Chapter 9
Mycorrhizal Associations in Agroforestry Systems

André Mundstock Xavier de Carvalho, Rodrigo de Castro Tavares, Irene Maria Cardoso, and Thomas W. Kuyper

9.1 Introduction

Since its first appearance 8,000 years BP, agriculture has caused large impacts on local to global scales (Ruddiman 2003), and it currently remains a major driver of human-induced environmental change. Agriculture impacts on biological, chemical, and physical properties of soils, leading to biodiversity losses, decreases in soil coverage, changes in element cycles and water balance of ecosystems, degradation of soil structure, erosion, and contamination of groundwater, amongst other consequences (Tilman et al. 2001; Foley et al. 2005). Many, if not all, of these unwanted side effects are due to the practices of agro-ecosystem simplification, where ecosystem services provided by the soil are increasingly bypassed. The problems that this simplification has generated have highlighted the need to utilize soil resources efficiently — not only water and nutrients, but also the biological resources of the soils. It is expected that increased ecological sustainability through alternative use of soil resources will feed back to increased social sustainability of agricultural systems. The perceived need to seek alternatives to current agricultural practices has resulted in an enhanced interest in agroforestry systems. Under agroforestry, the needs for ecological sustainability can be reconciled with the needs for sustainable food production (Young 1997). Agroforestry systems are based on a combination of tree with crop and/or animal species simultaneously or sequentially in the same area, and have as their major aim the optimization of beneficial ecological interactions among ecosystem components (Farrell and Altieri 2002).

A.M.X. de Carvalho, R. de Castro Tavares, and I.M. Cardoso (✉)
Department of Soil Science, Federal University of Viçosa, Viçosa, Minas Gerais, Brazil 36570-000
e-mail: irene@ufv.br

T.W. Kuyper
Department of Soil Quality, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

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Tropical agroforestry systems are planned with the objective of mimicking tropical forests. Agroforestry systems put much emphasis on species diversity, and on the interactions between these different species. It is generally assumed, on the basis of ecological principles, that agroforestry systems can be as productive as monocrop systems. Agroforestry systems also show larger resilience and resistance to attacks by pest species and diseases, in addition to maintaining organic matter, soil fertility, and biological activity at satisfactory levels (Souza 2006; Young 1997; Ewel 1999; Van Noordwijk and Ong 1999). However, we are confronted with a paradox. Whereas the path towards ecosystem simplification can successfully go along the path of methodological reductionism with the study of individual components in isolation, the route to sustainable agroforestry systems needs to take complexity and context-dependency as its point of departure. Therefore, knowledge on how to introduce and manage agroforestry systems is lagging behind, due to the specificity of each ecosystem and the great diversity and complexity of the interactions involved.

Among the interactions that occur in soils of agroforestry systems, we will focus in this chapter on interactions between plants and microbiota, especially those formed by roots and mycorrhizal fungi. However, mycorrhizal interactions cannot be studied in isolation, since further interactions with nitrogen-fixing bacteria and with other rhizosphere micro-organisms are an integral part of belowground complexity. The importance of mycorrhizal fungi and mycorrhizal associations is evidenced by the observation that they are ubiquitous in tropical soils. They have been present since the conquest of the terrestrial environment by higher plants (Brundrett 2002).

Mycorrhizas are mutualistic associations between the roots of plants and certain soil fungi, which can be grouped into four types: ectomycorrhiza, orchid mycorrhiza, ericoid mycorrhiza, and arbuscular mycorrhiza (Smith and Read 2008). In tropical agroforestry systems, the arbuscular mycorrhizal fungi (AMF) form the most important group. These fungi belong to the phylum Glomeromycota. At present, around 160–200 species have been described (INVAM 2008; Souza et al. 2008), and over 100 species of AMF have been recorded from Brazilian agroecosystems (Stürmer and Siqueira 2008).

A large part of the soil microbial biomass can be constituted of AMF material (Olsson et al. 1999). AMF can colonize virtually all plant types among Angiosperms and Gymnosperms. Some Pteridophytes and Bryophytes can also be colonized by AMF (Smith and Read 2008). Observations that the overwhelming majority of agroforestry tree species form arbuscular mycorrhiza confirm this overall picture. In a study of 101 tree species belonging to different families in southeastern Brazil, 93 of the evaluated species were colonized by AMF (Carneiro et al. 1998).

According to Siqueira et al. (2007) studies dealing with mycorrhizal associations in tropical tree species have been conducted in increasing numbers over recent decades, and about 500 noncrop species have been investigated for the occurrence, or the effect of mycorrhizal associations. Among the known mycorrhizal species, many are used by Atlantic Forest family farmers in agroforestry coffee systems (Cardoso et al. 2001; Siqueira 2008; Table 9.1). However, studies examining

Table 9.1 Mycorrhizal tree and shrub species used by smallholder farmers in agroforestry coffee systems, Zona da Mata of Minas Gerais, Atlantic Coastal Rainforest, Brazil

Family	Species	Reference
Anacardiaceae	*Mangifera indica*	Silveira and Gomes (2007)
	Miracroduon urundeuva	Siqueira et al. (2007)
	Schinus terebentifolium	Zangaro et al. (2003)
Annonaceae	*Annona muricata*[a]	Silveira and Gomes (2007)
Apocynaceae	*Aspidosperma polyneurum*	Zangaro et al. (2002)
Araucariaceae	*Araucaria angustifolia*	Siqueira et al. (2007)
Bignoniaceae	*Tabebuia impetiginosa*	Carneiro et al. (1998)
	T. schysotricha	Zangaro et al. (2003)
	T. serratifolia	Siqueira and Saggin-Júnior (2001)
Bixaceae	*Bixa orellana*[a]	Carneiro et al. (1998)
Bombacaceae	*Chorisia speciosa*	Zangaro et al. (2003)
Cannabaceae	*Trema micrantha*	Carneiro et al. (1996)
Caricaceae	*Carica papaya*[a]	Silveira and Gomes (2007)
Casuarinaceae	*Casuarina equisetifolia*	Carneiro et al. (1998)
Cecropiaceae	*Cecropia glaziovii*	Zangaro et al. (2002)
	C. pachystachya	Zangaro et al. (2003)
Ebenaceae	*Diospyrus kaki*	Silveira and Gomes (2007)
Euphorbiaceae	*Manihot esculenta*[a]	Silveira and Gomes (2007)
Lauraceae	*Persea americana*	Silveira and Gomes (2007)
Leguminosae–Caesalpinioideae	*Caesalpinea ferrea*	Siqueira et al. (2007)
	C. peltophoroides	Siqueira et al. (2007)
	Copaifera langsdorffii	Carneiro et al. (1998)
	Hymenaea courbaril	Zangaro et al. (2003)
	Pterogyne nitens	Zangaro et al. (2002)
	Schizolobium parahyba	Carneiro et al. (1998)
	Senna macranthera	Carneiro et al. (1998)
	S. multijuga	Carneiro et al. (1998)
Leguminosae–Mimosoideae	*Annadenanthera peregrina*	Siqueira et al. (2007)
	Enterolobium contortisiliquum	Zangaro et al. (2003)
	Inga sessilis	Zangaro et al. (2003)
	Leucaena leucocephala	Siqueira and Saggin-Júnior (2001)
	Piptadenia gonocantha	Carneiro et al. (1998)
	Mimosa caesalpiniaefolia	Siqueira et al. (2007)
Leguminosae–Papilionoideae	*Cajanus cajan*[a]	Siqueira et al. (2007)
	Machaerium nictitans	Carneiro et al. (1998)
	M. stipitatun	Zangaro et al. (2003)
Malpighiaceae	*Malpighia emarginata*[a]	Silveira and Gomes (2007)
Malvaceae	*Luehea divaricata*	Zangaro et al. (2002)
	L. grandiflora	Siqueira and Saggin-Júnior (2001)
Melastomataceae	*Tibouchina granulosa*	Siqueira and Saggin-Júnior (2001)
Meliaceae	*Azadirachta indica*	Siqueira et al. (2007)
	Cedrella fissilis	Carneiro et al. (1998)
	Melia azedarach	Carneiro et al. (1998)
Musaceae	*Musa* sp.[a]	Silveira and Gomes (2007)
Myrsinaceae	*Rapanea ferruginea*	Siqueira et al. (2007)

(*continued*)

Table 9.1 (continued)

Family	Species	Reference
Myrtaceae	*Campomanesia xanthocarpa*	Zangaro et al. (2002)
	Eugenia uniflora	Zangaro et al. (2003)
	Psidium guajava	Zangaro et al. (2002)
Palmae	*Euterpe edulis*	Zangaro et al. (2003)
	Syagrus romanzofianum	Zangaro et al. (2003)
Rhamnaceae	*Colubrina glandulosa*	Zangaro et al. (2003)
	Hovenia dulcis	Carneiro et al. (1998)
Rutaceae	*Citrus* sp.	Silveira and Gomes (2007)
Solanaceae	*Solanum argenteum*	Zangaro et al. (2002)
	S. granulosum	Siqueira and Saggin-Júnior (2001)
Verbenaceae	*Aegiphila sellowiana*	Zangaro et al. (2003)
	Cytharexyllum mirianthum	Zangaro et al. (2002)
	Vitex montevidensis	Zangaro et al. (2003)

[a] Shrub species

arbuscular mycorrhizal colonization in a complete agroforestry system (and not only with individual tree species) are scarce (Pande and Tarafdar 2004).

A search on the Scopus database with the words “agroforestry” and “mycorrhiza” yielded around 50 articles. However, fewer than 20 articles went beyond the evaluation of mycorrhizal responses of individual tree species. As a consequence of this meager database, many mycorrhizal aspects of agroforestry, related to relations between plant and fungal species diversity, ecological succession, effect of tree management such as pruning or shading, and interactions between plants under agroforestry systems, remain underinvestigated.

9.2 The Multi-Functionality of AMF in Agro-Ecosystems

The most obvious role of AMF in agro-ecosystems is to increase the soil volume exploited by the host plant. This leads to increased water and nutrient uptake, which in turn may enhance acquisition of other nutrients, for instance through associated N fixation (Bolan 1991; Garg et al. 2006; Smith and Read 2008). Other roles of AMF concern protection of the root system against pathogens (Pozo and Azcón-Aguilar 2007; Elsen et al. 2008), salinity (Al-Karaki 2000; Tavares 2007), phytotoxic elements such as Al (Rufyikiri et al. 2000), or heavy metals (Andrade et al. 2003). AMF are also involved in the formation and maintenance of soil structure (Rillig and Mummey 2006), and increase C input to soils (Rillig et al. 2001; Zhu and Miller 2003), both of these effects contributing to reduce erosion. Finally AMF also play a role in the maintenance of plant biodiversity (Van der Heijden et al. 1998). Mycorrhizal associations, therefore, are multifunctional in agro-ecosystems (Newsham et al. 1995). They have the potential to improve physical, chemical, and biological soil quality, including feedbacks between soil biota and plant communities.

A large body of literature on mycorrhizal associations has centered on a comparison between costs and benefits of the symbiosis, often expressed in the same carbon currency. Such studies have concentrated on conditions where nonmycorrhizal plants outperformed (in terms of biomass) mycorrhizal plants and have given rise to the concept of parasitic behavior of mycorrhizal fungi, or of a continuum between mutualism and parasitism (Bethlenfalvay et al. 1983; Johnson 1993; Johnson et al. 1997). Implicit in many of these studies is the argument that, considering the high costs for symbiosis which occur under conditions of nutrient, especially phosphorus, sufficiency, the mycorrhizal association represents a net carbon cost for the plant host in simplified agro-ecosystems, where plant nutrient uptake capacity almost matches plant needs (Bucher 2007). Bhadalung et al. (2005) observed that in soils where maize was grown for 27 years and with application levels of 180 kg ha^{-1} $year^{-1}$ of N and P_2O_5 (in the form of ammonium sulfate and triple superphosphate) there was a reduction of 70% in density and 40% in the diversity of AMF compared to the same soil without the application of fertilizers. Such conditions are hardly, if ever, found under agroforestry management, and the concept of the mutualism–parasitism continuum might be unimportant in such cases.

However, under conditions of severe nutrient limitation, the ability of the fungal mycelium to immobilize nutrients in its tissues, and hence to reduce the transfer of nutrients to the plant, could also result in lower performance of mycorrhizal plants compared to nonmycorrhizal plants. Such conditions could possibly occur in the most nutrient-depleted sites, hence diminishing the usefulness of agroforestry as a means for ecosystem rehabilitation.

The cost-benefit models of Johnson et al. (1997) and Schnepf and Roose (2006) propose that plants monitor the carbon-to-nutrient exchange rate, and that any deviation from the mean exchange rate is interpreted as a shift along the mutualism–parasitism continuum because of decreased coordination between plant and fungal responses. However, if carbon and nutrient fluxes are quantitatively unlinked, a larger context-dependency of mycorrhizal responses can be observed. The spatial and temporal heterogeneity of nutrient availability could result in larger variations in exchange rates between plants and fungus, without the need to invoke the parasitism terminology (Landis and Fraser 2008). Especially in pulsed environments, characterized by periods of prolonged drought alternated with periods of higher water and nutrient availability, adjustment of the mutualism–parasitism balance could then be context-dependent. Under such conditions, the dynamics of a mycorrhizal network should differ, depending on whether it is synchronized with perennial agroforestry trees or else with the growth cycle of annual crops.

9.2.1 Implications of the AMF Mycelium Network

Several functions performed by AMF are linked to the formation and maintenance of the mycelium network. In order for such a network to exist and be ecologically relevant, it is needed that at least some mycorrhizal species show low selectivity, and hence have the capacity to establish mycelial linkages between different plant species. Low fungal selectivity may or may not result in comparable responses of different plants to the same fungal species. The existence of such networks allows, at least from a theoretical perspective, the movement of carbon, water, and nutrients between plants belonging to different species, genera, or even families. The existence of such mycorrhizal networks (the wood-wide web) could therefore bring ecological consequences that seem to fit poorly with conventional theories on plant interactions (Fitter 2001; Simard and Durall 2004; Selosse et al. 2006). It has been proposed that such networks may reduce differences in competitive ability between plants. Plants benefiting from the network would include seedlings (Van der Heijden 2004) or plants whose photosynthetic performance is poorer because of shading. Conceivably, mycorrhizal fungi could enhance plant species richness, in the case where competitively inferior plant species would be most prone to mycorrhizal associations, or decrease it, when the competitively superior plant species would be most responsive (Urcelay and Diaz 2003).

With their very low levels of soil disturbance, agroforestry systems are particularly conducive to the build up and maintenance of mycorrhizal networks, as compared to the annual cropping systems characterized by regular disturbances and bare fallows. The existence of such networks can result in faster establishment of the mycorrhizal symbiosis in seedlings under agroforestry systems (Kuyper et al. 2004), because plant colonization tends to be faster from the mycelium than through spore germination (Brundrett and Abbott 1994). However, the possibility of further ecological consequences of such networks remains disputed. With regard to the transfer of carbon in arbuscular mycorrhizal networks, the position now held by almost all mycorrhizal researchers is that such carbon movements remain completely under the control of the fungus and therefore interplant carbon transfer is unimportant (Pfeffer et al. 2004) — except in the case of completely or partly mycoheterotrophic plants that can completely reverse carbon flow. Transfer of nutrients, especially transfer of nitrogen from a N-fixing plant to a neighboring plant in the same network, remains a more controversial issue (He et al. 2003). A recent study in agroforestry systems is consistent with a potentially large mycorrhizal role in this respect. Sierra and Nygren (2006) estimated N transfer from the N-fixing tree *Gliricidia sepium* to the grass *Dichanthium aristatum*. They claimed that around 25%–35% of the N in the grass adjacent to agroforestry plots was atmospheric in origin. They also observed a positive correlation between *Gliricidia* root density and amount of N in the grass derived from atmospheric sources, but no correlation between the grass N isotopic signature and the soil isotopic signature. Sierra and Nygren (2006) therefore suggested direct N transfer from trees to grass, for instance through root exudates (termed here “direct soil transfer”) or via common mycorrhizal networks (corresponding to “direct transfer through the mycorrhiza”). Unfortunately, the mycorrhizal status of the plants examined in this study was not investigated. Lower N transfer levels were observed from leguminous trees to coffee plants in an agroforestry system, where 5% of fixed N was directly transferred; again, mycorrhizas were not studied (Snoeck et al. 2000).

In a simplified experimental design with nonmycorrhizal plants, Rao and Giller (1993) suggested that around 10%–15% of N found in the *Cenchrus ciliaris* grass was derived from N fixation by the legume *Leucaena diversifolia*.

Should urgently needed further research demonstrate the reality of direct N-transfer through the mycorrhizal network, then this recognition might lead to a re-evaluation of N-fixation studies based on ^{15}N natural abundance. Basically, such studies compare the differences in ^{15}N signal of legumes and reference plants, and make the implicit assumption that no N is directly transferred from legume to reference plants. Field data often show substantial variation in ^{15}N values of different reference plants, resulting in different estimates of the amounts of N fixed by the legume. Such variation in ^{15}N values of reference plants is poorly understood, and a re-evaluation of its possible mycorrhizal origin is a research priority.

Selosse et al. (2006) reported that phosphorus can be moved between plants (with unilateral transfer being more frequent than bidirectional transfer) and can end up in shoots of receiver plants. Because P is less mobile and required in lower amounts than N, the transfer of P is less than that of N (Johansen and Jensen 1996). Furthermore, the magnitude of P transfer is too small to significantly affect the nutrition of the recipient plant. However, more intense P transfer (and also N transfer) occurs from dying roots – with root death occurring, for instance, as a consequence of shoot pruning or root pruning, both regular processes in agroforestry management. How pruning would affect the carbon contribution of individual plants to the common mycorrhizal network, and how individual plants subsequently benefit from that network, remain to be determined.

The importance of common mycorrhizal networks for water transfer and redistribution has received remarkably little attention. However, the role of the mycorrhizal network in hydraulic redistribution could be of particular importance in agroforestry systems. After deeply-rooted plants have taken up water from profound soil layers, the activity of neighboring shallow-rooted plants could be sustained by nocturnal water efflux coupled to water uptake and transfer by mycorrhizal fungi in superficial soil layers. This process of mycorrhiza-mediated hydraulic redistribution has been demonstrated for ectomycorrhizal and arbuscular mycorrhizal systems (Allen 2007; Egerton-Warburton et al. 2007), but its importance for agroforestry still needs experimental proof.

9.2.2 *Ecological Implications for Plants*

Agroforestry systems are hypothesized to harbor a high AMF species richness and a large AMF biomass, due to increased productivity and species richness of host plants, whether cultivated or spontaneous, and to a greater extension of the fungal network. However, the relationship between plant species richness and AMF species richness remains to a large extent unexplained. Methodologically, addressing these questions is not easy. First, AMF species can be both drivers and passengers, determining or following changes in plant species richness (Hart et al. 2001). Second, with increasing numbers of plant species, the likelihood of including highly mycotrophic plants increases, resulting in a positive relation between plant and fungal species richness due to a sampling effect. However, from a management point of view, increasing AMF species richness in agroforestry systems is only relevant if the fungal species that associate with trees also associate with the agricultural crops in a common network. Ingleby et al. (2007) did in fact demonstrate the sharing of the mycorrhizal network between the agroforestry tree *Calliandra calothyrsus* and the crops maize and bean.

Methods for assessing AMF species richness may yield different outcomes. If a persistent fungal network, rather than an annual and labile mycorrhizal mycelium, characterizes agroforestry systems, then one would expect that the fungal population be preferentially comprised of K-selected rather than of r-selected species.

However, the more prolific spore formers may belong to the latter group, and in this case a diversity estimate based on spore data only would yield biased data. Molecular methods may yield better data, but application of such methods often lags behind in developing countries, due to the absence of well-equipped laboratories. Jefwa et al. (2006) observed lower species diversity in agroforestry systems with *Sesbania macrantha* and *S. sesban* than in maize monocrops, and suggested that the higher species diversity in the maize fields was due to the short maize cropping season, inducing rapid root dynamics and turnover, as compared to the much longer growth cycles of the agroforestry plots. Other studies yielded opposite data. In Ethiopia, Muleta et al. (2008) found higher abundance of AMF spores in agroforestry systems (especially when legumes served as shade crops) than in monocultural systems. Similar observations of higher spore abundance in agroforestry coffee systems than in monocultural systems were made in Brazil by Colozzi and Cardoso (2000) and Cardoso et al. (2003a).

Different plants show differential mycorrhizal dependence and responsiveness. This relation was first hypothesized by Baylis (1975) who argued that plants with a root system comprised of unbranched, relatively thick roots, with very few and short root hairs, will be more responsive to AMF than plant species with a finely branched root system, consisting of thin fine roots with numerous long root hairs. Janos (1980, 1996) further argued that mycorrhizal dependency increases during natural succession. In bare sites, colonizing plants tend to have a fine root system, allowing them to acquire nutrients even in the absence of AMF. Such plants are therefore often nonmycorrhizal or facultatively mycorrhizal. During succession, such plants are gradually replaced by plants that are obligatorily mycorrhizal. However, despite the conceptual clarity of the scheme, field data from Brazil do not fit with this pattern. Several studies demonstrated that responsiveness and susceptibility to mycorrhizal colonization were inversely related to succession (Siqueira et al. 1998; Siqueira and Saggin-Júnior 2001; Zangaro et al. 2003). Siqueira et al. (1998), working with a group of 28 native tree species belonging to different successional groups, observed that pioneer species responded relatively more to mycorrhizal inoculation than to P fertilizer, while climax species showed the opposite pattern. These findings support the hypothesis of a multifunctional nature of mycorrhizal associations. They also demonstrate, as already hypothesized by Newsham et al. (1995), that benefits of mycorrhiza other than P facilitation are important, particularly in plants with more effective root systems. However, the generality of this phenomenon and the implications for tree species choice in relation to agroforestry management deserve further study, because other plant traits besides root morphology, such as seed size and relative growth rate, are also correlated with susceptibility to mycorrhizal colonization and mycorrhizal responsiveness.

9.2.3 AMF and the Physical Quality of the Soil

AMF contribute in a direct way to the maintenance of soil structure, which is of fundamental importance for the stability of the agro-ecosystems (Rillig and Mummey 2006). The organization of soil particles determines the flow of water, gas, and nutrients in the soil (Rillig et al. 2002). In this context, the AMF are essential to the recovery of soil structure. Their actions cover a range of spatial scales, and include (1) directing clay particles around the hyphae, (2) producing polysaccharide secretions that connect clay particles, (3) performing a "packing" effect of particles by hyphae, leading to a new microstructure (Dorioz et al. 1993), and (4) directly transferring the carbon from plants to soil, which promotes aggregation.

Mycorrhizal effects do not depend only on the live mycelium. AMF produce and subsequently deposit on their hyphal walls a substance known as glomalin. For analytical reasons, this glycoprotein complex may be better referred to as "glomalin-related soil protein" (GRSP) rather than simply as "glomalin." The term GRSP points to the fact that other soil proteins may have similar properties and cannot always be separated from glomalin. Glomalin or GRSP is a very recalcitrant glycoprotein with high cementation capacity, which remains in the soil for longer time periods than the hyphae, thus contributing more persistently to the stabilization of aggregates (Driver et al. 2005). Hyphal residence time varies from days (for the smallest hyphae and the branched absorbing structures) to months (for runner hyphae of larger diameter) (Langley and Hungate 2003; Staddon et al. 2003) while residence time of GRSP varies from 6 to 42 years (Rillig et al. 2001).

GRSP is present in the soil in large quantities. In tropical forest soils of Costa Rica and Hawaii, GRSP levels reached values up to 12.5 and 60 mg of glomalin cm^{-3} respectively (Lovelock et al. 2004; Rillig et al. 2001). Lovelock et al. (2004) estimated that approximately 3.2% of soil total C and 5% of soil N in tropical forests was in the form of glomalin. Treseder and Turner (2007) suggested that as a rule of thumb around 10% of soil organic carbon is constituted by GRSP. These values suggest that the contribution of AMF to soil C sequestration is substantial. AMF also play a major role in the carbon dioxide fluxes through soil.

The mycorrhizal symbiosis implies carbon costs for the plants ranging from 10% to 20% of photoassimilates. If we scale up such levels (assuming that 15% of photosynthate are consumed by fungi) to the global scale, about 10 Pg

(10×10^{15} g) of C are annually used by fungi and (at equilibrium) returned to the atmosphere (Langley et al. 2006). Thus, estimates by Bago et al. (2000) that the annual C flux through AMF amounts to 10^{12} g, most certainly are far too low. Considering that tropical ecosystems are mainly composed of AMF-dominated vegetation, the role of AMF in the regulation of global carbon balance is substantial. By producing recalcitrant compounds such as GRSP, mycorrhizal agroforestry systems make a major contribution to the rehabilitation of degraded land, sequestration of carbon, and possibly reduction of emissions of other greenhouse gases such as N_2O (Lal 2005; Mutuo et al. 2005).

AMF do not act alone on soil structure. The interactions between soil fauna (especially soil ecosystem engineers such as earthworms and termites) and AMF in determining the balance between formation, stabilization, and breakdown of macro-aggregates and micro-aggregates could have a major impact. Synergistic effects between AMF and earthworms are probably very important in agroforestry systems, which provide an environment that is beneficial for both groups of organisms. However, such interactions have hardly been investigated.

Detrimental roles of mycorrhizal associations on soil carbon sequestration have also been reported. Chapela et al. (2001) observed that a reduction of soil organic carbon levels occurred over a 20-year period in Ecuador, following the massive introduction of non-native pines (*Pinus radiata*), which had been inoculated with the equally non-native ectomycorrhizal fungus *Suillus luteus*. This ecosystem was very productive in terms of edible fruitbody biomass, reaching levels up to 1,000 kg dry weight per hectare per year (Hedger 1986), thereby providing income for the rural population. However, this biomass production occurred at the expense of the soil organic carbon stock. While this study may well suggest a fundamental difference between ectomycorrhizal and arbuscular mycorrhizal associations in relation to soil carbon dynamics, it could also represent yet another example of the unexpected consequences of drastic ecosystem simplification, where one non-native tree and one non-native fungal species come to dominate the landscape. Presumably, most agroforestry systems would avoid this path towards excessive reduction of aboveground and belowground diversity, and the consequent reduction in the quality of ecosystem services.

9.2.4 AMF and the Chemical Quality of the Soil

9.2.4.1 AMF and Acquisition of Soil P

Agriculture under temperate climate conditions is often characterized by conditions of excess, while in tropical regions the problem is access (Van Noordwijk and Cadish 2002). This fundamental difference between both types of ecosystems translates into equally fundamental differences as regards the benefits to be expected from AMF, and the response of these fungi to agro-ecosystem management. In temperate agricultural systems, interest in mycorrhizal associations is increasing due to changes in the production system from conventional to organic (Mäder et al. 2002; Ryan and Graham 2002). It is still commonly held that mycorrhizal associations are unimportant under conventional agriculture, although this view neglects the multifunctionality of the arbuscular mycorrhizal symbiosis and overlooks the major contributions of AMF to soil structure (Ryan and Graham 2002). The situation in the tropics is very different. Most resource-poor tropical farmers are organic by default and under the force of circumstances, due to high agricultural input costs and low revenues. In agricultural systems under tropical climate, especially in agroforestry systems, AMF are essential for maximizing the utilization of P and other soil nutrients (Cardoso and Kuyper 2006).

Different nutrient inputs do not represent the only factor modulating the roles of mycorrhiza in temperate and tropical agro-ecosystems. Tropical soils are geologically older (on average) than soils in temperate regions, and this results in much stronger P deficiency in the tropics (see Chaps. 1 and 10). This P deficiency is not due to scarcity of phosphorus per se, but to the very low concentrations of P in the soil solution caused by the strong $H_2PO_4^-$ adsorption to iron (Fe) and aluminium (Al) oxides (Vance et al. 2003; Ticconi and Abel 2004). Because of this very strong adsorptive capacity of tropical soils, the greatest part of P occurs in chemical forms that are unavailable to plants (Novais and Smyth 1999). P fertilizer addition is also very inefficient, as most of the P fertilizer rapidly enters pools that are subsequently unavailable to plants.

In order to increase the efficiency of nutrient uptake and use by plants, enlarging the soil volume exploited by roots is imperative. The volume of exploited soil and the surface over which nutrients are taken up by hyphae of AMF (the total length of which is often in the range of 10–50 $\mathrm{m} \times \mathrm{cm}^{-3}$ soil) are generally substantially larger than those of plant root and root hairs (with a root length usually less than 5 $\mathrm{cm} \times \mathrm{cm}^{-3}$ soil). These measurements make it easy to grasp the crucial importance of mycorrhizal associations under conditions of low nutrient bioavailability, arising as a consequence of low water content and strong nutrient adsorption to oxides (Leake et al. 2004). Because the nutrient diffusion pathway is strongly dependent on soil water availability (both directly, and indirectly through soil moisture effects on tortuosity), water deficits contribute to limit the continuity of nutrient supply. In a pulsed climate, which is characterized by alternating wet and dry seasons, positive feedbacks between the mycorrhizal effects on water uptake and P uptake therefore occur (Augé 2001).

While enlarging the exploited soil volume is the most important mechanism for contribution of AMF to nutrient uptake, several other mechanisms have also been proposed, such as: (1) the kinetics of P absorption by hyphae differs from that of the roots, either because AMF have a higher affinity (lower K_m) or are less leaky (possess lower C_{min}) as compared to roots (Faquin et al. 1990; Silveira and Cardoso 2004); (2) roots and hyphae explore microsites differently, especially small amounts of organic matter and pores with small pore necks that can only be accessed by hyphae (Joner and Jakobsen 1995); (3) roots and hyphae of AMF have different means of solubilizing inorganic forms of P in the rhizosphere (Bolan 1991; Cardoso et al. 2006; Satter et al. 2006); (4) plants and mycorrhizal fungi make a differential contribution to the uptake of organic forms of P, because plants and fungi release to the soil different amounts of phosphatases and other enzymes (Hamel 2004).

There is disagreement in the literature with respect to possible differences in physiology of P uptake by roots and AMF. It is also unclear how such differences, where existent, would translate into significant differences in nutrient uptake. In a sensitivity analysis as part of a modeling study on nutrient uptake by plants, Williams and Yanai (1996) stated that changes in physiological parameters (K_m, C_{min}) of uptake models have little impact on uptake rates under nutrient-poor conditions. However, Schnepf and Roose (2006) reached the opposite conclusion using a mycorrhizal uptake model. Resolving this discrepancy would be a prerequisite for evaluating the potential for “mycorrhizal saturation” (O’Neill 1994), the condition where the density and spatial distribution of the mycorrhizal fungal mycelium is not optimal from the plant’s perspective but seems to optimize the fungal fitness. Mycorrhizal saturation models, such as the model by Landis and Fraser (2008), do not automatically assume near-perfect coordination between plant and fungus.

Several studies have shown that plants with or without association with AMF use the same sources of P from soil (Bolan 1991; Hernández et al. 2000). However, other studies claimed that mycorrhizal plants obtained P from sources of inorganic P (P_i) (and possibly also from organic P, P_o) that are normally unavailable to nonmycorrhizal plants (Jayachandran et al. 1989; Feng et al. 2003; Shibata and Yano 2003). The latter studies were performed in an artificial medium or in soils enriched with artificial P compounds (such as phytates), raising doubts about the ability of AMF to use sources of P adsorbed or complexed to organic matter under field conditions. It should also be remembered that mycorrhizal symbiosis induces further changes in the rhizosphere, and that the occurrence and activity of phosphate-solubilizing bacteria (PSB) may be modified in the mycorrhizosphere. Synergistic and antagonistic interactions between AMF and PSB have been repeatedly described (Muthukumar et al. 2001), although, to our knowledge, studies under natural agroforestry conditions have not yet been published.

In order to examine whether plants associated with AMF gain differential access to $\mathrm{P_i}$ pools as compared to nonmycorrhizal plants, Cardoso et al. (2006) analyzed the different P pools through P fractionation before and after treatment with mycorrhiza in a natural soil. On the one hand, no change was noted in the fractions of P_i and P_o in the presence of nonmycorrhizal maize plants, and P balance analysis indicated that growth of the nonmycorrhizal plants was completely determined by seed P reserves. This complete inability of the maize cultivar to capture P in the nonmycorrhizal condition was surprising, because plant-available P (9 mg P $\mathrm{kg^{-1}}$ soil for Resin-P_i and $\mathrm{NaHCO_3}$-P_i) in the soil exceeded the minimal concentration determined for plant growth (3 mg P $\mathrm{kg^{-1}}$ soil, according to Hayman (1983)).

On the other hand, the mycorrhizal maize plants completely used the pools of Resin-P_i and $\mathrm{NaHCO_3}$-P_i (both of which are immediately accessible pools) and around 20% of the pool of NaOH-P_i (which is accessible in the medium term). These results remain to be confirmed under field conditions (Cardoso et al. 2006).

The various P_o pools remained constant or even increased in magnitude over the course of the above-mentioned experiment. This observation is in keeping with earlier suggestions that AMF have no saprotrophic ability. Under field conditions, the mycorrhiza may intercept and capture the newly mineralized nutrients before their fixation to soil particles. This strategy, amounting to a tightening of the P soil cycle, may be of great practical significance (Joner et al. 2000).

Cardoso et al. (2006) were unable to explain the uptake of P from pools (NaOH-P_i) that are considered to be unavailable in the short term. However, they noted that glomalin might have a role in P acquisition. Glomalin seems to interact with metal in the soil, because in analytical GRSP fractions, iron, aluminum and copper can be found in relatively high amounts (Rillig et al. 2001; Lovelock et al. 2004; Gonzales-Chavez et al. 2004). Iron levels varying from 0.8% to 8.8% have been reported in glomalin (Wright and Upadhyaya 1998). The metallic ions in GRSP seem to have a role in protecting and stabilizing this protein (Nichols and Wright 2005). Through this interaction, GRSP may affect not only the dynamics of the bound metals, but also that of other ions that bind to Fe or Al, such as P.

In order to explain P uptake by mycorrhizal plants from Fe-P sources, Bolan et al. (1987) suggested that AMF may break Fe-P links, but without proposing a specific mechanism for this. Possibly, one such mechanism may involve GRSP production. Assuming that for every molecule of Fe that ends up in GRSP, one molecule of P could become available for uptake, Cardoso et al. (2006) calculated that a soil with GRSP levels of 0.5 mg g^{-1} (with 1% of Fe being bound to GRSP) could deliver enough P to fully explain the changes in the NaOH-P_i pool. Further investigation is required to confirm this putative role of GRSP in P mobilization, and thoroughly understand the interrelated effect of mycorrhizal associations on biological, physical, and chemical properties of the soil.

9.2.4.2 AMF and Protection Against Heavy Metals and Al

Besides their effects on the chemical properties of the soil and the ability to supply nutrients to the plants, AMF may mitigate phytotoxic effects caused by elements such as heavy metals and aluminium. Heavy metal concentrations in host plant tissues may decrease as a result of fungal association, and reductions of Pb concentrations were noted in the aerial parts of soybean (Andrade et al. 2003) and *Brachiaria* (Silva et al. 2006). Hence, mycorrhizal plants gain improved heavy metal tolerance.

Similarly, the concentration of Al^{3+} is reduced in mycorrhizal banana plants as compared to nonmycorrhizal banana (Rufyikiri et al. 2000). Tolerance to Al may be conferred as a result of increased P acquisition or through other mechanisms. Again, a study of P uptake and Al resistance in relation to the dynamics of GRSP would be helpful. On the other hand, acting through mechanisms similar to those that are involved in enhanced P uptake, the mycorrhizal association can enhance Zn and Cu uptake when concentrations of these metals are limiting.

9.2.5 AMF and the Biological Quality of the Soil

AMF can reduce damage caused by pathogens such as fungi, bacteria, and nematodes (Azcón-Aguilar and Barea 1996; Cardoso and Kuyper 2006). It has been debated whether this is mainly an indirect effect, caused by an improved nutritional status of mycorrhizal plants as compared to nonmycorrhizal plants; or whether there are direct, non-nutritional effects. While improved nutrition is clearly involved in the observed protection, non-nutritional mechanisms are also acting, since mycorrhizal and nonmycorrhizal plants with a similar nutritional status may be affected differently by the same pathogen. Non-nutritional mechanisms include activation of the plant defense system, changes in exudate patterns resulting in concomitant changes in the microbial community of the mycorrhizosphere, increased lignification of the cell walls, and competition for space and infected sites (Elsen et al. 2008; Pozo and Azcón-Aguilar 2007). The latter mechanism may be of particular significance when AMF colonization takes place prior to pathogen infection, as would be expected to occur in agroforestry and other agro-ecosystems that help maintain the mycorrhizal network. However, direct evidence for this is currently lacking in the published literature.

Although the nutritional and non-nutritional pathogen control mechanisms almost certainly interact, their conceptual separation remains imperative for the rational application of mycorrhizal technologies. Should nutritional mechanisms prevail, then mineral or organic fertilizer application could, under certain circumstances at least, be cheaper and more effective than mycorrhizal management. However, to benefit from non-nutritional protection mechanisms calls for different management options (Cardoso and Kuyper 2006).

AMF can also play a role in antagonistic (parasitic) interactions between plants. In greenhouse experiments, mycorrhizal sorghum (*Sorghum bicolor*) plants suffered less damage caused by the root hemiparasite *Striga hermonthica* than nonmycorrhizal sorghum (Lendzemo and Kuyper 2001; Gworgwor and Weber 2003). The presence of AMF also suppressed emergence and abundance of *Striga*, both in greenhouse and field conditions (Lendzemo et al. 2005). Root exudates of mycorrhizal sorghum plants strongly inhibited the germination of *Striga* seeds (Lendzemo et al. 2007), most probably through downregulation of strigolactones, a class of substances that are important both in the AMF–plant molecular dialog and as *Striga* germination stimulants. *Striga* numbers are also reduced under the canopy of certain agroforestry trees (such as *Faidherbia albida*) and on termitaria, which are commonly found under such trees. Crushed material of *Cubitermes* termitaria improved the rate of sorghum mycorrhization, pointing to important synergistic effects between agroforestry trees, soil fauna, and mycorrhizal associations in the control of the world's most devastating parasitic plant (Andrianjaka et al. 2007).

AMF interact, not only with antagonistic organisms, but also with nitrogen-fixing bacteria. As a consequence of enhanced P uptake by the plant, AMF promote an increased legume nodulation by rhizobia: indeed, P is often the limiting factor for nodulation and nitrogen fixation. Direct interactions also occur between the two microsymbionts, such as the synthesis by AMF of proteins immunologically related to legume nodulins (Perotto et al. 1994). Several of these interactions reflect the fact that the early molecular dialog between legumes and rhizobia is derived from the molecular dialog between higher plants and AMF.

Field studies on the interactions between rhizobia and AMF in agroforestry systems are scarce. Most publications refer to studies where agroforestry trees were inoculated, individually or jointly, with rhizobia and AMF. Such studies demonstrated that the combination of both symbionts is effective in boosting the growth of tropical tree legumes (Weber et al. 2005; Lesueur and Sarr 2008). Dual colonization by AMF and rhizobia increased plant dry matter, concentration and content of N and P and nutrient uptake efficiency by *Sesbania virgata*, compared to the uninoculated control (Rodrigues et al. 2003a,b). It has often been mentioned that interactions between AMF and rhizobia lead to synergism. However, synergism has almost never been defined. We propose to call the effects of AMF plus rhizobia additive if an analysis of variance (ANOVA) indicates that the interaction term AMF * rhizobia is not significant, and synergistic if the interaction term is significant. Synergism includes instances of both negative interactions, as in the case of *Dalbergia nigra* (Santiago et al. 2002), and positive interactions (although we are not aware of publications on agroforestry legumes that show such positive synergism). In most cases the effect of AMF and rhizobia turns out to be additive — which is consistent with the theory that both root symbionts enhance plant availability for different limiting nutrients.

The beneficial effects from dual inoculation might be only temporary. Lesueur and Sarr (2008) showed that the benefit of the joint inoculation of the agroforestry legume *Calliandra calothyrsus* was significant until 12 months after transplanting to the field, but not after 24 months. Such changes, which again stress the need for field experiments with naturally occurring symbionts, is possibly due to the symbiotic capacity of native symbionts naturally present in the field. Inoculum potential, effectiveness, and competitive ability of the symbionts that naturally occur in the field might well differ from those of carefully selected strains used for experimentation under controlled conditions. The fact that many agro-ecosystems, unless very poorly managed, harbor indigenous AMF which might be competitively superior to commercial strains, suggests that for the rational use of the microbial potential, management is preferable to artificial inoculation (Kuyper et al. 2004). It should also be noted that commercial inoculants are often expensive and of variable quality. Recently, commercial formulations of AMF have been made available in the form of powders, pellets, tablets, granules, gel beads, and balls (Adholeya et al. 2005; see Chap. 11), but we are unaware of published evaluations of their effectiveness.

9.3 AMF and Agroforestry Systems: Beyond Compatibility

Plant monocultures, cultivation of nonmycorrhizal plants, prolonged bare fallow, erosion, compaction, use of excessive amounts of fertilizers, and the use of systemic pesticides are among the main factors that contribute to the reduction or elimination of the AMF (Siqueira et al. 2007; Abbott and Robson 1991). These adverse processes all derive from a shared (and implicit) principle of ecosystem simplification. A reversal of the simplification trend is therefore imperative, and agroforestry is one of the strategies that will allow full advantage to be taken of the ecosystem services provided by the soil biota.

Agroforestry is not a standard recipe fit for indiscriminate use under all agro-ecological conditions. Competition for resources (water, nutrients, and light) between annual crops and tree species has often been mentioned as a factor that constrains the success of agroforestry (Farrell and Altieri 2002). Because of the major impact that AMF have on uptake of water and nutrients, they could both mitigate and enhance competition. Whether mitigation or enhancement prevails depends on tree management, on properties of both the tree and crop components of the agroforestry system, and on the extent and implications of communication between these two components through a common mycorrhizal network. In such a network, maintenance of a mycorrhizal inoculum would insure a more rapid establishment on host plants and hence a better annual crop seedling performance. If nutrients and water are transferred between plants, and if the dominant flow is towards the competitively inferior plant, AMF have great potential to mitigate restrictions on plant growth (He et al. 2003; Selosse et al. 2006).

In a greenhouse study, Ingleby et al. (2007) observed that trees maintain active AMF propagules, hence increasing the density of AMF populations prone to annual crop colonization. This enhancement effect occurs both with indigenous propagules and after inoculum addition, and is related to the maintenance of spore banks and a stimulation of fungal mycelium spread in the soil. Shoot pruning of trees, which is a common practice in some agroforestry systems, did not restrict the mycorrhizal colonization of, or the spread of the mycelium network to, the annual crops. This effect may be of particular importance given that the mycelium network is responsible for the fast colonization of new roots, and thus for a growth stimulation and improved P absorption in young plants (Brundrett and Abbott 1994). However, the rate of spread of the AMF mycelium (1–3 mm day^{-1}) suggests that benefits from the network will develop slowly.

The common mycorrhizal network may further enhance the benefits of agroforestry through vertical niche expansion of AMF. The presence of perennial mycorrhizal tree species with deep roots increases the volume of soil to be exploited (Fig. 9.1) and thereby improves the efficiency of P cycling by AMF (Cardoso et al. 2003a; Muleta et al. 2008). The increase in the efficiency of P cycling is also linked to the maintenance of larger pools of P_{o} and the greater abundance of roots, which reduce the possibility of fixation of the newly mineralized phosphate (Cardoso et al. 2003b). Such vertical niche expansion of AMF could also increase water use efficiency of the agroforestry system through mycorrhiza-mediated hydraulic distribution (Allen 2007; Egerton-Warburton et al. 2007).

Therefore, we propose that positive feedbacks exist between agroforestry practices and arbuscular mycorrhizal management. According to this hypothesis, agroforestry systems create conditions more conducive to arbuscular mycorrhizal functioning, while mycorrhizal management mitigates the competition between

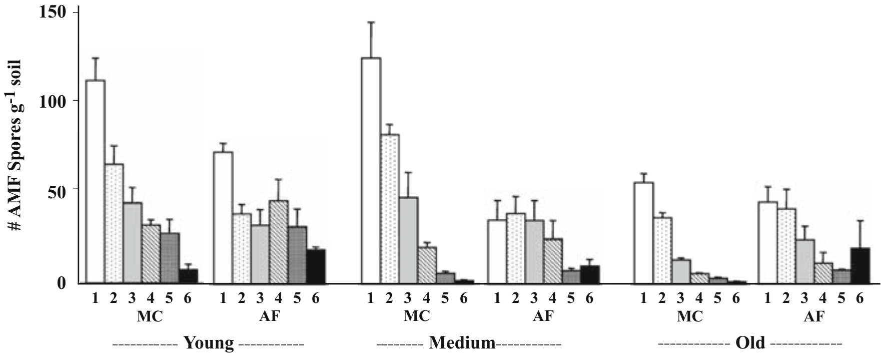

Fig. 9.1 Average (and standard error; n = 3) numbers (#) of arbuscular mycorrhizal fungi spores at different soil depths (1 = 0–1, 2 = 2–3, 3 = 5–7.5, 4 = 10–15, 5 = 20–30 and 6 = 40–60 cm depths) under monocultural coffee (MC) and agroforestry (AF) systems in the Atlantic Coastal Rainforest (Brazil). The agricultural systems were 5 years old (Young), 15–20 years old (Medium) and 20–24 years old (Old). Adapted from Cardoso et al. (2003a)

tree crops and annual crops. This beneficial impact between agroforestry management and mycorrhizal action may be depicted as a particular form of symbiosis. To confirm this hypothesis will require that mycorrhizal functions within agroforestry management be better understood.

9.4 Conclusions

Agroforestry systems can be a viable strategy for the preservation of natural resources while ensuring sustainable food production in the tropics. Agroforestry systems are designed with the objective of imitating tropical forests and optimizing beneficial ecological interactions among ecosystem components. In particular, the interactions between plants and soil as mediated by mycorrhizal fungi are of prime importance due to the wide range of functions that these fungi perform. Mycorrhizal fungi potentially improve physical, chemical, and biological soil quality. Several of these functions are linked to the formation of a common mycorrhizal network, which may mediate the transfer of water and nutrients between different plants. However, the ecological implications of these relationships remain poorly studied.

- Agroforestry systems are productive, in addition to containing a greater diversity of species than do simplified monoculture agro-ecosystems. However, the relationship of cause and effect between the diversity of AMF and diversity of plants, and the correlation of both with the productivity of agroforestry systems, remain largely undemonstrated.

- In tropical soils, which are commonly poor in nutrients and especially in available phosphorus, access to soil nutrients and the efficient use of these depend on the optimization of biogeochemical cycling and of the function of mycorrhizal fungi. The capacity and the access mechanisms to different fractions of soil P pools by AMF are not completely elucidated. The role of glomalin or GRSP in affecting P dynamics through GRSP interactions with Fe and Al needs to be further addressed.
- The practice of mycorrhizal inoculation remains very limited due to high inoculum costs, lack of quality standards, lack of technology adapted to resource-poor farmers, and especially the unresolved discrepancy between research results, obtained through short-term trials conducted under controlled conditions, and the phenomena occurring under long-term field conditions. In fact, management of native populations of mycorrhizal fungi might appear preferable to fungal inoculation.
- Agroforestry systems potentially maximize the benefits procured by AMF, which in turn could mitigate negative interactions between trees and annual crops. This positive mycorrhiza-agroforestry feedback, and the common mycorrhizal network which produces it, deserve closer attention.

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