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Mycorrhizal Associations in *Eucalyptus* spp.: Status and Needs

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ABSTRACT

In nature, there are some intra- or interspecific ecological relations with different dependence levels. Plant roots are good examples of this, because they develop ecological relations with many soil microorganisms, mainly with the fungi, forming mycorrhizae. The interest in studying this association has risen up due to increasing necessity of alternative handling methods that promote improvement in the plant growth and productivity. Arbuscular mycorrhiza have been known and explored for a long time due to the ecological significance and effects in the growth and nutrition of plants, playing an important role for the nutrient uptake system. The mycorrhizal establishment in eucalyptus has been known for many years, and the benefits of this symbiosis have been commercially explored. The most recent outcomes regarding the occurrence, importance and use of arbuscular mycorrhiza in *Eucalyptus* spp. are presented in this paper. Firstly, these will be grouped in various research topics (state of the art, mycorrhizal dependence; colonization and benefits; diversity of arbuscular mycorrhizal fungi in eucalyptus forests; coexistence of arbuscular-and ecto-mycorrhizal fungi; perspectives and needs). Then, a brief discussion will take place in order to define the real state of knowledge of this subject related to *Eucalyptus* spp.

Keywords: arbuscular mycorrhiza, ectomycorrhiza, fungi, symbiosis

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INTRODUCTION

In nature there are several intra- and inter-specific ecological relations, with diverse degrees of dependence, involving one or more organisms. Plant roots represent a good example of this, as they particularly develop ecological relations with many soil microorganisms. In natural ecosystems, plant roots are typically colonized by a wide range of fungi, mainly those that form the mycorrhizae. Some of these fungi are pathogenic, others seem to be opportunistic and have no apparent effect, while mycorrhizal fungi are generally regarded as mutualistic. They are classified into one of the following four major types: arbuscular mycorrhizas, ectomycorrhizas, ericaceous mycorrhizas and orchid mycorrhizas (Entry *et al*. 2002). The most abundant and widespread of all these types of mycorrhizal fungi are the arbuscular mycorrhizal (AM) which are found in more than 80% of plant species (Jeffries *et al*. 2003; Karandashov and Bucher 2005); however, these are estimatives based on an extrapolation from a limited number of studied plants (Wilkinson 2001). Botanists, ecologists, and agriculturalists have focused considerable attention on arbuscular mycorrhizal fungi (AMF) associations as they enhance growth, reproduction, and survival of the host plant (Smith and Read 1997). Furthermore, they play important role in succession and maintenance of plant community diversity (Brundrett 1991). AMF have good relations with the vegetative state of the mycotrophic plants (Carrenho *et al*. 2001), defining their ecological niches and, influencing the plant community structure, soil fertility and maintenance, the nutritional status of the plants and the nutrient cycle (Jeffries *et al*. 2003). Moreover, it is considered a cosmopolitan association, and an important and integral part of natural ecosystems (Gadkar *et al*. 2001). The mutualistic relation between roots and fungi is based on the bidirectional nutrient transfer between the symbionts. The plant benefits particularly through improved phosphorus, water and mineral nutrient uptake that often result in better growth (Entry *et al*. 2002). AMF can also protect plants against the toxic effects of excessive concentrations of heavy metals (Bagyaraj 1992), and promote beneficial alterations in soil physical properties, such as descompactation and formation of macroaggregates (Nadian *et al*. 1997; Yano *et al*. 1998; Miransari *et al*. 2007).

Eucalyptus species present many favorable characteristics to use in commercial scale, such as rapid growth, high cellulose production and resistance to diseases and to adverse environmental conditions (Santos *et al*. 2001). Due to

Received: 10 September, 2008. Accepted: 7 October, 2008.

Review

Table 1 Physiological profile of *Eucalyptus* species related as susceptible to form arbuscular mycorrhiza.

	Studies' data		
Eucalyptus	**Trial conditions**	**Locality**	**References**
calophylla	field	Australia	Jasper *et al.* 1991
	glasshouse	Australia	Malajczuk *et al.* 1975
camaldulensis	glasshouse	Algeria	Adjoud *et al.* 1996
	glasshouse	Burkina Faso	Kisa *et al.* 2007
	glasshouse	Brazil	Santos *et al.* 2001
	field	Brazil	Santos *et al.* 1995
	glasshouse	France	Boudarga *et al.* 1990
	field	Brazil	Alvarenga *et al.* 1999
citriodora	glasshouse	Brazil	Santos *et al.* 2001
cloeziana	field	Brazil	Santos 2001
	glasshouse	Brazil	Santos *et al.* 2001
	field	Brazil	Araújo *et al.* 2004
	field	Brazil	Amorin 1988
coccifera	glasshouse	United Kingdom	Jones *et al.* 1998
diversicolor	glasshouse	Australia	Malajczuk *et al.* 1981
dumosa	glasshouse	Australia	Lapeyrie and Chilvers 1985
dunnii	field	Brazil	Oliveira *et al.* 1997
globulus	glasshouse	Algeria	Adjoud *et al.* 1996
	glasshouse	Australia	Chen *et al.* 2000
	glasshouse	France	Joner *et al.* 2004
	field	Japan	Asai 1934
	glasshouse	Japan	Maeda 1954
	glasshouse	Scotland	Mason *et al.* 2000
	glasshouse	Spain	Arriagada *et al.* 2004, 2005
grandis	glasshouse	Australia	Malajczuk *et al.* 1981
	field	Brazil	Rodrigues *et al.* 2003
	field	Brazil	Mello *et al.* 2006
	field	Brazil	Zambolim and Barros 1982
	field	Brazil	Coelho *et al.* 1997
	field	Brazil	Alvarenga *et al.* 1999
	field	Brazil	Guimarães 1983
	glasshouse	Brazil	Santos *et al.* 2001
	glasshouse	Brazil	Fernandes *et al.* 1999
	glasshouse	Brazil	Reis and Krügner 1990
	glasshouse	Australia	Mulligan and Sands 1988
gummifera	glasshouse	Australia	Mulligan and Sands 1988
maideni	glasshouse	Algeria	Adjoud *et al.* 1996
marginata	field	Australia	Jasper *et al.* 1991
	glasshouse	Australia	Malajczuk *et al.* 1981
paniculata	field	Australia	Khan 1978
pilularis	field	Australia	Khan 1978
regnans	field	Australia	Ashton 1976
saligna	field	Brazil	Melloni *et al.* 2003
sideroxylon	glasshouse	Algeria	Adjoud *et al.* 1996
tereticornis	field	Brazil	Zambolim *et al.* 1982
	glasshouse	India	Sharma and Adholeya 2000
urophylla	glasshouse	Australia	Chen *et al.* 2000
	glasshouse	Brazil	Santos *et al.* 2001
	field	China	Gange *et al.* 2005
	field	Brazil	Guimarães 1983
viminalis	field	Brazil	Bellei *et al.* 1992
camaldulensis x *tereticornis*	glasshouse	India	Sastry *et al.* 2000
grandis x *urophylla*	field	Brazil	Santos *et al.* 2001
	field	Brazil	Grazziotti *et al.* 1998
	field	India	Methropa 1998
	glasshouse	Algeria	Adjoud *et al.* 1996

these characteristics, the use in reforestation programs in tropical regions has increased. The area in Brazil currently forested with *Eucalyptus* is of approximately 3.55 million ha (SBS 2007). Most plantations are driven to the production of pulp/paper and charcoal to supply steel plants, although the use of lumber, construction and essential oil extraction has increased (Silva *et al.* 2006). In Brazil, the majority of the eucalyptus reforested areas is in zones with low fertility soil that are associated with problems of water deficit which make the production of profitable wood difficult (Marques Júnior *et al.* 1996). In Brazilian soils in which eucalyptus species are cultured, there is a significant decrease in bioavailable nutrients has also been observed, affecting production, because nutrient uptake is higher than the nutrient inputs (Schumacher and Pogginari 1993; Leite 2001; Wadt 2004).

Also, it has been suggested that monoculture may reduce the spectrum of fungal species found in the soil after several years of continuous culture (Allen and Boosalis 1983; Sieverding 1991). Jasper *et al.* (1991), studying the level of mycorrhization by AMF in soils with different plant structure in Capel, Eneabba and Jarrahdale (Western Australia) observed that the colonization percentage, number of spores and AMF infectivity in eucalyptus forests were lower than that noticed in areas as pasture and native forests. According to those authors soils that support a productive vegetation dominated by AM plants are more likely to maintain the mycorrhizal infectivity. In contrast, infectivity in soil such as the heathland from Eneabba (*Eucalyptus* monoculture) is most vulnerable to disturbance because of relatively low number of potentially AM plants, and the low nutrient levels in the soil which limit the productivity of the vegetation. Eucalyptus are extremely ecologically damaging to many native plant species. The annual vegetation adjacent to naturalized stands of *Eucalyptus camaldulensis* was inhibited severely and annual herbs rarely survive to maturity when *Eucalyptus* litter accumulates (Kisa *et al.* 1970). Generally, *Eucalyptus* plantations are very common on sandy soils, predominantly acidic, and highly leached, in which fertilization is necessary to sustain high growth rates. In South China, the productivity of *Eucalyptus* plantation is very low and according to Gange *et al.* (2005) this is due to the infertile soils and lack of indigenous symbiotic mycorrhizal fungi. Where indigenous AMF population presents low colonization capacity, but it is effective, the soil handling to increase the abundance of AMF populations can be very viable (Dodd *et al.* 1990a, 1990b; Sieverding 1991).

Initially, in this review we will mention the results of studies about the mycorrhizal status in *Eucalyptus* species based on historical records, state of the art, mycorrhizal dependence; colonization and benefits; diversity of arbuscular mycorrhizal fungi in eucalyptus forests; coexistence of arbuscular- and ecto-mycorrhizal fungi; and perspectives and needs. Afterward, a brief discussion will be presented in order to define the real status of knowledge of this highly significant ecological relation to *Eucalyptus* spp.

STATE OF THE ART

Samuel (1926) was the first to recognize an ectotrophic mycorrhiza on *Eucalyptus rubida.* Although he suggested that "the roots of very many, if not all, *Eucalyptus* species may possess mycorrhizas", Chilvers and Pryor (1965) described the structure of eucalyptus mycorrhizas. The establishment of AM association in *Eucalyptus* was first described by Asai (1934) then by Maeda (1954), and the first synthesis in controlled conditions occurred in the 1980's (Malajczuk *et al.* 1981). AM already were verified in 20 species and two hybrids of *Eucalyptus* (**Table 1**), and the benefits of that symbiosis have been commercially exploited.

Generally, studies that approach the occurrence of AM are quantitatively-related, taking into account the radical colonization percentage (number of mycorrhizal roots/total number of roots), spore density (spores number for soil volume), and production of extraradical hyphae (through analysis of fluorescein fluorescence of hyphae for example) (Malacjuzuk *et al.* 1981; Bellei and Garbaye 1992; Grazziotti *et al.* 1998; Jones *et al.* 1998; Methropa 1998; Fernandes *et al.* 1999; Chen *et al.* 2000; Sastry *et al.* 2000; Rodrigues *et al.* 2003; Kisa *et al.* 2007). Also, the efficiency of mycorrhizal association in benefit plant growth such as dry matter and amino acids production, nutrient uptake, and the total stem length has been attested (Mulligan and Sands 1988; Reis and Krügner 1990; Jones *et al.* 1998; Fernandes *et al.* 1999; Chen *et al.* 2000; Sastry *et al.* 2000; Rodrigues *et al.* 2003; Kisa *et al.* 2007). Chen *et al.* (2000), for example, observed differences in plant height owing to fungal treatments were apparent after 10 wk for both *Eucalyptus globulus* and *E. urophylla* at the lower P but not at the higher P concentration. Inoculation with *Laccaria* but not AM significantly affected plant growth, especially at the lower P concentrations. It is possible to find studies about the production and use of AMF and ectomycorrhizal fungi inoculum (Dodd and Thomson 1994; Rola 2000). In general, spores of a natural or experimental soil are recovered by standard method (wet sieving), sterilized, washed with sterile distilled water and propagated on host plant. Following, the spores are reisolated from the host plant and again sterilized before application to eucalyptus seedlings (Sastry *et al.* 2000). Dodd and Thomson (1994) showed how successful exploitation of the AM association is favoured by rapid development of AMF infection in root systems. It was achieved with direct inoculation at sowing and use of a pre-crop on virgin land for subsequent crop growth in the following season. Moreover, several studies show the co-occurrence of both types of association (AMF and ectomycorrhizal fungi). Boudarga *et al.* (1990) verified colonization by *Gigaspora margarita* and *Pisolithus tinctorius* in an active state in roots of *Eucalyptus camaldulensis*, even when they were involved in a dual endo-ectomyzorrhiza association. Chen *et al.* (2000), evaluating the mycorrhization of *E. globulus* and *E. urophylla* by three species of AMF (*Glomus invermaium*, *Acaulospora laevis*, and *Scutellospora calospora*) and *Laccaria lateritia*, observed the AMF fungi colonized roots rapidly when inoculated with the ECM fungus, but the proportion of roots with AM declined to <10% of root length after 12-16 wk in these treatments. Santos *et al.* (2001) verified occurrence of AM and ectomycorrhizae in the same root system in seedlings of *Eucalyptus citriodora*, *E. urophyla*, *E. grandis*, *E. camaldulensis* and *E. cloeziana*, inoculated simultaneously with *Glomus etunicatum* and *Pisolithus tinctorius*. Although few studies had been conducted on the diversity of AMF species, in areas cultured with eucalyptus (Zambolim and Barros 1982; Guimarães 1993; Coelho *et al.* 1997; Gomes and Trufem 1998; Methropa 1998; Alvarenga *et al.* 1999; Stürmer and Morton 1999; Santos 2001; Melloni *et al.* 2003; Barbosa 2004; Mello *et al.* 2006; Chen *et al.* 2007), some studies have confirmed the susceptibility of *Eucalyptus* species to form arbuscular mycorrhiza and produce spores around their root systems. Alvarenga *et al.* (1999) verified percentages of root colonization varying from 9 to 31, average number of spores between 4.83 to 5.46 in 50 mL of soil, and nine species of AMF associated to *E. camaldulensis*. The root colonization varied from 10 to 44% in *E. grandis*, the number of spores, from 3.76 to 11.90, and seven taxa of AMF were identified in its rhizosphere. Melloni *et al.* (2003) observed low levels of colonization by AMF in roots of *E. saligna* (1-8%) as well richness of species (5-6).

MYCORRHIZAL DEPENDENCE

Gerdemann (1975) defined mycorrhizal dependence as the degree which a plant needs this association to reach maximum growth or production under a determined level of soil fertility. According to Menge *et al.* (1978), mycorrhizal dependence can be numerically defined as the relation of weight and dry matter between individuals with or without mycorrhiza, expressed as a percentage. Mycorrhizal dependence of a plant can be altered by factors as genotype due to establishment of species-specific or preferential relations (Janos 1993), soil type, levels of nitrogen and phosphorus in soil (Hayman and Mosse 1971), and fungi species and ecotypes (Jeffries and Barea 2000; Caravaca *et al.* 2005). Different species or cultivars of *Eucalyptus* show distinct nutrient requirements and growth rhythm, and probably have different levels of dependence to the mycorrhizal association. Also, differences on soil structure and fertility interfere on nutritional status of the plants, which can show bigger predisposition to the mycothrophic condition. In contrast, different fungal species or isolates may result in different responses on plant growth due to the genetic compatibility between the symbionts and/or levels of mycorrhizal efficiency. Adjoud *et al.* (1996) tested three AM fungi (*Glomus intraradices*, *G. mosseae* and *G. caledonium*) on 11 *Eucalyptus* species and found positive effects on growth in only 21% of the plant-fungus combinations. Chen *et al.* (2000) found positive growth effects in *E. urophylla* with three AM fungi (*Glomus invermaium*, *Acaulospora laevis* and *Scutellospora calospora*). The effects were not equal between fungal species, with *A. laevis* producing the greatest response and *G. invermaium* the least. Such results clearly indicate that AM species are more host specific than has previously been thought (Janos 1993). All these factors influence growth and other physiological processes of the seedlings transplanted to the field, as well as their mortality in greenhouses (Kormanik *et al.* 1981; Mosse *et al.* 1981; Pope *et al.* 1983).

Logically, under conditions in which plant growth is favored it is observed lesser mycorrhizal dependence. The increase in root production decreases the mycorrhizal dependence, mainly if associated to low concentration of shoot P (Azcón and Ocampo 1981). In low infective potential soils, Dodd and Thomson (1994) proposed the use of a mixed inoculum, containing more than one AMF species associated with ectomycorrhizal fungi to guarantee the persistence of this functional group. However, Howeler *et al.* (1987) and Hartnett and Wilson (2002) suggested that AM are beneficial to these plants only in stress conditions or in specific periods of its life cycle, in which the environmental conditions are not favourable to plants, increasing its mycorrhizal dependence. The mixed inoculum containing more than one species of AMF and ECM permits the establishment of mycorrhizal association as both fungal groups which present different capacity to explore resources and different characteristics as competitors, varying according to environment and to host plant susceptibility to infection and radical colonization. Habte and Manjunath (1987) verified that the dependence of *Leucena leucocephala* on the AM symbiosis decreased as phosphorus (P) concentration in soil increased; on the other hand, high concentrations of P in soil did not seem to alter the beneficial effects of mycorrhizal inoculation. Mycorrhizal dependency of plants may be substantially different and plants' ability to absorb P from low-P soils can be the main factor involved (Mosse 1973; Hall 1975). Root geometry also affects the mycorrhizal dependence as plants with few root hairs tend to be more dependent on mycorrhizal association (Mosse *et al.* 1973). The dependence of tree species has a strong relation with the morphology of its roots, because the benefits resulting from the association are due to intense and more frequent exploitation of soil by fungal hyphae at greater distances. There are numerous observations on the extent of the extra-matrical system of hyphae in soil with various types of mycorrhizas, although the gathering of quantitative data is extremely difficult and laborious. To arbuscular mycorrhiza data vary from 1.6 to 3.992 cm of hyphae per cm of infected root; it depends on the host plant, AMF species and period of colonization (Sanders and Tinker 1973; Abbott and Robson 1985; Abbott *et al.* 1992). In *Eucalyptus camaldulensis* inoculated with *Glomus intraradices*, Kisa *et al.* (2007) verified 4.2 m.g^{-1} soil of extraradical mycelium. According to Heinrich (1982), cited by Bowen (1984), the genus *Eucalyptus* generally presents a dense root system, with very fine, ramified and graminoid-type roots (Baylis 1975). This is in contrast to many other forest species that tend to have magnolioid morphology, allowing them to respond well to mycorrhizal colonization.

The production of AM propagules to be used as inoculum in *Eucalyptus* species is little studied. Zambolim *et al.* (1982) inoculated *E. grandis* and *E. tereticornis* with *Glomus* spp. and observed that the dependency variation of the association was related to the inoculated AMF species. Each host plant will present different susceptibility to mycorrhizal colonization and its effects will depend on fungus inoculated, because mycorrhizal dependence of a plant is influenced by genotype due to species-specific relation as mentioned formerly. Reis and Krügner (1990), assessing the inoculation influence with exotic (*Acaulospora morrowiae*, *A. scrobiculata*, *Glomus clarum*, *Gigaspora margarita*) or native AMF, and application of phosphorus on growth of *E. grandis*, did not observe differences between treatments with regards to any variables assessed (biomass, height and diameter), and considered that *E. grandis* are not dependent on AM association. It is generally acknowledged that many of the eucalyptus are adapted to soil with low nutrient level (Beadle 1966) and even extremely deficient sites can support a considerable biomass of some species (Westman and Rogers 1977; Heirinch and Patrick 1985). One of the basic features that could be argued as contributing to the continued success of a species in a nutrient-deficient habitat is the capacity of the seeds to sequester and concentrate a considerable proportion of the limiting nutrients (Pate and Dell 1984). Some members of the Myrtaceae growing in low nutrients soils also have seeds with high P contents (Bowen 1981), although there are large differences even between species of the same genus, including *Eucalyptus* (Barrow 1977). Mulligan and Sands (1988) showed that plants adapted to different soil fertility conditions present structural differences that explain the degree of dependence to the AM association. According to these authors, *E. grandis* is a species that forms small seeds with low P content and that develops small seedlings with a poorly developed root system, needing fertile soils for its establishment; on the other hand, *E. gummifera* possesses big seeds with high P content and with a more developed root system. *E. grandis* responds better to application of P in soil, and it is considered more dependent on the AM association than *E. gummifera*.

Adjoud *et al.* (1996) observed that *E. hybrid* (*E. grandis* x *E. urophylla*) grew more when inoculated with AMF; however these authors attested that this effect was not associated to the soil P levels or to P accumulated in the aerial parts. *Eucalyptus* seedlings' stem dry weight could be increased up to 49% more compared to non-inoculated control plants. Leaf P levels of non-inoculated *Eucalyptus* seedlings varied greatly between species. Increases in leaf phosphorus concentration following mycorrhizal infection were not necessarily associated with plant growth stimulation. The most mycorrhiza-dependent *Eucalyptus* species tended to be those with highest leaf phosphorus concentration in the absence of a symbiotic fungal. These mycorrhiza-dependent *Eucalyptus* species seem to have greater phosphorus requirements and consequently to rely more on the symbiotic association. Sharma and Adhouleya (2000) attested that *E. tereticornis* depended more on AM association when grew under low soil P available conditions. A positive response to mycorrhizal inoculation was evident at the first two levels of soil P (at 0.67 and 10 ppm) but not at the higher levels of soil P. Dry matter yield of inoculated plants beyond 20 ppm soil P was similar or even less compared to their uninoculated counterparts. Inoculated plants produced maximum dry matter (root and shoot) at 10 ppm soil P, whereas uninoculated plants did not produce until the level reached 20 ppm. Taking into account dry matter yield, *Eucalyptus* plants were found to be highly dependent on 10 ppm of soil P for maximum dry matter production. Any further amendment of P to soil was not beneficial either for AM symbiosis or for plant growth.

The increase in the growth of hybrids of *Eucalyptus* due to presence of mycorrhizal fungi has been reported by several authors (Chilvers *et al.* 1987; Boudarga *et al.* 1990; Adjoud *et al.* 1996). Sastry *et al.* (2000) verified that N and P uptake of *Eucalyptus hybrid* (*E. camaldulensis* x *E. tereticornis*) was highest at 20 ppm P with a sharp decline at higher P; mycorrhizal P uptake efficiency was reduced drastically at 30 ppm P. Bagyaraj and Machado (1996) found that an increased soil P concentration had an adverse effect on mycorrhizal colonization. Reduced mycorrhizal micronutrient uptake and suppression of AM activity at high P levels has been reported also by Habte and Manjunath (1991). Undoubtedly, there are several factors that exert influence on mycorrhizal dependency as mentioned above. A same plant will not be susceptible to mycorrhizal association in any situation. Mycorrhizal dependency of plants and mycorrhizal infectivity (quantity of AM propagules and the ability of the soil to favour their germination) are reciprocally linked since the latter is a condition of the expression of the former one which governs the level of the latter. Thus, mycorrhizal development in the field is largely dependent on cropping systems, and in particular, the cropping sequence of plants that exhibit a range of mycorrhizal dependencies.

COLONIZATION AND BENEFITS

The establishment of AM symbiosis begins with the colonization of a compatible root by the hyphae produced by AM fungal soil propagules, asexual spores or mycorrhizal roots. Even dead roots from annual plants might be a good source of inoculum as they protect the fungus from environmental hazards until when new hyphae are able to grow out of the roots and colonize other plants (Requena *et al*. 1996). After the attachment of hypha to the root surface by means of an appressorium the fungus penetrates into the cortex, filling the inter-cellular spaces, without however, having ever invaded the central cylinder. Inside the cells they may form ovoid structures known as vesicles and branched structures known as arbuscules, which are presumed to be the main site of nutrient exchange between symbionts. Malajczuk *et al*. (1981) observed that *E. diversicolor* and *E. marginata* formed typical arbuscular mycorrhizae, with the compact arbuscules occupying only a portion of the cortical cells. Most arbuscules were in the *Eucalyptus* short roots, and they were abundant close to the root tips. In addition, many hyphal coils were present in the root cortex. Nonetheless, there are many reports of Paris type mycorrhizal where arbuscules are completely absent (Requena *et al*. 2007). Methropa (1998) verified that the mycorrhizal infection percentage was low in *Eucalyptus hybrid* (20%), but all structures had been produced. Externally, the mycelium may expand around the root for some centimeters, thus nutrients are captured by networks of hyphae fungal radiating into soil around roots and are transported to the plant in exchange for carbon. The nutrient most often implicated in this process is phosphorus, a highly immobile element in soil that is therefore frequently limiting to plant growth (Newsham *et al*. 1995).

It is important to stand out that the benefits of AM association are not always related to levels of root colonization. McGonigle *et al*. (1990) have shown that the total percentage of root length colonized by an AM fungus is not a particularly good predictor of growth-promoting effects by that fungus. The length of external hyphae produced by a mycorrhizal fungus can be a better predictor of its relative ability to uptake P (Jones *et al*. 1990). In other cases, the average distance of extension from the root is more important (Jakobsen *et al*. 1992). In addition, the hyphae of different AM fungi can differ in the amount of P taken up per unit length (Jakobsen *et al*. 1992); thus, the total length of hyphae produced is not always a reliable indicator of the efficacy of P uptake. Arbuscular mycorrhizal fungi can absorb and transport to plants soil solution compounds containing nitrogen (Ames *et al*. 1983; He *et al*. 2003; Toussaint *et al*. 2004), and they can also absorb from neighbour plants by mycelial interconnection (Whittinghan and Read 1982; Francis and Read 1984; Martins 1993). Rodrigues *et al*. (2003), in a study performed under greenhouse conditions, observed that the efficiency of using N was greater in *E. grandis* inoculated with AMF (*Glomus macrocarpum, G. etunicatum* and *E. colombiana*). Also was verified a transfer of ^{15}N from *Sesbania virgata* (inoculated with *Rhizobium*) to *Eucalyptus* plants, by means of mycorrhizal hyphae.

The results of root colonization in *Eucalyptus cloeziana* found by Araújo *et al*. (2004) showed percentages of colonization ranging from 10% to 96.66%. In eucalyptus forests in renewal (seven months after cut), in the city Entre Rios (North littoral of Bahia State, Brazil), Santos (2001) found mean values of colonization from 27.77% and 58.33% in wet and dry stations, respectively. In adults plants (eight years) the means found by Santos (2001) were 61.9% in the rainy period, and 55.55% in the dry period. Zambolim and Barros (1982) found colonization in *Eucalyptus* spp. ranging from 25 to 50%; however small values (6.2 to 21.7%) were observed in *E. grandis* and *E. urophylla* (Guimarães 1993). These results indicate that colonization percentages by AMF in *Eucalyptus* genus are very varied. These variations are probably due to several factors, for instance soil physical-chemical and biological proprieties, nutrients availability, factors micro- and macroclimatic, development stage and genotype of the plants, root biomass, proximity with other mycotrophic species, AMF species presents, hyphae expansion in the soil, and soil handling can be influencing in the mycorrhizal status. There is no doubt about that the infection levels vary seasonally. If times of peak infection differ between species, much of the evidence of differences between species in infection levels could be a simple consequence of that (Fitter and Merryweather 1992; Grazziotti *et al*. 1998). In general, to represent an annual cycle of mycorrhizal infection on a species are performed studies in rainy and dry season; however, it is very important to know variations during several months. Observed differences in infection levels between plants can be attributed to phosphate availability and soil characteristics that vary at spatial and temporal scales (Fitter and Merryweather 1992). Since soil conditions are constantly changing, the soil environment may favor development of arbuscular mycorrhizae at one point in time, and inhibit them at others (Entry *et al*. 2002).

Other advantage attributed to symbiosis with mycorrhizal fungi is related to the capacity to protect plants of heavy metal-stress (Hildebrandt *et al*. 2007). The fact that heavy metals reduce availability of soil nutrients to plants which are essential for their normal development and growth reinforces the importance of AMF (Arriagada *et al*. 2007). The mechanisms which could better explain this is the selective immobilization of heavy metals in root tissues containing fungal structures or the metal sorption capacity of AMF extraradical mycelium (Kaldorf *et al*. 1999; Joner *et al*. 2000). Certainly, this benefit will depend on toxic levels present in the environment. Arriagada *et al*. (2007) showed that plants of *E. globulus* developed chlorosis and necrosis when were grown in heavy metal contaminated soil not inoculated with AM fungi; however these plants presented resistance to adverse soil conditions when were associated to AMF. According to the same authors, *Glomus mosseae* and *G. deserticola* contributed to a better development of the plants grown in contaminated soil since they increased the total N and the quantity of chlorophyll in *E. globulus* shoots. It was also reported that the fungus *Glomus mosseae* was able to restrict Cd transfer to the plant due to Cd inmobilization by the fungi (Joner *et al*. 2004). *Glomus deserticola* increased the resistance of plants to the presence of Cd and Pb (Arriagada *et al*. 2004, 2005).

DIVERSITY OF AMF IN EUCALYPTUS FORESTS

AMF colonizes the roots in different ways and intensity, and changes in soil conditions can modify the composition of fungus species that occur in mycorrhizal formation in yield. Several practices of handling and culture conditions showed that although mycorrhizal community is similar there will be differences in conditions of mycorrhizal association (Araújo *et al*. 2004). A community of mycorrhizal fungi has the capacity to influence (van der Heijden *et al*. 1998a, 1998b) and to be influenced (Bever *et al*. 1996) by vegetal community. This interaction is very relevant to agrosystems (Miranda *et al*. 2005). According to Bever *et al*. (1996), a host plant can be an important factor to regulate the composition and structure of AMF communities, because development phase such as spores germination, hyphae growth, root colonization and sporulation is influenced by plant roots. Abbott and Gazey (1994) suggest that can be advantageous to maintain high levels of AMF diversity in soil, independently of individual contribution of fungus to formation of AM. This can proportionate an opportunity to efficient species predominate when the soil conditions change due to cropping practices be propitiate (Miranda *et al*. 2005).

In Brazil, some check lists were performed in different regions and environmental conditions. Zambolim and Barros (1982) observed the dominance of *A. scrobiculata* in plantations of *E. grandis*, *E. saligna* and *E. citriodora* of different ages, growing in red latosoil in Viçosa (MG).

Table 2 Diversity of AMF in species of *Eucalyptus*.

Species of AMF	**Eucalyptus species[1]**								**Locality[2]**
	Eca	**Eci**	**Edu**	**Egr**	**Ehy**	**Esa**	**Esp.**	**Espp.**	
Acaulospora aff. *laevis*							+		BA (Brazil)
A. delicata					+				ES, MG (Brazil)
A. excavata							+		SP (Brazil)
A. foveata					+		+	+	BA, SP (Brazil); South China
A. longula	+				+		+		ES, MG (Brazil)
A. mellea					+		+		ES, MG (Brazil)
A. morrowiae	+				+		+		ES, MG (Brazil)
A. myriocarpa								+	South China
A. scrobiculata		+		+	+	+	+	+	BA, MG, RS (Brazil); South China
A. spinosa					+		+		BA (Brazil)
A. tuberculata					+				BA (Brazil)
Archaeospora leptoticha[3]					+		+		BA (Brazil)
E. colombiana[4]	+				+	+	+		BA, MG, RJ (Brazil); India
E. infrequens							+		BA (Brazil)
Gigaspora decipiens					+		+		BA (Brazil)
G. gigantea							+		BA (Brazil)
G. margarita				+		+	+	+	BA, MG, RS (Brazil); South China
G. ramisporophora							+		SP (Brazil)
Glomus aff. *constrictum*							+		BA (Brazil)
Glomus aff. *lamellosum*							+		BA (Brazil)
G. aggregatum								+	SP (Brazl); South China; India
G. ambispoprum					+				India
G. claroideum								+	South China
G. clarum				+	+				BA, RS (Brazil)
G. clavisporum					+				BA (Brazil)
G. constrictum								+	South China
G. coremioides								+	South China
G. deserticola					+				ES, MG (Brazil)
G. diaphanum					+				ES, MG (Brazil)
G. dolichosporum								+	South China
G. etunicatum	+			+	+		+		BA, ES, MG, RJ, RS (Brazil)
G. fasciculatum					+		+		BA (Brazil)
G. formosanum							+	+	BA (Brazil); South China
G. fuegianum							+		BA (Brazil)
G. geosporum					+		+	+	BA, ES, MG (Brazil); South China
G. glomerulatum					+		+		BA (Brazil)
G. halonatum							+		BA (Brazil)
G. heterosporum					+		+		BA (Brazil)
G. hoi					+				BA (Brazil)
G. intraradices							+	+	BA (Brazil); South China
G. invermaium					+		+		BA, ES, MG (Brazil)
G. macrocarpum					+		+	+	BA, ES, MG, RJ (Brazil); South China
G. microaggregatum					+			+	BA (Brazil); South China
G. microcarpum								+	South China
G. monosporum					+				BA (Brazil)
G. mosseae								+	South China
G. multisubstensum							+		SP (Brazil)
G. rubiformis								+	South China
G. sinuosum							+	+	BA (Brazil); South China
G. taiwanense		+						+	BA (Brazil); South China
G. versiforme							+	+	BA (Brazil); South China
Paraglomus occultum	+					+			MG (Brazil)
Scutellospora aff. *biornata*							+		SP (Brazil)
S. auriglоba					+				BA (Brazil)
S. calospora					+		+		BA (Brazil)
S. castanea								+	South China
S. dipurpurescens					+		+		BA (Brazil)
S. erythropa							+		SP (Brazil)
S. fulgida							+		BA (Brazil)
S. gilmorei							+		BA (Brazil)
S. heterogama	+			+					MG, RS (Brazil)
S. pellucida					+		+		BA (Brazil)
S. persica							+		BA (Brazil)
S. reticulata					+				BA (Brazil)
S. rubra			+						PR (Brazil)

[1] Eca – *E. camaldulensis*; ECi – *E. citriodora*; Edu – *E. dussii*; EGr – *E. grandis*; EHy – *E. hybrid* (*E. grandis* x *E. urophylla*); ESa – *E. saligna*; E.sp. – *Eucalyptus* sp.; E.spp. – *Eucalyptus* spp. (*E. camaldulensis*, *E. citriodora*, *E. exserta*, *E. globulus*, *E. grandis*, *E. hybrid*, *E. propinqua*, *E. robusta*, *E. urophylla*).

[2] BA, ES, MG, RJ, RS, SP correspond to the States of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, Rio Grande do Sul and São Paulo, respectively; South China corresponds to 155 plantations at 31 locations [Guangdong (11 locations), Guangxi (eight locations), Hainan (five locations), and Yunnan (seven locations) Provinces]. India corresponds to mine waste at Durgapur coal mine site.

[3] Recently renamed *Ambispora appendicula* (Walker 2008).

[4] Recently renamed *Kuklospora colombiana* (Sieverding and Oehl 2006).

Guimarães (1983), investigating the mycorrhizal status of eucalyptus plantations (*E. grandis* and *E. urophylla*) in States of Espírito Santo and Minas Gerais, identified 13 species of AMF. Coelho *et al.* (1997) verified higher abundance of *Acaulospora*, *Glomus* and *Scutellospora* in *E. camaldulensis* plantations, suggesting that those species have a higher range of ecological adaptation regarding to soil diversity and climate conditions. The AMF species diversity in eucalyptus forest associated to Atlantic forest fragment (São Paulo, SP) found by Gomes and Trufem (1998) was of 18 species, and the genus more abundant was *Acaulospora* (50% of all species). Alvarenga *et al.* (1999) investigated the presence of AMF in area of Cerrado in Minas Gerais, with different vegetal formations, and verified seven species associated to rhizosphere of *E. camaldulensis* in two distinct conditions: adult forest and a reformed area. Stürmer and Morton (1999) described *Scutellospora rubra*, an isolated species of rhizosphere of *E. dunnii*, in State of Paraná, Brazil. Eight species of AMF were registered by Santos (2001) in plantations of hybrid eucalyptus (*E. grandis* x *E. urophylla*) in North of Bahia State. Melloni *et al.* (2003), in an area of bauxite mining reforested with *E. saligna* in State of Minas Gerais, found five species of AMF. Barbosa (2004) registered 32 morpho-species of AMF in eucalyptus plantations in South of Bahia, under two scenarios: continuous and intercalated with Atlantic forest. Mello *et al.* (2006) evaluated the AMF diversity in eucalyptus plantations in State of Rio Grande do Sul of three and eight years old, and verified that the spores was significatively higher in younger zones. In India, Methropa (1998) found three species of AMF in rhizosphere of *Eucalyptus* hybrid growing on a reclaimed surface mining overburden situated at the Durgapur opencast coal mine site. In China, Chen *et al.* (2007) verified 21 species of AMF, mostly *Glomus* species, from 155 *Eucalypt* plantations (*E. camaldulensis*, *E. citriodora*, *E. exserta*, *E. globulus*, *E. grandis*, *E. grandis* x *E. urophylla*, *E. propinqua*, *E. robusta*, *E. urohylla)*, at 31 locations, over two years. *Glomus mosseae*, *G. formosanum*, *G. versiforme* e *G. geosporum* were frequently present in soils, but spore density and relative abundance of AMF were generally low. In studies performed with goal of identifying AMF species in *Eucalyptus* rhizosphere 65 species were discriminated, predominating the genus *Glomus* and *Acaulospora* (**Table 2**). The species total number studied area ranged from 3 to 32.

COEXISTENCE OF ARBUSCULAR- AND ECTO-MYCORRHIZAL FUNGI

The occurrence of AM to ecto-mycorrhizal (ECM) successsion on plants exhibiting both types of symbioses has been suggested for some host plants, including the genus *Eucalyptus.* Previous experiments have shown stimulation of growth and P uptake of *Eucalyptus* spp. by both ECM (Malajcuzk *et al*. 1975; Heinrich and Patrick 1985) and AM associations (Lapeyrie and Chilvers 1985; Adjoud *et al.* 1996). Jones *et al.* (1998) assessed growth of *Eucalyptus coccifera*, a relatively slow-growing shrub, simultaneously inoculated with AMF (*Glomus caledonium*, *G. mosseae* or *Glomus* E3) and an ECM fungus (*Laccaria bicolor* or *Thelephora terrestris*) and observed that the percentage of AMF colonization was generally higher (34.8% - *G. caledonium*; 48.5% - *Glomus* E3; 5.9% - *G. mosseae*) than the one observed only with ECM fungi (42.3% - *L. bicolor*; 40.8% - *T. terrestris*); however the association effects on plant growth (dry matter + total P content) were lower in plants inoculated with AMF. The same authors found an increasing in P inflow rates in plants with AM, which were comparable to those previously found (Sanders and Tinker 1973; Smith 1982). The ability to increase P inflow seems to be the most important factor to explain the differences in the growth response to ECM and AMF. Arbuscular mycorrhiza seems to be more prevalent on young seedlings whereas the ectomycorrhizas appear later (Chilvers *et al.* 1987). Lapeyric and Chilvers (1985) observed that initial colonization of young *Eucalyptus* was almost exclusively by AMF, and later ECM fungi predominated. Thus, it is possible to affirm that there is a succession of endo- to ectomycorrhiza. Nevertheless, both types of symbionts can be present simultaneously on the same root. In this situation, AMF colonizes the inner part of the cortex while the ectomycorrhizal is restricted to the outer cell layer (Chilvers *et al.* 1987). Each symbiont can form physiologically active and efficient mycorrhizas, as demonstrated with *E. dumosa* (Lapeyrie and Chilvers 1985), *E. camaldulensis* (Boudarga and Dexheimer 1988) and hybrid *Eucalyptus* (Garbaye *et al.* 1988). Some evidences show that the succession between AM and ECM during host plant ageing could be related to the competition for infections sites (Chilvers *et al.* 1987). Furthermore, the fungi could also compete for a limiting substrate. Additionally, the possibility of negative interactions among mycorrhizal fungi (AMF and ECM) has been suggested (Lodge and Wentworth 1990). Differences observed in roots percentage colonized by both AM and ectomycorrhizal fungi may be due to the competition between them (Chilvers *et al.* 1987). These authors discuss three probable and distinctive alternatives for the two-symbiont system. First, the root colonized by the AMF would leave a root cap/meristem region that was not colonized and open the later colonization by the ectomycorrhizal fungus. Second, the dual mycorrhizae result from the AM colonization extending internally into an ECM. The third alternative considers that when ectomycorrhizal colonization occurs first, the mantle persists and restricts the preferential entry sites for the arbuscular fungus (young differentiated epidermal cells) preventing subsequent entrance by the AMF (Lodge and Wentworth 1990). Furthermore, root colonization by AMF may be inhibited by chemical compounds produced by a resident fungus or by the host, by mechanical barriers, by competition for carbohydrates, and also by the rhizosphere community (Last *et al.* 1987; Duchesne *et al.* 1988). Simultaneous occurrence of AM (*Glomus etunicatum*) and ECM (*Pisolithus tinctorius*) in the same root system in five eucalyptus species (*E. urophyla*, *E. citriodora*, *E. grandis*, *E. cloeziana*, and *E. camaldulensis*) was investigated by Santos *et al.* (2001). The AM/ECM ratio values decreased after 45 days in all of *Eucalyptus* species. These observations showed a succession in the dual system, where increased colonization by ECM was accompanied by the decreasing of AM colonization. Initial dominance of AM may be due to the faster germination and growth of the propagules, the reserves available in these propagules which may support hyphal growth in the direction of roots or the quantity of existent propagules. Furthermore, Lodge (2000) considered the principal impact that ectomycorrhizal fungi may have on colonization by arbuscular mycorrhical fungi is due to their host to reduce production of fine roots, thereby limiting the availability of new roots to the fungus.

A study about joint inoculation of *Gigaspora margarita* (AMF) and *Pisolithus tinctorius* (ECM fungus) in *Eucalyptus camaldulensis* showed that the colonization by *P. tinctorius* was restricted to the external cell layer, forming a Hartig net between the cells and a thin sheath around the root (Santos *et al.* 2001). *G. margarita* was present as well, but it was restricted to the inner cortex where most of the cells were infected. The fungus formed arbuscules in the deeper layers on the inner cortex, but hyphal coils were observed in the more superficial ones. The percentage of lateral roots including both fungal symbionts varied between 60 and 70%. The anatomical structure of dual mycorrhizas synthetized *in vitro* resembled that of dual symbioses found in pot grown *Eucalyptus dumosa* on unsterile soil (Chilvers *et al.* 1987). According to these authors, the endomycorrhizal-ectomycorrhizal succession is simply related to spatial competition for infection sites. Santos *et al.* (2001) also observed that the proportion de AM and ECM colonization varied with the time of evaluation, but the sum of the percent root colonization of AM and ECM was close to a maximum and constant after 60 days. This result suggests that there is a limitation to how much fungal biomass a *Eucalyp-*

tus root system will support, and it may be due to the competition between both mycorrhizal fungi for infection sites and for carbohydrates. Positive effect of the simultaneous inoculation of both fungi in colonization percent by AMF was verified at initial stages (45 to 75 days), and a negative interaction between the two fungi at later stages (120 to 180 days) was observed. Schwan (1984) reported the co-existence of AM and ECM in plants collected in an experimental plantation area in Minas Gerais State, Brazil. In her work, she already had put forward the possibility that the incidence of each type of mycorrhizae could be related to environmental and host factors as the age of the plant.

Bellei *et al.* (1992) observed to *E. viminalis* in two areas in Santa Catarina State (Brazil) that arbuscular and ectomycorrhizal colonization followed a successional pattern with increasing stand age. As seedlings increased in age, colonization remained more or less constant, while the proportion attributable to AM decreased and that to ECM increased. Arbuscular mycorrhizal colonization was consistently predominant throughout the first months (eight months). Ectomycorrhizal colonization, on the other hand, gradually increased with plant age and was predominant in older stands (9-10 months nonwards). After planting *Eucalyptus dunnii*, virtually free of mycorrhizal colonization, at six sites in southern Brazil, Oliveira *et al.* (1997) discerned three distinctive patterns of root colonization by arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi during the ensuing 13 months which seemed to be very strongly related to previous cropping: 1) pattern A followed the AM-forming soya bean: the relatively large incidence of AM 5 months after planting progressively decreased while that of ECM increased; 2) pattern B followed the AM/ECM forming *Eucalyptus viminalis*: the incidence of AM remained minimal while the one of ECM relatively rapidly reached a high plateau; and 3) pattern C followed the ECM-forming *Pinus taeda*: both AM and ECM progressively increased but were never abundant. Although the results do not fully explain the three patterns of colonization, it is suggested that the inoculum potential and the specificity fungi-host are implicated. Gange *et al.* (2005) verified that *Glomus caledonium* reduced the growth of *E. urophylla* in the early stages, but the effect appeared to be transient. No effects of *Laccaria laccata* were detected on tree growth, but the ectomycorrhiza reduced colonization by AM. AM fungi appear to be rapid invaders of the root system, gradually being replaced by ECM. From an evolutionary point of view, plant species that can form either AM or ECM may be connecting links between the more primitive arbuscular mycorrhizal habit (Pirozynski and Malloch 1975) and the more advanced ectomycorrhizal habit.

PERSPECTIVES AND NEEDS

The increased demand for hardwood pulp has led to a rapid expansion, worldwide, of eucalypt plantations, including many locations known to be low in nutrients and suffering from water stress (Mason *et al.* 2000). Recent progress in the molecular and genetic analysis of mycorrhiza has provided new-fangled insights into the evolution of this symbiosis (Karandashov and Bucher 2005). Molecular results show that in the mycorrhiza symbiosis novel signaling components as well as conserved ones are directing the molecular dialogue between the fungus and plant. Major goals in the future will be to identify all players of these signaling networks, particularly the signals and receptors that open the door to symbiosis formation (Requena *et al.* 2007).

In spite of the very poor soils, sometimes productivity of *Eucalyptus* cultures is high due to favorable climate and the high growth potential of genetically improved plant material. As consequence, the main limiting factor for a further increase in productivity is mineral nutrition (Garbaye *et al.* 1988). Thus, due to the susceptibility of *Eucalyptus* species to mycorrhizal formation is necessary a better understanding of the biology and silviculture of this genus under conditions of mycorrhizal symbiosis. The relevance of this handling strategy show to be more evident because the main cultivated forest species, such as *Pinus* spp. and *Eucalyptus* spp., are dependents of these symbioses to survive and to obtain better growth (Wilcox 1990).

In recent years, considerable attention has been dedicated to the reforestation with native species (Janos 1996; Herrera *et al.* 1997), and due to this demand studies have searched to know the strategies and competitive abilities of different forest species. The success of the reforestation depends on the young plants capacity to uptake nutrients and water, and to resist diseases and survives the stress imposed by the environment, being of general knowledge, that AM can contribute to minimize those stresses (Siqueira and Saggin-Junior 1995). For this, it is necessary to maintain the vigour of the plants at the beginning of its development, which can be reached with an efficient AMF inoculation for determined host plant (Herrera *et al.* 1997; Siqueira *et al.* 1998). Therefore, AM is an important biological factor to regeneration of tropical forests in degraded areas, generally characterized by soil with deficiency in nutrients, mainly N and P. Similarly, to seek high productivity in *Eucalyptus* plantations without to take into account the mycorrhizal associations is practically unimaginable.

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