* or *Mucor* are examples of less studied
89 fungal genera defined as “endophytes” (Zahoor et al., 2017; Zubek et al., 2016).

90 Some authors defined the term “endophytes” as either bacterial or fungal symbionts within plant tissues that,
91 during at least part of their life cycle, do not cause any visible signs of tissue damage or adverse effects on the host
92 (Kageyama et al., 2008; Schulz and Boyle 2005; Wilson, 1995).

93 Numerous reviews on plant-fungus relationships, plant-MTE interactions and fungus-MTE interactions exist
94 (Figure 1). Some of them combine plant, fungi and heavy metal relationships, but most of them are restricted to some
95 plants (trees for example) or some microorganisms (AMFs mainly, DSEs, bacteria, etc.). Only a few studies
96 considered the tripartite plant-endophyte-metal system at the whole ecosystem level, and even fewer used *in situ*
97 analyses. Despite the fact that the roles of fungal endophytes on plant metal tolerance, including DSEs, were well and
98 recently reviewed by Domka et al. (2019), the contemporaneous bibliography did not explore the phylogeny of this
99 large taxonomical group that is formed by endophytic fungi. Fungal endophyte biology may be highly diverse, and as
100 a result, the mechanisms of metal stress alleviation may vary between these groups, although some might be
101 conserved between closely related species.

102 Consequently, the objectives of this review are (1) to report phylogenetic relationships of fungal endophytes
103 described to date and (2) to explore their mutualistic function in the context of metal contamination and by way of
104 taxonomy. As roots are directly in contact with contaminated soil where MTE transfer occurs, we chose to inventory
105 root fungal endophytes exclusively. Thus, we answered the following questions: which are the fungal endophytes
106 present in plant roots? Do they participate in plant tolerance to metal contamination? Is there any evident relationship
107 between their mutualistic function and their taxonomy?

108 This review identifies fungal endophytes described in various plant roots and environments and places them in
109 a global phylogeny of Fungi. Then, different aspects of metal stress alleviation by endophytes are reported in light of
110 taxonomy. We propose future investigations to further elucidate the roles of endophytic fungi in plant metal tolerance.
111

112 Identification and phylogenetic analysis

113

114 This first chapter presents an inventory of fungal endophytes that were identified in plant roots (Table 1); this review
115 does not include mycorrhizal fungi. A total of 144 articles studied fungal root communities and identified them by

116 sequencing approaches. The complete inventory is available in the supplementary data (Table S1), with more than
117 1500 different species referenced. Hereafter, all orders of identified species are presented.

118 Root endophytes were found wherever scientists searched for them by using molecular sequencing. Indeed, from
119 grasslands to aquatic systems, deserts, forests, bogs, dunes, mountains and metal-polluted environments, fungi
120 belonging to 101 orders, 40 classes and 12 divisions were retrieved and included in this review. However, many fungi
121 are still of undetermined order.

122 Fungal communities may vary according to the season, site, soil characteristics and host plant. Root fungal
123 communities were extremely different between the early and late seasons in *Bouteloua gracilis* and *Gutierrezia*
124 *sarothrae* (Kageyama et al., 2008), and root culturable endophytes were strictly different between spring and summer
125 in the carnivorous plant *Drosera rotundifolia* (Quilliam and Jones, 2010). The colonization percentage by DSEs was
126 6-fold higher in May (12%) than in April (2%) in *Salix humboldtiana* (Becerra et al., 2009). Thus, communities of
127 fungal endophytes are highly variable in quality and quantity during the growing season, indicating temporal
128 variability, which may be related to different fungal growth velocities, different fungal phenologies or variable fungal
129 recruitment by the plant, depending on its growth state and environmental changes.

130 Endophyte communities also vary in terms of diversity and colonization levels between geographical sites. For
131 example, the DSE colonization percentage in *Solanum nigrum* varied from 1 to 10% between four sites at three
132 different elevations (Muthukumar and Sathya, 2017), and endophyte richness was greater in *Festuca paniculata* roots
133 in unmown grasslands than in mown grasslands, with Eurotiomycetes being specific to mown grasslands
134 (Mouhamadou et al., 2011). Local pedoclimatic conditions may represent abiotic filters limiting fungal colonization
135 and include the variation of physico-chemical parameters such as elevation, slope orientation, climate, and soil
136 characteristics (pH, N and K concentrations, granulometry, etc.). For instance, in the halophyte plant *Inula*
137 *crithmoides*, one undetermined DSE belonging to the Pleosporales was positively correlated with the salt gradient
138 (Maciá-Vicente et al., 2012). Nevertheless, these differences between sites may also be explained by limited fungal
139 dispersion or biotic filters or even by the abundance of DSEs in soil that were not systemically recorded.

140 Each order of Fungi is found in several types of plants (e.g., Pleosporales and Chaetosphaeriales in Orchidaceae, trees,
141 subshrubs and shrubs, Poaceae, and forest plants, while Pleosporales is also reported in aquatic plants, forbs,
142 halophytes, and hyperaccumulators) (Table 1, Table 2), indicating rather generalist plant-fungus associations.
143 However, fungal endophyte communities depend on the host plant. Indeed, endophytic assemblages differ between
144 two plant species belonging to the same genera, for example, between the halophyte *Inula crithmoides* and the non-

145 halophyte *Inula viscosa* (Maciá-Vicente et al., 2012). The frequencies of association between endophytes and different
146 trees (*Betula papyrifera*, *Abies balsamea*, and *Picea glauca*) revealed the preferences of some fungi for a specific tree;
147 for example, *Phialocephala fortinii* associates preferentially with *P. glauca* and *Oidodendron* sp. with *B. papyrifera*
148 (Kernaghan and Patriquin, 2011). Similarly, in two grasses, *Phoma herbarum* and *Microdochium* sp. were found only
149 in *Bouteloua gracilis*, whereas *Lophiostoma* sp. was found only in *Gutierrezia sarothrae* (Kageyama et al., 2008).

150
151 Root fungal endophytes were found among the great majority of Ascomycota (52 identified orders, Table 1), followed
152 by Basidiomycota, Chytridiomycota, Mucoromycota, and Oomycota (32, 5, 3 and 2 orders, respectively, Table 2).
153 Orders that are found in a large number of studies (more than a quarter of studies) are Hypocreales (Sordariomycetes),
154 Pleosporales (Dothideomycetes), Helotiales (Leotiomyces), Eurotiales (Eurotiomycetes) and Xylariales
155 (Sordariomycetes) (Figure 2).

156
157 Thus, fungal root endophytes are highly diverse. We placed them on a phylogenetic tree of Eumycetes (Figure 3).
158 Similar to foliar endophytes (Higgins et al., 2007), root endophytes are found throughout the phylogeny of Eumycetes
159 and do not form a monophyletic group. This suggests, similar to mycorrhizae (Fitter and Moyersoen, 1996), that the
160 ability to live within plant roots without harming them appeared several times in evolution.

161
162 Among all fungal endophytes, the dark septate endophyte (DSE) morphological group is commonly – and more than
163 other endophytes - studied for its potential beneficial association with plants. Several orders were reported to contain
164 DSEs: Capnodiales, Chaetosphaeriales, Chaetothyriales, Dothideales, Elaphomycetales, Eurotiales, Helotiales,
165 Hypocreales, Leotiales, Microascales, Onygenales, Pleosporales, Pezizales, Saccharomycetales, Sordariales,
166 Taphrinales, and Xylariales (Grünig et al., 2011; Jumpponen and Trappe, 1998; Knapp and Kovács, 2016; Newsham,
167 2011). DSEs therefore constitute a paraphyletic group (Yuan et al., 2011), defined by their similar morphology (*i.e.*,
168 intercellular melanised and septate hyphae and intracellular microsclerotia). We note that the seven orders that were
169 the most often found from our results (Hypocreales, Pleosporales, Helotiales, Eurotiales, Xylariales, Capnodiales and
170 Sordariales) are known to contain DSEs (Knapp and Kovács, 2016; Jumpponen and Trappe 1998; Newsham 2011).

171
172 Root fungal endophytes are commonly found in metal-contaminated soils (Domka et al., 2019; Lacercat-Didier et al.,
173 2016) and increase plant metal tolerance (Domka et al., 2019). The high diversity of root endophytes observed in this

174 study suggests that their roles in plant metal tolerance may strongly differ as well as their mechanisms of tolerance to
175 metal. Thus, in this work, the role of these organisms in plant metal tolerance and accumulation is analysed and
176 compared with respect to their taxonomic diversity.

178 Fungal endophytes and plant metal tolerance

179 We made an inventory of root endophytes that were experimentally tested on plants in the context of metal
180 contamination (Table 3). When described, we reported the effect of those endophytes on plant growth, metal uptake
181 and metal translocation from roots to aerial parts. A complete inventory of the effects of endophytes on other plant
182 traits in the context of metal contamination is available in the supplementary data.

183
184 Of the 118 plant-fungus associations for which the MTE was specified, Cd was the most commonly studied (49),
185 followed by Pb (24) and Zn (15) (Figure 4A). These contaminants are particularly abundant in anthropized soils,
186 especially originating from coal combustion (Bourennane et al., 2010; Senesil et al., 1999) and agriculture for Cd
187 (Bourennane et al., 2010). These three elements presented enrichment factors from 10 to 30 in soils of industrial
188 regions, much higher than those of other trace elements (Bourennane et al., 2010). A relatively equal number of
189 studies examining monocontamination (35 associations) or polycontamination (27 associations) was observed (Figure
190 4B). Nine pot experiments directly tested field soil or wastewater contamination, in contrast to the rest of the studies
191 that used artificially mono- or polycontaminated soils. Metal availability for plants is related to its speciation in soil
192 (Kabata-Pendias, 2004), which cannot be controlled in greenhouses. Using field soil as a substrate for experiments
193 limits this bias and should be encouraged, although it makes the interactions between different metals more complex.
194 Almost all tested endophytes led to better welfare of plants in the presence of MTE (Table 3, Table 4, Figure 5A).
195 Plant metal tolerance may be associated with both metal accumulation in roots - metal uptake (Figure 5B) or shoots -
196 metal translocation (Figure 5C) or with a reduction in the metal concentrations of plant parts (i.e., exclusion). This
197 shows two strategies of metal tolerance: MTE avoidance and MTE storage, confirming the previously reported smaller
198 inventory of Domka et al. (2019).

199 Metal uptake and metal translocation are not correlated (Table 4): fungi may increase metal concentrations in roots but
200 decrease metal translocation to shoots (like AMF (Miransari, 2011)). Fungi may also decrease metal uptake but
201 increase its translocation. Finally, metal uptake and translocation may both vary together, either increasing or

202 decreasing in the presence of fungi. These effects depend on fungus/plant/metal identities, with the same fungal
203 species having various effects according to its host plant and the contaminant. For example, *Trichoderma asperellum*
204 does not have any effect on *Lactuca serriola* growth (Ważny et al., 2018), whereas it favours onion and *Suaeda salsa*
205 growth in association with decreased metal uptake and translocation (Li et al., 2019; Téllez Vargas et al., 2017).
206 Similarly, *Penicillium janthinellum* facilitates metal exclusion in *Solanum lycopersicum* in the presence of Cd (Khan
207 et al., 2014) but increases metal accumulation in the presence of Al (Khan et al., 2015). Unfortunately, data are
208 lacking concerning metal uptake and translocation induced by many fungal endophytes.

209
210 These strategies are not linked with taxonomy, and much variability in strategies is observed, including within a single
211 species. We observed that some fungi, such as *Fusarium oxysporum*, commonly considered pathogens (Michielse and
212 Rep, 2009; Poletto et al., 2020), may have positive effects on plant growth in the context of metal contamination
213 (Mostafa et al., 2019). This fungus has also been shown to decrease some biomarkers of oxidative stress in the legume
214 *Cicer arietinum* under Cd contamination, probably acting like a filter (Laib et al., 2020).

215 Considering plant taxonomy, we did not observe any common strategies for trees or members of the Poaceae. Even for
216 a given plant species, different fungi may have different effects. Indeed, under Cd/Pb polycontamination, *Brassica*
217 *napus* is always stimulated by endophytes, but the metal uptake and translocation strategies differ; the fungal
218 endophyte *Lasiodiplodia* sp. increases metal uptake and translocation (Deng et al., 2014), whereas *Fusarium* sp.,
219 *Mucor circinelloides* and *Mucor racemosus* have no effect on these parameters (Shi et al., 2017; Zhu et al., 2015).
220 *Penicillium* sp. have no effect on metal uptake but increase Cd (but not Pb) translocation to shoots (Shi et al., 2017).
221 For *Zea mays*, metal uptake and translocation may be increased by some strains of the endophyte *Peyronellaea* sp.
222 (Shen et al., 2013), but metal translocation is decreased by *Exophiala pisciphila* (He et al., 2017; Li et al., 2011). Thus,
223 in the presence of metal, the different fungi present in a given plant could have antagonistic effects.

224
225 Therefore, fungal endophytes have more than one way to improve metal tolerance in plants, and the different
226 strategies are not linked to taxonomy. Different mechanisms of plant protection against MTE by fungal endophytes
227 were reviewed in Domka et al. (2019) : for example, endophytic fungi can accumulate high quantities of MTE in their
228 mycelia (48.6 mg Cr/g dry fungal biomass, corresponding to 81% of the total Cr in media concentrated at 600 µg/mL)
229 (Zahoor et al., 2017). The accumulation occurs through the production of metal chelating molecules such as
230 glutathione (GSH), phytochelatins and metallothioneins (Domka et al., 2019). These small molecules bind toxic

231 metals and lead to their detoxification and storage in the vacuole. Endophytic fungi may also secrete chelating
232 molecules in the rhizosphere, preventing metals from entering the root. These molecules include citrates, organic
233 acids, siderophores, exopolysaccharides (EPSs), and phenolic compounds. Melanin, present in the fungal cell wall, is
234 reported for its ability to bind metal ions. In contrast, fungi may improve plant metal accumulation by stimulating
235 plant detoxification systems. Endophytes may indirectly improve plant growth in contaminated soil in other ways,
236 such as the production of phytohormones or the mobilization of nutrients (Domka et al., 2019). If the global metal
237 content in roots or shoots is not an indicator of plant tolerance, it is possible that subcellular locations of metal ions
238 would be more important for plant welfare. The DSE *Exophiala pisciphila* was shown to increase the subcellular
239 compartmentalization of *Zea mays* in response to Cd and to engage in the remodelling of plant cell walls, correlating
240 with an increase in Cd content (Shen et al., 2020).

241 Thus, endophytic fungi may immobilize MTE in the rhizosphere or within their mycelia. They may also favour plant
242 (hyper)accumulation and storage and/or favour plant health independently of MTEs. All three strategies lead to better
243 tolerance of host plants to MTEs.

244 Perspectives on the roles of endophytic fungi in plant metal tolerance

245 Ecology and evolution of plant-endophyte associations

246 This review, including major inventories of root fungal endophytes and their effect on plant metal tolerance, highlights
247 the high taxonomic diversity of endophytes and their different effects on metal accumulation (uptake and
248 translocation) in plants.

249 We referenced endophytes identified in plants growing in all types of environments and representing a large
250 taxonomic diversity of Fungi. This suggests the convergent and redundant appearance of endophytism in different
251 times and spaces during the co-evolution of plants and fungi. Present in plants without generating any symptom of
252 disease, endophytes can shift their lifestyle, being latent saprotrophs or pathogens, temporary residents, mutualists or
253 commensal (Suryanarayanan, 2013). Some endophytes can survive as decomposers on leaves after the death of plant
254 tissues, suggesting that mutualism could derive from saprophytism (Suryanarayanan, 2013). This theory relates
255 directly to the saprotrophism, symbiosis and pathogenesis continuum described by Veneault-Fourrey and Martin
256 (2011) and the potential transition of some fungi from saprotrophism to the ectomycorrhizal lifestyle (e.g., brown-rot
257 fungi). Using a phylogenetic approach, Delaye et al. (2013) showed that at least four changes occurred in fungi when
258 shifting from endophytism to necrotrophism (fungi living in dead tissues) and at least four other different shifts occur

259 when the transition occurs in the opposite direction. However, when shifts occurred towards biotrophic pathogenicity,
260 no return towards endophytism occurred. Thus, pathogenicity is an evolutionarily stable trait, but endophytism is not
261 (Delaye et al., 2013). According to paleobotany, endophytism (including all living fungi in unharmed plant tissues)
262 dates as far back as 400 MYA in terrestrial plants with differentiated organs as well as in prostrate plants (Krings et
263 al., 2012). The major groups of Fungi were already diversified, and the structures involved in plant-fungus interactions
264 were similar to those of today. The association of plants with fungi may have been a prerequisite for land colonization
265 by plants.

266 This wide association between plants and fungi and the evolutionary convergence and redundancy of this association
267 raises the question of the costs and benefits of the association for both partners. Leaf endophytes may protect plants
268 against fungal pathogens, herbivory and abiotic stress but probably also interfere with photosynthesis (change the
269 photosynthetic spectrum, consume photosynthetates, and use CO₂ for respiration) (Suryanarayanan, 2013). Under
270 extreme resource limitation, because they utilize host photosynthates, endophytes are thought to be a cost for plants.
271 Indeed, the leaf endophyte *Neotyphodium lolii* was shown in *Lolium perenne* to reduce photosynthetic activity and the
272 proportion of living shoots (Cheplick, 2007). However, the costs and benefits of root endophyte associations in plants
273 as well as the costs and benefits from the point of view of the fungus are rarely discussed (but see Kusari et al.
274 (2012)).

275 MTE avoidance or accumulation

276 In this review, we particularly explored the benefits of root endophytes in plant metal tolerance. Two main strategies
277 of plant tolerance via fungi are observed: MTE avoidance and MTE accumulation.

278 We were not able to retrieve any fungal taxonomic patterns related to a given effect on plant metal tolerance:
279 taxonomy does not seem to be a good predictor of the diversity of mechanisms of plant metal stress alleviation by
280 endophytes. Furthermore, the same fungal species showed antagonistic effects on different plants, decreasing or
281 increasing metal accumulation. This is the case for *Piriformospora indica*, which increases wheat but decreases maize
282 metal uptake (Asilian et al., 2019; Shahabivand et al., 2012), or *Trichoderma asperellum*, which has no effect on
283 *Lactuca serriola* metal uptake and translocation but shows a negative effect on onion and *Suaeda salsa* metal uptake
284 and translocation (Li et al., 2019; Téllez-Vargas et al., 2017; Ważny 2018). It has been shown for AMF that fungal
285 tolerance may vary individually, with local adaptation to metal contamination at the intraspecific level (Colpaert et al.,
286 2004; Jourand et al., 2010; Vallino et al., 2011). Similarly, the endophyte *Peyronellaea* sp. displays various effects on
287 metal uptake and translocation, depending on the tested strain (Shen et al., 2013). Thus, further studies should be

288 developed to analyse the effects of each fungal species at the infraspecific level before integrating them at the fungal
289 community level to better assess their effect on plant metal tolerance. Fundamental studies should further identify
290 functional similarities between fungi that share the same strategies or the conditions that determine the balance
291 between different strategies.

292 **Mechanisms and evolution of metal tolerance in the plant-endophyte association**

293 Cellular mechanisms of metal tolerance pre-exist (i.e., are present but not necessarily expressed), including in some
294 plants growing in uncontaminated sites. These plants are able to grow when transferred to contaminated soil (Meyer et
295 al., 2016). In *Arabidopsis halleri*, the plasma membrane pump HMA4 (HEAVY METAL ATPASE 4) involved in
296 metal translocation and detoxification pre-existed before metal adaptation (Meyer et al., 2016). Metal tolerance may
297 also be the exaptation of another trait: “the current function of a trait may not be that for which the trait originally
298 evolved (the latter being adaptation)” (Boyd, 2004). Indeed, uptake and translocation of toxic elements use the same
299 mechanisms as those dedicated to the acquisition and transport of micronutrients (Tangahu et al., 2011). Plant metal
300 tolerance results from the presence of metal chelators (phytochelatins, metallothioneins, phenols, organic acids, etc.),
301 but also from the presence of molecules limiting oxidative stress, such as alpha-tocopherol or polyphenols, which
302 scavenge ROS and prevent lipid peroxidation (Singh et al., 2016). Glutathione is involved in the production of
303 phytochelatins and the reduction of oxidative stress (Zenk, 1996). Glutathione may be induced by the growth hormone
304 salicylic acid, which is known for regulating many physiological processes, such as local and systemic plant-pathogen
305 resistance and tolerance against abiotic stress (Singh et al., 2016). For both mycorrhizal and nonmycorrhizal fungi,
306 similar mechanisms have been described. Fungi may immobilize metal ions in soil through the excretion of chelators,
307 such as the glycoprotein glomalin from *Glomus* spp., and those on chitin-containing cell walls, which offer many
308 binding sites to metals (Bellion et al., 2006; González-Guerrero et al., 2009). DSEs constitutively produce melanin in
309 their cell walls, and melanin is an important antioxidant (Zhan et al., 2011). This pigment is shown to increase in the
310 presence of Cd (Zhan et al., 2011) and Pb (Ban et al., 2012), suggesting exaptation. In the cytosol, glutathione and
311 metallothioneins chelate metal ions, and efflux pumps are activated to transport these chemical complexes out of the
312 cell or into vacuoles. Finally, oxidative stress induced by metals is neutralized by the induction of superoxide
313 dismutase and the production of antioxidant molecules (Bellion et al., 2006; González-Guerrero et al., 2009).
314 Common molecules to both plant and fungal partners, such as polyphenols (Michalet et al., 2017; Pham et al., 2017),
315 glutathiones, metallothioneins, and metal transporters (González-Guerrero et al., 2009; Zenk, 1996), suggest a

316 potential interaction between the two partners. In particular, plant defences against MTEs (glutathione,
317 phytochelatins and metallothioneins) were reported to be either lowered when associated with an arbuscular
318 fungus (Ferrol et al., 2016; González-Guerrero et al., 2009), or increased (Ferrol et al., 2016). Those correlations
319 between symbiotic fungi and plant defences may be either related to direct production of defence molecules by
320 fungi, or induction of plant gene expression and protein synthesis by fungi (Ferrol et al., 2016). Basal (metabolic)
321 oxidative stress may be amplified by environmental stresses such as salt, cold or drought stresses (Xiong et al., 2002).
322 Thus, metal tolerance mechanisms could derive from plant adaptation to other abiotic stresses. In the same way, plant
323 metal tolerance inherited from the endophyte association may also be an exaptation of the plant-endophyte association
324 that could be seen as an extension of plant functional traits.

325 Conclusion

326 A wide variety of fungal endophytes are present in plant roots, all over the world and in all ecosystems where they
327 were searched. They belong in majority to Ascomycota, with some Mucoromycotina and Basidiomycota species. They
328 participate in plant tolerance to metal stress, improving plant growth and physiology. However, if root fungal
329 endophytes influence root metal uptake and root-to-shoot translocation, this is in an inconsistent way. Plant MTE
330 tolerance through the association with root endophytes may result from the beneficial interactions of this association
331 compared to plant investment in their own defence systems and common defensive molecules. The mutualistic
332 function of root fungal endophytes do not seem to be related to their taxonomy, since different association types are
333 observed intraspecifically.

335 Research perspectives

336 Endophyte research is often oriented to applications in phytoremediation, agricultural yield improvement or
337 metabolite production. Isolation of endophytes is therefore a purely technical step for many researchers, who thus do
338 not provide information such as plant tissue provenance (e.g., Biswas et al., 2020). It would be of great value to share
339 this information, which can be useful for more fundamental research (the previously cited article and others could not
340 have been included in this inventory for this reason).

341 Current research mainly focuses on Cd, letting the effects of other anthropically emitted MTEs, such as Cr and Ni, go
342 largely unexplored. Although approximately half of the studies combine several MTEs, we still do not have a clear
343 understanding of the interactions between MTEs *in situ* (Påhlsson, 1989). Studies using contaminated field soil are

344 encouraged. In amended soils, added metals will not be complexed as they would be *in situ*, leading to different
345 availabilities for plants. Using field soil as a substrate would help to control the bias of metal availability and gain
346 insights into interactions between MTEs. In addition, using field soil could help to determine the processes of
347 microflora recruitment and thus the stability of plant-fungi associations.

348 One could find here potential applications for phytoremediation: as endophytes stimulate plant growth and, in some
349 cases, phytoaccumulation of MTEs in aerial parts, we could argue that carefully chosen endophytes may be inoculated
350 into polluted soils with particular plants to increase the degree of phytoextraction of metals (Berthelot et al., 2017;
351 Deng and Cao, 2017). However, endophytes will be amended to existing communities, and though some studies have
352 been conducted on the competition between various fungi *in vitro* (Berthelot et al., 2019), we have little idea of their
353 competitive abilities against endogenous communities *in situ*. Further studies should thus include soil collected from
354 the field to disentangle those processes.

355 Competitive abilities of endophytes are not only determined by direct interactions between fungi, but also by their
356 interactions with the host plant and other microbial and biotic communities. Indeed, plants have evolved some
357 mechanisms to distinguish pathogens from beneficial microbes, through specific receptors, nutrient monitoring,
358 damage sensing, and probably other ways that remain to be explored (Plett and Martin, 2018). Some authors
359 hypothesised that under abiotic stresses, plants may recruit beneficial microbes through the modulation of root
360 secondary metabolism, helping them to better cope with these stress – the “plant call for help hypothesis” (Thijs et al.
361 2016). Future research should follow considering the mechanisms of the association between plant and fungi and its
362 dynamic: is this association randomly occurring? To what extent does plant recruit fungi that are the most beneficial
363 for it and how?

364 365 Conflict of Interest

366 The authors declare that the research was conducted in the absence of any commercial or financial relationships that
367 could be construed as a potential conflict of interest.

369 Funding and acknowledgements

370 This study was funded by a CDSN (Contrat Doctoral Spécifique Normalien). The authors thank the Initiative
371 Structurante EC2CO (Ecosphère Continentale et Côtière) - ECODYN (ECotoxicologie, EcoDYNamique des
372 contaminants) for their support. The authors also thank the two reviewers for their corrections and constructive
373 commentaries and Dr Laszlo Nagy and Dr Gergely Szöllösi for the authorization of the reuse of their figure.

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Figure Legends

Figure 1: Existing reviews on plant-fungi-MTE interactions. EM: Ectomycorrhiza Fungi, AMF: Arbuscular Mycorrhizal Fungi.

Figure 1: Number of references per order of fungal endophytes.

Figure 3: Endophytes in the phylogeny of Eumycetes. Root fungal occurrences are defined as one fungus/one plant host/one environment/one reference article. Modified from Nagy and Szöllősi (2017).

Figure 4: Research on fungal endophytes in relation to plant tolerance to MTE: which MTE and which protocol? A: number of counts for each metal; B: Number of counts for each protocole of contamination (mono-, poly- contamination or field soil). Each count corresponds to a line of the table 3, i.e. one fungus * one plant host genera * one response dynamic * one reference.

Figure 5: Fungal endophyte effects in the presence of metal on plant growth (A), metal uptake (B) and MTE translocation (C). Green: positive effect, red: negative effect, grey: neutral effect.

Table Legends

Table 1: Fungal root plant endophytes: Ascomycota. ND: not determined, NS: not specified.

Table 2: Fungal root plant endophytes except Ascomycota. ND: not determined, NS: not specified.

Table 3: Fungal endophytes and their effects on plant growth, metal uptake and translocation on metal-contaminated soil. Oth: other endophyte. Root metal concentration was included in metal uptake, and shoot metal concentration was included in metal translocation. A line corresponds to one fungus * one plant host genera * one response dynamic * one reference. Green: positive effect, red: negative effect, ocher: neutral effect. Rs: research, Rv: review.

Table 4: Correlation between the effects of fungal endophytes metal uptake and translocation. Green and bold writing: positive effect on plant growth, *: no effect on plant growth. Lines and columns: effects on metal translocation (lines) and uptake (columns): green: positive effect, red: negative effect, grey: neutral effect.

References Table 1 & 2

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Fungi

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Vergara 2019: *Trichoderma* and DSE
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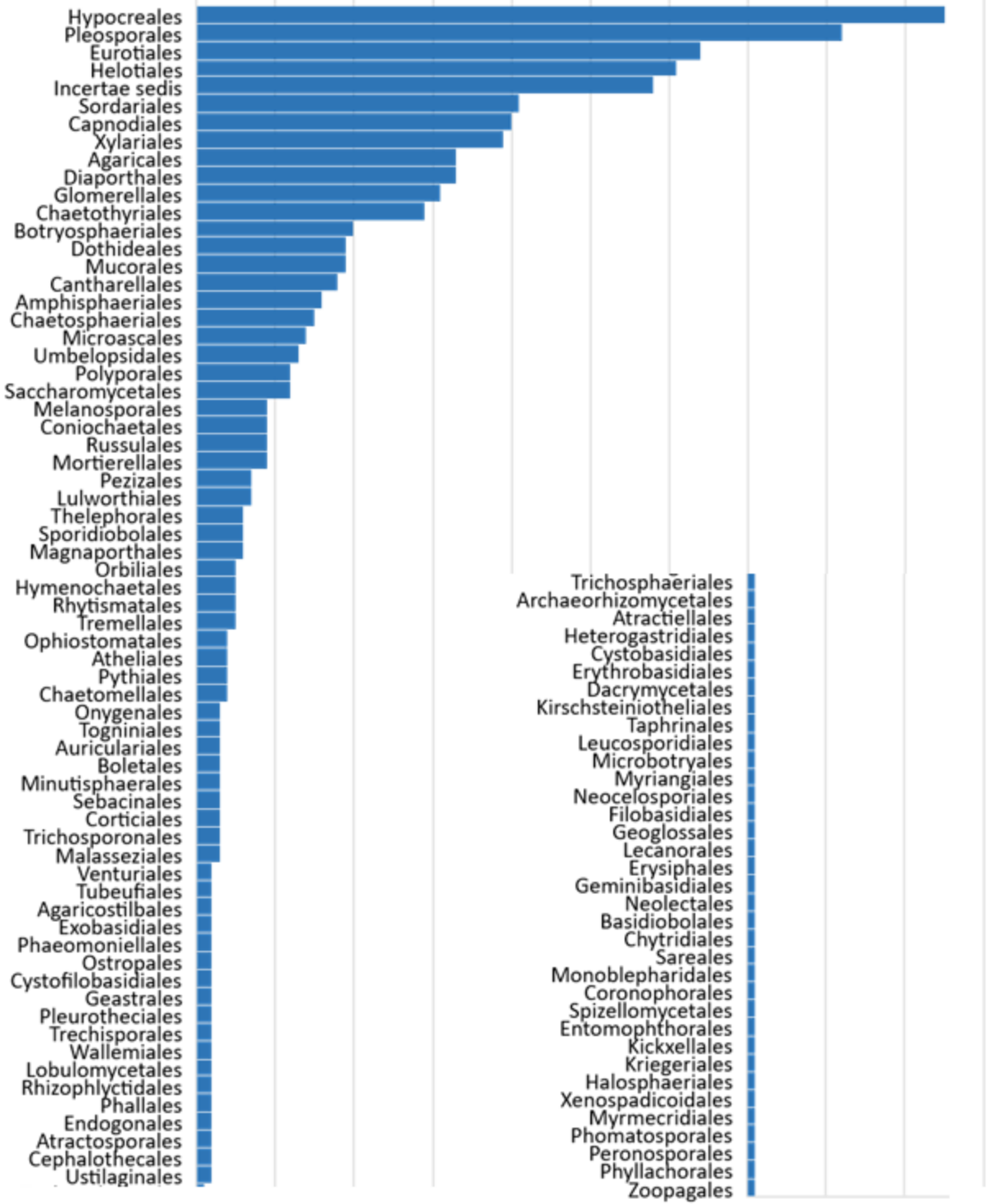
Plants

Heavy metals

Ghosh and Singh 2005
Yadav 2010
Singh 2016

Number of references

0 10 20 30 40 50 60 70 80 90 100

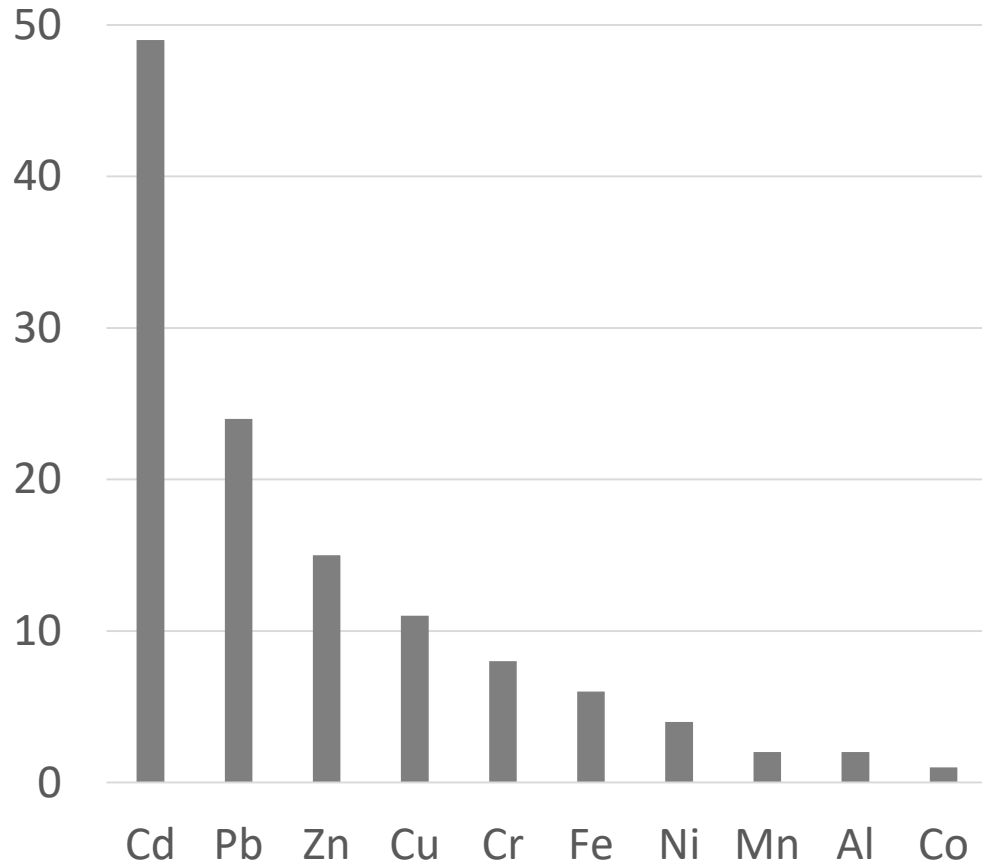




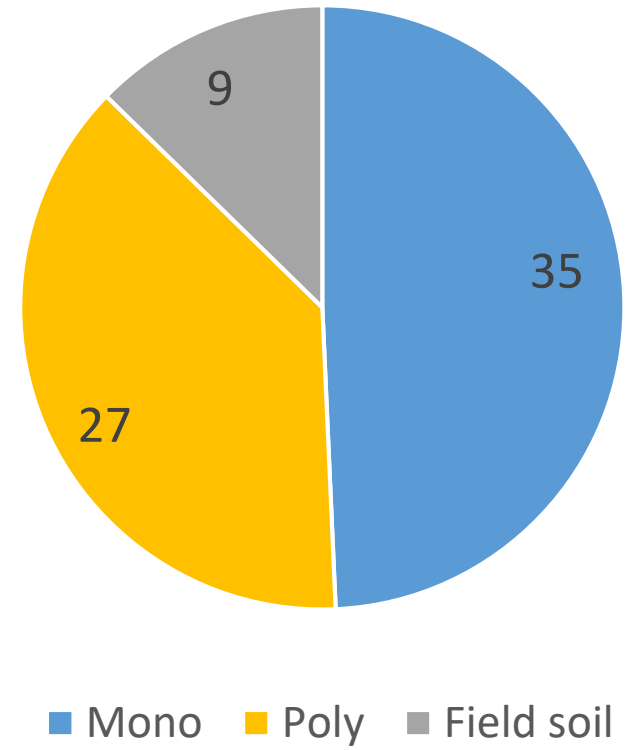
100 ≤ nb of occurrences
 10 ≤ nb of occurrences < 100
 nb of occurrences < 10

* Clade containing Dark Septate Endophytes (DSE)

A

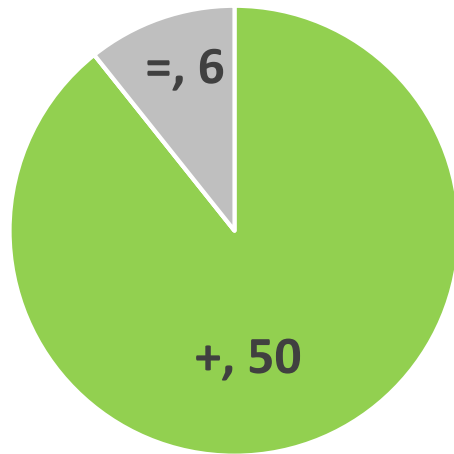


B



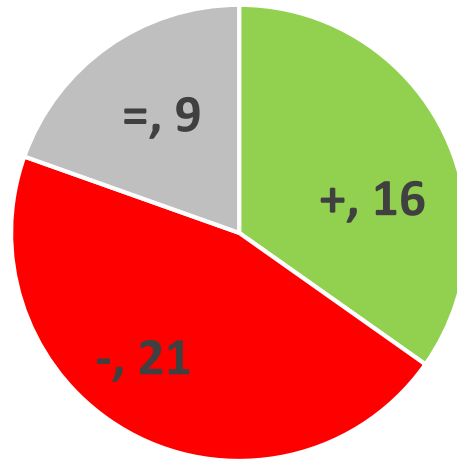
A

Plant growth, nutrition



B

Metal uptake



C

Metal translocation

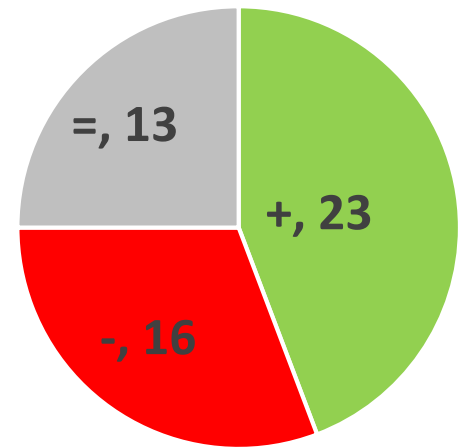


Table 1: Fungal root plant endophytes: Ascomycota. ND: not determined, NS: not specified.

Class (-mycetes)	Order	Type of plant	References
Archaeorhizo-	Archaeorhizomycetales	Forest plants	102
Asco-	Incertae sedis	Forb, Orchidaceae, Poaceae, Shrub, Subshrub, Tree	12, 17, 22, 48, 61, 68, 95, 120, 142
Asco-	ND	Forb, Orchidaceae, Poaceae, Shrub, Tree	3, 13, 33, 47, 82, 83, 91, 99, 100, 103, 110, 113, 120, 122
Chaetothyrio-	ND	Shrub	17
Coelo-	ND	Forb	13
Dothideo-	Botryosphaerales	Forb, Forest plants, Halophytes, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Subshrub, Tree	2, 6, 12, 20, 21, 28, 33, 48, 49, 62, 67, 81, 82, 85, 89, 102, 107, 109, 115, 116
Dothideo-	Capnodiales	Aquatic plant, Arborescent Poaceae, Forb, Forest plants, Halophytes, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Subshrub, Tree	2, 8, 12, 17, 19, 20, 21, 28, 29, 31, 38, 43, 49, 51, 54, 55, 57, 58, 62, 66, 68, 70, 74, 81, 82, 85, 90, 91, 92, 98, 102, 107, 109, 110, 112, 113, 116, 117, 122, 129
Dothideo-	Dothideales	Forb, Forest plants, Orchidaceae, Poaceae, Subshrub, Tree	9, 12, 16, 21, 28, 30, 32, 33, 43, 51, 57, 61, 87, 90, 91, 92, 102, 113, 131
Dothideo-	Incertae sedis	Forb, Forest plants, Orchidaceae, Poaceae, Shrub, Subshrub, Tree	4, 12, 33, 53, 70, 76, 81, 82, 87, 101, 102, 116, 120
Dothideo-	Kirschsteiniotheliales	Forest plants	102
Dothideo-	Minutisphaerales	Forest plants, Orchidaceae, Poaceae	12, 63, 102
Dothideo-	Myriangiales	Forest plants	102
Dothideo-	ND	Forest plants, Poaceae, Shrub, Tree	33, 64, 72, 76, 81, 90, 102
Dothideo-	Neocelosporiales	Shrub	81
Dothideo-	Pleosporales	Aquatic plant, Forb, Forest plants, Halophytes, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Subshrub, Tree, NS	2, 3, 4, 8, 9, 10, 12, 13, 16, 20, 21, 23, 27, 28, 29, 31, 32, 33, 34, 35, 36, 37, 41, 42, 43, 44, 45, 49, 50, 51, 53, 54, 57, 58, 62, 65, 66, 67, 68, 69, 70, 73, 76, 77, 78, 79, 80, 81, 82, 83, 85, 86, 87, 89, 90, 91, 92, 93, 97, 98, 101, 102, 104, 105, 107, 108, 109, 110, 113, 115, 116, 117, 120, 123, 128, 129, 131, 140, 141, 142, 143, 145
Dothideo-	Tubeufiales	Forest plants, Tree	65, 102
Dothideo-	Venturiales	Forb, Forest plants	102, 139
Eurotio-	Chaetothyriales	Forb, Forest plants, Halophytes, Orchidaceae, Poaceae, Subshrub, Tree, NS	4, 8, 12, 14, 20, 21, 22, 36, 43, 49, 51, 52, 55, 57, 62, 63, 66, 70, 72, 76, 83, 85, 91, 99, 101, 102, 118, 120, 121
Eurotio-	Eurotiales	Aquatic plant, Arborescent Poaceae, Carnivorous, Forb, Forest plants, Halophytes, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Subshrub, Tree, NS	1, 2, 9, 12, 13, 15, 16, 17, 19, 25, 29, 33, 34, 36, 39, 43, 44, 46, 48, 49, 51, 53, 54, 57, 61, 62, 66, 67, 68, 70, 73, 74, 81, 82, 85, 87, 88, 89, 90, 91, 92, 96, 101, 102, 104, 106, 107, 109, 110, 113, 115, 116, 117, 119, 120, 123, 125, 129, 131, 134, 135, 136, 137, 140
Eurotio-	ND	Forest plants, Tree	76, 102
Eurotio-	Onygenales	Hyperaccumulator, Poaceae	62, 86, 92
Eurotio-	Phaeomoniellales	Forest plants, Poaceae	102, 120
Geoglosso-	Geoglossales	Forest plants	102
Incertae sedis	Incertae sedis	Arborescent Poaceae, Fern, Forb, Forest plants, Orchidaceae, Poaceae, Shrub, Tree	2, 9, 10, 12, 13, 19, 21, 29, 45, 56, 57, 63, 82, 83, 93, 97, 102, 103
Incertae sedis	ND	Forb, Forb or Poaceae, Subshrub	44, 66, 87
Lecanoro-	Lecanorales	Poaceae	63
Lecanoro-	ND	Forest plants	102
Lecanoro-	Ostropales	Forest plants, NS	101, 102
Leotio-	Chaetomellales	Forb or Poaceae, Hyperaccumulator, Orchidaceae	20, 21, 62, 66
Leotio-	Erysiphales	Poaceae	120
Leotio-	Helotiales	Aquatic plant, Arborescent Poaceae, Carnivorous, Fern, Forb, Forest plants, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Subshrub, Tree, NS	2, 3, 4, 10, 12, 17, 19, 21, 29, 30, 33, 34, 36, 40, 44, 47, 48, 51, 52, 53, 54, 55, 56, 57, 58, 59, 61, 62, 63, 67, 68, 70, 72, 76, 79, 81, 82, 83, 87, 88, 92, 93, 95, 97, 98, 99, 100, 101, 102, 103, 107, 109, 114, 115, 118, 120, 122, 124, 128, 131, 145
Leotio-	Incertae sedis	Forb, Forest plants, Orchidaceae, Shrub, Tree, NS	10, 44, 51, 55, 61, 76, 81, 101, 102, 141
Leotio-	ND	Tree, Orchidaceae, Forest plants	20, 48, 102

Leotio-	Rhytismatales	Forest plants, Poaceae, Shrub, NS	81, 91, 92, 101, 102
ND	ND	Aquatic plant, Carnivorous, Forb, Forest plants, Halophytes, Orchidaceae, Poaceae, Shrub, Subshrub, Tree	17, 48, 51, 54, 55, 67, 72, 80, 81, 82, 88, 102, 106, 110, 129
Neolecto-	Neolectales	Forest plants	102
Orbilio-	ND	Orchidaceae	55
Orbilio-	Orbiliales	Forest plants, Orchidaceae, Shrub, Subshrub, Tree	12, 29, 78, 95, 102
Pezizo-	Pezizales	Forb, Forest plants, Poaceae, Shrub, Tree	12, 58, 81, 82, 86, 102, 103
Saccharo-	Saccharomycetales	Aquatic plant, Forb, Forest plants, Orchidaceae, Poaceae, Tree, NS	21, 51, 54, 55, 77, 90, 91, 92, 101, 102, 115, 144
Sareo-	Sareales	Shrub	81
Sordario-	Amphisphaeriales	Fern, Forb, Forest plants, Halophytes, Orchidaceae, Poaceae, Tree, NS	12, 21, 23, 28, 29, 49, 57, 68, 93, 101, 102, 107, 112, 113, 130, 138
Sordario-	Atractosporales	Forest plants, Tree	76, 102
Sordario-	Cephalothecales	Forest plants, Poaceae	91, 102
Sordario-	Chaetosphaeriales	Forest plants, Orchidaceae, Poaceae, Shrub, Tree, NS	4, 12, 33, 48, 55, 57, 58, 76, 92, 94, 101, 102, 107, 109, 145
Sordario-	Coniochaetales	Forb, Forest plants, Poaceae, Shrub, Tree	36, 48, 63, 66, 81, 87, 102, 126, 131
Sordario-	Coronophorales	Forest plants	102
Sordario-	Diaporthales	Forb, Forest plants, Halophytes, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Tree, NS	2, 12, 22, 23, 28, 29, 33, 34, 45, 51, 62, 65, 66, 67, 68, 73, 78, 81, 87, 90, 91, 92, 98, 101, 102, 109, 112, 115, 117, 119, 120, 144, 145
Sordario-	Glomerellales	Forb, Forest plants, Halophytes, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Tree	3, 4, 9, 12, 13, 20, 21, 22, 28, 34, 37, 43, 45, 49, 53, 62, 66, 73, 78, 79, 81, 91, 96, 98, 102, 104, 107, 110, 112, 115, 144
Sordario-	Halosphaeriales	Poaceae	86
Sordario-	Hypocreales	Aquatic plant, Arborescent Poaceae, Carnivorous, Fern, Forb, Forest plants, Halophytes, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Subshrub, Tree, NS	2, 3, 4, 5, 6, 7, 10, 12, 13, 15, 16, 17, 18, 19, 21, 22, 24, 28, 29, 31, 32, 33, 35, 36, 37, 41, 42, 44, 48, 49, 50, 51, 52, 57, 58, 60, 61, 62, 63, 66, 67, 68, 69, 70, 71, 72, 73, 74, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 96, 97, 98, 101, 102, 104, 105, 106, 107, 109, 110, 111, 113, 115, 117, 118, 119, 120, 123, 125, 126, 129, 130, 133, 136, 140, 141, 144, 145
Sordario-	Incertae sedis	Orchidaceae, Poaceae, Subshrub	12, 21, 33, 116
Sordario-	Lulworthiales	Forb, Poaceae, Shrub, Subshrub, Tree	2, 13, 51, 76, 82, 108, 116
Sordario-	Magnaporthales	Forb, Poaceae, Shrub	8, 33, 41, 62, 70, 145
Sordario-	Melanosporales	Forb, Forb or Poaceae, Orchidaceae, Shrub, Subshrub, Tree	12, 20, 21, 57, 66, 68, 81, 116, 140
Sordario-	Microascales	Forb, Forest plants, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Tree	2, 4, 5, 12, 13, 45, 57, 62, 67, 82, 91, 92, 102, 106
Sordario-	Myrmecridiales	Forest plants	102
Sordario-	ND	Forest plants, Orchidaceae, Poaceae, Shrub, Tree	33, 55, 76, 102, 145
Sordario-	Ophiostomatales	Forest plants, Poaceae, Tree	43, 50, 57, 102
Sordario-	Phomatosporales	Orchidaceae	12
Sordario-	Phyllachorales	Poaceae	92
Sordario-	Pleurotheciales	Forest plants, Poaceae	63, 102
Sordario-	Sordariales	Climber, Forb, Forest plants, Halophytes, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Subshrub, Tree	2, 5, 12, 13, 16, 20, 21, 23, 28, 29, 30, 41, 42, 49, 51, 53, 57, 61, 62, 63, 66, 67, 68, 69, 70, 72, 73, 81, 85, 86, 87, 91, 92, 102, 106, 107, 116, 123, 127, 129, 145
Sordario-	Togniniales	Forb, Forest plants, Tree	90, 102, 140
Sordario-	Trichosphaeriales	Poaceae	92
Sordario-	Xenospadicoidales	Forest plants	102
Sordario-	Xylariales	Forb, Forest plants, Halophytes, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Subshrub, Tree	2, 4, 5, 8, 11, 12, 20, 21, 22, 23, 28, 30, 32, 33, 34, 36, 37, 41, 45, 57, 62, 63, 66, 70, 72, 81, 85, 91, 92, 102, 103, 107, 112, 116, 119, 120, 123, 129, 140
Taphrino-	Taphrinales	Forest plants	102

Table 1: Fungal root plant endophytes except Ascomycota. ND: not determined, NS: not specified.

Division (-mycota)	Class (-mycetes)	Order	Type of plant	References
Basidio-	Agarico-	Agaricales	Aquatic plant, Forb, Forest plants, Orchidaceae, Poaceae, Shrub, Subshrub, Tree, NS	12, 17, 18, 21, 24, 28, 32, 33, 41, 42, 48, 50, 52, 54, 57, 58, 63, 64, 76, 85, 86, 91, 92, 94, 100, 101, 102, 108, 109, 120, 122, 140, 145
Basidio-	Agarico-	Atheliales	Forb, Forest plants, Shrub, Subshrub, Tree, NS	47, 52, 102, 131
Basidio-	Agarico-	Auriculariales	Forest plants, Orchidaceae, Tree	12, 76, 102
Basidio-	Agarico-	Boletales	Forest plants, Tree	76, 94, 102
Basidio-	Agarico-	Cantharellales	Aquatic plant, Forb, Forest plants, Orchidaceae, Poaceae, Shrub, Tree	2, 12, 16, 22, 33, 35, 54, 55, 58, 64, 75, 81, 83, 85, 94, 98, 102, 115
Basidio-	Agarico-	Corticiales	Forest plants, Poaceae, Subshrub, Shrub	52, 92, 102
Basidio-	Agarico-	Gastrales	Forest plants, NS	101, 102
Basidio-	Agarico-	Hymenochaetales	Forest plants, Orchidaceae, Poaceae, Shrub	12, 24, 42, 81, 102
Basidio-	Agarico-	Incertae sedis	Orchidaceae	12
Basidio-	Agarico-	ND	Forest plants, Shrub	102, 106
Basidio-	Agarico-	Phallales	Forest plants, Poaceae	86, 102
Basidio-	Agarico-	Polyporales	Aquatic plant, Forb, Forest plants, Orchidaceae, Poaceae, Shrub, Tree	8, 12, 61, 64, 68, 81, 92, 102, 106, 108, 132, 134
Basidio-	Agarico-	Russulales	Forest plants, Orchidaceae, Shrub, Tree	12, 43, 68, 76, 81, 86, 94, 102, 109
Basidio-	Agarico-	Sebacinales	Forest plants, Orchidaceae, Subshrub, Shrub	22, 52, 102
Basidio-	Agarico-	Thelephorales	Forest plants, Orchidaceae, Tree, NS	12, 47, 59, 94, 101, 102
Basidio-	Agarico-	Trechisporales	Forest plants	101, 102
Basidio-	Agaricostilbo-	Agaricostilbales	Forest plants, Poaceae	92, 102
Basidio-	Agaricostilbo-	ND	Forest plants	102
Basidio-	Atractiello-	Atractiellales	Tree	76
Basidio-	Basidio-	ND	Forb, Orchidaceae, Poaceae, Shrub	12, 23, 34, 52, 120, 122
Basidio-	Botryo-	Heterogastridiales	Forest plants	102
Basidio-	Cystobasidio-	Cystobasidiales	Forest plants	102
Basidio-	Cystobasidio-	Erythrobasidiales	Forest plants	102
Basidio-	Dacry-	Dacrymycetales	Forest plants	102
Basidio-	Exobasidio-	Exobasidiales	Forest plants, Halophytes	49, 102
Basidio-	Exobasidio-	Malasseziales	Forest plants, Poaceae	63, 102, 108
Basidio-	Incertae sedis	Incertae sedis	Forest plants	102
Basidio-	Microbotryo-	Incertae sedis	Forest plants	102
Basidio-	Microbotryo-	Leucosporidiales	Forest plants	102
Basidio-	Microbotryo-	Microbotryales	Forest plants	102
Basidio-	Microbotryo-	ND	Forest plants	102

Basidio-	Microbotryo-	Sporidiobolales	Forest plants, Orchidaceae, Poaceae, Subshrub, Tree	57, 91, 92, 102, 105, 116
Basidio-	ND	ND	Forest plants, Shrub, Tree	17, 57, 102
Basidio-	Puccinio-	ND	Forest plants	102
Basidio-	Tremello-	Cystofilobasidiales	Forest plants, Poaceae	92, 102
Basidio-	Tremello-	Filobasidiales	Forest plants	102
Basidio-	Tremello-	ND	Forest plants	102
Basidio-	Tremello-	Tremellales	Aquatic plant, Forb, Forest plants, Poaceae, Tree	43, 54, 92, 102, 142
Basidio-	Tremello-	Trichosporonales	Forb, Forest plants, Poaceae	37, 102, 120
Basidio-	Ustilagino-	Ustilaginales	Forest plants, Poaceae	92, 102
Basidio-	Wallemio-	Geminibasidiales	Forest plants	102
Basidio-	Wallemio-	Wallemiales	Forest plants, Poaceae	102, 120
Basidiobolo-	Basidiobolo-	Basidiobolales	Forest plants	102
Chytridio-	Chytridio-	Chytridiales	Aquatic plant	54
Chytridio-	Lobulo-	Lobulomycetales	Forest plants, Poaceae	102, 108
Chytridio-	Monoblepharido-	Monoblepharidales	Aquatic plant	54
Chytridio-	ND	ND	Aquatic plant, Poaceae	54, 108
Chytridio-	Rhizophlyctido-	Rhizophlyctidales	Aquatic plant, Forest plants	54, 102
Chytridio-	Spizello-	Spizellomycetales	Poaceae	64
Entomophthoro-	Entomophthoro-	Entomophthorales	Forest plants	102
Incertae sedis	Deutero-	ND	Forb	13
Incertae sedis	Incertae sedis	Incertae sedis	Tree	65
Kickxello-	Kickxellomycetes	Kickxellales	Forest plants	102
Kickxello-	Kickxellomycetes	Kriegeriales	Forest plants	102
Mortierello-	Mortierello-	Mortierellales	Forest plants, Halophytes, Poaceae, Orchidaceae, Shrub, Tree, NS	49, 52, 55, 58, 63, 68, 81, 92, 102
Mucoro-	Incertae sedis	Endogonales	Aquatic plant, Forest plants	54, 63
Mucoro-	Mucoro-	Mucorales	Forb, Forest plants, Hyperaccumulator, Non-hyperaccumulator, Orchidaceae, Poaceae, Shrub, Tree	12, 15, 26, 29, 43, 44, 57, 62, 66, 67, 68, 81, 85, 89, 96, 102, 107, 115, 135
Mucoro-	ND	ND	Tree	72, 76
Mucoro-	Umbelopsido-	Umbelopsidales	Forest plants, Orchidaceae, Poaceae, Shrub, Subshrub, Tree, NS	43, 48, 57, 61, 68, 72, 81, 100, 101, 102, 116, 118, 145
ND	ND	ND	Aquatic plant, Arborescent Poaceae, Carnivorous, Forb, Forest plants, Hyperaccumulator, Orchidaceae, Poaceae, Shrub, Subshrub, Tree	2, 9, 13, 16, 17, 19, 21, 22, 23, 24, 29, 30, 33, 35, 37, 40, 41, 43, 45, 48, 54, 58, 62, 65, 66, 67, 72, 79, 81, 83, 86, 88, 92, 95, 98, 99, 102, 103, 105, 108, 110, 120, 122, 133
Oo-	Oo-	ND	Forb	131
Oo-	Oo-	Peronosporales	Forb	131
Oo-	Oo-	Pythiales	Forb, Poaceae, Shrub, Tree	58, 78, 115, 131
Zoopago-	Zoopago-	Zoopagales	Tree	93
Zygo-	Zygo-	ND	Poaceae, Shrub	81, 96

Table 1: Fungal endophytes and their effects on plant growth, metal uptake and translocation on metal-contaminated soil. Oth: other endophyte. Root metal concentration was included in metal uptake, and shoot metal concentration was included in metal translocation. A line corresponds to one fungus * one plant host genera * one response dynamic * one reference. Green: positive effect, red: negative effect, ocher: neutral effect. Rs: research, Rv: review.

Division -mycota	Class -mycetes	Order	Fungal endophytes	Type of endophyte	Metal	Contamination	Plant	Type of article	Plant growth / nutrition	Metal uptake	Metal translocation	References
-	-	-	Endophyte community	Oth	Pb, Zn, Cd	poly (field soil)	<i>Arabis alpina</i>	Rs	+		-	Sharma 2019
-	-	-	Endophyte fungus	Oth	Cd	mono	<i>Lolium arundinaceum</i>	Rs	+	+	+	Ren 2011
Asco-	-	-	-	DSE	-	-	<i>Salix caprea</i>	Rv		-		Terhonen 2019
Asco-	-	-	-	DSE	-	-	-	Rv				Veragarame 2019
Asco-	Dothideo-	Botryosphaeriales	<i>Lasiodiplodia</i>	Oth	Cd, Pb	poly	<i>Brassica napus</i>	Rs	+	+	+	Deng 2014
Asco-	Dothideo-	Pleosporales	<i>Acrocalymma vagum</i>	DSE			<i>Tobacco</i>	Rs	+		-	Jin 2017
Asco-	Dothideo-	Pleosporales	<i>Acrocalymma vagum</i>	DSE	Cd	mono	<i>Medicago sativa</i>	Rs	+		+	Hou 2020
Asco-	Dothideo-	Pleosporales	<i>Acrocalymma vagum</i>	DSE	Cd	mono	<i>Ammopiptanthus mongolicus</i>	Rs	+		+	Hou 2020
Asco-	Dothideo-	Pleosporales	<i>Alternaria alternata</i>	Oth	Cd	mono	<i>Solanum nigrum</i>	Rs	+	-		Khan 2017a
Asco-	Dothideo-	Pleosporales	<i>Lewia sp.</i>	Oth	Pb	mono	<i>Festuca arundinacea</i>	Rs	+	+	no effect	Ortega-Aguilar 2020
Asco-	Dothideo-	Pleosporales	<i>Peyronellaea sp.</i>	Oth	Pb	mono	<i>Zea mays</i>	Rs	+ with some strains	+ with some strains	+ with some strains	Shen 2013
Asco-	Dothideo-	Pleosporales	<i>Peyronellaea sp.</i>	Oth	Zn	mono	<i>Zea mays</i>	Rs	+	+ with some strains	+	Shen 2013
Asco-	Dothideo-	Pleosporales	<i>Peyronellaea sp.</i>	Oth	Cd	mono	<i>Zea mays</i>	Rs	+	+ with some strains	+ with some strains	Shen 2013
Asco-	Eurotio-	Chaetothyriales	<i>Exophiala pisciphila</i>	DSE	Cd, Pb, Zn	mono	<i>Zea mays</i>	Rs			-	Li 2011
Asco-	Eurotio-	Chaetothyriales	<i>Exophiala pisciphila</i>	DSE	Cd	mono	<i>Zea mays</i>	Rs	+		-	He 2017
Asco-	Eurotio-	Chaetothyriales	<i>Phialophora mustea</i>	DSE	Cd	poly (field soil)	<i>Betula pendula</i>	Rs	+		no effect	Berthelot 2017
Asco-	Eurotio-	Chaetothyriales	<i>Phialophora mustea</i>	DSE	Cd	poly (field soil)	<i>Populus tremula x alba</i>	Rs	no effect		no effect	Berthelot 2017
Asco-	Eurotio-	Eurotiales	<i>Aspergillus flavus</i>	Oth	Cd, Ni	mono	-					Oyewole 2019
Asco-	Eurotio-	Eurotiales	<i>Aspergillus niger</i>	Oth	Cd, Ni	mono	-					Oyewole 2019
Asco-	Eurotio-	Eurotiales	<i>Paecilomyces</i>	Oth	Al, Cd,	poly (+ drought	<i>Glycine max</i>	Rs	+	-	-	Bilal 2020

Asco-	Sordario-	Glomerellales	<i>Glomerella truncata</i>	Oth	Cd	mono	<i>Solanum nigrum</i>	Rs	+ (Cd 15 mg/kg) or - (Cd 5 mg/kg)			Khan 2017b	
Asco-	Sordario-	Hypocreales	<i>Fusarium oxysporum</i>	Oth	Cd	mono	<i>Wheat</i>	Rs	-			Rahimi Tamandegani & Zafari 2019	
Asco-	Sordario-	Hypocreales	<i>Fusarium oxysporum</i>	Oth	Cd	mono	<i>Barley</i>	Rs	+			Mostafa 2019	
Asco-	Sordario-	Hypocreales	<i>Fusarium sp.</i>	Oth	Cd	mono	<i>Brassica napus</i>	Rs	+	no effect		no effect	Shi 2017
Asco-	Sordario-	Hypocreales	<i>Fusarium sp.</i>	Oth	Pb	mono	<i>Brassica napus</i>	Rs	+	-		no effect	Shi 2017
Asco-	Sordario-	Hypocreales	<i>Fusarium sp.</i>	Oth	Pb, Cd	poly	<i>Brassica napus</i>	Rs	+	no effect		no effect	Shi 2017
Asco-	Sordario-	Hypocreales	<i>Neotyphodium</i>	Oth	Cd	mono	<i>Festuca arundinacea, Festuca pratensis</i>	Rs	+	+		+	Soleimani 2010
Asco-	Sordario-	Hypocreales	<i>Purpureocillium sp.</i>	Oth	Cu	mono	<i>Kandelia candel</i>	Rs	+	-		-	Gong 2017
Asco-	Sordario-	Hypocreales	<i>Trichoderma asperellum</i>	Oth	Zn, Cd, Pb, Fe	Poly	<i>Lactuca serriola</i>	Rs	no effect			no effect	Wazny 2018
Asco-	Sordario-	Hypocreales	<i>Trichoderma asperellum</i>	Oth	Cu	mono	<i>Onion</i>	Rs	+	-		-	Télléz-Vargas 2017
Asco-	Sordario-	Hypocreales	<i>Trichoderma asperellum</i>	Oth	Pb	poly	<i>Suaeda salsa</i>	Rs	+	-		-	Li 2019
Asco-	Sordario-	Hypocreales	<i>Trichoderma asperellum</i>	Oth	Pb, Cd	mono	<i>Arabidopsis thaliana</i>	Rs	+			Zhang 2018	
Asco-	Sordario-	Hypocreales	<i>Trichoderma harzianum</i>	Oth	-	-	-	Book				Zaidi 2014	
Asco-	Sordario-	Hypocreales	<i>Trichoderma harzianum</i>	Oth	Cd, Mn, Ni, Pb, Zn	poly	<i>Salix fragilis</i>	Rs	+	no effect		+	Adams 2007
Asco-	Sordario-	Hypocreales	<i>Trichoderma logibrachiatum</i>	Oth	Pb	mono	<i>Helianthus annuus</i>	Rs				Devi 2017	
Asco-	Sordario-	Hypocreales	<i>Trichoderma pseudokoningii</i>	Oth	Cd, Cr, Cu, Fe, Zn	poly	<i>Pennisetum glaucum</i>	Rs	+	+			Firdaus-e-Bareen 2012
Asco-	Sordario-	Sordariales	<i>Chaetomium cupreum</i>	Oth	Cu	mono	<i>Eucalyptus globosus</i>	Prod of IAA and siderophores	+	-			Ortiz 2019
Basidio-	Agarico-	Polyporales	<i>Trametes hirsuta</i>	Oth	Pb	mono	<i>Triticum aestivum</i>	Rs	+	+		+	Malik 2020
Basidio-	Microbotryo-	Sporidiobolales	<i>Rhodotorula sp.</i>	Yeast	Cd, Cu, Pb	poly	<i>Brassica napus, B. alboglabra, B. campestris ssp. Cinensis var. utilis</i>	Rs	no effect			+	Wang 2013
Basidio-	Microbotryo-	Sporidiobolales	<i>Rhodotorula sp.</i>	Yeast	Cd, Cu, Pb	poly	<i>Brassica campestris ssp. Cinensis var.</i>	Rs				+	Wang 2013

										<i>communis</i>			
Mucoro-	-	-	<i>Mucor circinelloides</i>	Oth	Pb, Cd	mono	<i>Arabidopsis thaliana</i>	Rs	+				Zhang 2018
Mucoro-	-	-	<i>Mucor circinelloides,</i> <i>Mucor racemosus</i>	Oth	Pb, Cd	poly	<i>Brassica napus</i>	Rs	+	no effect	no effect		Zhu 2015
Mucoro-	-	-	<i>Mucor sp.</i>	Oth	Zn, Cd, Pb, Fe	poly	<i>Lactuca serriola</i>	Rs	+	+	+		Wazny 2018
Mucoro-	-	-	<i>Mucor sp.</i>	Oth	Zn, Fe	-	<i>Arabidopsis arenosa</i>	Rv		-	+		Rozpadek 2018
Mucoro-	-	-	<i>Mucor sp.</i>	Oth	Cd	-	<i>Arabidopsis arenosa</i>	Rs	+	no effect	+		Rozpadek 2018
Mucoro-	-	-	<i>Mucor sp.</i>	Oth	Zn, Cr, Co, Mn, Cu	poly	<i>Brassica campestris</i>	Rs	+	-			Zahoor 2017
Mucoro-	-	-	<i>Mucor sp.</i>	Oth	Zn, Fe	poly (field soil)	<i>Arabidopsis arenosa</i>	Rs	+	-	+		Rozpadek 2018
Mucoro-	-	-	<i>Mucor sp.</i>	Oth	Zn, Fe, Cd	poly (field soil)	<i>Arabidopsis arenosa</i>	Rs	+				Domka 2019

Table 1: Correlation between the effects of fungal endophytes metal uptake and translocation. Green and bold writing: positive effect on plant growth, *: no effect on plant growth. Lines and columns: effects on metal translocation (lines) and uptake (columns): green: positive effect, red: negative effect, grey: neutral effect.

		Metal uptake			No information on metal uptake
		-	=	+	
Metal translocation	-	<i>Trichoderma asperellum</i> <i>Rhizodermea veluwensis</i> <i>Phialocephala fortinii</i> <i>Penicillium roqueforti</i> <i>Penicillium funiculosum</i> <i>Penicillium janthinellum</i> <i>Purpureocillium sp.</i> <i>Paecilomyces formosus</i>		<i>Piriformospora indica</i>	<i>Endophyte community</i> <i>Exophiala pisciphila</i> <i>Phialocephala fortinii*</i> <i>Phialophora/Cadophora complex*</i> <i>Acrocalymma vagum*</i>
	=	<i>Fusarium sp.</i>	<i>Trichoderma asperellum*</i> <i>Fusarium sp.*</i> <i>Penicillium sp.</i> <i>Peyronella sp.*</i>	<i>Lewia sp.</i>	<i>Phialophora mustea</i> <i>Leptodontidium sp.</i> <i>Phialophora mustea</i> <i>Leptodontidium sp.</i> <i>Cadophora sp.</i>
	+	<i>Mucor sp.</i> <i>Penicillium sp.</i> <i>Glomerella truncata*</i>	<i>Mucor sp.*</i> <i>Penicillium sp.</i> <i>Peyronella sp.*</i>	<i>Lasodiplotia</i> <i>Phomopsis fukushi*</i> <i>Endophyte fungus*</i> <i>Neotyphodium</i> <i>Mucor sp.</i> <i>Peyronella sp.</i> <i>Penicillium janthinellum</i> <i>Glomerella truncata</i> <i>Trametes hirsuta</i>	<i>Acrocalymma vagum</i> <i>Scytalidium lignicola</i> <i>Trichoderma harzianum</i>
No information on metal translocation		<i>Alternaria alternata</i> <i>Fusarium oxysporum*</i> <i>Chaetomium cupreum</i> <i>Piriformospora indica*</i> <i>Mucor sp.</i>		<i>Aspergillus flavus*</i> <i>Aspergillus niger*</i> <i>Penicillium terreus*</i> <i>Aspergillus flavus</i> <i>Penicillium chrysogenum</i> <i>Trichoderma pseudokoningii</i> <i>Rhodotorula sp.*</i>	<i>Aspergillus flavus*</i> <i>Aspergillus niger*</i> <i>Penicillium notatum*</i> <i>Exophiala pisciphila</i> DSE* <i>Trichoderma harzianum*</i> <i>Trichoderma logibrachiatum*</i> <i>Trichoderma asperellum</i> <i>Fusarium oxysporum</i> <i>Mucor circinelloides</i> <i>Mucor racemosus</i> <i>Mucor sp.</i>