Mycorrhiza (2006) 16: 125–132
DOI 10.1007/s00572-005-0024-7

ORIGINAL PAPER

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Displacement of an herbaceous plant species community by mycorrhizal and non-mycorrhizal *Gmelina arborea*, an exotic tree, grown in a microcosm experiment

Received: 24 February 2005 / Accepted: 26 September 2005 / Published online: 19 November 2005
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Abstract *Gmelina arborea* Roxb. (Gmelina, Yemane) is a fast growing tree, native from India and considered as a potentially invasive woody plant in West Africa. Mycorrhizal inoculation of seedlings with *Glomus intraradices* was performed to study (1) the effect on the growth of *G. arborea*, (2) the impact on the catabolic diversity of soil microbial communities and (3) the influence on the structure of herbaceous plant species communities in microcosms. Treatments consisted of control plants, pre-planting fertilizer application and arbuscular mycorrhizal (AM) inoculation. After 4 months' culture in autoclaved soil, *G. arborea* seedlings were either harvested for growth measurement or transferred into containers filled with the same soil but not sterilized. Other containers were kept without *G. arborea* seedlings. After 12 months' further culture, effects of fertilizer amendment and AM inoculation on the growth of *G. arborea* seedlings were recorded. AM colonization was significantly and positively correlated with plant diversity. The substrate-induced respiration response to carboxylic acids was significantly higher in the absence of *G. arborea* and in the presence of *G. intraradices* as compared to the other treatments. The influence of AM symbiosis on plant coexistence and on allelopathic processes of invasive plants are discussed.

Keywords AMF · Plant diversity · Catabolic diversity · *Glomus intraradices* · *Gmelina arborea*

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Introduction

The biological processes by which plant biodiversity and species composition are regulated and maintained in terrestrial ecosystems could be explained from competition between neighbouring plants (Aarsen 1990; Grace and Tilman 1990), spatial and temporal resource partitioning (Ricklefs 1977; Tilman 1982), disturbance creating new patches for plant colonization (Grubb 1977; Huston 1977) and interactions with other organisms in the ecosystems (Brown and Gange 1989; Bever et al. 1997). The relationship between diversity and ecosystem functioning has generally been assessed by taking into account diversity, structure and productivity of the above-ground compartment of terrestrial ecosystems. However, plant population dynamics may be associated with the development of the below-ground community. It has been suggested that the composition and activity of microbial communities are mainly determined by plant factors such as species composition and formation age (Grayston and Campbell 1996; Westover et al. 1997; Priha et al. 1999; Grayston et al. 2001) as well as various environmental factors such as soil type, nutrient status, pH and moisture (Anderson and Domsch 1993; Stotzky 1997). In turn, feedback processes have also been proposed to consider the

influence of soil micro-organisms on the composition of plant community (Callaway 1995; van der Heijden et al. 1998; Bever 2002).

Among soil microbial communities, arbuscular mycorrhizal (AM) fungi form a key component of sustainable soil–plant systems (Bethlenfalvay 1992; van der Heijden et al. 1998; Schreiner et al. 2003; Johansson et al. 2004; Selosse et al. 2004). For instance, van der Heijden et al. (1998) have shown that plant species composition, variability, productivity and biodiversity were mainly influenced by species composition and species richness of AM fungi in artificial microcosms and macrocosms. In natural undisturbed ecosystems, AM fungi form a permanent external mycelium network and plants are linked by a common hyphal network that helps them to access and exploit the nutrient-rich zone or patches (Chiarello et al. 1982; St John et al. 1983; Ravnskov et al. 1999). In addition, AM symbiosis establishment may induce changes in both qualitative and quantitative release of exudates by the roots (Graham et al. 1981; Azaizeh et al. 1995). Moreover, some plant species may exude secondary compounds from their roots that are detrimental to the growth of other plants (Whittaker and Feeny 1971). This phenomenon called allelopathy has been suggested as a mechanism that contributes to the success of particular exotic species to become dominant in invaded plant communities (Vaughn and Berhow 1999; Ridenour and Callaway 2001). However, little attention has been paid to the effects of the AM symbiosis on the interactions among plants.

The aims of our experiments were (1) to study the effect of *Glomus intraradices* on the growth of *Gmelina arborea*, a fast growing tree, native to India and a potentially invasive woody plant in West Africa; (2) to study the impact of the AM symbiosis on the catabolic diversity of soil microbial communities and (3) to study its influence on the structure of herbaceous plant species communities, in artificial microcosms.

Materials and methods

Plant and fungal inoculum

Seeds of *G. arborea* Roxb. (Provenance Peni, Burkina Faso) were surface-sterilized with concentrated sulphuric acid (36 N) for 10 min. The acid solution was then decanted off, and the seeds were rinsed and imbibed for 24 h in sterile distilled water (120°C, 20 min). They were then transferred aseptically in Petri dishes filled with 1% (w/v) water agar. After 8 days of incubation in the dark at 25°C, the germinating seeds were used when rootlets were 2–3 cm long.

G. intraradices Schenk & Smith (DAOM 181602, Ottawa Agricultural Herbarium) was multiplied on leek (*Allium porrum* L.) for 12 weeks under greenhouse conditions on a calcined clay (particule size average 5 mm), Oil-Dri US-special Ty/IIIR (Oil-Dri Company, Chicago, USA) suitable for propagation of AM fungi (Plenchette et al. 1996). Before inoculation of the *G. arborea* seedlings, the leek plants were uprooted, gently washed and cut into infected pieces 0.5 cm long (around 250 vesicles cm^{-1}). Non-mycorrhizal leek roots, prepared as described previously, were used for the control treatment without AM inoculation.

Experimental design

G. arborea seedlings were grown in 1-l pots filled with an autoclaved sandy soil (140°C, 40 min) collected in an experimental station localized at Gampela (20 km from Ouagadougou, Burkina Faso). After autoclaving, the physico-chemical characteristics of the soil were as follows: pH (H_2O) 5.6, clay 4.6%, fine silt 0.0%, coarse silt 0.8%, fine sand 25.5%, coarse sand 69.1%, carbon 2.04%, total nitrogen 0.04%, Olsen phosphorus 4.3 mg kg^{-1}, total phosphorus 116 mg kg^{-1}.

Control, pre-planting fertilizer application (FA) and AM inoculation treatments were carried out. For AM inoculation, 1 g fresh mycorrhizal leek roots was placed in a hole (1×5 cm) in the soil of each pot. Non-mycorrhizal leek roots were introduced into control and FA treatments. The FA treatment was performed by mixing 0.5 g Osmocote (N/P/K, 11:8:17) into the soil of each pot. Pots were kept in a greenhouse in the IRD experimental station of Ouagadougou (Burkina Faso) (daylight, approximately 12 h, daily mean temperature 25°C) and were watered regularly with tap water (pH=6.5) without fertilizer. They were arranged in a randomised complete block design with 14 replicates per treatment.

After 4 months' culture, ten plants were randomly chosen from each treatment. Height was measured, and shoot dry biomass was determined after drying at 60°C for 1 week. For each plant, the entire root system was gently washed, cleared and stained according to the method of Phillips and Hayman (1970). Roots were cut into 1-cm pieces, mixed and placed on slides for microscopic observations at 250× magnification (Brundett et al. 1985). About 100 root pieces were observed per plant. The extent of AM colonization was expressed as a percentage mycorrhizal root pieces. Then, for each plant, the stained roots were collected and weighed (60°C, 1 week).

For each treatment, the remaining four plants were transferred into 50-l containers filled with the same soil as before but not disinfected and carefully mixed to ensure the homogeneity of the seed bank in the soil. Four other containers, prepared as describe previously, were kept without *G. arborea* seedlings (WGA). The pots were arranged in a complete randomised block design. They were placed outside in the IRD experimental station of Ouagadougou (Burkina Faso), in a clean area without any solar protection and grown at ambient temperature from 15 to 40°C with daily watering.

After 12 months' culture, the height of the *G. arborea* trees was measured. Herbaceous plant species naturally growing in each pot were identified, and for each species, shoot biomass was determined (60°C, 1 week). Plant biodiversity was assessed using species richness (S) and

Table 1 Organic compounds and their appropriate concentrations used to assess patterns of ISCP of soil treatments

Organic substrates	Concentrations (mM)	Organic substrates	Concentrations (mM)
Amino acids		Carboxylic acids	
L-Phenylalanine	15	Ascorbique acid	100
L-Glutamine	15	Citric acid	100
L-Serine	15	Fumaric acid	100
L-Arginine	15	Gluconic acid	100
L-Asparagine	15	Quinic acid	100
L-Histidine	15	Malonic acid	100
L-Lysine	15	Formic acid	100
L-Glutamic acid	15	α-Ketoglutaric acid	100
L-Tyrosine	15	α-Ketobutyric acid	100
L-Cysteine	15	Succinic acid	100
Carbohydrates		Tartaric acid	100
D-Glucose	75	Uric acid	100
D-Mannose	75	Oxalic acid	100
Sucrose	75	Gallic acid	100
Amides		Malic acid	100
D-Glucosamine	15	Tri-citrate	100
N-methyl-D-glucamine	15	DL-α-Hydroxybutyric acid	100
Succinamide	15	Polymers	
		Cyclohexane	100

Table 3 Growth response, AM colonization and on-leaf mineral content of *G. arborea* seedlings grown soils inoculated with *G. intraradices* or fertilized after 12 months' culture in a non-disinfected soil and above- and below-ground biomasses recorded from each treatment (means of four replicates)

	Treatments			
	WGA[a]	Control	FA[b]	*G. intraradices*
Height (cm)		226.0 (31.8)[c] a[d]	265.1 (7.6) a	240.4 (28.1) a
Stem biomass (g dry weight)		916 (248.5) a	1,395 (58.7) a	1,150 (60.9) a
Leaf biomass (g dry weight)		654 (32.4) a	1,300 (50.2) b	1,275 (48.1) b
Total shoot biomass (g dry weight)		1,570 (75.1) a	2,695 (86.1) b	2,425 (250) b
Root biomass (g dry weight)		520 (135.3) a	750 (22.4) a	710 (28.9) a
AM colonization		32.3 (3.4) a	25.6 (10.3) a	69.3 (9.1) b
P (mg per plant)		1.78 (0.46) a	3.56 (0.32) b	3.55 (0.28) b
N (mg per plant)		16.6 (2.35) a	30.1 (1.84) b	27.2 (9.1) ab
Above ground biomass (mg dry weight)	65.9 (3.6) c	12.1 (6.1) ab	1.64 (0.46) a	16.8 (1.56) b
Below ground biomass (mg dry weight)	18.2 (2.3) c	2.8 (1.3) ab	0.5 (0.27) a	3.6 (0.63) b

[a]Without *G. arborea* seedlings
[b]Pre-planting fertilizer application
[c]Standard error of the mean
[d]Data in the same line followed by the same letter are not significantly different according to the one-way analysis of variance ($P<0.05$)

Simpson–Yule's diversity index (Krebs 1989) on individual species shoot biomass data. Total below-ground herbaceous plant biomass was determined in each pot. The leaves and the stems of each *G. arborea* plant were divided, and their oven-dried weights (2 weeks at 60°C) were assessed. After drying, 1 g of leaf tissue from each plant was ground, ashed (500°C), digested in 2 ml HCl 6N and 10 ml HNO_3 N and then analysed by colorimetry for P (John, 1970). Another 1 g sub-sample of leaf tissue was grounded and digested in 15 ml H_2SO_4 36N containing 50 g l^{-1} salicylic acid for N (Kjeldahl) determination. The *G. arborea* trees were uprooted, and their root systems were gently washed. Two grams of fresh root was randomly sampled along the root systems of *G. arborea*, and the intensity of AM symbiosis was determined as described before. Then the roots were oven-dried (1 week, 65°C) and weighed.

Table 2 Growth response of *G. arborea* seedlings and AM colonization in soils inoculated with *G. intraradices* or fertilized after 4 months' culture in a disinfected soil (means of ten replicates)

Treatments	Height	Shoot biomass (mg dry weight)	Root biomass (mg dry weight)	AM colonization (%)
Control	22.7 (1.8)[b] a[c]	876 (28.9) a	330 (12.7) a	0
FA[a]	36.1 (2.1) b	1,540 (53.8) b	760 (20.6) b	0
G. intraradices	34.2 (2.37) b	1,573 (66.5) b	890 (53.2) b	22.2 (3.1)

[a]Pre-planting fertilizer application
[b]Standard error of the mean
[c]Data in the same column followed by the same letter are not significantly different according to the one-way analysis of variance ($P<0.05$)

The soil collected from each pot was carefully mixed, and 2 kg sub-samples were taken and kept at 4°C for further analysis.

Catabolic diversity of microbial communities in soil treatments

Patterns of in situ catabolic potential (ISCP) of microbial communities were determined to provide microbial functional diversity in soil treatments (Degens and Harris 1997). A range of amino acids, carbohydrates, organic acids and amides, were screened for differences in substrate-induced respiration (SIR) responsiveness between soil treatments (Table 1). The substrate concentrations providing optimum SIR responses were indicated in Table 2 (Degens and Harris 1997). One gram of equivalent dry weight soil was added to 2 ml substrate solution (West and Sparling, 1986) in 10-ml bottles. CO_2 production from basal respiratory activity in the soil samples was also determined by adding 2 ml sterile distilled water to 1 g equivalent dry weight of soil. The bottles were immediately closed after the addition of the substrate solutions to soil samples and kept at 28°C for 4 h. CO_2 fluxes from the soils were measured using an infrared gas analyser (IRGA) (Polytron IR CO_2, Dräger) in combination with a thermal flow meter (Heinemeyer et al. 1989). Results were expressed as µg CO_2 g^{-1} soil h^{-1}. Catabolic diversity was assessed using catabolic richness and catabolic evenness. Catabolic richness, R, represented the number of substrates used by micro-organisms in each soil treatment. Catabolic evenness, E, (variability of substrate used among the range of substrates tested) was calculated using the Simpson–Yule's index, $E=1/\sum p^2_i$, with p_i=respiration response to individual substrates/total respiration activity induced by all substrates for a soil treatment (Magurran 1988).

Statistical analysis

All data were subjected to a one-way analysis of variance using the Super Anova Computer program, and means were compared with the Newman–Keuls multiple range test (P=0.05). Mycorrhizal indexes were transformed by arcsin (sqrt %) before statistical analysis.

Results

After 4 months' culture in the disinfected soil, the pre-planting fertilizer application significantly increased the growth of *G. arborea* seedlings (Table 2) by ×1.50, ×1.76 and ×2.31 for height, shoot and root dry weight, respectively, compared to the controls. There was no significant difference between the FA and *G. intraradices* treatments (Table 2). AM structures (vesicles and hyphae) were observed in the latter treatment, but no AM structure was recorded in the FA and the control treatments.

After 12 months' further culture in non-disinfected soil, the positive effects of the fertilizer amendment and AM inoculation were only recorded on the leaves and the total shoot biomasses, whereas no significant difference was found for the height, the stem and root biomasses compared to the control (Table 3). The growth of *G. arborea* seedlings was not significantly different in the FA and *G. intraradices* treatments. Highest nitrogen leaf content was recorded for the FA treatment, whereas highest P leaf contents were found for FA and *G. intraradices* treatments (Table 3). AM

Table 4 Above-ground biomass (mg dry weight) of individual plant species recorded in each treatment after 12 months' culture in a non-disinfected soil

Plant species	Families	Treatments			
		WGA[a]	Control	FA[b]	*G. intraradices*
Alysicarpus ovalifolius (Schumach. & Thonn)	Fabaceae	0 a[c]	0 a	80 (80)[d] a	0 a
*Cassia obtusifolia*L.	Caesalpinaceae	0 a	0 a	40 (40) a	0 a
Commelina subulata Roth	Commelinaceae	560 (49) a	0 a	0 a	433 (30) a
Cyperus rotundus L.	Cyperaceae	7,700 (3,917) a	6,767 (4,548) a	840 (241) a	6,000 (1,769) a
Dactyloctenium aegyptium (L.) Willd	Poaceae	4,640 (2,367) b	267 (267) ab	0 a	233 (233) ab
Digitaria horizontalis Willd	Poaceae	20,100 (5,897) b	0 a	40 (40) a	4,000 (1,337) a
Euphorbia forskalii Gay	Euphosbiaceae	160 (81) a	0 a	0 a	0 a
Euphobia E. hirta L.	Euphorbiaceae	13,580 (5,694) b	333 (333) a	180 (112)a	67 (34) a
Eragrostis E. aspera (Jacq.) Nees	Poaceae	11,740 (4,863) b	833 (833) a	20 (20) a	3,367 (2,468) ab
Mitracarpus M. villosus (Sw.) Cham. & Schlecht. Ex DC	Fabaceae	1,880 (394) b	460 (460) ab	0 a	33 (33) ab
Pennisetum P. pedicellatum Trin.	Poaceae	2,140 (1,209) b	0 a	0 a	0 a
Setaria pumila (Poir.) Roem. & Schult	Poaceae	740 (356) a	3,433 (2,503) a	380 (380) a	2,700 (1,532) a
Zornia Z. glochidiata Reichb. Ex DC	Fabaceae	2,620 (1,620) b	0 a	0 a	0 a

[a]Without *G. arborea* seedlings
[b]Pre-planting fertilizer application
[c]Data in the same line followed by the same letter are not significantly different according to the one-way analysis of variance (P< 0.05)
[d]Standard error of the mean

Table 5 Effect of the treatments on the plant species richness, Simpson–Yule's diversity index, catabolic richness and evenness after 12 months' culture in a non-disinfected soil

	Treatments			
	WGA[a]	Control	FA	*G. intraradices*
Plant species richness	7.8 (0.66) [b] c[c]	3.0 (1.15) ab	2.8 (0.74) a	5.7 (0.33) bc
Simpson–Yule's diversity index	3.46 (0.29) b	1.62 (0.31) a	1.69 (0.31) a	3.16 (0.26) b
Catabolic richness	24.8 (1.43) a	28.3 (0.67) ab	30.8 (1.16) b	28.1 (2.89) ab
Catabolic evenness	12.7 (0.79) a	15.4 (0.32) b	15.4 (0.51) b	14.4 (0.46) ab

[a]Without *G. arborea* seedlings
[b]Standard error of the mean
[c]Data in the same line followed by the same letter are not significantly different according to the one-way analysis of variance ($P<0.05$)

colonization was significantly greater for the AM inoculated seedlings than in the other treatments (Table 3).

Above- and below-ground herbaceous plant biomasses ranged among the treatments as follows: WGA treatment >*G. intraradices* >Control >FA treatment (Table 3). In the FA treatment, above- and below-ground biomasses decreased by ×0.24 and ×0.15, respectively, compared to the WGA treatment. Thirteen herbaceous plant species were found within all the treatments (Table 4). Seven species were predominant in the WGA treatment (*Dactyloctenum aegyptium*, *Digitaria horizontalis*, *Euphorbia hirta*, *Eragrostis aspera*, *Mitracarpus villosus*, *Pennicetum pedicellatum* and *Zornia glochidiata*), whereas no significant differences were recorded for plant species in the other treatments (Table 4). Plant species richness ranged from 7.8 (WGA treatment) to 2.8 (FA treatment), and the Simpson–Yule's index was significantly higher in WGA and *G. intraradices* treatments than in control and FA treatments (Table 5). The extent of AM colonization along *G. arborea* root systems was significantly and positively correlated with each of the plant diversity parameters (Fig. 1a,b). Compared to the WGA treatment, the catabolic richness was significantly higher in the FA treatment, whereas the catabolic evenness was significantly higher in the control and FA treatments (Table 5). The average SIR response to carboxylic acids was significantly higher in soil from WGA and *G. intraradices* treatments than in the other treatments (Table 6). A significant response to amino acids was recorded in soil from *G. arborea* planted treatments (Table 6). No significant differences were found with amides. Average SIR response to carbohydrates was significantly higher in soil from the FA treatment than in other treatment (Table 6). Significant positive correlations were recorded between *G. arborea* root growth and both catabolic diversity indexes (r^2=0.542 for catabolic richness and r^2=0.425 with the catabolic evenness). No significant relation was found between these catabolic diversity indexes and the extent of AM colonization in *G. arborea* root systems.

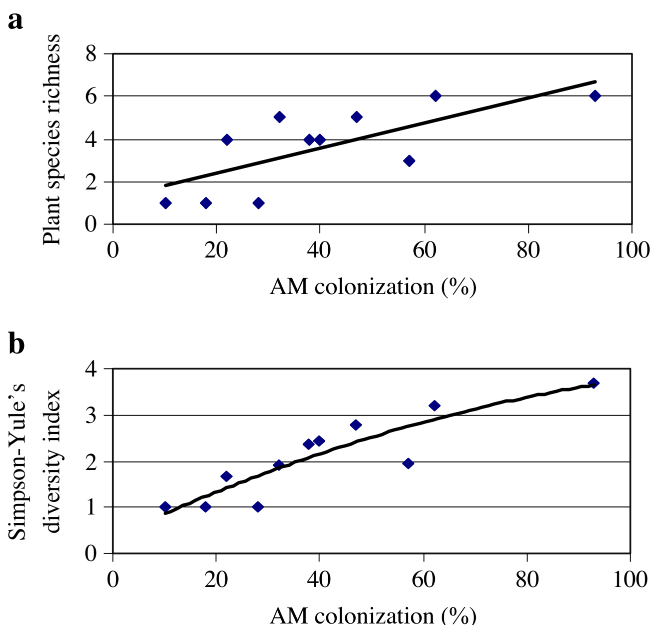

Fig. 1 Correlations between percentage of AM colonization of *G. arborea* root systems and **a** plant species richness (y=8.114+8.935x, r^2=0.526, p=0.011) and **b** Simpson–Yule's diversity index (y=0.405+0.05x+0.00016x^2, r^2=0.801, P=0.0016)

Table 6 Average SIR responses (μg CO_2 g^{-1} soil h^{-1}) in the four treatments with each substrate group (carboxylic acids, amino acids, amides and carbohydrates)

	Treatments			
	WGA[a]	Control	FA	*G. intraradices*
Carboxylic acids	14.86 (0.66)[b] b[c]	10.96 (0.48) a	12.12 (0.87) a	14.59 (0.72) b
Amino acids	1.68 (0.36) a	3.94 (0.13) b	3.31 (0.31) b	3.45 (0.52) b
Amides	7.01 (1.30) a	8.27 (0.91) a	7.91 (1.21) a	11.56 (2.69) a
Carbohydrates	8.72 (0.58) a	9.87 (1.77) ab	13.06 (0.96) b	9.41 (1.71) a

[a]Without *G. arborea* seedlings
[b]Standard error of the mean
[c]Data in the same line followed by the same letter are not significantly different according to the one-way analysis of variance ($P<0.05$)

Discussion

From this research work, two main points deserve discussion: (1) whether an exotic tree species, *G. arborea*, potentially invasive in West Africa, can modify the microbial community function in the soil and can alter the herbaceous plant community structure and (2) whether these effects can be modified by massive AM establishment on *G. arborea* root systems.

Previous research has shown that some exotic plant species can cause an increased pH in soils as well as higher nitrification rates and available nitrate (Callaway 1995; Kourtev et al. 1998, 1999, 2003; Ehrenfeld et al. 2001). In the present study, no significant differences have been found between each treatment for these soil characteristics (nitrogen and pH) (data not shown). In contrast, the analysis of ISCP patterns in soil in which *G. arborea* had been planted (control and FA treatments) or not (WGA treatment) showed a strong differentiation of microbial community functions. It has been well established that the structure and functional diversity of microbial communities in the soil were mainly dependent on plant composition above-ground (Grayston and Campbell 1996; Priha et al. 1999; Grayston et al. 2001). Our data also clearly showed that the highest catabolic richness and evenness indexes were found in soil in which *G. arborea* had been cultured without previous *G. intraradices* inoculation. Although recent studies have assessed that catabolic abilities of microbial communities can be modified by exotic plants (Kourtev et al. 2003), the responses of catabolic diversity indexes to exotic plant species have been rarely assessed. In addition, the opposite effects of this exotic tree species on carboxylic acid, amino acid and carbohydrate responses showed that it also creates changes in functional groups within the microbiota (Meyer 1994). These changes in soil community functions could influence the structure of plant communities and modify the outcome of competition between neighbouring plants (West 1996; Watkinson and Freckleton 1997).

The influence of *G. arborea* on native herbaceous plant community structure and microbial community function is significantly modified by the massive AM inoculation of *G. arborea* seedlings. *G. intraradices* is highly beneficial to the growth of *G. arborea* seedlings in the disinfected sandy soil, and this positive effect was maintained during 12 months' culture in a non-disturbed soil. It has already been shown that AM inoculation of plants is very efficient in establishing plants on disturbed soils (Estaun et al. 1997). In addition, it has been previously established that the *G. intraradices* isolate (DAOM 1802) was very efficient on the growth of other plant hosts such as native or exotic leguminous plant species from West Africa (Villenave et al. 2003; Duponnois and Plenchette 2003). More recently, it has been demonstrated that the AM symbiosis between *Acacia holosericea* and *G. intraradices* affected the microbial activities in hyphosphere soil (Duponnois et al. 2005).

AM fungi modify root functions (i.e. root exudation) (Marshner et al. 1997), influence carbohydrate metabolism of the host plant (Shachar-Hill et al. 1995) and modify rhizosphere populations (Azaizeh et al. 1995; Andrade et al. 1998). In addition, chemical compounds that are exuded from AM hyphae have a selective effect on the microbial community in the rhizosphere and in the soil (Hobbie 1992). Together, these microbial compartments are commonly named "mycorrhizosphere" (Linderman 1988). Among all the substrates tested for the SIR measurement, our results show that carboxylic acids are the substrates yielding the highest respiratory responses and eliciting significantly different responses. These results corroborate those of Degens and Harris (1997) who found that carboxylic acids showed the most variable response in soils under different agriculture management and the highest responses on the average. As the SIR responses of microbial communities reflect soil potential in utilization of simple substrates, our results suggest that in the soil where *G. arborea* has been inoculated with *G. intraradices*, there was a higher availability of these. In addition, Duponnois et al. (2005) have also found that carboxylic acid SIR responses were highly correlated with mycorrhizal soil infectivity (MSI). In the present study, the MSI may be increased by *G. intraradices* inoculation, as resulting in the highest carboxylic acids SIR response.

It has been suggested that AM fungi might be important agents promoting plant coexistence (Janos 1980; Allen and Allen, 1990; Hart et al. 2003). van der Heijden et al. (1998) argued that an increase in hyphal lengths and nutrient exploitation occurred with increasing AM fungi richness that, in terms, led to a higher plant biodiversity, ecosystem variability and productivity. Several recent papers emphasized the role of AM fungi in influencing plant diversity (O'Connor et al. 2002; Urcelay and Diaz 2003; Dhillion and Gardsjord 2004). Although hyphal length was not measured in the present study, results suggest that a well-developed mycelial network could increase the diversity and the development of herbaceous plant species communities by equalising the distribution of soil resources among competitively dominant and sub-dominant species (Wirsel 2004).

It is usually observed that many plant species coexist with neighbours in species-diverse systems in their native habitat, whereas they exclude and eliminate their neighbours after their introduction into a novel environment. Several hypotheses have been proposed to explain the success of invasive plants such as the "natural enemies hypothesis" (Gillet 1962), the existence of empty niches in recipient communities, and rapid genetic changes in invader populations in response to new selection pressure in the novel environment (Mack et al. 2000; Sakai et al. 2001). Although it has been suggested that possible allelopathic effects in degraded soils may have important implications for the susceptibility of plant communities to invasion (Lonsdale 1999), little attention has been paid to the potential role of AM fungi in such mechanisms (Callaway 1995; Ridenour and Callaway 2001). Among biotic factors, it is well known that soil degradation generally results in loss of AM propagules (Mosse 1986), particularly in semi-arid ecosystems (Mc Gee 1989), which

decreases the MSI potential and thus limits the re-establishment of indigenous plants communities (Sylvia 1990). In contrast, introduced fast growing tropical trees are usually associated with a high diversity of AM fungi in their undisturbed native area (Helgason et al. 1998). As an increase in AM fungi richness is linked with an increase in hyphal length (van der Heijden et al. 1998), the highest AM soil colonization could prevent their negative effect on neighbours because of the environmental fungal influences as describe previously. It is known that micro-organisms can act as allelochemical mediators, inactivating or metabolising toxic compounds, and mycorrhizal fungi have been hypothesized to protect seedlings against allelopathy (Pellissier and Souto 1999). This effect of mycorrhiza could also be indirect through a modification of bacterial community, as bacteria are able to break down phenolic allelochemical compounds (Blum et al. 2000; Renne et al. 2004).

In conclusion, AM fungal inoculation affected plant community structure associated with *G. arborea*. However, field-based experimental research must be undertaken to assess AM species richness and shared mycelium networks associated with this fast growing, introduced, tropical tree in its native and exotic areas using genetic markers. These experimental approaches need to be undertaken in different ecosystem types as the influence of AM fungi is probably influenced by biotic and abiotic environmental characteristics.

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