

Arbuscular Mycorrhizas Alleviate Plant Stress: Analysis of Studies from South America

MARCELA CLAUDIA PAGANO^{1*} AND MARTA NOEMÍ CABELLO²

ABSTRACT

Interest in stressful conditions is rising with increasing the recognition that global changes can negatively affect plant diversity and ecosystem function. It is known that arbuscular mycorrhizas (AM) permit the plant to perform better under stressful and unfavorable conditions, recruiting their symbiont in the soil. Recent reports on plant growth under different levels of stress and AM account for 94% of the published papers on AM. Stress affects soil physical and chemical properties, influencing the population, diversity and activities of soil microbes, including symbiotic fungal populations. This review was done to explore the current information on the benefits of AM symbioses in stressed systems, with respect to the research results in South America. The increasing appreciation that in-arid regions most trees are mycorrhizal has also deep consequences for rehabilitation efforts of woodlands and forest showing that underground processes are crucial for understanding of ecosystem function. Thus, relevant findings related to the benefits of AM management by increasing stress tolerance are emphasized. Accordingly, research paths that are necessary for the increased understating of

¹ Department of Physics, Federal University of Minas Gerais, Belo Horizonte, Minas Gerais, Brazil.

² Instituto Spegazzini, Av 53 No 477, B1900AVJ La Plata, Argentina

* Corresponding author: E-mail: marpagano@gmail.com

The effect of abiotic environmental factors (temperature, humidity, light, water supply, nutrients, and CO₂) varied with their intensity and determine plant growth (Schulze *et al.*, 2002). Moreover, wind or pollutants are also abiotic factors, the latest of increasingly research nowadays. It is known that plant tolerances to abiotic stresses such as drought, cold, and salinity have been reported for different plant species, such as eucalypts. Stress can be used on a scale of intensity (from deficiency to excessive supply), thus the environmental factors become stress factors (Schulze *et al.*, 2002).

As plants are sessile organisms exposed to natural climatic or edaphic stresses (drought, high irradiation, heat, frost, flooding, nutrient differences) and to environmental changes from human activities (air and soil pollution, soil degradation, etc.) (Schützendübel and Polle, 2002) biotechnological techniques of stress tolerance in plants are increasingly sought. For example, under stress arbuscular mycorrhizal fungi (AMF) are able to modify plant physiology in a way to cope with those environmental factors (Miransari *et al.*, 2008). Several reports have showed that mycorrhizal symbiosis improves plant health through increased protection against environmental stresses, either biotic (*e.g.*, pathogen attack) or abiotic (*e.g.*, drought, salinity, heavy metals, organic pollutants) (Azcón and Barea, 2010; Barea *et al.*, 2005a,b).

It is known that abiotic stresses adversely affect plant growth, productivity and trigger morphological, physiological, biochemical and molecular changes in plants. For example, cold stress limits the agricultural productivity of plants in hilly areas.

Mineral salts deficiency are usually recomposed by using commercial fertilizers (labeled with a formula that indicates the percentage of each element, *e.g.*, 04-30-10 NPK fertilizer contains 4% N, 30% P and 5% K). Additionally, some micronutrients (iron, sulfur, magnesium, zinc, and boron) are incorporated to soil as they can sometimes become limiting factors (Raven *et al.*, 2005). New directions in microbial ecology have need of integration of microbial physiological ecology, population biology, and process ecology as microorganisms have a diversity of evolutionary adaptations and physiological mechanisms to cope environmental stress (Schimel *et al.*, 2007).

Nevertheless, little attention has been paid to soil stresses and their effect in roots. For example, tillage promote disruption of the AMF hyphal network and dilution of the propagule-rich in topsoil (Schalamuk and Cabello, 2010) and affects the soil physical and chemical properties, modifying the number, diversity and activity of the soil microflora,

including both free and symbiotic fungal populations (Pagano, 2011). In this sense, AMF enhances soil structure through the formation of hydro-stable aggregates necessary for good soil tilth (Rillig and Mummey, 2006; Ruíz-Lozano *et al.*, 2008).

AMF can improve plant growth and production under different conditions, including various soil stresses (reviewed by Miransari 2010). It is known that heavy metals, compaction, drought and salinity can decrease plant growth and production. However, AMF can promote plant growth increasing plant production under stress due to their benefits: establishment of extensive hyphal networks and secretion of biochemicals like glomalin, which enhance water and nutrient uptake meliorating soil structure (reviewed by Miransari, 2010).

It is interesting to mention that Biotechnology offers new strategies that can be used to develop transgenic crop plants with improved tolerance to stresses. Moreover, germplasm collected from high altitude and low temperature areas, cold tolerant mutant, and wild species can be exploited for improved tolerant genotypes in other areas. Then, the impacts of two important plant stressors, drought and freezing, on microbial and plant physiology will be also addressed here.

Lastly, biochar soil amendment not only can contribute to improved soil fertility and plant productivity, but can benefit microorganism populations that promote plant growth and resistance to biotic stresses (soil borne diseases and foliar pathogens). The mechanisms by which it is benefic are scarcely understood, and indirect effects (increased water and nutrient retention, improvements in soil pH, increased soil cation exchange capacity, effects on P and S transformations and turnover, neutralization of phytotoxic compounds in the soil, improved soil physical properties, and alteration of soil microbiota (Elad *et al.*, 2011). Interestingly, biochar promote AMF and in this regard, further studies are needed (Warnock *et al.*, 2007).

This chapter examines the current information on the benefits of AM symbioses in stressed plant systems, with respect to the research results in South America. Additionally, soil amendments that may have a synergistic influence are discussed.

ARBUSCULAR MYCORRHIZAL FUNGI AND PLANTS

Plants provide several services (provisioning of plant products, erosion control, invasion resistance, pathogen and pest regulation and soil

fertility regulation)(Quijas *et al.*, 2010). The vegetation cover is the most important vegetation parameter for soil erosion (interrill or rill erosion) control as well as the influence of plant roots is increasingly studied in this sense (*e.g.* for rill and ephemeral gully erosion) (Gyssels *et al.*, 2005).

Additionally, plants interact with below-ground group of microorganisms (Kuyper and Goede, 2005) as well as above-ground (Zheng and Dicke, 2008).

For example, the numbers of worldwide species of rhizobia (98 species in 13 genera) (<http://www.rhizobia.co.nz/>) and of AMF (230 species in 13 genera) (www.mycobank.org) is much lower than that of legumes (18,000) or AM plants (3,617 species in 263 families) (Wang and Qiu, 2006), totaling more than 3,941 [over 324 AM plant species compiled by Pagano (2012)] and estimated in 200,000 (Kuyper and Goede, 2005).

To know the mycotrophic status in plant species is an important tool for various purposes such as seedling production, plant cultivation (greenhouse or field), ecological restoration, endangered species protection, to differentiate plant functional types and for screening for plant stress tolerance. Information on parasitic AMF association is also needed.

It is known that parasitic interactions show a larger degree of selectivity of species than mutualisms; but selectivity is also the rule in the last associations, mostly at lower taxonomic level (Kuyper and Goede, 2005).

Little is known about the perception of abiotic stress by plants at the molecular level (Schulze *et al.*, 2002). However, mycorrhizosphere conditions are part of the common plant-microbe strategies and plant-defending mechanisms that can result in a better stress-alleviation at chronic metal-exposures (Biró *et al.*, 2012), for example. There are signaling compounds produced by the host plant to promote root colonization by AMF such as strigolactones (Bouwmeester *et al.*, 2007). It is also known that isoprenoids and Jasmonic acid (JA) play a role in plant defense protection, which is related to the establishments and functionality of mycorrhizal symbiosis (Pozo and Azcón-Aguilar, 2007).

The AMF symbiosis can potentiate C allocation to root exudates and give more resources to plant, to synthesize essential isoprenoids and to use them for its growth. The JA application might contribute to the shoot response to root colonization by AM fungi (Isayenkov *et al.*, 2005)

with potential enhance of defense status (Augé, 2001; Cordier *et al.*, 1998; Hause and Schaarschmidt, 2009; Asensio *et al.*, 2012).

Thus, increasing experiments worldwide are subjecting the plants to stressors such as drought and to exogenous application of plant hormones or pesticides, in order to test the interaction between AM symbiosis, biochar and plants.

Since the publication of the seminal books of Sieverding (1991), Smith and Read (2008), van der Heijden and Sanders (2003) and Miransari *et al.* (2008) and several reports (see Table 2) it was highlighted the need for more information on how AMF influence plant stress in different crop species. However, to increase our ability to optimize management of AMF in field situations is still urgently needed.

Table 2: Some recent book and reports dealing with occurrence of AMF in stressed conditions

<i>Reports on AMF and plant stress</i>	<i>Biome/ ecosystems/ country</i>	<i>References</i>
AMF in native species and soil/ climatic stress	Cerrado, Brazil	Detmann <i>et al.</i> (2008)
AMF in <i>Calolisianthus</i> species/ water deficit and nutritional stress	Rupestrian field, Brazil	Delgado <i>et al.</i> (2011)
Mycorrhizal biotechnology, AMF, phytoremediation, climatic changes	Several ecosystems	Tangadurai <i>et al.</i> (2010)
AMF and soil stresses	Several ecosystems	Miransari (2010)
AMF and heavy metals stress, phytoextraction greenhouse experiments	Brazil	Cabral <i>et al.</i> (2010); Silva <i>et al.</i> (2006)
Drought tolerance and AMF in three perennial grasses	Grassland, Argentina	Busso <i>et al.</i> (2008)
AMF and alleviation of soil stresses	Several ecosystems	Miransari <i>et al.</i> (2008)
AMF and alleviation of soil stresses	Several ecosystems	Siddiqui <i>et al.</i> (2008)
AMF and soil and environmental stresses	Several ecosystems	Smith and Read (2008)
AMF and hydrocarbon soil stress	Polluted soils Argentina and Germany	Cabello (2001)

ARBUSCULAR MYCORRHIZAL PLANTS AND DROUGHT STRESS

Of serious significance are the effects of global change on soils: increased soil temperatures, increased nutrient availability, increased ground instability in mountainous regions, and increased erosion from floods.

As nutrient and water limitations increase, plants can allocate more photosynthate to mycorrhizal hyphae to increase soil resource uptake, which can be seen particularly in high latitude and high altitude ecosystems (See Simard and Austin, 2010).

Plant responses to water deficiency are complex (and include stress avoidance or tolerance). It is known that stomata close in response to water deficit; however, it is more related to soil moisture than to leaf water status, involving chemical signals produced by roots (Chaves *et al.*, 2002).

Mycorrhizal plants under drought conditions increase stomatal conductance, transpiration rate and leaf water potential due to a higher water uptake (Augé, 2001) than non-mycorrhizal plants. However, the mechanism by which the fungus modifies host-plant water relations remains unknown (different hypotheses have been tested with inconclusive results (Morte *et al.*, 2000) and the contribution of AM symbiosis to plant drought tolerance is nowadays seen as the result of accumulative effects (physical, nutritional, physiological and cellular) (Ruiz-Lozano, 2003).

In 2009, Monroy Ata and Sánchez compiled the benefits of AMF in semiarid plants of Mexico. They showed better water relations and plant growth in such environments in comparison with uninoculated control plants.

Recently, Barea *et al.* (2011) compiled the diversity of mycorrhizas found in semiarid Mediterranean ecosystem in SE Spain. They showed the benefit of mycorrhizal fungi to help plants to establish and deal with nutrient deficiency, drought, soil disturbance and other environmental stresses characteristically involved in soil degradation.

In Brazil, reports from highland fields from deciduous forest (See Pagano and Araújo, 2011; Pagano, 2012) pointed out a total of ~28 AM plant species and at least 36 AM species that occurs in those ecosystems (Pagano *et al.*, 2013). Additionally, Carvalho *et al.* (2012) reported 49 AMF species in highland fields from Minas Gerais State, Brazil, of them 23 AMF species are in common with the reports cited above.

Argentinean arid and semiarid regions present in general xerophytic plants, forming dry forests, open scrublands, shrub steppe, etc. Lugo *et al.* (2002, 2008) studied different vegetal types such as Jarillal and Puna vegetation and compiled information on mycorrhizal status of 225 AM plant species (see Pagano *et al.*, 2012), some of them also

associate with dark septate endophytic fungi (DSE). In dry Puna ecosystem (2000 to 4400 m. a. s. l.) ten AMF species were found, and *Glomus* was the predominant genus.

ARBUSCULAR MYCORRHIZAL PLANTS AND FLOODING STRESS

Flooding has proved to be a usual stress affecting agriculture and forestry, being able to change soil microbial abundances, including rhizobial composition as seen in experiments of land restoration in the Rio Doce valley, Minas Gerais, Brazil (Pagano, 2008). The tropical legume tree (*Centrolobium tomentosum*) tested for functional and structural riparian restoration showed renodulation by fast-growing strains after flood disturbance (plants were inoculated with a fast growth *Rhizobium* strain) than uninoculated plants.

In general, less research has been focused on conditions of excess water, although some aquatic and wetland plants associate with AMF (see Pagano 2012). The function of AM fungi in Florida wetland, for example, do not appeared to be restricted by hydroperiod. Root colonization is probable controlled by plant factors such as carbon availability (Ipsilantis and Sylvania, 2007).

Using phylogenetic analysis, Wang *et al.* (2011) also showed that flooding plays an important role in AMF diversity, and its effects appear to depend on the degree (duration) of flooding. Both host species and tide level affected community structure of AMF, indicating the presence of habitat and host species preferences (Wang *et al.*, 2011). Additionally, Radhika *et al.* (2012) showed the benefits of AM association in mangroves from Ganges river, India, to cope soil physical and chemical stress.

In the Argentinean flooding pampa the mycorrhizal colonization of the community of *Paspalum dilatatum* (a highly palatable, dominant species) was higher in the continuous grazing plots (Grigera and Oosterheld, 2004) than in enclosure sites.

ENVIRONMENTAL STRESS FROM HUMAN ACTIVITIES

Arbuscular Mycorrhizal Fungi and Tillage

Anthropogenic alterations to improve the productivity of field crops (*e.g.* tillage, monoculture, crop rotation, irrigation, amendments and

crop protection) can be denominated as perturbation stresses, result in disturbance of the native soil microbial ecosystem. While moderate perturbation will be benefic in the short term, higher levels of stress may result in degraded soils (Sturz and Christie, 2003).

Nowadays, the conventional tillage system is still commonly used in most countries, usually consisting in the use of moldboard plowing and additional secondary operations to prepare the seedbed. However, field traffic or intensive tillage result in excessive soil compaction and soil water loss.

It is known that tillage reduce AMF spore and hyphal length densities, as well as decreased glomal concentrations in both temperate and tropical soils (Wright *et al.*, 1999; Boddington and Dodd, 2000). The composition and diversity of AMF spore communities were affected by tillage in a number of studies (Pagano, 2011). Moreover, direct effects of tillage on AMF propagules are the following: the disruption of the hyphal network; the dilution of the propagule-rich topsoil; and accelerated root decomposition (Schalamuk and Cabello, 2010).

In addition, AM fungi can be strongly decreased by conventional agricultural practices, possibly due to disturbance of AM fungal hyphal networks, changes in soil nutrient content, altered microbial activity, or changes in weed populations (Jansa *et al.*, 2003; 2006).

In Argentina, earlier studies have found less management of AMF in order to increase plant productivity (Covacevich and Echeverria, 2009). Soils of the Pampas region present high native AMF that colonize crop plants under different management systems (Covacevich *et al.*, 2006; 2007, Schalamuk *et al.*, 2006; Covacevich *et al.*, 2008); however, they are not yet manipulated.

More recently, Schalamuk and Cabello (2010) showed that different types of AM inocula from a field experiment with tilled and no-tilled wheat and from nondisturbed treatments (spontaneous vegetation), presented different proportions of AM families (*Acaulosporaceae*, *Gigasporaceae*, *Glomeraceae*), between field and trap cultures. *Glomeraceae* were higher in the trap cultures, which was attributed to the use of intra- and/or extra radical mycelium, showing advantages in the use of these propagules.

ARBUSCULAR MYCORRHIZAL FUNGI AND PLANT BIOTIC STRESSES

Biotic stresses (disease, herbivory and/or the presence of competitors) as much as abiotic stresses such as nutrient deficiency and drought can affect both plant and symbiont fitness. Damage caused by biotic factors such as herbivory have often enhance secondary metabolism, however response depends on the particular species. It is known that many plants species respond to herbivory or pathogens attack by increasing synthesis and releasing jasmonic acid and methyl jasmonate, starting in damaged organs.

With regard to AMF symbioses, Wehner *et al.* (2010) indicate the mechanisms of protection of host plants from root pathogenic fungi by different AMF species. They pointed out the little evidence and the focus on *Glomus* species, such as *Glomus intraradices* and *Funneliformes mosseae*, which do not represent of the whole fungal biodiversity. Only one report (Maherali and Klironomos, 2007) refers to abundance of AMF species and suggest their coexistence by reduced competition between them, enhancing ecosystem health.

ARBUSCULAR MYCORRHIZAL FUNGI AND HEAVY METALS

While many heavy metals (zinc, copper, cobalt, nickel, mercury, lead, cadmium, silver and chromo) (Berry and Wallace, 1981) have considerable toxicity, others are essential micronutrients for animals, plants and many micro-organisms. It is known that most vascular plants need 17 essential elements for normal growth and development (see Raven *et al.*, 2005).

Certain elements that are normally toxic are, for certain organisms or under certain conditions, beneficial (vanadium, tungsten, and cadmium). It is known that most metallophytes plants belong to the families *Brassicaceae* and *Caryophyllaceae*, which are known as non-mycorrhizal plants (de Mars and Boerner, 1996). However, some species in these families, *e.g.*, *Biscutella laevigata* and *Thlaspi* spp., are able to develop symbioses with AM species such as *Glomus intraradices* (Hildebrandt *et al.*, 2007).

Alleviating heavy metal toxicity by AMF colonization can vary to a large extent, depending on the heavy metal, its concentration in the soil, the fungal partner, and the conditions of plant growth (Hildebrandt *et al.*, 2007). Plant tolerance can be enhanced by inoculation with specific AMF (Cicatelli *et al.*, 2010; Lingua *et al.* 2008).

More recently, Cicutelli *et al.* (2012) showed the improvement of poplar growth associated with increased uptake of Cu and Zn when inoculated with *Glomus* spp. (specially with *Glomus mosseae*) as compared with non-mycorrhizal plants.

In Brazil, some of the studies dealing with heavy metals such as those by Dr Siqueira (Cabral *et al.*, 2010; Silva *et al.*, 2006; Siqueira *et al.*, 2011) showed the retention capacity of Cu, Zn, Cd, and Pb by AMF mycelium, which differed amongst the different AMF species. Moreover, soil amendments for remediating metal contaminated soil in the tropics were indicated.

Dr Marta Cabello's pioneer work conducted in hydrocarbons polluted areas in Argentina, showed that native AMF, its isolation, quantification of infectivity of indigenous propagules and its effectiveness could be applied in bioremediation programs (Cabello, 1997, 2001). Her results confirmed the beneficial effects of AMF as inoculants due to the increased hosts efficient adaptation to contamination. Furthermore, those results suggested a huge importance of the selection of AMF species to be included in revegetation/restoration practices. A protocol for studying the effect of hydrocarbon pollution on AM plants is presented in Fig. 1.

It is known that the presence of gold and their exploration results in fine sulphidic, saline wastes (tailings), which contain toxic elements and compounds such as cadmium, lead, manganese, cyanide, and particularly arsenic. In Spain, for example, strong evidence that AM plants can develop arsenate resistance has been presented by González-Chávez *et al.* (2002).

In Brazil, Pagano *et al.* (2007) have studied differences in P response of native Brazilian trees to inoculation with arbuscular mycorrhizal fungi. One of them, *Anadenanthera peregrina* Speg., has increased potential use in recuperation of degraded lands; however, the nutritional requirements are scarcely known and the AMF symbioses have been showed in greenhouse (Pereira *et al.*, 1996; Carneiro *et al.*, 1998; Pagano, 2007). Pagano *et al.* (2007) have found that young *Anadenanthera peregrina* is AMF-independent, but a P-responsive species. In this way, P fertilizer should be applied in order to guarantee adequate seedling development. Moreover, those authors showed that inoculation of selected AMF species (*Scutellospora heterogama*) improved growth parameters and P concentration in leaves (Table 3). To know the response to fertilization and inoculation with AMF species of trees species is a very useful information. In the case of P, the competition

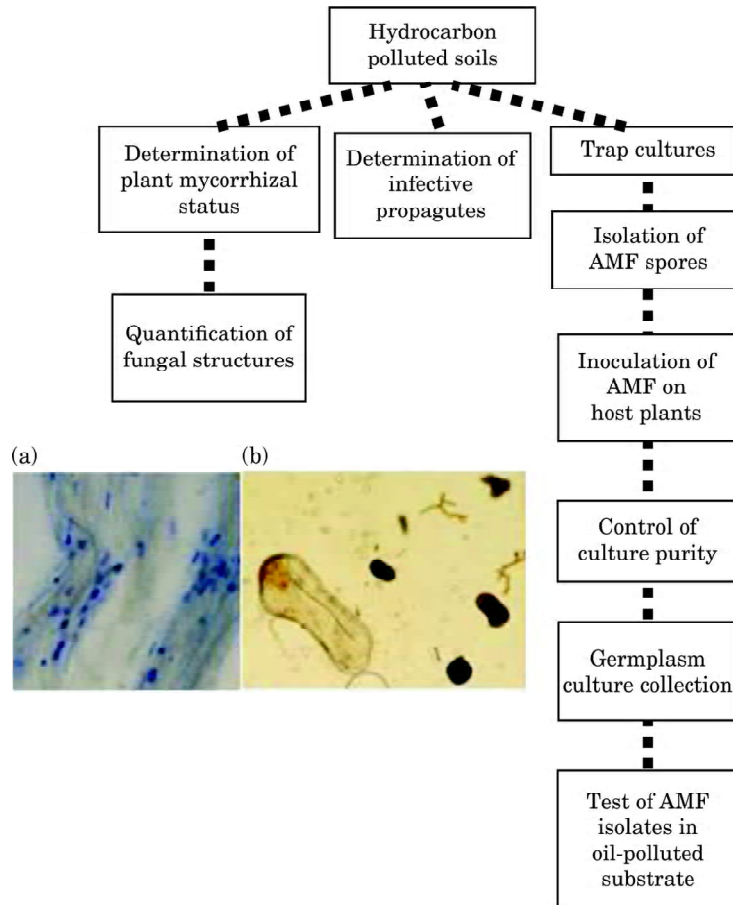


Fig. 1: Protocol for studying the effect of hydrocarbon pollution on AM plants. Roots of plants growing in the polluted soils are stained for AM colonization (a). Determination of infective propagules including spores (b) and trap cultures against soil samples are required (Adapted from Cabello, 2001; Photos by M. Pagano).

between arsenate (and As) and phosphate for adsorption sites in soils and absorption by plants have been showed. Moreover it is known that P addition to soil can increase phytotoxicity realizing more As for the soil solution (Melo *et al.*, 2007). This can be explained in terms of similarity between As and P. Plants with high P doses also decreased arsenate levels in nectar, even when subjected to high arsenate levels. Additionally, other reports suggest that the sequestration of As is not performed in leaves, which will result in litter without As. Surprisingly, a recent report showed that *A. peregrina* did not tolerate As without

Table 3: Response of *A. peregrina* to AMF inoculation and P fertilization 150 days after sowing. Values followed by the same letter in each column do not differ significantly by One way ANOVA and Tukey's HSD test $p < 0.05$. Adapted from Pagano *et al.* (2007).

AMF inoculation	P fertilization	Plant height (cm)	P concentration in leaves (mg g^{-1})
<i>Glomus</i>	32.5 mg dm^{-3}	16.5 ^a	1.15 ^a
	65 mg dm^{-3}	24.0 ^b	1.82 ^a
	136 mg dm^{-3}	17.1 ^a	1.92 ^a
<i>Gigaspora</i>	32.5 mg dm^{-3}	16.5 ^a	1.36 ^a
	65 mg dm^{-3}	14.3 ^a	1.63 ^a
	136 mg dm^{-3}	28.1 ^{ab}	2.84 ^{ab}
<i>Scutellospora</i>	32.5 mg dm^{-3}	13.5 ^a	1.14 ^a
	65 mg dm^{-3}	14.5 ^a	1.33 ^a
	136 mg dm^{-3}	33.6 ^b	4.00 ^b
<i>Acaulospora</i>	32.5 mg dm^{-3}	12.3 ^a	0.99 ^a
	65 mg dm^{-3}	20.9 ^b	2.29 ^a
	136 mg dm^{-3}	25.6 ^{ab}	1.98 ^a
Non inoculated	136 mg dm^{-3}	32.1 ^{ab}	2.73 ^{ab}

the AMF symbiosis (Gomes *et al.*, 2012). In this sense *A. peregrina* showed great potential for phytoremediation, particularly for As (with toxicity and potential risk to ecosystems as well as to human health) and abundant in contaminated sites (*e.g.* mining tailings in Minas Gerais State, Brazil). Given the potential benefits to environment of *A. peregrina*, it is not surprising that manipulation of AMF communities needs to be more carefully investigated.

Moreover, AMF inoculation can reduce the uptake of HM and arsenic from metal contaminated biosolids and tailings and thus diminish the risk for the food chain. However, it will depend on the part of the plant that accumulates the HM and the part that is use for food. The native legume species *A. peregrina* also showed tolerance to *E. camaldulensis* and *E. grandis* oils, being tested, in field conditions, inoculated (AMF and rhizobia) and mixed with *E. camaldulensis* plants (Duarte *et al.*, 2012). In this sense it is known that the production of allelochemicals is regulated by diverse factors (environmental: temperature, light intensity, water and nutrient availability, soil texture and microorganisms) (Chou and Kuo, 1986; Carmo *et al.*, 2007). Furthermore, factors related to stress can increase their biologic activity (Rizvi and Rizvi 1992; Einhellig, 1999; Inderjit *et al.* 2006). Once more we detected AMF, and also ectomycorrhiza, in plants of *E. camaldulensis* (monoculture and mixed plantations) (Pagano and Scotti, 2008).

BIOCHAR STIMULATION OF BENEFICIAL SOIL MICROBIOTA

Given the potential benefits to agricultural productivity, biochar soil amendment not only can contribute to improved soil fertility, but can benefit microorganism populations that promote plant growth and resistance to biotic stresses (soil borne diseases and foliar pathogens). However, the mechanisms by which it is beneficial are scarcely understood, as well as the indirect effects (increased water and nutrient retention, improvements in soil pH, increased soil cation exchange capacity, effects on P and S transformations, neutralization of phytotoxic compounds, improved soil physical properties, and alteration of soil microbiota (Elad *et al.*, 2011)). Interestingly, biochar promote AMF and in this regard, further studies are needed (Warnock *et al.*, 2007). It must be stressed that there is much future research to elucidate the “Biochar Effect” (Elad *et al.*, 2011). Recent studies, for example, showed that biochar addition to asparagus field soil resulted in reductions in root lesions caused by *Fusarium* sp. compared with a non-amended control (Elmer and Pignatello, 2011). Moreover, biochar amendments improved AM colonization of asparagus roots, contributing to control diseases (Elmer and Pignatello, 2011). It is also known that biochar may help to remove allelopathic effects via adsorption and detoxification, as pointed by Wardle *et al.* (1998).

Further studies evaluating the types of biochar (depending on original feedstock and pyrolysis conditions) (Downie *et al.*, 2009; Krull *et al.*, 2009) that induce resistance responses in plants against a broad range of pathogens and parasites including fungi, bacteria, viruses and nematodes, are urgently needed.

CONCLUSION

In the introduction to this chapter, we briefly described plant stress factors and the benefits that mycorrhizal fungi provide to their plant hosts.

Throughout the chapter, we have showed that stress affects soil physical and chemical properties, influencing the population, diversity and activities of soil microbes, including symbiotic fungal populations. To know the mycotrophic status of plant species is essential, and drought stress increasingly link plant to soil. Additionally, flooding and anthropogenic alterations (tillage) were discussed although the lack of more detailed studies.

The alleviation of heavy metal stress would have great implication in the manipulation of AMF species able to colonize plants in polluted soils approving the potential of AMF to be incorporated in phytoextraction technologies as mycorrhizo remediation.

This chapter argues that AMF alleviate biotic stresses which have greater effect on plant growth than increasing the amount of pesticides or fertilizer commonly added; however, to develop technologies and protocols are crucial. Consequently, further research is needed to cope plant stresses.

Finally, as cattle and agriculture are increasing activities, the potential benefits to agricultural productivity of biochar soil amendment and their interactions with mycorrhizal plants were also pointed.

ACKNOWLEDGEMENTS

M. Pagano is grateful to the Council for the Development of Higher Education at Graduate Level, Brazil (CAPES), and to the Minas Gerais State Agency for Research and Development (FAPEMIG) for the postdoctoral scholarships granted. M.N. Cabello is a researcher from Comisión de Investigaciones Científicas (CIC) Provincia Bs. As., Argentina.

REFERENCES

- Asensio, D., Rapparini, F. and Penuelas, J. (2012). AM fungi root colonization increases the production of essential isoprenoids vs. nonessential isoprenoids especially under drought stress conditions or after jasmonic acid application. *Phytochemistry*, 77: 149–161.
- Augé, R.M. (2001). Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza*, 11: 3–42.
- Azcón, R. and Barea, J.M. (2010). Mycorrhizosphere interactions for legume improvement. In: Khan, M.S., Zaidi, A. and Musarrat, J. (Eds.), *Microbes for Legume Improvement*. Springer, Vienna, pp. 237–271.
- Bainard, L.D., Koch, A.M., Gordon, A.M. and Klironomos, J.N. (2012). Temporal and compositional differences of arbuscular mycorrhizal fungal communities in conventional monocropping and tree-based intercropping systems. *Soil Biology and Biochemistry*, 45: 172–180.
- Barea, J.M., Azcón, R. and Azcón-Aguilar, C. (2005a). Interactions between *mycorrhizal* fungi and bacteria to improve plant nutrient cycling and soil structure. In: Buscot, F. and Varma, A. (Eds.), *Microorganisms in Soils: Roles in Genesis and Functions*. Springer-Verlag, Berlin, Heidelberg, pp. 195–212.

- Barea, J.M., Pozo, M.J., Azcón, R. and Azcón-Aguilar, C. (2005b). Microbial co-operation in the rhizosphere. *Journal of Experimental Botany*, 56: 1761–1778.
- Barea, J.M., Palenzuela, J., Cornejo, P., Sánchez-Castro I., Navarro-Fernández, C., López-García, A., Estrada, B., Azcón, R., Ferrol, N. and Azcón-Aguilar, C. (2011). Ecological and functional roles of mycorrhizas in semi-arid ecosystems of Southeast. *Spain Journal of Arid Environments*, 75: 1292–1301.
- Berry, W.L. and Wallace, A. (1981). Toxicity: The concept and relationship to the dose response curve. *J. Plant Nutr.*, 3: 13–19.
- Biró, B., Kádár, I., Lampis, S., Gullner, G. and Kőmives, T. (2012). Inside and outside rhizosphere parameters of barley and dose-dependent stress alleviation at some chronic metal exposures. *Acta Phytopathologica et Entomologica Hungarica*, 47(2): 373–383.
- Boddington, C.L. and Dodd, J.C. (2000). The effect of agricultural practices on the development of indigenous arbuscular mycorrhizal fungi. I. Field studies in an Indonesian ultisol. *Plant and Soil*, 218: 137–144.
- Busso, C.A., Bolleta, A., Flemmer, A.C. and Montani, T. (2008). Influence of soil water status on arbuscular mycorrhizas in three perennial grasses in central Argentina. *Ann. Bot. Fennici.*, 5: 435–447.
- Cabello, M.N. (1997). Hydrocarbon pollution: Its effect on native arbuscular mycorrhizal fungi (AMF). *FEMS Microbiology Ecology*, 22: 233–236.
- Cabello, M.N. (2001). Mycorrhizas and hydrocarbons *In: Fungi In Bioremediation* Gadd, G.M. Eds., pp. 456–471.
- Cabral, L., Siqueira, J.O., Soares, C.R.F.S. and Pinto, J.E.B.P. (2010). Retenção de metais pesados em micélio de fungos micorrízicosarbusculares. *Quim. Nova*, 33(1): 25–29.
- Carneiro, M.A.C., Siqueira, J.O., Moreira, F.M.S., Carvalho, D., Botelho, S.A. and Saggin-Junior, O.J. (1998). Micorriza arbuscular em espécies arbóreas e arbustivas nativas de ocorrência no Sudeste do Brasil. *CERNE*, 4: 129–145.
- Chaves, M.M., Pereira, J.S., Maroco, J., Rodrigues, M.L., Ricardo, C.P.P., Osório, M.L., Carvalho, I., Faria, T. and Pinheiro, C. (2002). How plants cope with water stress in the field. Photosynthesis and growth. *Annals of Botany*, 89: 907–916.
- Cicatelli, A., Lingua, G., Todeschini, V., Biondi, S., Torrigiani, P. and Castiglione, S. (2012). Arbuscular mycorrhizal fungi modulate the leaf transcriptome of a *Populus alba* L. clone grown on a zinc and copper-contaminated soil. *Environmental and Experimental Botany*, 75: 25–35.
- Cordier, C., Pozo, M.J., Barea, J.M., Gianinazzi, S. and Gianinazzi-Pearson, V. (1998). Cell defense responses associated with localized and systemic resistance to *Phytophthora parasitica* induced in tomato by an arbuscular mycorrhizal fungus. *Mol. Plant-Microbe Interact.*, 11: 1017–1028.
- Covacevich, F., Marino, M.A. and Echeverría, H.E. (2006). The phosphorus source determines the arbuscular mycorrhizal potential and the native mycorrhizal colonization of tall fescue and wheatgrass in a moderately acidic Argentinean soil. *European Journal of Soil Biology*, 42: 127–138.
- Covacevich, F., Echeverría, H.E. and Aguirrezaba, L.A.N. (2007). Soil available phosphorus status determines indigenous mycorrhizal colonization of field and glasshouse-grown spring wheat from Argentina. *Applied Soil Ecology*, 35: 1–9.
- Covacevich, F. and Echeverría, H.E. (2008). Receptivity of an Argentinean pampas soil to arbuscular mycorrhizal *Glomus* and *Acaulospora* strains. *World Journal of Agricultural Sciences*, 4(6): 688–698.

- De Mars, B.G. and Boerner, R.E.J. (1996). Vesicular arbuscular mycorrhizal development in the *Brassicaceae* in relation to plant life span. *Flora*, 191: 179–189.
- Delgado, M.N., Azevedo, A.A., Silva, L.C., Valente, G.E. and Kasuya, M.C.M. (2011). Comparative anatomy of *Calolisianthus* species (*Gentianaceae*–*Helieae*) from Brazil: Taxonomic aspects. *Edinburgh Journal of Botany*, 68(1): 139–155.
- Detmann, K.S.C., Delgado, M.N., Rebello, V.P.A., Leite, T.S., Azevedo, A.A., Kasuya, M.C.M. and Almeida, A.M. (2008). Comparison of methods to visualize arbuscular mycorrhizal and dark septate endophytic fungi innative Cerrado species. *R. Bras. Ci. Solo*, 32: 1883–1890.
- Downie, A., Crosky, A. and Munroe, P. (2009). Physical properties of biochar. In: *Biochar for Environmental Management: Science and Technology*. (Lehmann, J. and Joseph, S. Eds.), Earthscan, London, UK, pp. 13–32.
- Duarte, N.F., Karam, D., Bucek, E.U. and Muzzi M.R.S. (2012). Tolerance of *Anadenanthera peregrina* to *Eucalyptus camaldulensis* and *Eucalyptus grandis* essential oil as condition for mixed plantation. *Braz. Arch. Biol. Technol.*, 55(3): 417–424.
- Elad, Y., Cytryn, E., Meller Harel, Y., Lew, B. and Graber, E.R. (2011). The Biochar Effect: Plant resistance to biotic stresses. *Phytopathol. Mediterr.*, 50: 335–349.
- Elmer, W.H. and Pignatello, J.J. (2011). Effect of biochar amendments on mycorrhizal associations and *Fusarium* crown and root rot of asparagus in replant soils. *Plant Disease*, 95: 960–966.
- El-Khawas, S.A. and Shehata, M.M. (2005). The allelopathic potentialities of *Acacia nilotica* and *Eucalyptus rostrata* on monocot (*Zea Mays* L.) and dicot (*Phaseolus vulgaris* L.). *Plant Biotechnol.*, 4: 23–24.
- Firbank Les, G., Petit, S., Smart, S., Blain, A. and Fuller, R.J. (2008). Assessing the impacts of agricultural intensification on biodiversity: A British perspective. *Phil. Trans. R. Soc. B*, 363: 777–787.
- Gomes, M.P., Carvalho, M., Marques, T.C.L.L.S.M., Duarte, D.M., Nogueira, C.O.G., Soares, Á.M. and Garcia, Q.S. (2012). Arsenic-Sensitivity in *Anadenanthera peregrina* due to arsenic-induced lipid peroxidation. *International Journal of Applied Science and Technology*, 2(2): 55–63.
- Gonzalez-Chavez, M.C., Carrillo-Gonzalez, R., Wright, S.F. and Nichols, K. (2004). The role of glomalin, a protein produced by arbuscular mycorrhizal fungi, in sequestering potentially toxic elements. *Environ. Pollution*, 130(3): 317–323.
- Grigera, G. and Oesterheld, M. (2004). Mycorrhizal colonization patterns under contrasting grazing and topographic conditions in the flooding Pampa (Argentina). *Journal of Range Management*, 57: 601–605.
- Gyssels, G., Poesen, J., Bochet, E. and Li, Y. (2005). Impact of plant roots on the resistance of soils to erosion by water: A review. *Progress in Physical Geography*, 29(2): 189–217.
- Hause, B. and Schaarschmidt, S. (2009). The role of jasmonates in mutualistic symbioses between plants and soil-born microorganisms. *Phytochemistry*, 70: 1589–1599.
- Hildebrandt, U., Regvar, M. and Bothe, H. (2007). Arbuscular mycorrhiza and heavy metal tolerance. *Phytochemistry*, 68: 139–146.
- Ipsilantis, I. and Sylvania, D.M. (2007). Abundance of fungi and bacteria in a nutrient-impacted Florida wetland. *Applied Soil Ecology*, 35: 272–280.

- Isayenkoy, S., Mrosk, C., Stenzel, I., Strack, D. and Hause, B. (2005). Suppression of allene oxide cyclase in hairy roots of *Medicago truncatula* reduces jasmonate levels and the degree of mycorrhization with *Glomus intraradices*. *Plant Physiol.*, 139: 1401–1410.
- Jansa, J., Mozafar, A., Kuhn, G., Anken, T., Ruh, R., Sanders, I.R. and Frossard, E. (2003). Soil tillage affects the community structure of mycorrhizal fungi in maize roots. *Ecological Applications*, 13: 1164–1176.
- Jansa, J., Wiemken, A. and Frossard, E. (2006). The effects of agricultural practices on arbuscular mycorrhizal fungi. *Geological Society, London, Special Publications*, 266: 89–115.
- Krull, E., Baldock, J.A., Skjemstad, J. and Smernik, R. (2009). Characteristics of biochar: Organo-chemical properties. *In: Biochar for Environmental Management: Science and Technology*. Lehmann, J. and Joseph, S. Eds., Earthscan, London, UK, pp. 53–66.
- Kuyper, T.W. and Goede, R.G.M. (2005). Interaction between higher plants and soil-dwelling organisms. *In: der Maarel E., Vegetation Ecology*, Blackwell, UK, pp. 286–308.
- Leicach, S.R., Sampietro, D. and Narwal, S. (2009). Allelopathy, *In: Allelochemicals: Role in Plant-Environment Interactions*, Studium Press LLC, ISBN 1933699442, Texas, USA. pp. 34–41.
- Lugo, M.A. and Cabello, M.N. (2002). Native arbuscular mycorrhizal fungi (AMF) from mountain grassland (Córdoba, Argentina) I. Seasonal variation of fungal spore diversity. *Mycologia*, 94: 579–586.
- Lugo, M.A., Ferrero, M.A., Menoyo, E., Estévez, M.C., Siñeriz, F. and Anton, A.M. (2008). Arbuscular mycorrhizal fungi and rhizospheric bacteria diversity along an altitudinal gradient in South American Puna grassland. *Microbial Ecology*, 55: 705–713.
- Maherali, H. and Klironomos, J. (2007). Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science*, 316: 1746–1748.
- Miransari, M. (2010). Contribution of arbuscular mycorrhizal symbiosis to plant growth under different types of soil stress. *Plant Biology*, 12: 563–569.
- Miransari, M. (2011). Mycorrhizal fungi and ecosystem efficiency. Nova Science Publishers, Inc., Hauppauge, p. 41.
- Melo, R.F., Dias, L.E., Assis, I.R. and Faria, A.F. (2007). Influência do arsênio e fósforo sobre o crescimento de duas essências florestais. *In: XXXI Congresso Brasileiro de Ciência do solo*, Gramado, 5p. (In Portuguese).
- Monroy Ata, A. and Sánchez, R.G. (2009). Plantas y hongos. Micorrizas arbusculares: Un mutualismo esencial en zonas semiáridas. Universidad Nacional Autónoma de México, México, DF, p. 96. (In Spanish).
- Morte, A., Lovisolo, C. and Schubert, A. (2000). Effect of drought stress on growth and water relations of the mycorrhizal association *Helianthemum almeriense*-*Terfezia claveryi*. *Mycorrhiza*, 10: 115–119.
- Pagano, M.C. (2007). Characterization of Glomalean mycorrhizal fungi and its benefits on plant growth in a semi-arid region of Minas Gerais (Jaíba Project), Brazil. PhD thesis. Federal University of Minas Gerais, Belo Horizonte, Brazil.
- Pagano, M.C., Cabello, M.N. and Scotti, M.R. (2007). Phosphorus response of three native Brazilian trees to inoculation with four arbuscular mycorrhizal fungi. *Journal of Agricultural Technology*, 3(2): 231–240.
- Pagano, M.C. (2008). Composition of rhizobia associated with neotropical tree legume *Centropogon tomentosum* used in riparian restoration. *Plant Soil and Environment*, 54: 498–508.

- Pagano, M.C. and Scotti, M.R. (2008). Arbuscular and ectomycorrhizal colonization of two *Eucalyptus* species in semiarid Brazil. *Mycoscience*, 49: 379–384.
- Pagano, M.C., Cabello, M.N. and Scotti, M.R. (2010). Agroforestry in dry forest, Brazil: Mycorrhizal fungi potential. In: Kellymore, L.R. Ed. Handbook on Agroforestry: Management Practices and Environmental Impact. Nova Science Publishers, New York, pp. 367–388.
- Pagano, M.C. and Araújo, F.S. (2011). Semiarid vegetation in Brazil: Biodiversity, Impacts and Management. In: Degenovine, K.M., Ed. *Semi-Arid Environments: Agriculture, Water Supply and Vegetation*. Nova Science Publishers, Inc., Hauppauge, New York, pp. 99–114.
- Pagano, M.C. (2012). Soil tillage in agroforestry and agroecosystems: Mycorrhizal Benefits. In: Miransari, M. Ed. Soil Tillage and Microbial Activities. Research Signpost Publications, India. pp. 65–84.
- Pagano M.C., Zandavalli R.B., Araújo F.S. (2013). Biodiversity of arbuscular mycorrhizas in three vegetational types from the semiarid of Ceará State, Brazil. *Applied Soil Ecology* 67 (2013) 37–46.
- Pagano, M.C., Lugo, M., Araújo, F., Ferrero, M., Menoyo, E. and Steinaker, D. (2012). Native species for restoration and conservation of biodiversity in South America. In: *Native Species: Identification, Conservation and Restoration*, Marín, L. and Kovaè, D. (Eds.), Nova Science Publishers, New York, USA. pp. 1–55.
- Pagano M.C. (ed.) Mycorrhiza: Occurrence and Role in Natural and Restored Environments. Nova Science Publishers, Hauppauge, NY. 327p.
- Pereira, E.G., Siqueira, J.O., Curi, N., Moreira, F.M.S. and Purcino, A.A.C. (1996). Efeitos da micorriza e do suprimento de fósforo na atividade enzimática e na resposta de espécies arbóreas ao nitrogênio. *Revista Brasileira Fisiologia Vegetal*, 8: 59–65.
- Quijas, S., Schmid, B. and Balvanera, P. (2010). Plant diversity enhances provision of ecosystem services: A new synthesis. *Basic and Applied Ecology*, 11: 582–593.
- Radhika, K.P., D’Souza, J. and Rodrigues, B.F. (2012). Arbuscular mycorrhizae in aquatic plants, India. In: Pagano, M.C. (Ed.) Mycorrhiza: Occurrence and Role in Natural and Restored Environments. Nova Science Publishers, Hauppauge, NY, pp. 265–274.
- Raven, P.H., Evert, R.F. and Eichhorn, S.E. (2005). *Biology of Plants*. 7th edition. W.H. Freeman and Company Publishers. New York.
- Ruiz-Lozano, J.M. (2003). Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress. New perspectives for molecular studies. *Mycorrhiza*, 13: 309–317.
- Schalamuk, S. and Cabello, M.N. (2010). Effect of tillage systems on the Arbuscular Mycorrhizal Fungi (AMF) Propagule Bank in Soils. CAB International. *Management of Fungal Plant Pathogens* (eds A. Arya and A.E. Perelló) pp. 162–170.
- Scherr, S.J. and McNeely, J.A. (2008). Biodiversity conservation and agricultural sustainability: Towards a new paradigm of ‘ecoagriculture’ landscapes. *Phil. Trans. R. Soc. B*, 363: 477–494.
- Schimel, J., Balsler, T.C. and Wallenstein, M. (2007). Microbial stress-response physiology and its implications for ecosystem function. *Ecology*, 88: 1386–1394.
- Schulze, E., Beck, E. and Müller-Hohenstein. (2002). *Plant Ecology*. Springer-Verlag, Berlin, p. 702.

- Schützendübel, A. and Polle, A. (2002). Plant responses to abiotic stresses: Heavy metal-induced oxidative stress and protection by mycorrhization. *Journal of Experimental Botany, Antioxidants and Reactive Oxygen Species in Plants Special Issue*, 53, 372: 1351–1365.
- Siddiqui, Z. and Pichtel, J. (2008). *Mycorrhiza: Sustainable Agriculture and Forestry*. Siddiqui, Z.A., Akhtar, M.S. and Futai, K. (Eds.). Springer, p. 359.
- Siqueira, J.O., Vangronsveld, J., Soares, C.R., Sousa, F. and Curi, N. (2011). Inorganic materials as ameliorants for soil remediation of metal toxicity to wild mustard (*Sinapis arvensis* L.). *International Journal of Phytoremediation*, 13: 498–512.
- Silva, S., Siqueira, J.O. and Soares, C.R.F.S. (2006). Mycorrhizal fungi influence on brachiaria grass growth and heavy metal extraction in a contaminated soil. *Pesq. Agropec. Bras.*, 41(12): 1749–1757.
- Simard, S.W. and Austin, M.E. (2010). The role of mycorrhizas in forest soil stability with climate change. In: *Climate Change and Variability edited by Simard, S.W. and Austin, M.E.* Sciyo, Rijeka, pp. 275–302.
- Smith, S.E. and Read, D.J. (2008). *Mycorrhizal Symbiosis*, New York: Elsevier; 2008.
- Sturz, A.V. and Christie, B.R. (2003). Beneficial microbial allelopathies in the root zone: The management of soil quality and plant disease with rhizobacteria, *Soil Till. Res.*, 72: 107–123.
- Takahashi, T., Kokubo, R. and Sakaino, M. (2004). Antimicrobial activities of *Eucalyptus* leaf extracts and flavonoids from *Eucalyptus maculate*. *Letters in Applied Microbiology*, 39(1): 60–64.
- Tangadurai, D., Busso, C.A. and Hijri, M. (eds.) (2010). *Mycorrhizal Biotechnology*. Capital Publishing Company, New Delhi, p. 216.
- Zheng, Si.J. and Dicke, M. (2008). Ecological genomics of plant-insect interactions: From gene to community. *Plant Physiology*, 146: 812–817.
- Wang, B. and Qiu, Y.L. (2006). Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza*, 16: 299–363.
- Wang, Y., Huang, Y., Qiu, Q., Xin, G. and Yang, Z. (2011). Flooding greatly affects the diversity of arbuscular mycorrhizal fungi communities in the roots of Wetland Plants. *PLoS ONE*, 6(9): 24512.
- Wardle, D.A., Zackrisson, O. and Nilsson, M.C. (1998). The charcoal effect in Boreal forests: Mechanisms and eco-logical consequences. *Oecologia*, 115: 419–426.
- Warnock, D. D., Lehmann, J., Kuyper, T.W. and Rillig, M.C. (2007). Mycorrhizal responses to biochar in soil – concepts and mechanisms. *Plant Soil*, 300: 9–20.
- Wehner, J., Antunes. P.M., Powell. J.R., Mazukatow. J. and Rillig, M.C. (2010). Plant pathogen protection by arbuscular mycorrhizas: A role for fungal diversity? *Pedobiologia*, 53: 197–201.