

Review

Arbuscular mycorrhizal fungi: Essential belowground organisms for earth life but sensitive to a changing environment

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Changes in the soil and environment rarely occur in isolation and new insights into their impacts on arbuscular mycorrhizal fungi (AMF) in moderating ecosystems processes are needed. Any climate, soil and/or plant type change affects activity and biomass of extra radical mycelia of AMF and can consequently impact on the physiology of the host plant as well as on soil structure and rhizospheric microorganisms. Mycorrhizae have immediate access to plant root exudates and can alter the chemical composition and relative abundance of these exudates, which are a source of nutrients for many soil organisms. Thus, mycorrhizal symbiosis can directly and indirectly influence soil microbes, nutrient cycling and plant growth. Studies have revealed that AMF are cosmopolitan organisms which are present around the world and in particular in tropical dry forests, in temperate grasslands and in riparian forests. However, mycorrhizae formation is susceptible to environmental changes in both soils as well as in host plant populations. Due to the large number of factors affecting mycorrhizas the symbiosis is still little understood and it is not yet been efficiently used despite their enormous potentiality. This work explores the current research on the effects of environmental changes produced by human activities on the mycorrhizal symbioses, drawing on results mainly in agroecosystems and succession on disturbed ecosystems from Argentina and Brazil. Additionally, factors affecting indigenous mycorrhiza from different successional stages in the semiarid region of Brazil ecosystems and their possible role in the composition and stability of plant communities are discussed.

Key words: Arbuscular mycorrhiza, environmental changes, human activities.

INTRODUCTION

Many natural systems are being affected by global change (GC), especially climate change (CC), a process that has been speed up by human beings in recent years. Current scientific evidence indicates that global warming is progressing due to an increase in anthropogenic, that is, man-made, greenhouse gas concentrations, mostly due to industrial activity. Communities in South America are heavily dependent on the continent's natural resources (rangelands, plants and animals, fisheries, etc.)

as well as agricultural (crops, livestock) and forestry production. Agriculture is the major transforming agent of natural landscapes (Solbrig, 2005), spreads over an extensive area of the Argentinean and Brazilian territories and remains an important part of the economy in both countries. In Brazil, the expansion of soybean crops is concentrated in Goiás and Mato Grosso States, displacing the rich native biota of the savannas and the Amazonian forest (Solbrig, 2005). Brazil lost nearly 80% of Amazon rainforest, which have been devastated by the actions of poor subsistence cultivators and land clearing for pastureland for commercial exploitation of forest resources associated with government subsidized

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agriculture and colonization programs encouragement (Davidson et al., 2012). In Argentina, the native vegetation structure cover has also been displaced by agriculture. In comparison to the rest of the agroecological areas, grain crops had faster expansion in the rolling pampas, replacing the pristine natural lands. Since 1990, soybean production has increased by 66% worldwide (from 108 million tons in 1990 to 179 million tons in 2002) (Mattson et al., 2004) being the United States, Brazil and Argentina, which account for most of it (88%). The major change in the agricultural production of Argentina over the last 20 years was also the dominance of soybean as the principal crop of the Pampa (Grau et al., 2005; Solbrig, 2005). As a consequence and according to the National Directorate of Forests, Argentina is experiencing the most intense deforestation in its history due to the replacement of forests with soybean plantations, Córdoba being the province with the most devastating environmental damage. On the other hand, the high deforestation rate in the country resulted in numerous areas which suffer water shortages due to CC caused by the felling of the forests (Grau et al., 2005; Boletta et al., 2006).

There is now an emerging consensus that any changes occurring aboveground (in the atmosphere or land) undoubtedly will affect plant, animal and belowground microbial biodiversity (van der Putten et al., 2009) because those compartments are intimately linked. However, studies on how climate is changing, and how these changes differ along latitudes, are much more advanced than studies on how GC will affect plant community structure (Ausmus, 2009). Furthermore, there is a little knowledge yet about how CC is related to soil plant-symbionts along different ecosystems despite their influence on numerous functions such as decomposition and nutrient cycle and their role linking plant biodiversity and ecosystem functioning (Marshall et al., 2011). This is due to the fact that aboveground changes are easier to measure (Zheng et al., 2003) than those occurring belowground such as using remote sensing. However, more recent studies are conducting to understand the belowground relationships (de Carvalho et al., 2012; Pagano and Covacevich, 2011; Covacevich and Berbara, 2011; Pagano, 2011).

Arbuscular mycorrhizal fungi (AMF) are belowground plant symbionts of plant roots that add another dimension to the plant-soil-microbe system because mycorrhizae can directly and indirectly influence others soil microbes and nutrient cycling. Mycorrhizal fungi are able to develop a symbiotic association with most (over 90%) of vascular or non-vascular terrestrial plants (van der Heijden et al., 1998; Pongrac et al., 2007; Feddermann et al., 2010) and with some aquatic plants (reviewed by Pagano, 2011). Mycorrhizal symbiosis is usually non-host-specific, displaying abundant ecological differentiation and specialization to both their biotic and abiotic environments, which resulted in fungal types that are highly

specialized to unusual ecological niches (Fitter et al., 2004). AMF form a uniformly distributed mycelium in soil and hyphal proliferation occurs in response to several types of organic material deposition, improving physical and chemical soil quality. The AMF mycelium also interconnects root system of neighboring plants of the same or different species (Allen et al., 2003).

The high amount of hyphae produced by AMF is correlated with significant increases in the aggregate stability of soils (Jastrow et al., 1998; Tisdall et al., 1997; Rillig, 2004a; Treseder and Turner, 2007), modifying the soil's ability to mobilize nutrients, water content, as well as root penetration in soil and soil erosion potential. In this sense, mycorrhizal networks can create indefinitely large numbers of fungal linkages connecting together many plants in a community (Newman, 1988). This suggests that AMF formation could be an important element in the plant succession of ecosystems. Consequently, AMF are of increasingly interest for agriculture, agroforestry, restoration of degraded lands and conservation of natural ecosystems. The contribution of AMF on plant nutrition is widely documented: the symbiosis links the biotic and geochemical components of the ecosystem enhancing the uptake of nutrients with low mobility as phosphorus (P) but also zinc (Zn), nitrogen (N) and iron (Fe) (Shaw et al., 1990; Chen et al., 2007; Parniske, 2008; Siddiqui et al., 2008; Smith and Read, 2008; Miransari, 2011a) and their transfer to plants.

AMF also provide other benefits to their host plants than mineral nutrition such as stabilizing soil structure, increasing tolerance to water stress, soil salinity and drought, soil compaction, root pathogens and heavy metals or others toxic substances present in the soil (Davies et al., 1993; Augé, 2001; Feng et al., 2002; Trotta et al., 2006; Hildebrandt et al., 2007; Siddiqui and Pichtel, 2008; Raviv, 2010; Miransari, 2011b).

In low-fertility soils, plants usually maintain high levels of arbuscular mycorrhizal colonization (AMC) of its roots (Treseder, 2004; Powers et al., 2005). For that, AMF are extremely relevant in tropical soils, where they make symbiosis with a wide variety of plant species (Smith and Read, 2008). Studies from South America reported a high occurrence and diversity of AMF in preserved and reforested riparian areas of Brazil, in contrast with degraded sites, invaded by herbaceous species or used for agropecuary sector (Pagano et al., 2010a). Moreover, semiarid biomes are also expected to show a high AMF diversity in the future, as research by Goto et al. (2011) who pointed out for the Caatinga biome of Brazil. The Caatinga biome is increasingly studied for AMF, which resulted in more published researches (Pagano et al., 2012) as well as new AMF species (Silva et al., 2008; Pagano, unpublished), that point strong interactions between plant communities and AMF (Pagano et al., 2011; Pagano et al., 2012). The Brazilian rupestrian fields were recently focus of pioneer studies showing a high

AMF diversity (de Carvalho et al., 2012) and plant AMC (Pagano and Cabello, 2012) resulting in important directions for restoration programs as these ecosystems are affected by intense mining and other human activities. With regard to agronomic plants, Miranda et al. (2010) identified different indigenous AMF species associated with mixed pastures of *Arachis pintoii* (a native legume) in the state of Acre (Brazil), showing that its cultivation increase the AMF populations in production systems, improving the biological soil quality.

Mycorrhizal fungi also showed high diversity - activity in temperate grasslands such as the Argentinean Pampas (Schalamuk and Cabello, 2010) where available soil P limit both crop growth and indigenous mycorrhizal formation in native as well as and agricultural crops (Covacevich and Echeverría, 2000; Menéndez et al., 2001; Covacevich et al., 2006; Covacevich et al., 2007). Furthermore, Yungas forests are among the ecosystems most affected by human activity, with loss of biodiversity. Becerra et al. (2009) found that at two montane cloud forests from Tucumán and Catamarca Provinces (Argentina) dominant plant species were very low to medium colonized; *Alnus acuminata* formed facultative AMC showing the highest AMF spore number (SN) and the lowest AMC which was mainly explained by high soil fertility. Furthermore, Becerra et al. (2011) found twenty-two AMF morphotaxa at that environment being *Acaulospora*, the genera that most contributed to the biodiversity index at Tucumán and *Glomus* for Catamarca provinces, respectively.

In the last 20 years, publications (original articles and reviews) in relation to environmental changes (GC+CC) as well to AMF increased (Figure 1). However, publications of AMF associated to environmental changes still not show so obvious increases. Even less are available publications about AMF + (GC+CC) in South America. In this review, we discussed the mycorrhizal associations in the wider context that goes beyond their impact on mineral nutrition of host plants, as important as they are, apparently, more complex aspects are still to be revealed. Mycorrhiza-soil interactions can be affected by changes in the environment due to CC and in turn it may result in the modification of soil structural properties (Rillig and Mummey, 2006) as well as in a modified availability of nutrients (Marschner and Dell, 1994; Smith and Read, 2008). So we evaluate these interactions and consider their implications for both agricultural and disturbed natural ecosystem mainly from Argentina and Brazil.

MYCORRHIZA DEVELOPING IN A CHANGING ENVIRONMENT: CASE STUDIES AT CAATINGA AND RUPESTRIAN SOILS (BRAZIL)

In terms of biodiversity and functioning of agroecosystems, the mycorrhizal role is now being more recognized, particularly due to their known effect on plant

diversity and productivity (van der Heijden et al., 1998). The concept of using mycorrhizas as indicators of quality (Barea et al., 2002) or soil disturbance is just beginning and mycorrhizal response to changes in soil management is the focus of current several studies. However, few consistent results evidence the link between plant and soil AMF community composition. It is unclear whether diversity and abundance of AMF are associated with properties of soils, plant diversity or ecosystem management. Mycorrhizal fungi have a widespread presence in all environments, and within the tropics (Fuchs and Haselwandter, 2004; Moreira et al., 2007) although most of the knowledge regarding the effect of soil management on mycorrhizae comes from temperate regions (Raviv, 2010) and conclusive results in tropical regions are still scarce. Observations on the pattern of plant succession in semiarid regions of Brazil reported that AMF could play a key role in the composition and stability of plant communities (Sturmer et al., 2006). Changes in vegetation as a result of environmental disturbance may affect also the infectivity of native AMF (Alguacil et al., 2011). However, there are still no conclusive results on the relationship between AMF infectivity and the spatial heterogeneity of environmental disturbance (Boerner et al., 1996) because it was shown to be associated to sampling effort (Whitcomb and Stutz, 2007).

Rupestrian fields

De Carvalho et al. (2012) studied the relationship among diversity of AMF under field conditions, soil physical-chemical attributes and the plant diversity in five rupestrian fields of Serra do Cipó (Minas Gerais State, Brazil): sandy bogs (periodic flooding/rainy seasons; main vegetation: herb), peat bogs (wet during the rainy season, retaining moisture in the dry; main vegetation: herb), rocky outcrops (main vegetation: herb growing in rock crevices), quartz gravel field (main vegetation: herb; soil surface covered by quartzite rocks) and cerrado (predominance of tree and shrub species). They found that AMF spore densities and AMF richness were more related to physical soil parameters (content of gravel, sand and silt) than the chemical attributes being the quartz gravel fields the environment with highest abundance and diversity of AMF. *Glomus* was the genus with the highest number (19) of recovered species, followed by *Acaulospora* (13) and *Scutellospora* (4), which corroborates data obtained from other Brazilian environments (de Souza et al., 2010). There were 171 species of plants recorded (classified in 110 genera and 44 families). Rupestrian fields shelter 23% AMF species described all over the world and 41% of identified species in Brazilian ecosystems. That research also showed significantly higher richness in plant species, but sandy bogs showed low AMF richness and the lowest AMF diversity index. In the rocky outcrops, the plant communities

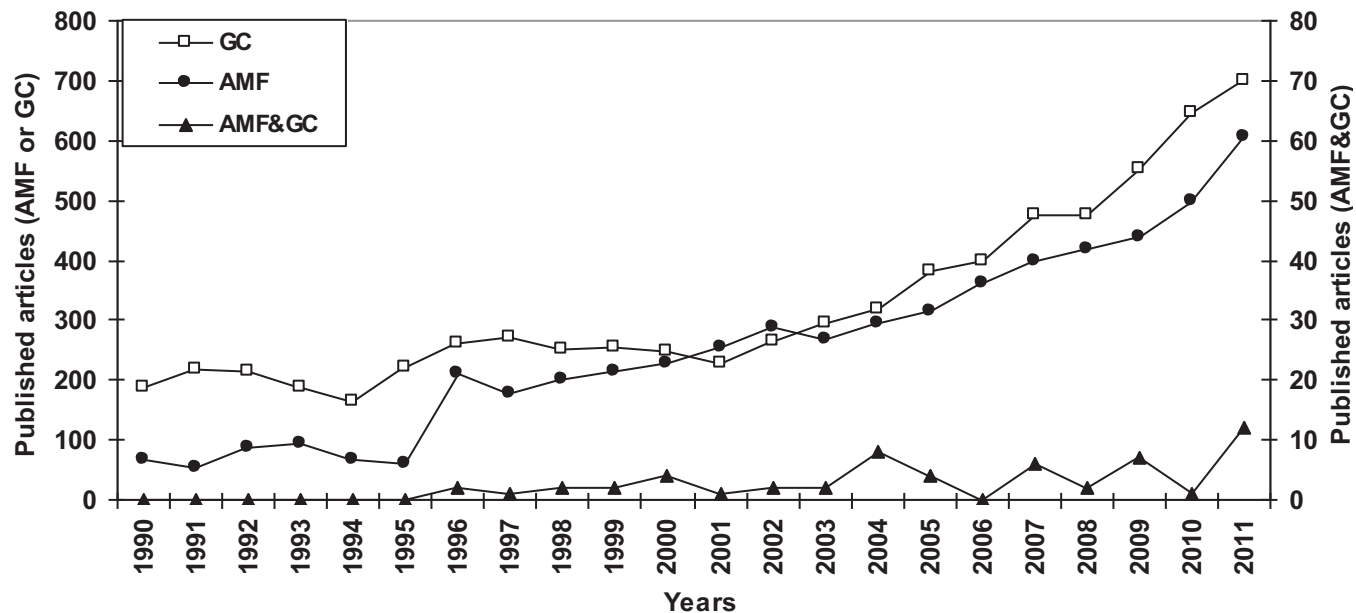


Figure 1. Number of articles (original papers and reviews) on AMF and GC published annually since 1990, included in the SCOPUS. Database survey conducted on March, 2012.

showed high plant species richness but the AMF communities exhibited low richness. Studies by de Carvalho et al. (2012) concluded that rupestrian fields AMF are highly diverse and this can help to show this ecosystem as a hot spot.

The high diversity of AMF found in the rupestrian fields of Serra do Cipó was attributed both to heterogeneity within the habitats and with soil physical attributes (mainly grain size and texture). De Carvalho et al. (2012) also pointed that diversity of AMF was related to the variability among the mosaic of habitats of the rupestrian fields and may contribute to the heterogeneity of the assessed environments. In sandy bogs, they found intermediate-low richness and diversity associated with *Lagenocarpus rigidus*, which is a species of the Cyperaceae family. In rocky outcrops, the dominant species was *Trachypogon spicatus*, a slow-growing climax Poaceae, slightly dependent on AMF association (Pasqualini et al., 2007). Highest AMF richness was found in gravel fields, with *Vellozia* sp. as the dominant plant species in this habitat. Earlier studies conducted by Pagano and Scotti (2009) showed that *Paepalanthus bromelioides* (Eriocaulaceae, a probably endemic species that inhabits the high altitude rocky-substrate) and *Bulbostylis* sp. (Cyperaceae, common of in rocky fields or flooding soils) at the Serra do Cipó soils (pH 5.3 and organic matter content 2.72%, sand >78%, clay>7%) effectively formed indigenous AMF. In the rooting zone soil, they found four taxa of AMF, two belonging to the *Glomus* genus, one to *Acaulospora*, and one to *Scutellospora*. Although they found the lowest diversity of AMF in comparison to the study reported by de Carvalho

et al. (2012), highest *Glomus* taxa supported the hypothesis pointed by de Carvalho et al. (2012) that rupestrian fields are a hotspot for Glomeromycetes. The lower diversity in AMF found by Pagano and Scotti (2009) could be attributed in part to a higher sand content (and lower in larger granulometry as 'rock' soil) in the fields where the samples were collected. Another consideration could be the fact that the Cyperaceae (sedges) studied by Pagano and Scotti (2009) is recognized as non-mycorrhizal (Trappe, 1987) or mycorrhizal with low incidence (Muthukumar et al., 2004). Contrarily, they found that it was a mycotrophic host and their report was in accordance with Lovera and Cuenca (1996) about mycorrhiza formation of Cyperaceae in the restored savannas in La Gran Sabana, Venezuela. Although the results sometimes seem contradictory between different studies, it appears that the diversity of the plant communities is closely linked with the AMF diversity.

Semiarid caatinga

The tropical dry forest commonly named *caatinga* is of considerable importance because is the only biome of exclusively Brazilian distribution and much of the world's biological richness is found in that ecosystem (Queiroz, 2006). Although Stürmer and Siqueira (2008) listed 30 AMF species from the Caatinga biome, little is known about the possible relationship between infectivity capacities of native AMF from that environment.

More recently, Covacevich and Berbara (2011) compared the AMF SN, genus contribution and mycotrophic

capacity (in pots experiments) among some *caatinga* soils (Manga, Minas Gerais State, Brazil): a pasture (5 years without human activity, covered mainly by *Panicum maximum*); and three different successional stages areas: initial (8 years in process of spontaneous recovery), intermediate (17 years without human activity) and late (no recorded human activity). Mycorrhizal development of *Braquiaria* trap plants roots decreased from 45 to 90 days after planting (DAP), probably due to the fact that most of the photosynthates were allocated in the aerial part at 90 DAP and therefore less C was available in the roots to support the mycorrhiza. AMC was highest in roots growing in pots filled with pasture soil and lowest AMC was recorded on roots grown in the intermediate soil. This could be probably associated with a lower pH in the intermediate soil (5.06) than in the other sites (which were in the range of 6.42 to 7.02). Soil acidity normally affects the development of mycorrhizal symbiosis (Sieverding, 1991; Bartolome-Esteban and Schenck, 1994; Fuchs and Haselwandter, 2004; Kittiworawat et al., 2010), mainly when the soil has high Al^+ and H^+ contents, which are toxic to AMF (Porter et al., 1987) and sometimes interferes with roots colonization, because P adsorption makes it unavailable to the plant. In accordance with that, Covacevich and Berbara (2011) found highest Al^+ and H^+ contents in intermediate soils, which could explain the lowest presence of AMC in this site. However, although Siqueira et al. (1990) mentioned that root colonization of *Brachiaria* was not greatly different between Brazilian soils of pH 4.51 to 6.0, in a previous study (Siqueira et al., 1986) they also showed that the ability to colonize maize roots on Brazilian soil ranging in pH 4.5 to 6.3 varied among AMF species and that, in general, mycorrhiza formation increased gradually as soil pH increased to pH 5, and decreases at the highest soil pH of 6.3. Because Covacevich and Berbara (2011) also found lowest plant dry matter production at the intermediate soil, they pointed that if the pH was not the cause of lower AMC at the Intermediate soil, the lower amount of C in roots as a consequence of lower plant growth could restrict the symbiosis development. This is because AMF are obligate symbionts of plants that consume photosynthates from roots (Smith and Read, 2008).

Changing environments can induce the predominance of intermediate-sized spores, such as *Glomus* species that in general modulate the production of spores directly according to C availability, showing a direct reproduction investment as expected for r-strategists (Ijdo et al., 2010), as well as a reduction in AMF abundance and in richness species. However, sometimes AMC as well as SN could not necessarily reflect the actual AMF populations in the soils. For example, Ahulu et al. (2006) showed that species with an abundant production of spores in the field or in greenhouse do not always dominate the AMF community in coastal sand-dune ecosystem of USA. Covacevich and Berbara (2011) found that the most

abundant genus in soil samples collected at the *caatinga* biome after trap plants were grown until 3 months was *Glomus*. *Acaulospora* was the second most frequent genus and showed the highest frequency at intermediate soils reaching the same proportion of *Glomus* in late ones. Moreover, Silva (2010), who collected field samples from the same areas as Covacevich and Berbara (2011), also found that *Acaulospora* showed the highest frequency at the intermediate site under field conditions. These results agree with other studies in Brazil reporting that *Acaulospora* could be found preferably under moderately acid soil-conditions at pH <6.2 (Stürmer, 1999) and preferably within the range 3.5 to 5.8 (Trufem, 1995). Interestingly, Covacevich and Berbara (2011) found no spores belonging to the genus *Archaeospora* in pots filled with the initial soils, as well as, Silva (2010) did not also found any spores belonging to that genus at the late site under field conditions.

Sometimes freshly formed AMF spores can often not be readily distinguished from spores formed earlier in the season (Lee and Koske, 1994). According to Pianka (1970), AMF that sporulates early in trap cultures could potentially be representatives of the r-strategy because they could dominate resource-rich uncolonized habitats in early successional stages of the fungal community. In the study of Covacevich and Berbara (2011), *Glomus* also seems to have shown an r-strategy and could be found also in highest proportion in soils coming from early and late successional stages. The k-strategists would follow the opposite strategy showing slow growth rates under resource-limited conditions and occurrence in late successional areas (Pianka, 1970). In that sense because *Acaulospora* increased in soils coming from intermediate and late sites, it probably followed a k-strategy. However, it is still difficult to draw direct conclusions about the life history strategy of the AMF detected by their spores; this topic need more research studies.

Covacevich and Berbara (2011) found highest SN in soils from pasture while the lowest SN was found in pots with intermediate area soil. Silva (2010) also found that pasture had highest SN. However, she found that the late was the area with the lowest SN and pointed that it could be an indicative of a highest environmental stability of soils. The SN quantified at the study of Covacevich and Berbara (2011) was about 3.5 to 6 folds lower than the amounts reported by Silva (2010). Differences between pots and field conditions could be attributed to the fact that AMF sporulation varies with host and AMF species and also with growing conditions (affecting fungus directly and indirectly through host physiology). Many studies have demonstrated that not necessarily the same AMF species are found in a field site and in greenhouse cultures with soil from the same site and growing in "trap cultures" (Jansa et al., 2002; Oehl et al., 2004), although there is usually a considerable overlap between the same species groups. The period of time during which the

cultures are grown appears to be important. Sporulation often occurs within 3 to 4 weeks after onset of mycorrhizal colonization under almost any conditions except the high availability of soil P, which could depress or inhibits all fungal growth phases (INVAM, 2011). While Declerck et al. (2001) pointed that sporulation under controlled conditions increased from 4 to 5 weeks to approximately 10 weeks and after this time sporulation was stabilized, Oehl et al. (2004) reported a longer time range for sporulation (4 to 20 months).

It is known that diversity of AMF is a major factor contributing to the maintenance of plant biodiversity and to ecosystem functioning; however, the increase/decrease of SN with plant succession is still controversial. In Brazil, Carrenho et al. (2001) developed a plant restoration study along the river Moji-Guaçu, using a mixture of pioneer, secondary (early and late) and climax plant species. They found that the rhizosphere of pioneer species (*Croton urucurana*) had the lowest number of spores, and this increased progressively until the occurrence of climax species such as *Genipa americana*. They concluded that the number of AMF spores increases with the stage of succession. Contrarily, Zangaro et al. (2007, 2008) found that fast-growing native woody species in southern Brazil showed higher levels of AMC compared to slow growing ones. The last authors suggested that the occurrence of mycorrhiza and the density of AMF spores decreased along the succession, and it could be probably due to morphological root traits in fast-growing species that favored the contact with AMF propagules in the soil. Additionally, studies by Pagano et al. (2008, 2010b) in semiarid fields of Minas Gerais State, showed higher mycorrhizal sporulation in disturbed sites (Carrasco) with highest soil P content and pioneer species such as *Anadenanthera peregrina*, *Piptadenia moniliformis*, and others.

Covacevich and Berbara (2011) pointed that the physicochemical characteristics of *caatinga* soils of Brazil affected mycorrhizal symbiosis more than the successional stages of the sites. Recently, Oehl et al. (2010) also reported that soil type strongly affect AMF composition and the occurrence of many species. When a soil loses its natural condition (mainly by human action or when agricultural practices are installed) changes in the physical, chemical and biological soil properties undoubtedly occur and the adaptation to the 'new' environment is mediated largely by soil microorganisms whose activity depends on the presence of indigenous AMF (Johansson et al., 2004; Jin et al., 2010). According to Lejon et al. (2005), these are the main factors controlling the transformation of organic matter and nutritional status in soils. In this sense, the monitoring of microbial populations (particularly AMF) and the physicochemical properties of soils can be useful tools to determine the state of disturbance in different sites. However, mechanisms regulating and maintaining AMF

species composition, spore density and fungus infectivity (as a measure of activity) among different life story sites are still not well understood. In Brazil, the AMF have been reported to depend on the physical characteristics and chemical soil sometimes; however, at other times also showed dependence on productivity and plant diversity. The disparity in results is due to the still misconduct of global interdisciplinary studies, conducted under the same methodology in order to monitor large (ecological) areas. Future studies on the effects of AMF on the growth of native species present in the Brazilian environments are essential to the preservation and maintenance of these ecosystems. This will contribute to the knowledge of AMF diversity and function not only in Brazil but also worldwide.

MYCORRHIZA DEVELOPING IN HUMAN-CHANGED ENVIRONMENTS: CASE STUDIES OF FERTILIZATION, TILLAGE AND CROP ROTATION AT AGRICULTURAL LANDS (ARGENTINA AND BRAZIL)

In the last decade's deforestation, over grazing, over cropping plus a non-suitable technology has changed the atmosphere, the soil microbiota and the symbiotic associations such as mycorrhizas. Although Argentina and Brazil are not primarily responsible for global CC, they have too incurred unsustainable environmental management and environmental conditions have changed in both countries. Many forms of crop management have been used systematically by farmers both in Argentina and Brazil for many decades with the aim of rapidly increasing crop productivity. Among them, mineral fertilizers now represent one of the main expenses in intensive agricultural management practices. Yet, the use of chemical fertilizers and pesticides has a number of negative secondary effects both above and belowground. Studies revealed that indigenous AMF are present in tropical ecosystems, as well as in agroforestry systems (Cardoso and Kuyper, 2006), whose native vegetation is used to produce fuel wood, and where cattle and agriculture are increasing activities, which results in declines in soil fertility. Mixing cropping is little practiced; and the symbiotic plant association with AMF has not been sufficiently studied.

The deficiency of P in tropical, subtropical (Fernández et al., 2001) as well in temperate soils (García and Berardo, 2005) is a problem of recognized importance, which constitutes a central restriction for crop production. Thus, the main strategy to cope with P deficiency in South America has been the addition of fertilizers, either in the form of synthetic fertilizer or in the form of rock phosphate (RP). Land use and yield average of main crops were remarkably increased in the last 20 years in the Pampas region of Argentina. This situation has generated a progressive decrease of P, and therefore, a generalized crop response to P application (García and

Berardo 2005; Covacevich et al., 2005; Covacevich et al., 2008). Chemical fertilizers are very soluble and amounts not used immediately by the plant tend to run-off into surface watercourses or into the water table contaminating urban water supplies (Solbrig, 2005). In other cases, the use of synthetic fertilizer is relatively inefficient because of P fixation. Furthermore, in general, crops supplied with high rates of synthetic fertilizers rich in N, P and K, are inhibited in their mycorrhizal development (Velázquez and Cabello, 2010).

Studies in Argentinean Pampas conducted by Covacevich et al. (2007) showed that P fertilization with the inorganic soluble P source superphosphate (SP) increased available soil P but depressed indigenous AMC of wheat monoculture from temperate agroecosystems, suggesting that the primary effect of P on mycorrhizal symbiosis seems to be a reduction in AMF caused by high available soil P concentration. Authors established that available soil P content depressed indigenous AMC of wheat until a threshold of 27 mg P kg soil⁻¹. Above this threshold, AMC was stabilized at a minimum of 10%. At 15.5 mg P kg soil⁻¹ highest relative shoot dry matter was obtained under field conditions and AMC reached 39%. They pointed that both the soil P content threshold and the minimum AMC values must be considered in planning the fertilization regime to be applied in order to increase crop growth without depressing mycorrhizae. Alternatively, fertilizer placement also affects indigenous AMC of agricultural crops. Covacevich et al. (2005, 2008) found that fertilization of wheat crops with banded SP depressed indigenous mycorrhizal formation as compared with broadcast applications both under no-tillage (NT) and under conventional tillage (CT). It is probably that the high mycorrhizal formation, which was not depressed when P was broadcast, connected the soil P with the roots allowing adequate access of the nutrient to plant. It could be due to absence of differences in yield and plant P content between P placement treatments obtained under NT. This could indicate a high accessibility of wheat roots to soil P, mainly under broadcast P applications. It is probably that without mycorrhizal formation, wheat plants of broadcast P treatments were at a greater distance from the root system, which could make difficult P access to the root, in relation to P line-banded adjacent to the seed. This could allow speculation that the AMF could have functioned as 'facilitators' of available soil P for wheat plants when P is broadcast.

It is clear that synthetic fertilizer sources of P depress AM. For that, the use of RP, mainly consisting of apatite, has been proposed as alternative of synthetic fertilizer in view of its very large deposits in Africa (Mowo et al., 2006). Covacevich et al. (2006) found that fertilization with SP or RP produced similar available soil P contents and grass productions at the Argentinean Pampas. However, while indigenous AMC decreased after fertilization with SP, RP did not decrease mycorrhizal

formation or indigenous mycorrhizal potential (12 to 14 AM propagules g soil⁻¹), which were higher than in SP fertilized soils (0.7 to 0.9 AM propagules g soil⁻¹). This indicates that soils of low-input of synthetic P have a higher capacity to initiate mycorrhizal symbiosis and could be less dependent on the inoculation.

Several studies indicate that growth response of AMF inoculated plant depends on genetic and functional compatibility between plant species and the strain of mycorrhizal fungus, as well as prevailing environmental conditions, such as soil type, pH and nutrient availability, especially P (Fuchs and Haselwandter, 2004; Siddiqui et al., 2008; Covacevich and Echeverría, 2009). The role of AMF range from their relationships with host plants (mainly for uptake of nutrients), with plant communities (acting on their diversity and abundance) and finally with processes related to ecosystem stability by participating actively and significantly in the dynamics of C and soil aggregation. Thus, perceived not only from the perspective of the plant, but of the soil in its multiple relationships, mycorrhizal formation are now recognized as a fundamental and integral component in the construction and stability of ecosystems worldwide (van der Heijden et al., 1998, 2003; Rillig, 2004b). In this regard, available conclusive results about involved mechanisms come just from controlled conditions and environmental monitoring is still missing. Olsson et al. (2010) described that under controlled conditions the allocation of C to the AMF was strongly reduced by P fertilization under good light conditions. Although shading reduced a Ri T-DNA-transformed carrot root growth, the C limitation did not reduce colonization by the mycorrhizal fungus *Glomus intraradices*, known to be tolerant to high P levels (Douds and Schenck, 1990), which may indicate that it is able to act as a parasite under certain conditions. Covacevich and Echeverría (2009) showed that inoculation of grasses with *Glomus claroideum* increased plant growth, P uptake and mycorrhizal response in non-fertilized or RP supplied soils but SP fertilization did not increase mycorrhizal growth responses. It could be then likely that also in that situation of high P availability mycorrhizal symbiosis has changed parasitic. Thus, one way to minimize the environmental risk of fertilization is to use moderate doses of fertilizers and/or non-synthetic sources. For perennial crops, the strategy would be to use RP as a natural and cheap source which shows a slower P release mainly in moderately acidic soils, which, in combination with mycorrhiza, could increase the grass productivity. Organic fertilization improves soil's quality due to increase on availability of organic matter which benefits physical, chemical and microbiological soil properties as microbial activity. This includes soil aggregation, aeration and fertility levels, providing energetic substrates that potentially can be degraded by the edaphic microbiota, increasing the oxidative metabolism (Sampaio et al., 2008). Freitas et al. (2011) found that although AMC of grapes was relatively low (less than 18

%) both under conventional and organic manure (amended with compost of plant debris), number of AMF spores, diversity and propagules as well as higher microbial activity were found in the organic system at the semiarid region of São Francisco Submedium Valley (Pernambuco State, Northeast Brazil). Therefore, if the alternative is to use sources of synthetic P fertilizer (for example, for seasonal crops), a strategy could be a minimum fertilizer dose which may allow the attainment of acceptable yield levels, while also reducing costs and environmental pollution risk. That may be a promising way for obtaining high agricultural crop yields with low agrochemical inputs in order to support sustainable agriculture.

Contrary to expected but in agreement with results obtained in Brazil (Covacevich and Berbara, 2011) preliminary studies conducted by Covacevich et al. (2012a,) found that the mycotrophic ability was not significantly different in relation to land management of 29 agricultural sites from Buenos Aires Province (Argentina) all under with or without agricultural management (pristine). Available soil P content, together with the Fe and to a lesser extent Mn soil content, depressed mycotrophic ability, mainly under of moderate-low content of CO conditions. The confirmation of these results could change the previous concepts in relation to the impacts of soil disturbance as a result of agricultural practices on indigenous AMF of agroecosystems.

Some reports have shown that tillage can reduce either AMF spore density (Kabir et al., 1999) or root AMC of crops and the potential for P uptake (McGonigle and Miller, 1996), mainly because the damage to the hyphal network which reduce AMF growth and root colonization (Goss and de Varennes, 2002). In Argentina and Brazil, NT farming has currently become widespread for most of crop production. NT produces physical, chemical and biological changes in the soils compared to soil under CT, that is, increases of P available and organic matter in soil surface layers (Calviño et al., 2000), higher soil phosphatase activity (Doran, 1980) and greater root density in the soil surface layers (Qin et al., 2004). In cultivated sites (wheat, barley or clover) of the Pampas (Buenos Aires Province, Argentina) the most widely recognized influence of tillage on AMF species diversity and SN was the decrease of some unidentified species of *Glomus*, plus *Glomus aggregatum*, *Glomus microaggregatum*, *Acaulospora denticulata*, *Entrophospora* spp. and *Glomus coremioides*. In contrast, other unidentified species (*Glomus mosseae* and *Scutellospora pellucida*) of larger size persisted after several decades of CT (Menéndez et al., 2001). Furthermore, composition of the AMF population decreased compared to a grassland soil. Schalamuk et al. (2006) also identified, in agricultural field crops of Argentinean Pampas, 24 species of Glomeromycota belonging to six genera of AMF: *Acaulospora*, *Archaeospora*, *Entrophospora*, *Gigaspora*, *Glomus* and

Scutellospora. Contrarily to others, they showed that AMF biodiversity was higher in tilled plots than in untilled ones and that the contribution of species belonging to Glomeraceae increased in NT plots to the detriment of Acaulosporaceae and Gigasporaceae, contradicting reports by Jansa et al. (2002). Those authors suggested that the higher contribution of Glomeraceae previously found by Jansa et al. (2002) in NT systems from a long-term field experiment in Switzerland could be related to the lack of disruption of the hyphal network and the composition of the soil propagules in that system. Covacevich et al. (2011) also found no significant differences in AMC of wheat by tillage from a long-term field experiment in Buenos Aires Province (Argentina) under fertilization treatments with micro and macro-nutrients. Generalization is often difficult because mycorrhizal communities are site specific and each AMF species can be affected in several ways by different agricultural management practices. In this way, it is probably that different species of AMF respond differently to soil disturbance and variations in temperature, humidity and microbiota result of tillage.

In Brazil, NT systems are increasingly used, especially in the *cerrado* West Central Brazil (Mello and van Raij, 2006). Research interest of AMF and NT in *cerrado* and *caatinga* biome is nowadays more favored, with increasing selection of the crop, cultivars and the rotation to be used. For maximum effect, NT requires crop rotation (CR) to decrease accumulation of plant's diseases and pests. From the point of view of the host plant some annual crops (soybean, bean, maize) and green manure (*mucuna*, *Crotalaria*, *Canavalia ensiformes*, *Cajanus*, sunflower, millet, *Ricinus communis*) as well as some fodder (*Stylosanthes*, andropogon) show high AMF dependency and they can increase the native AMF community, which benefit subsequent crops (Miranda et al., 2010). For example, rice and *Raphanus sativus* (green manure), show low or no AMF dependency, respectively, and the introduction of them in rotation could decrease the fungal community in soil and their benefits to the subsequent crop. Nevertheless, effects of hyphae on soil structure can persist in the absence of mycotrophic host plants, thus non-mycorrhizal plants can benefit from the improved soil when they are cultivated before mycorrhizal crops (Smith et al., 2010). Miranda et al. (2010) confirmed the hypothesis that the presence of forage peanut *A. pintoi* in crop rotations systems (monoculture, with grass pasture and others legumes intercropped, coffee plant under cover of *A. pintoi*, besides brush and forest) at Rio Branco (Acre State, Brazil) increased mycorrhiza formation. They found that presence of grass species favored the *Glomus* species development while *Acaulospora* species were present in areas with trees and shrubs (coffee, capoeira and forest), especially in the dry season. Previous studies conducted by de Miranda et al. (2005) of a 6-year field experiment in Brazil, reported

changes in the indigenous AMF populations after crop rotation (andropogon grass/soybean) and seasonal variations in *cerrado* soils. They found that spore numbers and AMC varied according to cropping time, soil moisture, crops and rotation system and were higher in the cultivated soil than in undisturbed *cerrado* soil. Moreover, they estimated that AMF contributed 53 and 95% to the growth of soybean and andropogon grass, respectively, in a greenhouse experiment. They concluded that the number of AMF genus and species increased according to cropping time and management, being higher under annual crops in rotation.

Another big problem in Brazil is mining pollution. In this regard, studies on mycorrhizas in mined areas are increasing, such as in reclaimed areas after the bauxite mining in Porto Trombetas by Caproni et al. (2005, 2007). The study determined that AMF species have different characteristics of sporulation: *Glomus clarum* showed the highest spore density in early planting, declining with time, and *Gigaspora margarita* increased in sporulation with time, suggesting different adjustments of species to the early stages of reclamation in bauxite mining. While in Argentina Mining is currently conducted and is growing, the country's current policies do not carry environmental impact assessments or how the exploitation affects soil microbial communities, including the AMF.

Information on AMF is generated monitoring their populations in both natural and disturbed sites; however, in most of the cases its identification is difficult and this may negatively influence the effective implementation of global comparative studies. The main impediment is the inability to isolate these fungi, because they form obligate symbiotic associations with the partner (Smith and Read, 2008). Occasionally, difficulties to identify AMF could be a result of lack of skills of the researches morphological identification. For that, in the last decades molecular methods contributed to increase the knowledge of identity and variability of the AMF because molecular techniques based on DNA analysis seem to offer a wider range of advantages. However, in South America, molecular biology studies of mycorrhizae are still in their infancy. Even so, increasingly research groups are adopting molecular tools to study the biodiversity of AMF, such as Mergulhão et al. (2008), who distinguished some indigenous AMF species (*Paraglomus occultum*, *G. mosseae*, *G. intraradices* and *Glomus etunicatum*) from an impacted gypsite mining area (Araripina, Pernambuco State, Brazil) by using the polymerase chain reaction (PCR)-restriction fragment length polymorphism approach. Barreto de Novais et al. (2010) characterized phenotypically and genotypically by PCR-denaturing gradient gel electrophoresis isolates of AMF extracted from different sites of Brazil. In Argentina, preliminary studies conducted by Covacevich et al. (2012b) found changes in Single Stranded Conformation Polymorphism patterns of the PCR-amplified 28S ribosomal DNA genome of AMF (*Glomus* sp.) as a result of changes in the management

of agro-ecosystems (Conventional-Agricultural versus Pristine, for the same sites) of the Buenos Aires Province. Those studies agree with the fact that the combination of molecular and traditional methods may be the most promising way to monitor the community structure and biodiversity of AMF in the field.

CONCLUSIONS AND PERSPECTIVES

The understanding of the impacts of agriculture on belowground AMF is just beginning and an effective collaboration between mycorrhizobiologist and other specialist groups are required. Contradictory results do not easily allow reaching general conclusions because it is difficult to control completely the environment in which the symbiosis develops in a way that may be representative of the conditions that will occur. In several cases, the deleterious effects on the symbiosis seem to be more associated with the incorporation of chemicals in the environment that the disturbance of the soil system. Moreover, even having found the best environmental strategy for soil management, there is resistance from farmers and companies that cause environmental impacts to modify practices and thereby minimize the negative environmental impact on microbial populations (in particular on AMF). The first conceptual change should be the need for farmer recognition about the conversion from intensively-cultivated conventional land to low input and sustainable management. They must also understand that times are different between chemical reactions and biological processes. As most of other biological processes the mycorrhiza formation is a slow and gradual process that is related to building up the soil fertility. For example, the period of time required for the establishment of a stable mycorrhizal population is longer than that for the solubilization of synthetic fertilizers. Furthermore, AMF communities and the species abundances may fluctuate throughout seasons and years because of changes in abiotic and biotic conditions. For that we need to identify each plant/mycorrhizal combination, suitable to each region and crop aimed to maximize biological processes appropriate to each ecosystem.

Our review has highlighted soil disturbance, plant diversity and soil (physical and chemical) conditions as main contributors to determining of mycorrhizal fungal infectivity and diversity. There are different agricultural practices adversely affecting AMF functioning in the field (soil tillage, chemical fertilization, biocides, monocropping and nonmycorrhizal plants). It has been shown that the loss of biodiversity in soils represents a poorly understood field of research which requires more attention. The reduction of biodiversity in the earth and its potential threat to ecosystem stability and sustainability can only be reversed or stopped if whole ecosystems (including ecosystem components other than plants) were

protected and conserved (van der Heijden et al., 1998). The current production and environmental trajectories indicate that in many farming systems still resemble the intensive models. In response, we need a new productive and environmental view to replace the traditional one. This explains why in the last decades some Brazilian and Argentinean farmers have become increasingly interested in managing their soils more ecologically for minor risks of erosion. Although cropped areas with minimum or NT are increasing yearly, farmers also want to get good yields from their crops and thus they need the help of soil scientists (Borie et al., 2006). Therefore, the selection of appropriate agricultural practices could enhance efficiency of AM symbiosis in field in order to use it as biological fertilizers (Gentili and Jumpponen, 2005).

Main current limitation is that there are many ways in which humans interacts and affects the environment, but in comparison there are few studies to assess this impact and there are not management alternatives offered that allow a sustainable economic development with the environment. Additionally, our knowledge of the basic biology of the AMF is still limited and to report general conclusions about the effects of CC and human practices on mycorrhizal symbiosis is still arduous. This is because changes do not always involve only one factor, and to make useful predictions about the effects of all involved factors is ambitious. Governments need consistent and reliable information to design policies, and science and technology organizations are capable to provide that. Some necessary policies are being implemented by means of appropriate mitigation and adaptation. The former targets the causes of the problem and the latter helps to minimize their impact and maximize opportunities. Governments are developing programs; the next step now is to achieve the implementation of measures by local farmers.

Finally, for better nutrient management in the agroecosystems and also for ecological management of degraded and/or contaminated areas, an increased use of the biological potential is important. In that sense, mycorrhizal association has received attention as an active and diverse soil fungal community essential for increasing the sustainability of agricultural systems. The complexity of the interactions (nutrients, moisture, temperature, plants, others microorganisms, etc) involved requires an interdisciplinary work and coordination to design and implement the necessary measures to reduce the negative effects of CC and anthropogenic practices on environmental sustainability.

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