The role of mycorrhizal symbioses in phytotechnology

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Abstract

There is a growing interest in using plants to provide low-cost ecosystem services in a diversity of environments (e.g., polluted, degraded, urban). These utilizations of plants are collectively referred to as phytotechnologies. Many plants used in phytotechnological applications are naturally found to associate with mycorrhizal fungi. These fungal associates can provide numerous ecosystem services, or help plants to do so. There is thus an obvious incentive to better understand how mycorrhizal symbioses can assist phytotechnologies. For some phytotechnological applications, the benefits of using mycorrhizal fungi seem well established while for others, these benefits are either uncertain or simply unexplored. In all cases, a trait-based, mechanistic understanding of what allows mycorrhizal fungi to provide any benefit/service is urgently needed. This will help to develop reliable, mycorrhizas-assisted phytotechnologies in the future, while also improving our fundamental understanding of the evolution of stress tolerance in these important plant-associated symbionts.

Keywords: phytoremediation, phytostabilization, green roofs, pollution, treatment wetlands, constructed wetlands, ecological restoration.

In the last two or three centuries, the rapid development of urban centers, and more recently the intensification of agricultural practices, have given rise to a myriad of environmental issues. These include the pollution of soils with heavy metals and organic compounds, the loss of soil structure, and the increase in wastewater volumes. Phytotechnology is a domain of applied science and engineering that focuses on the use of plants to provide cost-effective, sustainable solutions to these environmental issues (Mangkoedihardjo 2007). Treatment (or constructed) wetlands, soil phytoremediation, green roofs and green stormwater facilities are all examples of phytotechnological approaches. Although phytotechnologies are plant-based systems, their driving mechanisms often involve microbial processes taking place in the rhizosphere. Among the plants' microbial associates, mycorrhizal fungi (MF) are especially important, as they can receive up to 20% of plants' photosynthates and constitute around the third of soil microbial biomass (Leake et al. 2004). In the context of phytotechnology, MF can alleviate plant stress through a wide variety of mechanisms, including the provision of growth-limiting nutrients, the alteration of the host hormonal balance and the sequestration of heavy metals in the soil. This allows plants to provide more efficiently some key phytotechnological services. Also, MF can provide by themselves some services, for example by ameliorating soil structure (Kohler et al. 2017). However, for many phytotechnological applications, the role of MF remains unclear, either because it has only been rarely investigated (e.g., green roofs) or because it is expected to have little influence (e.g., treatment wetlands dealing with nutrient-rich wastewaters, considering that MF typically reduce in abundance in nutrient-rich systems [Smith and Read 2008]). Here, we broadly review

the empirical evidence that MF can influence the success of phytotechnologies. We also identify key traits of MF that are likely to promote specific phytotechnological applications. We focus our review on four of the most familiar phytotechnologies: (1) phytoremediation, (2) stabilization of degraded soils, (3) treatment wetland, and (4) green roofs and green walls (Table 1).

1. Phytoremediation

Contamination of soils with toxic compounds such as heavy metals or oil products is a pervasive environmental problem (Varkey et al. 2012). These contaminants are associated with a variety of human activities such as mining, combustion of fossil fuels, and the application of pesticides in agriculture (Clemens 2006). Their accumulation in the environment represents a hazard to human health, and also compromises plant and microbial growth. However, their removal from soils is often very costly, such that large contaminated areas often cannot be remediated through chemical extraction. The use of plants to either stabilize, volatilize or extract these inorganic or organic pollutants (referred to as phytoremediation), on the other hand, may represent a cost-effective way to ameliorate soil conditions.

For phytoremediation of heavy metals, many studies have aimed at identifying plants that can both (1) tolerate high soil metal concentrations and (2) produce large amounts of biomass where heavy metals can be highly concentrated (the so-called “hyperaccumulators”) (Gamalero and Glick 2012). However, a large amount of

research trying to identify metal-accumulating plants focused on *Brassica*, a plant genus that does not form symbiotic associations with MF. Yet, MF could be expected to increase the efficiency of phytoremediation practices, in various ways (reviewed in Hassan et al. 2010). For example, arbuscular mycorrhizal (AM) fungi have sometimes been shown to promote the immobilization of metals in soil (Wu et al. 2016), which could be explained by the binding of heavy metal cations to (1) cell wall components (i.e., glomalin; Gonzalez-Chavez et al. 2004; Wu et al. 2014) or (2) vacuolar polyphosphates bearing negative charges (Leung et al. 2013). Janouskova et al. (2006) showed, in fact, that extraradical hyphae of some AM fungi could be up to 20 times more efficient in binding Cadmium (Cd) than tobacco roots. Joner et al. (2000) also showed that AM fungal strains isolated from sites polluted with heavy metals were even more efficient at binding Cd and Zn on their hyphae than strains isolated from unpolluted environments. Other studies have also found that AM fungi could prevent the translocation of metals from roots to shoots (Marques et al. 2007; Affholder et al. 2014), which can be due to the accumulation of metals bound to plant cell walls (Almeida-Rodriguez et al. 2016). Similarly to AM fungi, some ectomycorrhizal (ECM) and ericoid mycorrhizal (ERM) fungi have also been shown to protect plants from heavy metals through various mechanisms (Colpaert et al. 2011; Daghino et al. 2016), including the sorption to cell wall components, the segregation into cellular structures, or the chelation in the cytosol by metallothioneins (Nguyen et al. 2017).

Regarding the impact of MF on net metal uptake, empirical evidence is mixed, some studies showing that MF could acidify neighbouring soil and promote solubilisation and uptake of metals (Leyval and Joner 2001), and others showing that metal uptake could be reduced by MF, thus reducing toxicity to plants (Wang et al. 2007). We still need to clarify what mycorrhizal fungal traits are important to influence metal uptake. For example, many studies have shown that MF could promote rock weathering through the production of organic acids (ectomycorrhizal fungi: Jongmans et al. 1997; Quirk et al. 2014; Schmalenberger et al. 2016 / arbuscular mycorrhizal fungi: Burghela et al. 2015): these could also solubilize heavy metals or other toxic elements. For example, organic acids can complex with Al and reduce its toxicity (Seguel et al. 2013). Mycorrhizal fungi can also produce chelating, metal-binding agents (Haselwandter et al. 2006; Winkelmann et al. 2007) or promote the growth of siderophore-producing bacteria in their hyphosphere (Franco-Correa et al. 2010). These traits, and potentially others as well (see Hassan et al. 2010), could be linked to increased metal uptake and transfer to plants. More work will thus be needed to evaluate the net impact of MF on the phytoextraction of metals. Even if MF often increase metal tolerance of hosts, if they accomplish this through reduced uptake of metals, or reduced transfer to hosts, then the goal of phytoextraction is not met (provided that the goal is to extract, and not only stabilize, metals). On the other hand, it must be noted that even if MF reduce metal uptake by the plant (thus reducing metal concentration per unit of plant tissue), the total amount of metal extracted from the soil can still be increased by MF if mycorrhizal plants produce much more biomass overall, as it is often seen in stressful environments (Smith and Read 2008).

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133 Phytoremediation also addresses the role of plants in detoxifying soils contaminated
134 with persistent organic pollutants (POPs, e.g., polychlorinated biphenyls [PCB],
135 dichlorodiphenyltrichloroethane [DDT]) (Infante et al. 2012). Here, the role of plants
136 is rather to promote the activity of soil microbes having the ability to degrade these
137 organic compounds. It is expected that root exudates can promote the growth of POP-
138 degrading microbes, since those exudates can provide a labile carbon (C) source and
139 sometimes a N source to support microbial metabolism (Alkorta and Garbisu 2001).
140 Accordingly, rhizosphere microbial populations are much larger than in the
141 surrounding bulk soil (e.g., Lopes et al. 2016). This was correlated with an enhanced
142 degradation of pesticides in rhizosphere soil (Anderson et al. 1994). MF associated
143 with plants are also well known to exude labile C compounds (Jansa et al. 2013),
144 which in turn can stimulate bacterial growth (e.g., Toljander et al. 2007) and could be
145 expected to favor the growth of POP-decomposing microbial populations (Lenoir et
146 al. 2016). In fact, it has recently been shown by Paterson et al. (2016) that AM fungi
147 can strongly prime the decomposition of soil organic matter; they could therefore
148 prime the degradation of POPs through similar mechanisms. Moreover, AM fungi
149 have been shown to modify plant exudates (e.g., Hage-Ahmed et al. 2013), which
150 could indirectly influence, and potentially promote, POP-degrading microbial
151 populations. This is consistent with the study published by Corgié et al. (2006),
152 showing increased population sizes of POP-degrading culturable bacteria in soils
153 colonized by AM roots. MF may also directly influence POP degradation through
154 their own enzyme secretion. For example, ECM and ERM fungi are known to express

laccases (Burke and Cairney 2002), which can attack organic matter through oxidative mechanisms (Lindhal and Tunlid 2015): these could thus break down POPs more specifically. Accordingly, several studies using pure liquid ECM fungal cultures have found them to be sometimes almost as efficient as white rot fungi, which are well known to oxidize soil organic matter (e.g., Braun-Lülleman et al. 1999). Regarding AM fungi, several genes in the genome of the model species *Rhizophagus irregularis* have been identified as potentially associated with POPs degradation (Lenoir et al. 2016). However, some studies have shown that MF can in fact delay organic matter decomposition (e.g., ECM fungi: Gadgil and Gadgil 1971 /AM fungi: Verbruggen et al. 2016), and more specifically POP degradation (Genney et al. 2004), which could be explained by competitive/antagonistic interactions between MF and other soil microorganisms.

Future work addressing the potential for MF to assist phytoremediation of sites contaminated with heavy metals or POPs should aim at identifying the fungal traits associated with increased remediation (Table 1). For example, tropical grasses producing large amounts of thin roots have been shown to better promote POPs breakdown in their rhizosphere in a greenhouse assay (Merkl et al. 2005). Likewise, similar studies must identify what traits best promote the phytoremediation potential of MF, which is known to vary among species (Liu and Dalpé 2009; Hassan et al. 2013). Since local, stress-adapted strains of MF have often been shown to be more effective to remove contaminants or at least promote plant growth in stressful environments (e.g., Cabello et al. 1999; Joner et al. 2000; Vivas et al. 2006; Lacercat-

Didier et al. 2016), comparing the traits of these strains to the traits of strains from nearby, unpolluted environments may be a useful starting point. Indeed, it has been shown several times that polluted soil can retain a high diversity of AM fungi (e.g., de la Providencia et al. 2015), although these communities are often dominated by closely related members of specific families (Hassan et al. 2014; de la Providencia et al. 2015; Krishnamoorthy et al. 2015), which further suggests that key traits favor the success of MF in such stressful habitats (see Hassan et al. 2010). Other studies have found that organic contaminant spills decreased ECM fungal community diversity, retaining only (and potentially favouring) strains that were resistant to the pollutant (Nicolotti and Egli 1998). The nature of these resistance traits still remains elusive. They may relate to changes in enzyme secretion, or membrane or cell wall composition, but may also be behavioural. For example, since POPs may harm fungal membranes (Robertson et al. 2007), they could be expected to favour more intraradical biomass production, at the expense of less soil hyphal biomass. However, less soil hyphal production could mean less C transfer from MF to POP-degrading microbial populations and fewer nutrients transferred to plants. The latter may influence plant performance, because high loads of POPs in the soil can strongly increase carbon:nutrients ratios, and exacerbate plant-microbial competition for nutrients (Robertson et al. 2007). A reduced transfer of nutrients by plants through their mycorrhizal symbionts may thus strongly decrease their fitness. The upcoming challenges are thus to (1) clarify what fungal traits favour their resistance to environmental contaminants and (2) evaluate whether resistance-traits make MF more

or less efficient in dissipating these contaminants, either through direct removal or through altered plant performance.

2. Stabilization of degraded soils

Human activities worldwide greatly contribute to soil erosion and loss of structure (Pimentel et al. 1995). A major cause for increased slope instability or soil erosion is the loss of plant cover (Auzet et al. 2006), and various approaches and technologies have been developed to limit soil erosion by re-establishing vegetation and applying various amendments to the soil (Blanco-Canqui and Lal 2010). It has been shown that an efficient management of degraded soils can reduce soil erosion by a factor of 50 (de Santisteban et al. 2006). MF are known to ameliorate soil structure in various ways, including shifts in host root system architecture, enmeshment of soil particles with hyphae and changes in soil moisture regimes (Rillig and Mummey 2006). However, plant and fungal species vary substantially in their effect on soil aggregation (e.g., Rillig et al. 2002; Piotrowski et al. 2004). We still lack a predictive framework linking root and hyphal traits to soil structure (Rillig et al. 2015). However, through a meta-analysis, Leiheit et al. (2015) have identified in what experimental conditions AM fungi have been found to be most efficient in promoting soil aggregation: they reported, for example, that AM fungi were more likely to improve soil structure in pot studies with near neutral soil pH. Such analyses, combined with additional experimental work, will provide some guidelines regarding the environmental conditions where MF are expected to be most useful in soil conservation and management practices. But as stressed by Rillig et al. (2015), there

is a need to develop a trait-based framework in order to predict the ability of various MF (both AM and ECM) to improve soil structure (Table 1). The authors highlighted traits for further investigation such as hyphal length density or growth rate, as well as longevity. We could add to this list traits related to the amount of C transferred by MF to soil bacteria: the latter are expected to stabilize microaggregates (Tisdall 1994). It would also be valuable to investigate how shifts in root system architecture due to root colonization by MF influence soil aggregation: the reduced specific root length and branching intensity found in some colonized plants (e.g., Hetrick et al. 1988) could in fact reduce the positive impact of roots on soil aggregation.

We also need to gather data about trait-environment linkages. When developing mycorrhizal fungal inocula (AM, ECM or ERM) for application in soil restoration projects, it is not only important to select and multiply fungal species with optimal traits: we need to ensure that our inocula will perform well under the environmental conditions where they will be applied. Such knowledge about trait-environment relationships is especially scarce in the mycorrhizal literature. There are some data linking, for example, spore size and phenology to disturbance regimes (e.g., Oehl et al. 2009), but regarding traits of interest in the context of soil aggregation (see Rillig et al. 2015), virtually nothing is known. Data on trait-environment relationships would also be useful in situations where fungal inoculation is hardly feasible: it could rather be envisaged to apply various amendments to modify the abiotic environment in a way that is expected to favor specific, desired fungal traits. For example, if high soil hyphal biomass is a desirable trait in a given applied context, applying N

fertilizers may promote a P limitation of some AM fungi that will favour their soil hyphal biomass production (Johnson et al. 2003).

Similar data are also needed to evidence linkages between plant and fungal traits. To quickly restore a dense vegetation cover that will efficiently ameliorate soil structure, we need to apply optimal mixtures of plants and mycorrhizal fungal species. It has been shown that soil-based inocula can influence our success in establishing a target vegetation (Middleton and Bever 2012). Likewise, various methods to establish a plant cover differentially impact the AM fungal community: van de Voorde et al. (2010) found that sowing plant communities (compared to unsown communities relying on plant propagule bank) led to more spatially homogeneous AM fungal communities (i.e., reduced beta-diversity). Future research will have to dissect these community-level patterns to evidence linkages between plant and fungal traits. For example, Chagnon et al. (2015) have sampled young regenerating forests, and correlated plant traits to the identity of their AM fungal partners. They found that plants with resource-conservative leaf traits (e.g., *Spiraea alba* var. *latifolia* having high leaf dry mass content) associated with different AM fungi as compared to plants with resource-acquisitive traits (e.g., *Clematis virginiana* having high specific leaf area). The next frontier will be to ask what fungal traits are promoted in the rhizosphere of a plant bearing specific root traits, and vice versa. Better understanding the linkages between the traits of plants and their mycorrhizal symbionts will help to design specific plant-fungal mixtures that are most efficient in restoring structure in degraded soils.

3. Treatment wetlands

Treatment wetlands (TW), also known as “constructed wetlands”, are artificial wetlands that can be designed to treat a variety of water types (e.g., agricultural runoff, industrial contaminated water, domestic wastewater) in order to improve its quality (e.g., by removing pollutants, nutrients and/or dissolved organic matter). Their use has increased tremendously since the 1990’s, as there were some clear examples of successful implementations of this phytotechnology over the years. For example, TW were established under a cold climate in Norway in order to treat domestic wastewaters, and they allowed the reduction of BOD (biological oxygen demand, which is the oxygen required by aerobic organisms to degrade the organic matter in a water body) of these wastewaters by 90% (Paruch et al. 2016). TW, at least those referred to as “sub-surface”, are typically planted with large aquatic plants such as reed (*Phragmites australis*) and cattails (*Typha* spp.), which produce large amounts of roots and rhizomes (Brisson and Chazarenc 2009; Vymazal 2011). It is often assumed that pollutant removal efficiency in TW is correlated with enhanced plant (especially root) biomass production. It is also recognized that transformation and removal of most pollutants in TW is primarily due to bacterial activity (Faulwatter et al. 2009).

Now, can MF be of any help here? The soil environment in TW is typically very nutrient rich, especially TW receiving domestic wastewater, and the rhizosphere environment is flooded or highly humid. Both AM and ECM fungi are well known to

decrease in abundance in fertile systems (e.g., Smith and Read 2008; Bahr et al. 2013), and there is some evidence that low oxygen pressure is also detrimental to AM fungi (Le Tacon et al. 1983). On the other hand, some AM fungi are known to persist in fertile soils (e.g., Johnson et al. 1993) and poorly oxygenated substrates such as peat bogs (Thormann 2006). In surveys of natural wetland plants, symbioses with AM fungi have been found to be the norm rather than the exception (extensively reviewed by Xu et al. 2016). Moora et al. (2016) also have found that AM fungi colonizing the roots of a submerged aquatic plant comprised a high proportion of novel taxa and a non-random subsample of already known taxa, suggesting that AM fungi growing in these habitats may bear specific traits allowing them to adapt to such unique conditions.

Likewise, in a TW, Fester (2013) found extensive AM fungal colonization, and molecular analyses revealed that the community was largely dominated by generalist taxa recognized as ruderals (e.g., *Funneliformis mosseae* and *Rhizophagus irregularis*, Chagnon et al. 2013). This suggests that in the context of TW, AM fungi could be expected to successfully colonize plants and potentially favor their growth. In fact, Lingua et al. (2015) did find that AM fungal inoculation improved NO_3^- removal from wastewaters. However, other reports from natural wetlands or TW suggested that AM fungal abundance could decrease due to flooding (Cantelmo and Ehrenfeld 1999), high water P concentrations (Cornwell et al. 2001; Wang et al. 2014) or high organic matter content (Confer and Niering 1992). Some studies have also shown a decrease in arbuscule formation as compared to other fungal structures

in flooded and high-nutrient wetlands or TW (e.g., Cantelmo et al. 1999; Wang et al. 2014; but see Miller et al. 2000). Given that the arbuscules are the main site of nutrient delivery to plants in the AM symbiosis (Smith and Read 2008), these results might suggest that in natural wetlands or in TW, the main function of the symbiosis shifts from nutrition to, for example, pathogen protection. Little is known about the accumulation of root pathogens by TW plants, but we know that some AM fungi can be very efficient at protecting their hosts against pathogens (e.g., Sikes et al. 2009).

Overall, empirical assessment of the presence, the importance or even the role of MF in TW remains scarce in the literature. Future work will be required to better evaluate their importance, quantify their impact on plant growth and functioning, and elucidate traits which allow MF to persist in TW (Table 1). We could then envisage the development of inoculation strategies aimed at introducing TW fungal strains that either possess traits that favor a given ecosystem service (e.g., larger hyphal networks stabilizing contaminated sediments) or traits that better promote the growth of plants, which can in turn provide services through their own root systems. For example, plants can provide a substrate and exudates to support microbial biofilm formation and metabolic activity (Brix 1997), or take up nutrients from eutrophicated waters. However, compelling evidence that MF do provide benefits in TW must first be produced.

4. Green roofs and walls

Green roofs have recently emerged as a promising phytotechnology providing, in urban ecosystems, a variety of benefits including the reduction of stormwater outputs through roof leachates and the regulation of building temperatures (Oberndorfer et al. 2007). Likewise, green or vegetated walls can also help to regulate indoor building temperatures: Hoyano (1988) found that vegetated walls could reduce indoor air temperature by 7 °C. However, green roofs and walls present unique challenges to plants, namely a thin substrate and a strong exposure to winds (Sutton 2015). This can make plants highly susceptible to drought. AM fungi are well-known to ameliorate water relations in plants, through various mechanisms (reviewed in Augé 2001), including regulation of stomatal closure and hormonal balance. However, there is large interspecific variation in the ability of AM fungi to improve plant water relations (Dixon et al. 1994; Mathur and Vyas 1995). As for the effect of MF on soil aggregation, we still lack a mechanistic understanding of the fungal traits responsible for the amelioration of plant water relations. The best MF could be those that possess the finest hyphae, able to reach water in finer micropores (Drew et al. 2003). Alternatively, the ability for MF to alter the host hormonal balance (e.g., abscisic acid production) and thus trigger a better plant response to drought could be another key trait to investigate (Estrada-Luna and Davies 2003). Comparative studies linking mycorrhizal fungal traits to amelioration of plant response to drought will be required to identify and select optimal fungal strains that may be used as inoculum in green roofs and walls. Knowledge advancement on how MF traits favour drought tolerance would also be useful to the study of POP-contaminated sites, which are also known to lose a large part of their water retention capacity (Robertson et al. 2007).

Another benefit that could be provided by MF in such phytotechnologies relates to the cycling of organic matter. In most installations, the substrate used for green roofs and walls is highly organic (e.g., coco husk, peat moss) for two reasons: it is lightweight and it provides a nutrient reserve made available progressively through mineralization (Sutton 2015). However, the low clay content of such substrates reduces their water retention, which can limit nutrient mineralization. The ability of some MF to prime organic matter decomposition (Paterson et al. 2016) or at least scavenge for nutrient mineralized by saprotrophs or soil fauna (e.g., Leigh et al. 2009; Koller et al. 2013), could promote nutrient transfer to plants. On the other hand, MF have also been shown to sometimes reduce organic matter decomposition (e.g., Verbruggen et al. 2016), which could be due to antagonistic interactions between MF and saprotrophs (Bending 2003) or to water consumption by MF that reduces the activity of saprotrophs (Leifheit et al. 2015). Again, more studies will be needed to better grasp the role of MF in green roof or wall ecosystems, and especially identify the fungal traits that best promote plant performance in these systems (Table 1). For now, data are very scarce. We know that fungal colonization (John et al. 2014), as well as taxonomic richness (McGuire et al. 2013) can be high in those systems. However, we still lack studies identifying the impact of MF on green roof/wall plants, and the optimal strains to use as inoculum (McGuire et al. 2015). Studies will also be needed to better understand the nature of the interactions between MF and the substrate microbiome, and their impact on plants: these interactions could be synergistic and provide even more benefits to host plants, but conversely, they could

be antagonistic and lead to a reduced plant performance (e.g., Molineux et al. 2014) or survival.

Conclusion

From what is presented in this mini-review, in many cases the use of inocula containing MF seems to be promising in assisting phytotechnologies. However, for certain phytotechnologies (e.g., TW, green roofs and walls), there is a lack of data comparing ecosystem services with or without MF, which calls for more empirical work. Also, in some cases, MF may prove to be disadvantageous to phytotechnological applications. For example, MF may reduce plant uptake of metals, and thus delay phytoextraction. Similarly, under severe nutrient limitations, MF may decrease nutrient transfer to hosts by first satisfying their own nutritional needs (Treseder and Allen 2002). These aspects need to be considered to provide a balanced view on the potential benefits derived from mycorrhizal symbioses in phytotechnology. Below we outline major knowledge gaps that we believe need to be addressed in future research:

- 1- A mechanistic framework is needed to identify the fungal traits required to provide a given ecosystem service for each phytotechnological application (Table 1). Only such a trait-based approach will allow a predictable application of MF in various applied systems. This is especially true for phytoremediation, where it is commonly found that stress-adapted fungal strains are better in promoting plant

performance in stressful systems (e.g., Cabello et al. 1999): we thus need to identify what traits allow for stress adaptation. Likewise, for TW, we could study natural analogous systems (i.e., natural wetlands) to investigate fungal traits associated with flooded, nutrient-rich systems. Surface or thin forest soils could provide cues about the fungal traits associated with organic substrates prone to drying (i.e., green roofs and walls). As a whole, the need to better predict the utility of MF in phytotechnologies further emphasizes the need for a trait-based approach in fungal ecology, pointed out previously (e.g., Chagnon et al. 2013; Aguilar-Trigueros et al. 2014; Rillig et al. 2015; Treseder and Lennon 2015). Such an approach will require a significant amount of work in highly controlled systems, where fungal traits of individual species can be measured. However, we also stress that care must be taken when studying phytotechnologies in simplified systems. For example, it is well-known that environmental pollutants are typically not homogeneously distributed in soil profiles, and MF could avoid stress in nature by preferentially placing biomass in less stressful soil microsites: pot-based experiments with well-mixed substrates cannot meaningfully address this issue.

- 2- Another challenge is the production of large quantities of fungal inoculum. While *in vitro* cultivation allows the mass-production of clean AM fungal propagules, easily extracted and free of contaminating microorganisms, only a few species can be successfully produced using this method (~5%, Declerck et al. 2005). On the other hand, while many identified AM fungal species can be pot-propagated, optimal conditions for inoculum production are quite variable among species:

different fungi prefer different hosts (Struble and Skipper 1988; Dodd et al. 1990; Bever et al. 1996), different nutrient concentrations (Egerton-Warburton et al. 2007), or different soil textures (Lekberg et al. 2007). Here, again, more research linking fungal traits to environmental conditions could be useful, and it will allow more predictability in the identification of the optimal growing conditions for a fungus based on its traits. Moreover, another characteristic that should be considered for inoculum production is its adaptability to changing abiotic conditions: it may be useful to develop multispecies inocula that not only include the most efficient strains to provide a given service under a given environmental context, but also include a set of functionally complementary strains that may be more resilient and/or resistant to environmental fluctuations, as expected under an insurance hypothesis scenario (Yachi and Loreau 1999). More fundamental research on the plasticity of mycorrhizal fungal traits (Johnson et al. 2012; Behm and Kiers 2014) and their evolution (e.g., Angelard et al. 2010) will also provide crucial knowledge on our eventual ability to not only screen for best fungal inocula, but purposely breed for fungal strains bearing specifically desired traits (Angelard and Sanders 2011).

- 3- We also need to better identify collateral benefits derived from the use of MF in phytotechnologies. For example, MF may not only improve the ecosystem service that we specifically aim at maximizing (e.g., water retention in green roofs, extraction of metals in phytoremediation), they may also provide additional services. For example, there is evidence that MF can promote plant community

diversity in some contexts (e.g., Grime et al. 1987; van der Heijden et al. 1998; Urcelay and Diaz 2003), and limit the success of invasive plants (e.g., Seifert et al. 2009; Vogelsang and Bever 2009). MF could thus provide an additional, parallel tool in conservation biology.

- 4- Empirical results linking MF to the efficiency of phytotechnological applications often show very contrasted results, and this may be due, at least in part, to a lack of concertation in methodological approaches. It might be useful to improve coordination among research groups to develop more standardised approaches to conduct controlled experiments involving MF.

As a whole, there is no doubt that MF are part of the equation for the future of phytotechnologies, and the adoption of a trait-based approach will greatly improve our predictive power in this regard. Conversely, the trait-based study of these stressful, anthropogenic environments may provide new insights regarding phenotypic plasticity and the evolution of stress tolerance in microorganisms.

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References

- Affholder, M.C., Pricop, A.D., Laffont-Schwob, I., Coulomb, B., Rabier, J., Borla, A., Demelas, C., and Prudent, P. 2014. As, Pb, Sb, and Zn transfer from soil to root of wild rosemary: Do native symbionts matter? *Plant and Soil*, **382**(1-2): 219–236. doi:10.1007/s11104-014-2135-4.
- Aguilar-Trigueros, C.A., Hempel, S., Powell, J.R., Anderson, I.C., Antonovics, J., Bergmann, J., Cavagnaro, T.R., Chen, B., Hart, M.M., Klironomos, J., Petermann, J.S., Verbruggen, E., Veresoglou, S.D., and Rillig, M.C. 2015. Branching out: Towards a trait-based understanding of fungal ecology. *Fungal Biol. Rev.* **29**(1): 34–41. doi:10.1016/j.fbr.2015.03.001.
- Alkorta, I., and Garbisu, C. 2001. Phytoremediation of organic contaminants in soils. *Bioresour. Technol.* **79**(3): 273–276. doi:10.1016/S0960-8524(01)00016-5.
- Almeida-Rodriguez, A.M., Gomes, M.P., Loubert-Hudon, A., Joly, S., and Labrecque, M. 2016. Symbiotic association between *Salix purpurea* L. and *Rhizophagus irregularis*: Modulation of plant responses under copper stress. *Tree Physiol.* **36**(4): 407–420. doi:10.1093/treephys/tpv119.
- Anderson, T.A., Kruger, E.L., and Coats, J.R. 1994. Enhanced degradation of a mixture of three herbicides in the rhizosphere of a herbicide-tolerant plant. *Chemosphere*, **28**(8): 1551–1557. doi:10.1016/0045-6535(94)90248-8.
- Angelard, C., and Sanders, I.R. 2011. Effect of segregation and genetic exchange on arbuscular mycorrhizal fungi in colonization of roots. *New Phytol.* **189**(3): 652–657. doi: 10.1111/j.1469-8137.2010.03602.x
- Angelard, C., Colard, A., Niculita-Hirzel, H., Croll, D., and Sanders, I.R. 2010. Segregation in a mycorrhizal fungus alters rice growth and symbiosis-specific gene transcription. *Curr. Biol.* **20**(13): 1216–1221. doi:10.1016/j.cub.2010.05.031.
- Audet, P., and Charest, C. 2007. Heavy metal phytoremediation from a meta-analytical perspective. *Environ. Pollut.* **147**(1): 231–237. doi:10.1016/j.envpol.2006.08.011.
- Auge, R.M. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza*, **11**(1): 3–42. doi:10.1007/s005720100097.
- Auzet, A.V., Le Bissonnais, Y., and Souchère, V. 2006. France. *In* Soil erosion in Europe. Edited by J. Boardman, and J. Poesen. Wiley, Chichester. pp.369–383
- Bahr, A., Ellström, M., Akselsson, C., Ekblad, A., Mikusinska, A., and Wallander, H. 2013. Growth of ectomycorrhizal fungal mycelium along a Norway spruce forest

- 510 nitrogen deposition gradient and its effect on nitrogen leakage. *Soil Biol. Biochem.*
511 **59**: 38–48. doi:10.1016/j.soilbio.2013.01.004.
- 512 Behm, J.E., and Kiers, E.T. 2014. A phenotypic plasticity framework for assessing
513 intraspecific variation in arbuscular mycorrhizal fungal traits. *J. Ecol.* **102**(2): 315–
514 327. doi:10.1111/1365-2745.12194.
- 515 Bellion, M., Courbot, M., Jacob, C., Blaudez, D., and Chalot, M. 2006. Extracellular and
516 cellular mechanisms sustaining metal tolerance in ectomycorrhizal fungi. *FEMS*
517 *Microbiol. Lett.* **254**(2): 173–181. doi:10.1111/j.1574-6968.2005.00044.x.
- 518 Bending, G.D. 2003. Litter decomposition, ectomycorrhizal roots and the “Gadgil” effect.
519 *New Phytol.* **158**: 228–229. doi:10.1046/j.1469-8137.2003.00753.x.
- 520 Bever, J.D., Morton, J.B., Antonovics, J., and Schultz, P. a. 1996. Host-dependent
521 sporulation and species diversity of arbuscular mycorrhizal fungi in a mown
522 grassland. *J. Ecol.* **84**(1): 71–82. doi:10.2307/2261701.
- 523 Blanco-Canqui, H., and Lal, R. 2010. Principles of soil conservation and management.
524 Springer, New York.
- 525 Braun-Lüllemann, A., Hüttermann, A., and Majcherczyk, A. 1999. Screening of
526 ectomycorrhizal fungi for degradation of polycyclic aromatic hydrocarbons. *Appl.*
527 *Microbiol. Biotechnol.* **53**(1): 127–132. doi:10.1007/s002530051625.
- 528 Brisson, J., and F. Chazarenc. 2009. Maximizing pollutant removal in constructed
529 wetlands: should we pay more attention to macrophyte species selection? *Sci. Total*
530 *Environ.* **407**: 3923–3930
- 531 Brix, H. 1997. Do macrophytes play a role in constructed treatment wetlands? *Wat. Sci.*
532 *Technol.* **35**(5): 11–17. doi:10.1016/S0273-1223(97)00047-4.
- 533 Burghilea, C., Zaharescu, D.G., Dontsova, K., Maier, R., Huxman, T., and Chorover, J.
534 2015. Mineral nutrient mobilization by plants from rock: influence of rock type and
535 arbuscular mycorrhiza. *Biogeochemistry*, **124**(1-3): 187–203. doi:10.1007/s10533-
536 015-0092-5.
- 537 Burke, R.M., and Cairney, J.W.G. 2002. Laccases and other polyphenol oxidases in ecto-
538 and ericoid mycorrhizal fungi. *Mycorrhiza*, **12**(3): 105–116. doi:10.1007/s00572-
539 002-0162-0.
- 540 Cabello, M. N. 1999. Effectiveness of indigenous arbuscular mycorrhizal fungi (AMF)
541 isolated from hydrocarbon polluted soils. *J. Basic Microbiol.* **39**(2) : 89-95. doi:
542 10.1002/(SICI)1521-4028(199905)39:2<89::AID-JOBM89>3.0.CO;2-D.

- 543 Cairney, J.W.G. 1991. Rhizomorphs: Organs of exploration or exploitation? *Mycologist*,
544 **5**(1): 5-10. doi: 10.1016/S0269-915X(09)80325-X
- 545 Cantelmo Jr, A.J., and Ehrenfeld, J. G. 1999. Effects of microtopography on mycorrhizal
546 infection in Atlantic white cedar (*Chamaecyparis thyoides* (L.) Mills.). *Mycorrhiza*,
547 **8**(4): 175-180. doi: 10.1007/s005720050231
- 548 Chagnon, P.L., Bradley, R.L., and Klironomos, J.N. 2015. Trait-based partner selection
549 drives mycorrhizal network assembly. *Oikos*, **124**(12): 1609–1616.
550 doi:10.1111/oik.01987.
- 551 Chagnon, P.L., Bradley, R.L., Maherali, H., and Klironomos, J.N. 2013. A trait-based
552 framework to understand life history of mycorrhizal fungi. *Trends Plant Sci* **18**(9):
553 484-491. doi:10.1016/j.tplants.2013.05.001.
- 554 Clemens, S. 2006. Toxic metal accumulation, responses to exposure and mechanisms of
555 tolerance in plants. *Biochimie*, **88**(11): 1707–19. doi:10.1016/j.biochi.2006.07.003.
- 556 Colpaert, J. V., Wevers, J.H.L., Krznaric, E., and Adriaensen, K. 2011. How metal-
557 tolerant ecotypes of ectomycorrhizal fungi protect plants from heavy metal
558 pollution. *Ann. For. Sci.* **68**(1): 17–24. doi:10.1007/s13595-010-0003-9.
- 559 Confer, S.R., and Niering, W.A. 1992. Comparison of created and natural freshwater
560 emergent wetlands in Connecticut (USA). *Wetl. Ecol. Manag.* **2**(3): 143–156.
561 doi:10.1007/BF00215321.
- 562 Corgié, S.C., Fons, F., Beguiristain, T., and Leyval, C. 2006. Biodegradation of
563 phenanthrene, spatial distribution of bacterial populations and dioxygenase
564 expression in the mycorrhizosphere of *Lolium perenne* inoculated with *Glomus*
565 *mosseae*. *Mycorrhiza*, **16**(3): 207–212. doi:10.1007/s00572-006-0049-6.
- 566 Cornwell, W.K., Bedford, B.L., and Chapin, C.T. 2001. Occurrence of arbuscular
567 mycorrhizal fungi in a phosphorus-poor wetland and mycorrhizal response to
568 phosphorus fertilization. *Am. J. Bot.* **88**(10): 1824–1829.
- 569 Daghino, S., Martino, E., and Perotto, S. 2016. Model systems to unravel the molecular
570 mechanisms of heavy metal tolerance in the ericoid mycorrhizal symbiosis.
571 *Mycorrhiza*, **26**(4): 263-274. doi:10.1007/s00572-015-0675-y.
- 572 Declerck, S., Séguin, S., and Dalpé, Y. 2005. The monoxenic culture of arbuscular
573 mycorrhizal fungi as a tool for germplasm collections. *In* *In vitro culture of*
574 *mycorrhizas*, Edited by S. Declerck, D.G. Strullu, and J.A. Fortin. Springer, New
575 York. pp.17-30.

- 576 De Deyn, G.B., Cornelissen, J.H.C., and Bardgett, R.D. 2008. Plant functional traits and
577 soil carbon sequestration in contrasting biomes. *Ecol. lett.* **11**(5): 516-531.
578 doi:10.1111/j.1461-0248.2008.01164.x.
- 579 de la Providencia, I.E., Stefani, F.O.P., Labridy, M., St-Arnaud, M., and Hijri, M. 2015.
580 Arbuscular mycorrhizal fungal diversity associated with *Eleocharis obtusa* and
581 *Panicum capillare* growing in an extreme petroleum hydrocarbon-polluted
582 sedimentation basin. *FEMS Microbiol. Lett.* **362**(12). doi:10.1093/femsle/fnv081.
- 583 de Santisteban, L.M., Casali, J., and López, J.J. 2006. Assessing soil erosion rates in
584 cultivated areas of Navarre (Spain). *Earth Surf. Process. Landforms*, **31**(4): 487–
585 506. doi:10.1002/esp.1281.
- 586 Dixon, R., Rao, M., and Garg, V. 1994. Water relations and gas exchange of mycorrhizal
587 *Leucaena leucocephala* seedlings. *J. Trop. For. Sci.* **6**(4): 542-552. Available from
588 <http://www.jstor.org/stable/43581779>.
- 589 Dodd, J.C., Arias, I., Koomen, I., and Hayman, D.S. 1990. The management of
590 populations of vesicular-arbuscular mycorrhizal fungi in acid-infertile soils of a
591 savanna ecosystem - II. The effects of pre-crops on the spore populations of native
592 and introduced VAM-fungi. *Plant and Soil*, **122**(2): 241-247.
- 593 Drew, E.A., Murray, R.S., Smith, S.E., and Jakobsen, I. 2003. Beyond the rhizosphere:
594 Growth and function of arbuscular mycorrhizal external hyphae in sands of varying
595 pore sizes. *Plant and Soil*, **251**(1): 105–114. doi:10.1023/A:1022932414788.
- 596 Egerton-Warburton, L.M., Johnson, N.C., and Allen, E.B. 2007. Mycorrhizal community
597 dynamics following nitrogen fertilization: A cross-site test in five grasslands. *Ecol.*
598 *Monogr.* **77**(4): 527–544. doi:10.1890/06-1772.1.
- 599 Estrada-Luna, A., and Davies, F.T. 2003. Arbuscular mycorrhizal fungi influence water
600 relations, gas exchange, abscisic acid and growth of micropropagated chile ancho
601 pepper (*Capsicum annuum*) plantlets during acclimatization and post-
602 acclimatization. *J. Plant Physiol.* **160**: 1073–1083. doi:10.1078/0176-1617-00989.
- 603 Fester, T. 2013. Arbuscular mycorrhizal fungi in a wetland constructed for benzene-,
604 methyl tert-butyl ether- and ammonia-contaminated groundwater bioremediation.
605 *Microb. Biotechnol.* **6**(1): 80–84. doi:10.1111/j.1751-7915.2012.00357.x.
- 606 Franco-Correa, M., Quintana, A., Duque, C., Suarez, C., Rodríguez, M.X., and Barea,
607 J.M. 2010. Evaluation of actinomycete strains for key traits related with plant
608 growth promotion and mycorrhiza helping activities. *Appl. Soil Ecol.* **45**(3): 209–
609 217. doi:10.1016/j.apsoil.2010.04.007.
- 610 Gadgil, R.L., and Gadgil, P.D. 1971. Mycorrhiza and litter decomposition. *Nature*, **233**:
611 133.

- 612 Gamalero, E., and Glick, B.R. 2012. Plant growth-promoting bacteria and metals
613 phytoremediation. *In* Phytotechnologies: Remediation of environmental
614 contaminants. *Edited by* N.A. Anjum, M.E. Pereira, I. Ahmad, A.C. Duarte, S.
615 Umar, and N.A. Khan. Taylor and Francis, New York. pp. 361-376.
- 616 Genney, D.R., Alexander, I.J., Killham, K., and Meharg, A.A. 2004. Degradation of the
617 polycyclic aromatic hydrocarbon (PAH) fluorene is retarded in a Scots pine
618 ectomycorrhizosphere. *New Phytol.* **163**(3): 641–649. doi:10.1111/j.1469-
619 8137.2004.01131.x.
- 620 González-Chávez, M.C., Carrillo-González, R., Wright, S.F., and Nichols, K.A. 2004.
621 The role of glomalin, a protein produced by arbuscular mycorrhizal fungi, in
622 sequestering potentially toxic elements. *Environ. Pollut.* **130**(3): 317–323.
623 doi:10.1016/j.envpol.2004.01.004.
- 624 Grime, J.P., Mackey, J.M.L., Hillier, S.H., and Read, D.J. 1987. Floristic diversity in a
625 model system using experimental microcosms. *Nature*, **328**(30): 420–422.
626 doi:10.1038/328420a0.
- 627 Hage-Ahmed, K., Moyses, A., Voglgruber, A., Hadacek, F., and Steinkellner, S. 2013.
628 Alterations in root exudation of intercropped tomato mediated by the arbuscular
629 mycorrhizal fungus *Glomus mosseae* and the soilborne pathogen *Fusarium*
630 *oxysporum* f.sp. *lycopersici*. *J. Phytopathol.* **161**(11-12): 763–773.
631 doi:10.1111/jph.12130.
- 632 Haselwandter, K., and Winkelmann, G. 2002. Ferricrocin - An ectomycorrhizal
633 siderophore of *Cenococcum geophilum*. *BioMetals*, **15**(1): 73–77.
634 doi:10.1023/A:1013188823076.
- 635 Haselwandter, K., Passler, V., Reiter, S., Schmid, D.G., Nicholson, G., Hentschel, P.,
636 Albert, K., and Winkelmann, G. 2006. Basidiochrome - A novel siderophore of the
637 orchidaceous mycorrhizal fungi *Ceratobasidium* and *Rhizoctonia* spp. *BioMetals*,
638 **19**(3): 335–343. doi:10.1007/s10534-006-6986-x.
- 639 Hassan, S.E., Labrecque, M., St-Arnaud, M. and Hijri, M. 2010. Prospects of plants and
640 arbuscular mycorrhizal fungi in phytoremediation of heavy metal contaminated soil.
641 *In* Mycorrhizal biotechnology, *Edited by* D. Thangadurai, C.A. Busso, and M. Hijri.
642 Taylor and Francis, New York. pp. 152-177.
- 643 Hassan, S.E., Hijri, M., and St-Arnaud, M. 2013. Effect of arbuscular mycorrhizal fungi
644 on trace metal uptake by sunflower plants grown on cadmium contaminated soil.
645 *New. Biotechnol.* **30**(6): 780–787. doi:10.1016/j.nbt.2013.07.002.
- 646 Hassan, S.E.D., Bell, T.H., Stefani, F.O.P., Denis, D., Hijri, M., and St-Arnaud, M. 2014.
647 Contrasting the community structure of arbuscular mycorrhizal fungi from

- hydrocarbon-contaminated and uncontaminated soils following willow (*Salix* spp. L.) planting. PLoS One, **9**(7). doi:10.1371/journal.pone.0102838.
- Hetrick, B.A.D., Leslie, J.F., Wilson, G.T., and Kitt, D.G. 1988. Physical and topological assessment of effects of a vesicular-arbuscular mycorrhizal fungus on root architecture of big bluestem. New Phytol. **110**(1): 85–96. doi:10.1111/j.1469-8137.1988.tb00240.x.
- Hoyano, A. 1988. Climatological uses of plants for solar control and the effects on the thermal environment of a building. Energy Build. **11**(1-3): 181–199. doi:10.1016/0378-7788(88)90035-7.
- Infante, C., Hernandez-Valencia, I., Lopez, L., and Toro, M. 2012. Phytoremediation of petroleum-contaminated soils in Venezuela. In Phytotechnologies: Remediation of environmental contaminants. Edited by N.A. Anjum, M.E. Pereira, I. Ahmad, A.C. Duarte, S. Umar, and N.A. Khan. Taylor and Francis, New York. pp.293-308.
- Jansa, J., Bukovská, P., and Gryndler, M. 2013. Mycorrhizal hyphae as ecological niche for highly specialized hypersymbionts - or just soil free-riders? Front. Plant Sci. **4**(May): 134. doi:10.3389/fpls.2013.00134.
- John, J., Lundholm, J., and Kernaghan, G. 2014. Colonization of green roof plants by mycorrhizal and root endophytic fungi. Ecol. Eng. **71**: 651–659. doi:10.1016/j.ecoleng.2014.08.012.
- Johnson, D., Martin, F., Cairney, J.W.G., and Anderson, I.C. 2012. The importance of individuals: Intraspecific diversity of mycorrhizal plants and fungi in ecosystems. New Phytol. **194**(3): 614-628. doi:10.1111/j.1469-8137.2012.04087.x.
- Johnson, N.C. 1993. Can fertilization of soil select less mutualistic mycorrhizae? Ecol. Appl. **3**(4): 749–757. doi:10.2307/1942106.
- Johnson, N.C., Rowland, D.L., Corkidi, L., Egerton-Warburton, L.M., and Allen, E.B. 2003. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. Ecology, **84**(7): 1895–1908. doi:10.1890/0012-9658(2003)084[1895:Neamaa]2.0.Co;2.
- Joner, E.J., Briones, R., and Leyval, C. 2000. Metal-binding capacity of arbuscular mycorrhizal mycelium. Plant and Soil, **226**(2): 227–234. doi:10.1023/A:1026565701391.
- Jongmans, A.G., Lundström, U.S., van Breemen, N., van Hees, P.A.W., Finlay, R.D., Srinivasan, M., Unestam, T., Giesler, R., Melkerud, P.A., and Olsson, M. 1997. Rock-eating fungi. Nature, **389**(6652): 682–683. doi:10.1038/39493.

- 682 Kohler, J., Roldán, A., Campoy, M., and Caravaca, F. 2017. Unraveling the role of
683 hyphal networks from arbuscular mycorrhizal fungi in aggregate stabilization of
684 semiarid soils with different textures and carbonate contents. *Plant and Soil*, **410**(1):
685 1–9. doi:10.1007/s11104-016-3001-3.
- 686 Koller, R., Rodriguez, A., Robin, C., Scheu, S., and Bonkowski, M. 2013. Protozoa
687 enhance foraging efficiency of arbuscular mycorrhizal fungi for mineral nitrogen
688 from organic matter in soil to the benefit of host plants. *New Phytol.* **199**(1): 203–
689 211. doi:10.1111/nph.12249.
- 690 Krishnamoorthy, R., Kim, C.G., Subramanian, P., Kim, K.Y., Selvakumar, G., and Sa,
691 T.M. 2015. Arbuscular mycorrhizal fungi community structure, abundance and
692 species richness changes in soil by different levels of heavy metal and metalloid
693 concentration. *PLoS One*, **10**(6): e0128784.
694 doi:UNSPe0128784\10.1371/journal.pone.0128784.
- 695 Lacercat-Didier, L., Berthelot, C., Foulon, J., Errard, A., Martino, E., Chalot, M., and
696 Blaudez, D. 2016. New mutualistic fungal endophytes isolated from poplar roots
697 display high metal tolerance. *Mycorrhiza*, **26**(7): 657–671. doi:10.1007/s00572-016-
698 0699-y.
- 699 Le Tacon, F., Skinner, F.A., and Mosse, B. 1983. Spore germination and hyphal growth
700 of a vesicular-arbuscular mycorrhizal fungus, *Glomus mosseae* (Gerdemann and
701 Trappe), under decreased oxygen and increased carbon dioxide concentrations. *Can.*
702 *J. Microbiol.* **29**(10): 1280–1285. doi:10.1139/m83-200.
- 703 Leake, J., Johnson, D., Donnelly, D., Muckle, G., Boddy, L., and Read, D. 2004.
704 Networks of power and influence: the role of mycorrhizal mycelium in controlling
705 plant communities and agroecosystem functioning. *Can. J. Bot.* **82**: 1016–1045.
706 doi:10.1139/b04-060.
- 707 Leifheit, E.F., Verbruggen, E., and Rillig, M.C. 2015. Arbuscular mycorrhizal fungi
708 reduce decomposition of woody plant litter while increasing soil aggregation. *Soil*
709 *Biol. Biochem.* **81**: 323–328. doi:10.1016/j.soilbio.2014.12.003.
- 710 Leigh, J., Hodge, A., and Fitter, A.H. 2009. Arbuscular mycorrhizal fungi can transfer
711 substantial amounts of nitrogen to their host plant from organic material. *New*
712 *Phytol.* **181**(1): 199–207. doi:10.1111/j.1469-8137.2008.02630.x.
- 713 Lekberg, Y., Koide, R.T., Rohr, J.R., Aldrich-Wolfe, L., and Morton, J.B. 2007. Role of
714 niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal
715 communities. *J. Ecol.* **95**(1): 95–105. doi:10.1111/j.1365-2745.2006.01193.x.
- 716 Lenoir, I., Lounes-Hadj Sahraoui, A., and Fontaine, J. 2016. Arbuscular mycorrhizal
717 fungal-assisted phytoremediation of soil contaminated with persistent organic
718 pollutants: a review. *Eur. J. Soil Sci.* **67**(5): 624–640. doi:10.1111/ejss.12375.

- 719 Leung, H.M., Wang, Z.W., Ye, Z.H., Yung, K.L., Peng, X.L., and Cheung, K.C. 2013.
720 Interactions between arbuscular mycorrhizae and plants in phytoremediation of
721 metal-contaminated soils: A review. *Pedosphere*, **23**(5): 549–563.
722 doi:10.1016/S1002-0160(13)60049-1.
- 723 Leyval, C., and Joner, E.J. 2001. Bioavailability of heavy metals in the mycorrhizosphere.
724 *In* Bioavailability of heavy metals in the mycorrhizosphere: Trace elements in
725 rhizosphere. *Edited by* G.R. Goran, W.W. Wenzel, and E. Lombi. CRC Press, New
726 York. pp. 165-185.
- 727 Lilleskov, E.A., Bruns, T.D., Dawson, T.E., and Camacho, F.J. 2009. Water sources and
728 controls on water-loss rates of epigeous ectomycorrhizal fungal sporocarps during
729 summer drought. *New Phytol.* **182**(2): 483–494. doi:10.1111/j.1469-
730 8137.2009.02775.x.
- 731 Lindahl, B.D., and Tunlid, A. 2015. Ectomycorrhizal fungi - potential organic matter
732 decomposers, yet not saprotrophs. *New Phytol.* **205**(4):1443-1447.
733 doi:10.1111/nph.13201.
- 734 Lingua, G., Copetta, A., Musso, D., Aimo, S., Ranzenigo, A., Buico, A., Gianotti, V.,
735 Osella, D., and Berta, G. 2015. Effect of arbuscular mycorrhizal and bacterial
736 inocula on nitrate concentration in mesocosms simulating a wastewater treatment
737 system relying on phytodepuration. *Environ. Sci. Pollut. Res.* **22**(23): 18616–18625.
738 doi:10.1007/s11356-015-5502-7.
- 739 Liu, A., and Dalpé, Y. 2009. Reduction in soil polycyclic aromatic hydrocarbons by
740 arbuscular mycorrhizal leek plants. *Int. J. Phytoremed.* **11**(1): 39-52. doi:
741 10.1080/15226510802363444.
- 742 Lopes, L.D., Pereira e Silva, M. de C., and Andreote, F.D. 2016. Bacterial abilities and
743 adaptation toward the rhizosphere colonization. *Front. Microbiol.* **7**(AUG).
744 doi:10.3389/fmicb.2016.01341.
- 745 Mangkoedihardjo, S. 2007. Phytotechnology integrity in environmental sanitation for
746 sustainable development. *J. Appl. Sci. Res.* **3**(10): 1037-1044.
- 747 Marques, A.P.G.C., Oliveira, R.S., Samardjieva, K.A., Pissarra, J., Rangel, A.O.S.S., and
748 Castro, P.M.L. 2007. *Solanum nigrum* grown in contaminated soil: effect of
749 arbuscular mycorrhizal fungi on zinc accumulation and histolocalisation. *Environ.*
750 *Pollut.* **145**(3): 691–699. doi:10.1016/j.envpol.2006.06.029.
- 751 Materechera, S.A., Kirby, J.M., Alston, A.M., and Dexter, A.R. 1994. Modification of
752 soil aggregation by watering regime and roots growing through beds of large
753 aggregates. *Plant and Soil*, **160**(1): 57–66. doi:10.1007/BF00150346.

- Mathur, N., and Vyas, A. 1995. Influence of va mycorrhizae on net photosynthesis and transpiration of *Ziziphus mauritiana*. *J. Plant Physiol.* **147**(3-4): 328–330. doi:10.1016/S0176-1617(11)82161-9.
- McGuire, K.L., Payne, S.G., Palmer, M.I., Gillikin, C.M., Keefe, D., Kim, S.J., Gedallovich, S.M., Discenza, J., Rangamannar, R., Koshner, J.A., Massmann, A.L., Orazi, G., Essene, A., Leff, J.W., and Fierer, N. 2013. Digging the New York city skyline: soil fungal communities in green roofs and city parks. *PLoS One* **8**(3). doi:10.1371/journal.pone.0058020.
- McGuire, K.L., Payne, S.G., Orazi, G., and Palmer, M.I. 2015. Bacteria and fungi in green roof ecosystems. *In* *Green roof ecosystems. Edited by R.K. Sutton*. Springer, New York. pp. 1-26.
- Merkl, N., Schultze-Kraft, R., and Infante, C. 2005. Assessment of tropical grasses and legumes for phytoremediation of petroleum-contaminated soils. *Water Air. Soil Pollut.* **165**(4): 195–209. doi:10.1007/s11270-005-4979-y.
- Middleton, E.L., and Bever, J.D. 2012. Inoculation with a native soil community advances succession in a grassland restoration. *Restor. Ecol.* **20**(2): 218–226. doi:10.1111/j.1526-100X.2010.00752.x.
- Miller, S.P. 2000. Arbuscular mycorrhizal colonization of semi-aquatic grasses along a wide hydrologic gradient. *New Phytol.* **145**(1): 145–155. doi:10.1046/j.1469-8137.2000.00566.x.
- Molineux, C.J., Connop, S.P., and Gange, A.C. 2014. Manipulating soil microbial communities in extensive green roof substrates. *Sci. Total Environ.* **493**: 632–638. doi:10.1016/j.scitotenv.2014.06.045.
- Moora, M., Öpik, M., Davison, J., Jairus, T., Vasar, M., Zobel, M., and Eckstein, R.L. 2016. AM fungal communities inhabiting the roots of submerged aquatic plant *Lobelia dortmanna* are diverse and include a high proportion of novel taxa. *Mycorrhiza*, **26**(7): 735–745. doi:10.1007/s00572-016-0709-0.
- Nguyen, H., Rineau, F., Vangrosveld, J., Cuypers, A., Colpaert, J.V., and Ruytinx, J. A novel, highly conserved metallothionein family in basidiomycete fungi and characterization of two representative SIMTa and SIMTb genes in the ectomycorrhizal fungus *Suillus luteus*. *Environ. Microbiol.* *In press*. doi:10.1111/1462-2920.13729
- Nicolotti, G., and Egli, S. 1998. Soil contamination by crude oil: Impact on the mycorrhizosphere and on the revegetation potential of forest trees. *Environ. Pollut.* **99**(1): 37–43. doi:10.1016/S0269-7491(97)00179-6.

- 789 Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin,
790 S., Köhler, M., Liu, K.K.Y., and Rowe, B. 2007. Green roofs as urban ecosystems:
791 Ecological structures, functions, and services. *Bioscience*, **57**(10): 823.
792 doi:10.1641/B571005.
- 793 Oehl, F., Sieverding, E., Ineichen, K., Mäder, P., Wiemken, A., and Boller, T. 2009.
794 Distinct sporulation dynamics of arbuscular mycorrhizal fungal communities from
795 different agroecosystems in long-term microcosms. *Agric. Ecosyst. Environ.* **134**(3-
796 4): 257–268. doi:10.1016/j.agee.2009.07.008.
- 797 Paruch, A.M., Maehlum, T., Haarstad, K., and Buseth, A.G. 2016. Performance of
798 constructed wetlands treating domestic wastewater in Norway over a quarter of a
799 century – options for nutrient removal and recycling. *In* *Natural and constructed*
800 *wetlands. Edited by J. Vymazal. Springer, New York. pp. 41-55.*
- 801 Paterson, E., Sim, A., Davidson, J., and Daniell, T.J. 2016. Arbuscular mycorrhizal
802 hyphae promote priming of native soil organic matter mineralisation. *Plant and Soil*,
803 **408**(1-2): 243–254. doi:10.1007/s11104-016-2928-8.
- 804 Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., Crist, S.,
805 Shpritz, L., Fitton, L., Saffouri, R., and Blair, R. 1995. Environmental and economic
806 costs of soil erosion and conservation. *Science*, **267**(5201): 1117–1123.
807 doi:10.1126/science.267.5201.1117.
- 808 Piotrowski, J.S., Denich, T., Klironomos, J.N., Graham, J.M., and Rillig, M.C. 2004. The
809 effects of arbuscular mycorrhizas on soil aggregation depend on the interaction
810 between plant and fungal species. *New Phytol.* **164**(2): 365–373.
811 doi:10.1111/j.1469-8137.2004.01181.x.
- 812 Quirk, J., Andrews, M.Y., Leake, J.R., Banwart, S.A., and Beerling, D.J. 2014.
813 Ectomycorrhizal fungi and past high CO₂ atmospheres enhance mineral weathering
814 through increased below-ground carbon-energy fluxes. *Biol. Lett.* **10**(7): 20140375–.
815 doi:10.1098/rsbl.2014.0375.
- 816 Reinoso, R., Torres, L.A., and Bécares, E. 2008. Efficiency of natural systems for
817 removal of bacteria and pathogenic parasites from wastewater. *Sci. Total Environ.*
818 **395**(2-3): 80–86. doi:10.1016/j.scitotenv.2008.02.039.
- 819 Rillig, M.C., Aguilar-Trigueros, C.A., Bergmann, J., Verbruggen, E., Veresoglou, S.D.,
820 and Lehmann, A. 2015. Plant root and mycorrhizal fungal traits for understanding
821 soil aggregation. *New Phytol.* **205**(4): 1385–1388. doi:10.1111/nph.13045.
- 822 Rillig, M.C., and Mummey, D.L. 2006. Mycorrhizas and soil structure. *New Phytol.*
823 **171**(1): 41–53. doi:10.1111/j.1469-8137.2006.01750.x.

- 824 Rillig, M.C., Wright, S.F., and Eviner, V.T. 2002. The role of arbuscular mycorrhizal
825 fungi and glomalin in soil aggregation: comparing effects of five plant species. *Plant*
826 *and Soil*, **238**(2): 325–333. doi:10.1023/a:1014483303813.
- 827 Robertson, S.J., McGill, B.W., Massicotte, H.B., and Rutherford, P.M. 2007. Petroleum
828 hydrocarbon contamination in boreal forest soils: a mycorrhizal ecosystems
829 perspective. *Biol. Rev. Camb. Philos. Soc.* **82**(2): 213–240. doi: 10.1111/j.1469-
830 185X.2007.00012.x
- 831 Schmalenberger, A., Duran, A.L., Bray, W., Bridge, J., Bonneville, S., Benning, L.G.,
832 Romero-Gonzalez, M.E., Leake, J.R., and Banwart, S. A. 2015. Oxalate secretion by
833 ectomycorrhizal *Paxillus involutus* is mineral-specific and controls calcium
834 weathering from minerals. *Sci. Rep.* **5**(January): 12187. doi:10.1038/srep12187.
- 835 Scholz, M., Höhn, P., and Minall, R. 2002. Mature experimental constructed wetlands
836 treating urban water receiving high metal loads. *Biotechnol. Prog.* **18**(6): 1257–
837 1264. doi:10.1021/bp0200503.
- 838 Schuler, R., and Haselwandter, K. 1988. Hydroxamate siderophore production by ericoid
839 mycorrhizal fungi. *J. Plant Nutr.* **11**(6): 907–913. doi: 10.1080/01904168809363855
- 840 Seguel, A., Cumming, J.R., Klugh-Stewart, K., Cornejo, P., and Borie, F. 2013. The role
841 of arbuscular mycorrhizas in decreasing aluminium phytotoxicity in acidic soils: A
842 review. *Mycorrhiza*, **23**(3): 167–183. doi:10.1007/s00572-013-0479-x.
- 843 Seifert, E.K., Bever, J.D., and Maron, J.L. 2009. Evidence for the evolution of reduced
844 mycorrhizal dependence during plant invasion. *Ecology*, **90**(4): 1055–1062.
845 doi:10.1890/08-0419.1.
- 846 Sikes, B.A., Cottenie, K., and Klironomos, J.N. 2009. Plant and fungal identity
847 determines pathogen protection of plant roots by arbuscular mycorrhizas. *J. Ecol.*
848 **97**(6): 1274–1280. doi: 10.1111/j.1365-2745.2009.01557.x
- 849 Smith, S.E., and Read, D.J. 2008. *Mycorrhizal Symbiosis*. Academic Press. New York.
- 850 Struble, J.E., and Skipper, H.D. 1988. Vesicular-arbuscular mycorrhizal fungal spore
851 production as influenced by plant species. *Plant and Soil*, **109**(2): 277–280.
- 852 Sutton, R.K. 2015. Introduction to green roof ecosystems. *In* *Green roof ecosystems*.
853 *Edited by* R.K. Sutton. Springer, New York. pp. 1–26.
- 854 Takaya, N. 2009. Response to hypoxia, reduction of electron acceptors, and subsequent
855 survival by filamentous fungi. *Biosci. Biotechnol. Biochem.* **73**(1): 1–8.
856 doi:10.1271/bbb.80487.

- 857 Thormann, M.N. 2006. Diversity and function of fungi in peatlands: a carbon cycling
858 perspective. *Can. J. Soil Sci.* **5**(October 2004): 281–293. doi:10.4141/S05-082.
- 859 Tisdall, J.M. 1994. Possible role of soil-microorganisms in aggregation in soils. *Plant and*
860 *Soil*, **159**(1): 115–121. doi:10.1007/BF00000100.
- 861 Toljander, J.F., Lindahl, B.D., Paul, L.R., Elfstrand, M., and Finlay, R.D. 2007. Influence
862 of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community
863 structure. *FEMS Microbiol. Ecol.* **61**(2): 295–304. doi:10.1111/j.1574-
864 6941.2007.00337.x.
- 865 Treseder, K.K., and Lennon, J.T. 2015. Fungal traits that drive ecosystem dynamics on
866 land. *Microbiol. Mol. Biol. Rev.* **79**(2): 243–262. doi:10.1128/MMBR.00001-15.
- 867 Urcelay, C., and Díaz, S. 2003. The mycorrhizal dependence of subordinates determines
868 the effect of arbuscular mycorrhizal fungi on plant diversity. *Ecol. lett.* **6**(5): 388-
869 391. doi:10.1046/j.1461-0248.2003.00444.x.
- 870 van de Voorde, T.F.J., van der Putten, W.H., Gamper, H.A., Gera Hol, W.H., and Martijn
871 Bezemer, T. 2010. Comparing arbuscular mycorrhizal communities of individual
872 plants in a grassland biodiversity experiment. *New Phytol.* **186**(3): 746–754.
873 doi:10.1111/j.1469-8137.2010.03216.x.
- 874 van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel,
875 R., Boller, T., Sanders, I.R., and Wiemken, A. 1998. Mycorrhizal fungal diversity
876 determines plant biodiversity, ecosystem variability and productivity. *Nature*,
877 **396**(6706): 69–72. doi:10.1038/23932.
- 878 Varkey, M., Lal, N., and Khan, Z.H. 2012. Phytoremediation: Strategies to enhance the
879 potential for toxic metal remediation of *Brassica* oilseed species. *In*
880 *Phytotechnologies: Remediation of environmental contaminants. Edited by N.A.*
881 *Anjum, M.E. Pereira, I. Ahmad, A.C. Duarte, S. Umar, and N.A. Khan. Taylor and*
882 *Francis, New York. pp.293-308.*
- 883 Verbruggen, E., Jansa, J., Hammer, E.C., and Rillig, M.C. 2016. Do arbuscular
884 mycorrhizal fungi stabilize litter-derived carbon in soil? *J. Ecol.* **104**(1): 261–269.
885 doi:10.1111/1365-2745.12496.
- 886 Vymazal, J. 2011. Plants used in constructed wetlands with horizontal subsurface flow: a
887 review. *Hydrobiologia*, **674**: 133–156
- 888 Vivas, A., Biro, B., Németh, T., Barea, J.M., and Azcon, R. 2006. Nickel-tolerant
889 *Brevibacillus brevis* and arbuscular mycorrhizal fungus can reduce metal acquisition
890 and nickel toxicity effects in plant growing in nickel supplemented soil. *Soil Biol.*
891 *Biochem.* **38**(9): 2694–2704. doi:10.1016/j.soilbio.2006.04.020.

- 892 Vogelsang, K.M., and Bever, J.D. 2009. Mycorrhizal densities decline in association with
893 normative plants and contribute to plant invasion. *Ecology*, **90**(2): 399–407.
894 doi:10.1890/07-2144.1.
- 895 Wang, F.Y., Lin, X.G., and Yin, R. 2007. Inoculation with arbuscular mycorrhizal fungus
896 *Acaulospora mellea* decreases Cu phytoextraction by maize from Cu-contaminated
897 soil. *Pedobiologia*, **51**(2): 99–109. doi:10.1016/j.pedobi.2007.02.003.
- 898 Wang, Y., Qiu, Q., Li, S., Xin, G., and Tam, N.F.Y. 2014. Inhibitory effect of municipal
899 sewage on symbiosis between mangrove plants and arbuscular mycorrhizal fungi.
900 *Aquat. Biol.* **20**(2): 119–127. doi:10.3354/ab00550.
- 901 Winkelmann, G. 2007. Ecology of siderophores with special reference to the fungi.
902 *BioMetals*, **20**: 379–392. doi:10.1007/s10534-006-9076-1.
- 903 Wu, S., Zhang, X., Chen, B., Wu, Z., Li, T., Hu, Y., Sun, Y., and Wang, Y. 2016.
904 Chromium immobilization by extraradical mycelium of arbuscular mycorrhiza
905 contributes to plant chromium tolerance. *Environ. Exp. Bot.* **122**: 10–18.
906 doi:10.1016/j.envexpbot.2015.08.006.
- 907 Wu, Z., McGrouther, K., Huang, J., Wu, P., Wu, W., and Wang, H. 2014. Decomposition
908 and the contribution of glomalin-related soil protein (GRSP) in heavy metal
909 sequestration: field experiment. *Soil Biol. Biochem.* **68**: 283–290.
910 doi:10.1016/j.soilbio.2013.10.010.
- 911 Xu, Z., Ban, Y., Jiang, Y., Zhang, X., and Liu, X. 2016. Arbuscular mycorrhizal fungi in
912 wetland habitats and their application in constructed wetland: a review. *Pedosphere*,
913 **26**(5): 592–617. doi:10.1016/S1002-0160(15)60067-4.
- 914 Yachi, S., and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating
915 environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* **96**(4): 1463–
916 1468. doi:10.1073/pnas.96.4.1463.

917

918 **Table 1.** Mycorrhizal fungal traits likely (or known) to play a role in phytotechnological applications. We specify whether each trait is
 919 expected to be relevant to arbuscular mycorrhizal (AM), ectomycorrhizal (ECM), and/or ericoid mycorrhizal (ERM) fungi. We also
 920 identify the function of this trait in a phytotechnological context (i.e., why this trait would be valuable in phytotechnology).

Phytotechnology	Mycorrhizal group involved	Trait	Function	Reference(s)
1 Phytoremediation i. Metals				
	AM, ECM, ERM	Production of metal-binding agents in cell walls (e.g., glomalin in AM fungi) or inside cytosol/vacuoles (e.g., polyphosphates, glutathione, metallothioneins)	Reduce transfer to host (i.e., phytostabilization)	Bellio et al. 2006; Colpaert et al. 2011; Leung et al. 2013; Wu et al. 2014; Nguyen et al. <i>in press</i> ;
	AM, ECM, ERM	Enhanced mechanisms for free radical scavenging (e.g., superoxide dismutase)	Mitigate the stress imposed by metal-mediated free radical production	Bellio et al. 2006
	AM, ECM, ERM	High metal absorption rates	Improved phytoextraction	Janouskova et al. 2006; Colpaert et al. 2011; Wu et al. 2016
	AM, ECM, ERM	High, or low, metal transfer rate to plants	Improved phytoextraction, or phytostabilization, respectively	Audet and Charest 2006
	AM, ECM, ERM	High rates of C transfer to heterotrophic soil microorganisms	Favour growth of metal-binding or metal-solubilizing microorganisms	Franco-Correa et al. 2010
	ECM, ERM	Direct siderophore production	Chelate metals	Schuler and Haselwandter 1988; Haselwandter and

Winkelmann 2002

ii. Organic pollutants

ECM, ERM	Expression of laccases	Oxidation of organic pollutants	Burke and Cairney 2002
AM, ECM, ERM	Exudation of large amounts of C, or priming of host exudation	Favor the growth of microorganisms that can attack organic pollutants	Toljander et al. 2007; Jansa et al. 2013; Lenoir et al. 2016
AM, ECM, ERM	Enhanced nutrient transfer to hosts	Large amounts of organic pollutants can increase soil C-to-nutrients ratio, thus inducing nutrient limitation and increasing plant-microbial competition for nutrients. Plants can gain competitive advantage by receiving nutrients from mycorrhizal fungi	Smith and Read 2008

2 Stabilization of degraded soils

AM, ECM, ERM	High hyphal density and/or growth rates	Rapidly establish a hyphal network likely to enhance aggregate formation and/or stabilization	Rillig et al. 2015
ECM	Formation of long-lived rhizomorphs	Fungal necromass contributing to aggregate stability	Cairney 1991
AM, ECM, ERM	Exudation of large quantities of C	Act as aggregate binding agents or promote the growth of heterotrophic microorganisms exuding binding agents	Rillig et al. 2015

AM, ECM, ERM	Promotion of host root production	High root density may favor initiation of macroaggregate formation and will increase amounts of C exuded to soils	Materechera et al. 1994
AM, ECM, ERM	High compatibility with hosts used in vegetation restoration practices	Symmetrical benefits derived by hosts from mycorrhizal fungi (and vice versa) will promote root and hyphal biomass production, eventually favoring aggregate formation and stabilization	Middleton and Bever 2012; Chagnon et al. 2015

3 Treatment wetlands

AM, ECM, ERM	Specialized electron transport chains	Tolerate hypoxia in submerged environments	Takaya 2009
AM, ECM, ERM	Promotion of host root production	Enhance plant beneficial impacts on nutrient uptake, exudate-driven decomposition of organic matter by microorganisms, or interception of pathogens propagules	Brix 1997
AM, ECM, ERM	High hyphal density and/or growth rates	As for plant roots, improve C transfer to heterotrophic microorganisms and take up nutrients	[this study]
AM, ECM, ERM	Low nutrient use efficiency	Increase nutrient consumption from wastewaters	[this study]
AM, ECM, ERM	Tolerance to pollutants found in wastewaters	Sustain activity even under abiotic stress	Bellio et al. 2006; Colpaert et al. 2011; Wu et al. 2014

4 Green roofs and walls

AM	Fine hyphal diameter	Improve water retention and uptake in fine soil pores	Drew et al. 2003
AM	Alter host hormonal balance (e.g., abscisic acid)	Ameliorate host tolerance to drought	Augé 2001
AM	High hyphal density and/or growth rates	Favor C transfer to heterotrophic microorganisms to prime decomposition of the organic substrate	De Deyn et al. 2008; Paterson et al. 2016
AM	High water use efficiency	Tolerate low water availability	Lilleskov et al. 2009