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ORIGINAL PAPER

Response of native soil microbial functions to the controlled mycorrhization of an exotic tree legume, *Acacia holosericea* in a Sahelian ecosystem

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Abstract Fifty years of overexploitation have disturbed most forests within Sahelian areas. Exotic fast growing trees (i.e., Australian *Acacia* species) have subsequently been introduced for soil improvement and fuelwood production purposes. Additionally, rhizobial or mycorrhizal symbioses have sometimes been favored by means of controlled inoculations to increase the performance of these exotic trees in such arid and semiarid zones. Large-scale anthropogenic introduction of exotic plants could also threaten the native biodiversity and ecosystem resilience. We carried out an experimental reforestation in Burkina Faso in order to study the effects of *Acacia holosericea* mycorrhizal inoculation on the soil nutrient content, microbial soil functionalities and mycorrhizal soil potential. Treatments consisted of uninoculated *A. holosericea*, preplanting fertilizer application and arbuscular mycorrhizal inoculation with *Glomus intraradices*. Our results showed that (i) arbuscular mycorrhizal (AM) inoculation and prefertilizer application significantly improved *A. holosericea* growth after 4 years of plantation and (ii) the introduction of *A. holosericea* trees significantly modified soil microbial functions. The results clearly showed that the use of exotic tree legume species should be directly responsible for important changes in soil microbiota with great disturbances in essential functions driven by microbial communities (e.g., catabolic diversity and C cycling, phosphatase activity and P availability). They also highlighted the importance of AM symbiosis in the functioning of soils and forest plantation

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performances. The AM effect on soil functions was significantly correlated with the enhanced mycorrhizal soil potential recorded in the AM inoculation treatment.

Keywords Arbuscular mycorrhizal symbiosis · Functional diversity · Mycorrhizal soil potential · *Acacia holosericea* · *Glomus intraradices* · Soil microbial communities · Exotic tree species

Introduction

Ecological resilience has been defined as the capacity of an ecosystem to absorb disturbances and to return to a similar state that existed before the disturbance with the same functions, structure, identity, etc. (Peterson et al. 1998; Boesch 2006). This concept of resilience has received regular interest since it has been suggested that ecological diversity (especially functional diversity) tends to increase resilience to biological disorders (Lavorel 1999). Severe disturbance to forest ecosystems leads to a dysfunctional (or desertified) landscape with reduced soil fertility and productivity (D'Odorico et al. 2005). As a result of a weak plant cover, soil erosion increases concurrently to a decrease of soil microbial activity, water infiltration, organic matter and nutrient contents (Garcia et al. 1997). Plant species composition is closely related to the structure and functional diversity of microbial communities (Grayston et al. 1996; Wardle 2002; Bardgett 2005). Numerous studies have reported that structurally and functionally distinct microbial communities develop under different plant species (Degens and Harris 1997; Bossio et al. 1998; Marilley and Aragno 1999; Kourtev et al. 2003). Desertification processes disturbed these close relationships between aboveground and belowground components of terrestrial ecosystems.

In order to achieve a fast recovery by woody vegetation and to increase soil fertility in arid and semiarid ecosystems, many revegetation programs have been conducted by planting fast growing exotic trees such as *Pinus* spp., *Eucalyptus* spp. and *Acacia* spp. Australian acacias are fast-growing pioneer species which have been highly planted in Australia and outside their natural range for their tannin, timber, fuelwood and paper-making properties (Cossalter 1987). West Africa has large areas of eroded lands resulting from inappropriate land use and deforestation over the last 50 years. This land needs to be rehabilitated for agricultural production, to provide fuelwood and other products for the expanding populations (Cossalter 1987). Hence, many experimental plantations have been conducted to identify and characterize Australian *Acacia* species with potential for soil improvement and fuelwood production (Cossalter 1986, 1987). The ability of these tree legume species to grow in low N and low P soils also depends on their biological ability of forming root symbioses with rhizobial bacteria and arbuscular mycorrhiza and/or ectomycorrhiza (Cossalter 1987; de la Cruz and Garcia 1991). It has also been shown that controlled rhizobial or mycorrhizal symbiosis could significantly improve the growth of Australian acacias in arid and semiarid conditions (Cornet et al. 1982; Galiana et al. 1994; Duponnois et al. 2005, 2007). However, numerous studies have underlined the hazards that can result from this widespread anthropogenic dispersal of exotic organisms that could alter ecological interactions among native species in the introduction area (Rejmanek 2000; Callaway and Ridenour 2004). Exotic plants could threaten ecosystems by different ways such as allelopathic interference with native plant ecosystem (del Moral and Muller 1970), higher performance in a new site (Thébaud and Simberloff 2001), etc. More recently, it has been suggested that exotic plants could interact with soil microbial communities and disrupt mutualistic associations between existing ecological associations within native communities (Richardson et al. 2000; Callaway and Ridenour 2004). Among microorganisms involved in soil biofunctioning, it has been clearly demonstrated that arbuscular mycorrhizal (AM) symbioses were key components of natural systems, particularly, in arid and semiarid ecosystems (Carpenter and Allen 1988; Brundrett 1991; Duponnois et al. 2001). Belowground diversity of AM fungi is an important determinant of plant diversity, ecosystem variability and productivity (Odum 1959; van der Heijden et al. 1998a; b). In this background, other studies have clearly demonstrated that the introduction of an exotic tree species could strongly alter the structure of AM fungus communities (Remigi et al. 2008) and reduce mycorrhizal soil infectivity (Kisa et al. 2007) as well as microbial soil functionalities (Kisa et al. 2007; Remigi et al. 2008). But it has also been shown that the negative effect of the exotic tree species was significantly lowered when it was inoculated with an efficient AM fungus (Kisa et al. 2007). The fungal inoculation tended to return the soil to its initial conditions with similar microbial functionalities and soil mycorrhizal potential (Kisa et al. 2007). However, contrasting results have been reported on the effects of exotic tree introduction on soil characteristics. In some cases, soil fertility and microbial functionalities have been enhanced under tree plantation (Duponnois et al. 2005), whereas in other ecological environments, opposite effects have been found (Remigi et al. 2008).

The aims of this study were to test in field conditions the impact of an Australian acacia species, *Acacia holosericea*, on soil nutrient content, microbial soil functionalities and mycorrhizal soil potential. Benefits expected from the AM inoculation on the host plant and soil (higher root growth, interactions between soil microbiota and extramatrical mycelium) were also evaluated. It has been previously

demonstrated that the extramatrical mycorrhizal mycelium influenced plant diversity, ecosystem stability and productivity (van der Heijden et al. 1998a; b). In order to assess the role of an extended soil mycorrhizal hyphal length compared to a high root system development, data resulting from the plantation of mycorrhized plants and prefertilized plants were compared. We hypothesized that in a highly degraded sahelian soil, exotic tree plantation will deplete microbial activities. We further hypothesized that controlled AM fungal inoculation of *A. holosericea* seedlings will counterbalance the effects of the exotic tree species introduction and that the AM effects will be highly linked with an improved mycorrhizal soil potential and more particularly by a well developed extramatrical mycelium.

Materials and methods

Plant and fungal inoculum

Seeds of *A. holosericea* ex G. Don, provenance Bel Air (Dakar, Senegal) were surface sterilized with concentrated 36 N sulfuric acid for 60 min. They were washed for 12 h in sterile distilled water and transferred aseptically to Petri dishes filled with 1% (w/v) agar per water medium. The plates were incubated at 25°C in the dark for 1 week. The germinating seeds were used when rootlets were 1−2 cm long.

The AM fungus *Glomus intraradices* Schenk and Smith (DAOM 181602, Ottawa Agricultural Herbarium) was multiplied on millet (*Pennisetum typhoides* L.) for 12 weeks under greenhouse conditions on Terragreen™ substrate. Before inoculation of the *Acacia* seedlings, the millet plants were uprooted, gently washed and roots cut into 0.5-cm-long pieces bearing around 150 vesicles cm^{-1}. Nonmycorrhizal millet roots, prepared as above, were used for the control treatment without AM inoculation.

Acacia seedlings were grown in 1-l pots filled with an autoclaved sandy soil (120°C for 40 min) collected in an experimental station localized at Gampella (20 km from Ouagadougou, Burkina Faso; 1°21′W, 12°25′N), crushed and passed through a 2-mm sieve. Its physicochemical characteristics were as follows: pH (H_2O) 5.6, clay (%) 7.75, fine silt (%) 2.75, coarse silt (%) 17.1, fine sand (%) 42.6, coarse sand (%) 29.8, total carbon (%) 0.35, total nitrogen (%) 0.04, Olsen phosphorus 4.3 mg kg^{-1}, total phosphorus 96.8 mg kg^{-1}. Control (C), preplanting fertilizer application (PFA) treatments and AM inoculation treatments (GI) were carried out. For AM inoculation, a hole (1×5 cm) was made in the soil of each pot and filled with 1 g of fresh mycorrhizal millet roots. Treatments without fungus (control and PFA) received the same amount of nonmycorrhizal millet roots. The PFA was performed by adding 0.5 g Osmocote™ granulates into the soil of each pot (N/P/K, 11:8:17; Sanon et al. 2006). 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. They were arranged in a randomized complete block design with 40 replicates $treatment^{-1}$.

After 4 months of culture, ten plants were randomly chosen from each treatment. Height was measured, and shoot dry biomass was determined after drying at 65°C for 1 week. The root systems were gently washed, cleared and stained according to the method of Phillips and Hayman (1970). About 50 1-cm root pieces were observed per plant under a microscope (magnification, ×250). The extent of mycorrhizal colonization was expressed as [the number of mycorrhizal root pieces]/[total mycorrhiza number of observed root pieces]×100. Remaining roots were oven-dried (1 week at 65°C) and weighed.

Experimental design, tree growth measures, and soil sampling

The study site was located in Burkina Faso at Kamboinse (12°28′N–1°32′W; 12 km at the north of Ouagadougou) on a ferruginous soil (Zerbo et al. 1995). The climate is Sahelo-Sudanian, tropical dry with an average annual rainfall of 710 mm and a mean annual temperature of 28°C. Two seasons are distinguished: (i) a long dry season from November to April and (ii) a rainy season from May to October. The physicochemical characteristics of the soil were as follows: pH (H_2O) 5.9, clay (%) 8.75, fine silt (%) 4.75, coarse silt (%) 15.1, fine sand (%) 43.6, coarse sand (%) 27.8, total carbon (%) 2.04, total nitrogen (%) 0.03, Olsen phosphorus 3.85 mg kg^{-1}, total phosphorus 95.6 mg kg^{-1}.

The experiment was arranged in a randomized block design with one factor and three replication blocks. The factor had three levels: uninoculated (control), inoculated with *G. intraradices* and PFA. An area of 900 m^2 was established in the Institut de l'Environnement et de Recherches Agricoles (INERA) experimental station of Kambouinse and cleaned from trees, shrubs and herbaceous species. *A. holosericea* seedlings were planted in individual holes at 3 m apart. There were at least 30 seedlings $treatment^{-1}$ and 30 seedlings per replication block (ten plants × three treatments in each block). After 4 years of plantation, soil cores (2 kg) were collected during the wet season at 1 m from the tree trunk and at 0- to 10-cm depth. In addition, six soil samples were taken from the surrounding grassland of the *A. holosericea* plantation. This area was mainly covered by herbaceous species such as *Pennisetum pedicellatum*, *Spermacoce radiata* and *Zornia glochidiata*. Soil samples were crushed and passed through a 2-mm sieve, the roots were collected and their dry

weights (1 week at 65°C) were measured. Soil samples were then kept at 4°C for further analysis. Then height of each tree was measured before clearing. Their diameter was measured at 30 cm over the ground. The leave and wood biomasses per tree were determined. Subsamples of leave biomass were collected from each tree. For P, they were ashed (500°C), digested in 2 ml HCl 6 N and 10 ml HNO_3–N and analyzed by colorimetry (John 1970). For N (Kjeldhal) determination, they were digested in 15 ml H_2SO_4 36 N containing 50 gl^{-1} salicylic acid.

Soil analyses

All soil samples were characterized by measuring total C, total N and soluble P (Olsen et al. 1954) in the LAboratoire des Moyens Analytiques (LAMA), ISO 9001–2000, Dakar, US Imago (Unité de Service Instrumentations, Moyens Analytiques, Observatoires en Geophysique et Océanographie), IRD, www.lama.ird.sn.

Measurement of microbial functional diversity

The functional diversity of soil microbial communities was assessed by measuring the patterns of in situ catabolic potential (ISCP) of microbial communities (Degens and Harris 1997). This physiological approach is based on the measurement of short-term respiration responses of soils amended with a range of simple organic compounds (Degens and Harris 1997; Degens et al. 2001). Each of the 31 substrates suspended in 2-ml sterile distilled water was added to 1 g of equivalent dry soil in 10-ml bottles (West and Sparling 1986). CO_2 production from basal respiratory activity in the soil samples was evaluated by adding 2 ml sterile distilled water to 1 g of equivalent dry soil. After the addition of the substrate solutions to the soil samples, the bottles were immediately sealed with a Vacutainer stopper and incubated at 28°C for 4 h in darkness. CO_2 fluxes from the soils were measured using an infrared gas analyzer (IRGA; Polytron IR CO_2, Dräger™) in combination with a thermal flow meter (Heinemeyer et al. 1989). Carbon dioxide measurements were subtracted from the CO_2 basal production and were expressed as μg $CO_2 g^{-1}$ soil h^{-1}. Among 31 substrates, there were eight amino-acids (L-serine, L-glutamic acid, L-phenylalanine, L-asparagine, L-lysine, L-cysteine, L-tyrosine, L-histidine); two amines (D-glucosamine, L-glutamine); two amides (*N*-methyl-D-glucosamine, L-succinamide); three carbohydrates (D-mannose, D-sucrose, D-glucose) and 16 carboxylic acids (α-ketobutyric acid, α-ketoglutaric acid, fumaric acid, oxalic acid, tartric acid, gluconic acid, ascorbic acid, malic acid, malonic acid, quinic acid, 3-OH-butyric acid, formic acid, gallic acid, succinic acid, uric acid, citric acid). The amines, amides and amino-acids were added at 10 mM, whereas the carbohydrates were added at 75 mM and the carboxylic acids at 100 mM (Degens and Vojvodic-Vukovic 1999). Catabolic evenness (a measure of relative variability in the catabolic functions) was determined using the Simpson–Yule index, $E=1/p_i^2$ with p_i = [respiration response to individual substrates]/[total respiration activity induced by all substrates for a soil treatment] (Magurran 1988). Microbial biomass C (MBC) was calculated with the substrate-induced respiration (SIR) method as described by Sparling (1995). Oven-dried weight of soil (1 g) was suspended in 2 ml of 75 mM glucose solution in 10 ml bottles, sealed with a Vacutainer stopper and incubated at 25°C for 4 h. After correction for CO_2 produced in bottles with only deionized water added, MBC was calculated as MBC (μg $C g^{-1}$ soil)=50.4×respiration rate (μl $CO_2 g^{-1}$ soil h^{-1}). The metabolic quotient (qCO_2) was calculated dividing the CO_2 basal respiration by the MBC content.

Total microbial activity in soil samples was measured using the fluorescein diacetate [3′, 6′-diacetylfluorescein (FDA)] hydrolysis assay (Schnürer and Rosswall 1982). FDA (Sigma-Aldrich Chimie, France) was dissolved in acetone and stored as a stock solution (5 mg ml^{-1}) at −20°C. Soil samples (1 g equivalent dry weight) were suspended in 200 μl FDA and 15 ml of sterile 60 mM sodium phosphate buffer, pH 7.6. The mixture was placed at 25°C for 1 h on a rotary shaker. Then, FDA hydrolysis reaction was stopped by adding 750 μl acetone. Soil suspensions were centrifuged (2,400×*g*, 10 min) and the supernatant was sampled, passed through a 45 μm filter. Then the absorbance readings were taken at 490 nm. Three replicates were prepared for each treatment and a fourth received 15 ml of buffer without substrate that served as a control used to correct for background. A standard fluorescein concentration curve, ranging from 0 to 0.5 mg l^{-1}, was prepared fresh using the stock solution of fluorescein diacetate in sodium phosphate buffer. The rate of fluorescein diacetate hydrolysis (μg of product corrected for background fluorescence per hour per gram of soil) was calculated to determine total microbial activity for each soil samples.

Dehydrogenase activity was measured following the method of Skujins (1976) modified by Garcia et al. (1997). Dehydrogenase activity was assessed in 1 g of soil at 60% of its field capacity, suspended in 0.2 ml of 0.4% INT (2-*p*-iodophenyl-3-*p*-nitrophenyl-5-phenyltetrazolium chloride) in distilled water for 20 h at 22°C in darkness. A mixture (10 ml) of 1:1.5 methanol was used to extract the formed iodo-nitrotetrazolium formazan (INTF) by shaking vigorously for 1 min and filtered through a Whatman No. 5 filter paper. INTF was measured spectrophotometrically at 490 nm.

Acid and alkaline phosphatase was measured using 1 g soil equivalent dry weight; 4 ml 0.1 M modified universal buffer

(pH 6.5 for acid phosphatase and pH 11.0 for alkaline phosphatase), and 1 ml 25 mM *p*-nitrophenyl phosphate (Tabatabai and Bremner 1969). The mixtures were incubated for 1 h at 37°C, and then the reaction was stopped by adding 4 ml 0.5 M NaOH and 1 ml $CaCl_2$. Three replicates were prepared for each soil samples and a fourth received 4 ml of buffer without substrate that served as a control used to correct for background. The absorbance was measured in the supernatant at 400 nm. Phosphate activities were expressed as μg *p*-nitrophenol released g^{-1} soil h^{-1}.

Assessment of the mycorrhizal soil infectivity

AM hyphal length was measured on membrane filters according to Jakobsen and Rosendahl (1990). Samples collected from each soil treatment (grassland, control, PFA and AM inoculation treatments) were pooled together. Then six dilutions were made of each soil sample by thoroughly mixing the original soil with the same soil but disinfected (120°C, 40 min) at the following percentages: 100%, 48%, 24%, 12%, 6% and 3% (v:v). There were ten replicates for each dilution. Seeds of *Sorghum vulgare* Pers. were surface sterilized with 10% sodium hypochlorite and washed with sterile distilled water (120°C, 20 min). Then they were pregerminated for 2 days in Petri dishes on humid filter paper. One germinated seed was then transplanted into each of 100-ml pots filled with 100 g of different soil dilution. The pots were placed in a glasshouse under natural light (daylight 12 h, mean temperature 30°C) and watered daily with deionized water. After 2 months of culture, seedlings were uprooted and their entire root systems were gently washed under tap water. The extent of AM colonization was on each plant as described above.

Statistical analyses

Data were treated with two-way analysis of variance (ANOVA). Means were compared using the Newman−Keul's test ($p<0.05$). The percentages of the mycorrhizal colonization were transformed by arcsin(sqrt) prior statistical analysis.

The patterns of ISCP of microbial communities from soil samples submitted to the four treatments (grassland, not inoculated, PFA, *G. intraradices* inoculation) were analyzed using the between-group analysis (BGA, Dolédec and Chessel 1989; Culhane et al. 2002). BGA is an ordination method considered as a robust alternative to the discriminant analysis (Huberty 1994). A permutation test (Monte-Carlo method) was used to check the statistical significance of the between-group differences. BGA computations were performed with the free ADE 4 software (Thioulouse and Dray 2007).

For the assessment of the mycorrhizal soil infectivity, the relationships between the extent of AM colonization and soil dilutions were fitted by covariance analysis models. Covariance analysis allowed comparing the slopes of the regression model for each treatment (grassland, uninoculated, PFA, *G. intraradices* inoculation). The *p*-values for model fits were calculated by ANOVA (Venables and Ripley 2002). Computations were performed with the R software (R Development Core Team 2010).

Results

Plant growth

After 4 months of culture under glasshouse conditions, AM inoculation significantly increased the growth of *A. holosericea* seedlings by factors of 1.51, 1.52 and 1.69 for height, shoot and root dry weight, respectively, compared with the control (Table 1).There were no significant differences between the PFA and *G. intraradices* treatments (Table 1). The extent of AM colonization was 24.9% for *G. intraradices*-inoculated seedlings, whereas no AM structures (vesicles, hyphae or arbuscules) were detected in the PFA and the control treatments (Table 1).

After 4 years of plantation, the growth of *A. holosericea* trees was significantly higher in the PFA and *G. intraradices* treatments than in the control (Table 2). No significant block effect was recorded. The stimulating effects of the fertilizer amendment and *G. intraradices* inoculation were found for all the measured parameters (height, diameter, leaf and wood biomass, leaf N and leaf P contents, root biomass; Table 2). No significant differences

Table 1 Growth response of *Acacia holosericea* seedlings and AM colonization in soils inoculated with *Glomus intraradices* or fertilized after 4 months' culture in a disinfected soil

Treatments	Height (cm)	Shoot biomass (mg dry weight)	Root biomass (mg dry weight)	AM colonization (%)
Control	21.6 (1.3)[a] a[b]	856 (25.6) a	321 (12.6) a	0
Preplanting fertilizer application	34.8 (2.3) b	1356 (42.6) b	552.3 (21.8) b	0
G. intraradices	32.6 (1.9) b	1298 (39.5) b	543.2 (19.8) b	24.9 (4.2)

[a] Standard error of the mean

[b] Data in the same column followed by the same letter are not significantly different according to the Newman–Keul's multiple range test ($p<0.05$)

Table 2 Growth response, AM colonization and leaf mineral content of *Acacia holosericea* trees after 4 years of plantation in the field

	Treatments		
	Control	Fertilizer application	*G. intraradices* inoculation
Height (m)	3.51 (0.28)[a] a[b]	4.62 (0.08) b	4.43 (0.20) b
Diameter (cm)	5.67 (0.82) a	8.77 (0.72) b	8.23 (0.49) b
Leaf biomass (kg dry weight)	1.71 (0.37) a	3.83 (0.95) b	3.44 (0.43) b
Wood biomass (kg dry weight)	7.20 (1.89) a	20.71 (3.87) b	17.73 (2.84) b
Total biomass (kg dry weight)	8.91 (2.25) a	28.54 (4.70) b	21.17 (3.25) b
Leaf N content (g $tree^{-1}$)	3.50 (0.77) a	7.5 (1.75) b	6.61 (0.82) b
Leaf P content (g $tree^{-1}$)	0.11 (0.024) a	0.36 (0.055) b	0.26 (0.032) b
Root biomass (g kg^{-1} of soil)	0.15 (0.03) a	1.8 (0.08) b	1.7 (0.07) b
AM colonization (%)	25.8 (2.6) a	21.6 (1.9) a	45.3 (2.9) b

[a] Standard error of the mean

[b] Data in the same column followed by the same letter are not significantly different according to the Newman–Keul's multiple range test ($p<0.05$)

were found between the PFA and *G. intraradices* treatments (Table 2). The AM colonization of *A. holosericea* trees inoculated with *G. intraradices* was significantly higher than those measured in the other treatments (Table 2).

Chemical and microbial functionalities of soils

The nitrogen and carbon contents of soils collected under the not inoculated *A. holosericea* trees was significantly lower than those measured in the other treatments (Table 3). Soil soluble P content was significantly higher in the *G. intraradices* inoculated *A. holosericea* trees (Table 3). The soil from the *G. intraradices* inoculation treatment had a higher pH than those measured in the other soil treatments (Table 3). Soil microbial biomasses and MBC/ Total organic carbon (TOC) ratios ranged among the treatments as follows: grassland > not inoculated and prefertilized trees > *G. intraradices*-inoculated trees (Table 3). The specific respiration rate of the soil microbial biomass (qCO_2) was significantly higher in the soil collected under *G. intraradices*-inoculated trees (Table 3). The hyphal network was more important in the soil samples collected from grassland and under inoculated *A. holosericea* trees than from the other treatments.

The soil catabolic evenness was significantly higher inside the *A. holosericea* plantation than in the grassland (Table 4). The catabolic diversity was significantly higher under *G. intraradices*-inoculated trees than under not inoculated trees (Table 4). The highest average respiration (SIRs) to amides and carbohydrates were recorded with the soils collected from the grassland and the lowest with soils from not inoculated tree treatment and *G. intraradices*-inoculated treatment for carbohydrates (Table 4). The highest SIR responses with carboxylic acid and amino-acids were recorded with the grassland soil followed by the AM-inoculated soil for the carboxylic acids and the prefertilized *A. holosericea* tree soil for the amino-acids (Table 4).

The permutation test of BGA on ISCP data table showed that microbial functionalities were very different according to the soil treatment ($p<0.001$). The soil samples collected inside the *A. holosericea* plantation and outside (grassland)

Table 3 Microbial biomass and chemical characteristics of the soils sampled inside the *Acacia holosericea* plantation (uninoculated plots, *Glomus intraradices*-inoculated plots and preplanting fertilizer application plots) and outside the *A. holosericea* plantation (Grassland)

	Treatments			
	Grassland	Control	Fertilizer application	*G. intraradices* inoculation
Total nitrogen (%)	0.058 (0.006)[a] b[b]	0.041 (0.002) a	0.051 (0.002) b	0.050 (0.002) b
Total carbon (%)	0.676 (0.064) b	0.577 (0.015) a	0.682 (0.037) b	0.669 (0.034) b
Soluble phosphorus (mg kg^{-1})	6.9 (1.4) a	8.4 (1.0) a	6.8 (0.6) a	17.4 (1.0) b
pH (H_20)	5.30 a	5.37 a	5.59 a	5.77 b
Microbial biomass (μg C g^{-1} soil)	378.0 (4.6) c	190.9 (27.5) b	240.5 (18.2) b	108.8 (15.1) a
Hyphal length (m g^{-1} soil)	1.3 (0.5) a	1.9 (0.3) a	2.1 (0.6) a	3.9 (0.4) b
qCO_2 (μg C-CO_2 g^{-1} MBC h^{-1})	0.10 (0.031) a	0.17 (0.014) a	0.13 (0.023) a	0.33 (0.023) b
MBC:TOC (%)	5.59 (0.07) c	3.31 (0.48) b	3.53 (0.27) b	1.63 (0.23) a

MBC Microbial biomass carbon, *TOC* total organic carbon

[a] Standard error of the mean

[b] Data in the same line followed by the same letter are not significantly different according to the Newman–Keuls test ($p<0.05$)

Table 4 Catabolic evenness and average SIR responses (μg CO_2 g^{-1} soil h^{-1}) with each substrate group (carboxylic acids, amino-acids, amides and carbohydrates) of the soils collected inside the *Acacia holosericea* plantation (uninoculated plots, *Glomus intraradices*-inoculated plots and preplanting fertilizer application plots) and outside the *A. holosericea* plantation (Grassland)

	Treatments			
	Grassland	Control	Fertilizer application	*G. intraradices* inoculation
Catabolic evenness	17.9 (0.37)[a] a[b]	20.4 (1.02) b	22.7 (0.45) bc	22.9 (0.19) c
Carboxylic acids	827.2 (4.02) c	188.5 (5.26) a	200.8 (7.22) a	228.9 (4.81) b
Amino-acids	166.3 (9.83) c	132.5 (1.25) a	150.9 (1.56) bc	142.2 (4.09) ab
Amines	100.0 (17.4) a	136.7 (16.4) a	127.5 (11.3) a	131.3 (10.1) a
Amides	197.5 (5.95) c	98.3 (14.53) a	167.5 (7.5) b	165.0 (3.53) b
Carbohydrates	145.1 (6.16) c	83.3 (6.67) a	115.8 (2.09) b	68.3 (9.18) a

[a] Standard error of the mean

[b] Data in the same line followed by the same letter are not significantly different according to the Newman–Keul's test ($p<0.05$)

were very well separated on the BGA first axis (Fig. 1). The substrates preferentially used in soils sampled under *A. holosericea* trees were uric acid, OH-butyric acid, glutamine and cystein (Fig. 1). In contrast, the substrates preferentially used in samples collected from the grassland were citric acid, ascorbic acid and oxalic acid (Fig. 1). On the BGA second axis, the four treatments were clearly distinguished and the substrates preferentially catabolized were OH-butyric acid for the soils sampled under not inoculated trees, sucrose, glucose, tartric acid, glutamic acid and fumaric acid for the soil sampled under *G. intraradices*-inoculated trees, serine and phenylalanine for the soil collected under prefertilized trees whereas most of the carboxylic acids were used in soils from the grassland (Fig. 1).

The FDA hydrolysis and alkaline phosphatase were significantly higher in the grassland soil compared with the soils collected under not inoculated *A. holosericea* trees (Fig. 2). In contrast, these enzymatic activities were not significantly different between the soils collected from the grassland and those under *G. intraradices*-inoculated trees (Fig. 2). The dehydrogenase activity was significantly lower in the soils collected inside the *A. holosericea* plantation for all the treatments than those from the surrounding grassland area (Fig. 2). The acid phosphatase activity in the soil under prefertilized *A. holosericea* trees was significantly higher than those recorded in the grassland and in the not inoculated tree soils. No significant differences were detected between acid phosphatase activities in the soils from prefertilized *A. holosericea* trees and fungal inoculated *A. holosericea* trees (Fig. 2).

The regression model between the extent of AM colonization and soil dilutions for the four different treatments showed that the treatment and the percentage of soil dilution had very strong effects ($p<0.0001$). The highest mycorrhizal potential was recorded in soil collected under *G. intraradices*-inoculated trees followed by those measured in the other soil tree treatments whereas the lowest was found in the grassland (Fig. 3). There were significant negative correlations between the mycorrhizal soil infectivity and the mean catabolic responses with carbohydrates, amino acids, carboxylic acids, the soil microbial biomass and the MBC:TOC ratio whereas positive correlations were recorded with the extend of extramatrical mycelium (hyphal length), the catabolic evenness, and the specific respiration rate of the soil microbial biomass (qCO_2; Table 5).

Discussion

The main results of this study show that (i) the introduction of the exotic fast growing tree, *A. holosericea*, without any treatments (AM inoculation or prefertilizer application), significantly modifies soil microbial functionalities and soil nutrient contents, (ii) AM inoculation with *G. intraradices* significantly improves *A. holosericea* growth after 4 years of plantation and enhances microbial and chemical soil characteristics, and (iii) these changes were significantly linked to a higher mycorrhizal soil infectivity and more particularly to the extend of extramatrical mycelium.

Impact of not treated *A. holosericea* trees on soil biological and chemical characteristics

Compared to the grassland, the introduction of not inoculated *A. holosericea* trees had significantly depleted soil nutrient contents (N and C) as well as some soil microbial functionalities (total microbial activity, alkaline phosphate activity, dehydrogenase activity, microbial biomass, etc.). These results are in accordance with previous studies where it has been reported that reforestation with exotic trees such as eucalypts significantly decreased soil C and N contents (Bargali et al. 1993; Sicardi et al. 2004) that further declined with plantation age (Bargali et al. 1993). Microbial biomass,

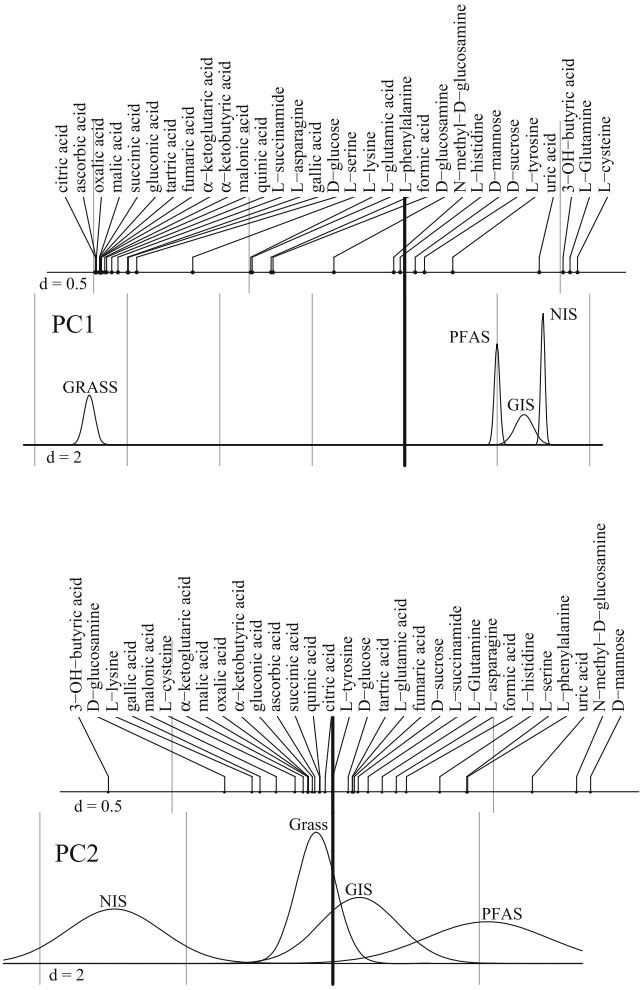

Fig. 1 Graphical display (biplot) of the first two BGA axes (PC1 and PC2) showing the relationships between SIRs and soil treatments. The *upper* part of each figure shows the scores of the 31 substrates on the first and second BGA axes. The four Gauss curves in the *lower* part of the figures represent the mean and the variance of the scores of the soil samples on the first and second BGA axes. Grass, grassland soil; NIS, soil of plantation with uninoculated *Acacia holosericea* trees; GIS, soil of plantation with *Glomus intraradices*-inoculated trees; PFAS, soil of plantation with prefertilized *A. holosericea* trees. Substrates placed in the same direction as a Gauss curve tend to be used more in the corresponding soil samples

specific respiration rate of the soil microbial biomass as well as some soil microbial enzymatic activities were greater under grassland than under uninoculated *A. holosericea* trees (total microbial activity, alkaline phosphate activity, dehydrogenase activity). This greater microbial activity under grassland could be due to a higher rhizosphere activity of the grass root systems than in *A. holosericea* adult trees. Since soil dehydrogenase, FDA hydrolysis, and alkaline phosphatase activities are directly involved in the transformation of soil organic matter, uninoculated *A. holosericea* trees have affected these processes leading to a depletion of C and N contents. However, it is also well known that litter accumulation under uninoculated *A. holosericea* trees could reduce soil microbial biomass (Wardle 2002). Previous studies have shown that genetic composition and microbial functionalities are different under forest and pasture (Bardgett and McAlister 1999; Stevenson et al. 2004). The chemical characteristics of soil organic matter that is different with plant genera could explain such changes. Litter quality from forest to grassland differs markedly from a woody and lignin substrate (high C/N ratio) to a more cellulosic substrate (low C/N ratio; Stevenson et al. 2004). Uninoculated *A. holosericea* trees have also depleted the relative SIR responses to carbohydrates, amino-acids, amides and carboxylic acids. Stevenson et al. (2004) compared the catabolic respiration responses of microbial communities from pastures and forest soils, and their results are in accordance with those of the present study for the SIR responses measured with amino acids and carbohydrates (higher levels in the grassland), but are opposed to the SIR responses with carboxylic acids (lower level in the not inoculated *A. holosericea* plantation). Low molecular weight organic acids play key roles in many soil processes such as nutrient uptake, soil structural improvement, metal decontamination, etc. (Jones et al. 2003). Root exudation and lysis provide most organic acids in soil (Ryan et al. 2001). For plant nutrition, organic acids have been hypothesized to be involved in the mobilization and solubilization of poorly soluble nutrients such as phosphorus (Marschner 1995; Micales 1997; Ma and Miyasaka 1998). Soil solutions from permanent pasture and forest soils have usually higher concentrations of di-, tri-carboxylic acids as compared to cultivated soil, whereas contents of monocarboxylic acids are not dependent from the vegetation type. In the present study, root density was higher than that recorded under uninoculated *A. holosericea* trees (data not shown) that suggested the presence of higher amounts of carboxylic acids in soils. Since uptake by soil microorganisms is considered as one of the primary mechanisms by which organic acids are removed from the soil solution (Lundström et al. 1995), it could explain the higher SIR response with carboxylic acids recorded in the grassland.

Soil chemical and biological changes resulting from AM inoculation

The AM fungal species *G. intraradices* was already found in the soil of the Kambouinse experimental station (Duponnois, R., personal communication); all the fungal inoculation effects recorded from the present study did not result from the introduction of a new AM fungal species. Inoculation with *G. intraradices* was highly beneficial to the growth of *A. holosericea* in the disinfected sandy soil during the nursery plantation and this plant growth promoting effect was retained during 4 years after outplanting in field conditions. This fungal effect on the tree growth was comparable to that recorded with the prefertil-

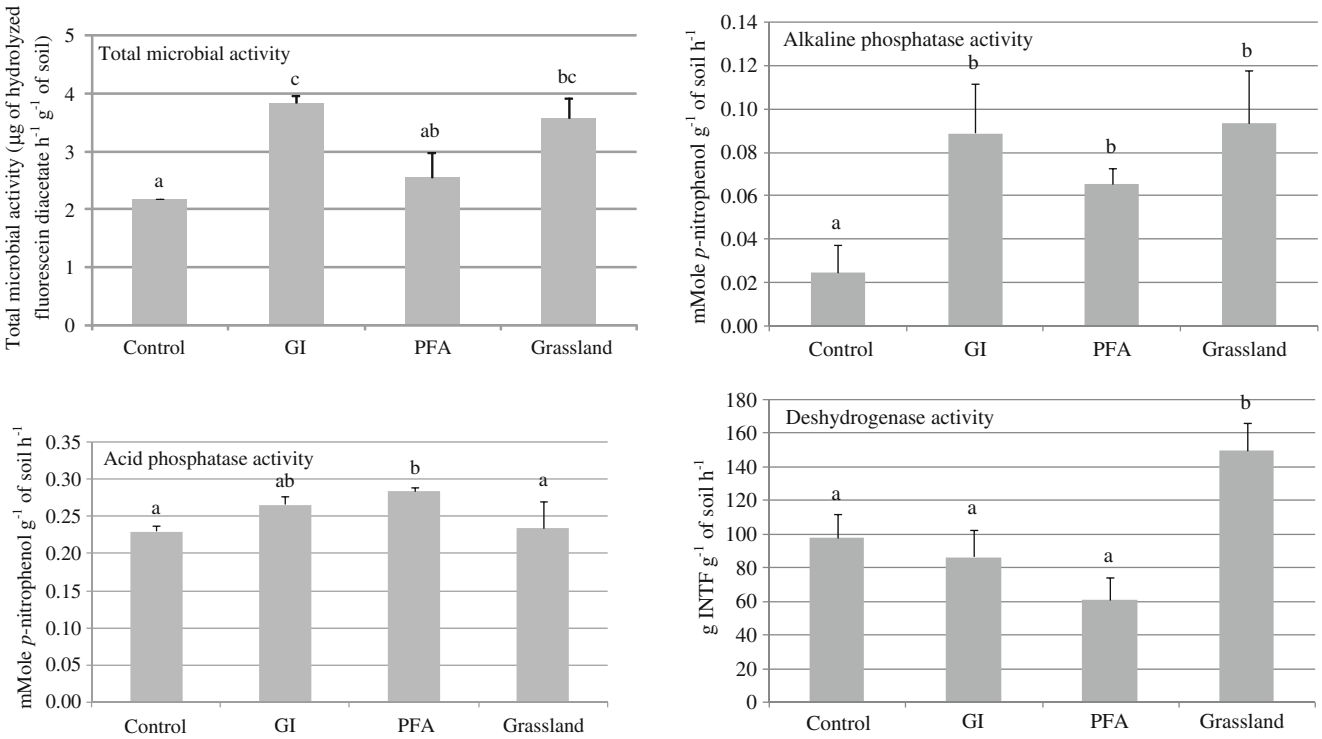

Fig. 2 Total microbial, acid phosphatase, alkaline phosphatase and dehydrogenase activities in soils under grassland, uninoculated *Acacia holosericea* trees, *Glomus intraradices*-inoculated *A. holosericea* trees and prefertilized *A. holosericea* trees. For each enzymatic activity, *bars with different letters* represent significant difference according to the Newman Keul's multiple range test ($p<0.05$). *Error bars* represent standard deviation

ized trees. These results are in accordance with other studies where it has been shown that this fungal isolate was very efficient on the growth of other plant species in controlled conditions (Duponnois and Plenchette 2003; Dabire et al. 2007; Kisa et al. 2007) and after outplanting (Duponnois et al. 2005). In addition, the fungal inoculation tends to limit the negative effects of the *A. holosericea* plantation on soil microbial functionalities, more particularly for the total microbial activity and alkaline phosphatase activity. Numerous studies have shown that AM symbiosis enhances root exudation (Grayston et al. 1996), alters carbohydrate metabolism of the host plant (Shachar-Hill et al. 1995), modifies microbial community equilibrium in the rhizosphere (Johansson et al. 2004) that leads to a microbial compartment commonly named "mycorrhizosphere" (Linderman 1988). AM inoculation has also induced a higher multiplication of AM fungal propagules reflected by a higher mycorrhizal soil potential. From the present study, it is clearly demonstrated that AM fungal inoculation influenced microbial functionalities compared to the results recorded from the prefertilizer application treatment (i.e., total microbial activity, average SIR response with carboxylic acids, etc.). It also suggests that AM fungal inoculation effect

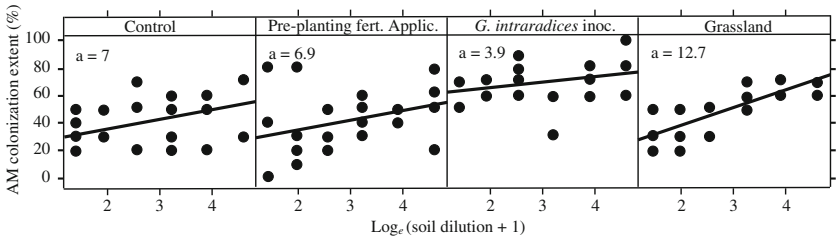

Fig. 3 Regression model between the extent of AM colonization and soil dilutions in each soil treatment. Control: uninoculated *Acacia holosericea* trees; Preplanting fert. applic.: prefertilized *A. holosericea* trees; *Glomus intraradices* inoc.: *G. intraradices*-inoculated *A. holosericea* trees; Grassland: soil sampled outside the *A. holosericea* plantation. The slope of the regression line (*a*) is given in each graphic. Log_e (soil dilution+1): Natural logarithm of the dilutions nondisinfected soil by the same soil but disinfected expressed in %. AM colonization extent (%): extent of mycorrhizal colonization expressed as [the number of mycorrhizal root pieces]/[total mycorrhiza number of observed root pieces]×100

Table 5 Correlation analysis between the mycorrhizal soil infectivity (expressed by the slope of the regression model for each treatment; grassland, uninoculated, preplanting fertilizer application, *G. intraradices* inoculation) and the catabolic evenness (Simpson–Yule index), mean catabolic responses with each category of organic substrates (carbohydrates, amides, amines, amino acids, organic acids), soil microbial biomass, hyphal length, Microbial Biomass C (MBC)/Total organic carbon (TOC) ratio and the specific respiration rate of the soil microbial biomass (qCO_2)

Parameters	Equation	r^2	p
Catabolic evenness	$y = 25.53 - 0.59x$	0.74	<0.0001
Carbohydrates	$y = 39.6 + 8.46x$	0.75	<0.0001
Amino acids	$y = 126.4 + 2.95x$	0.39	0.013
Amines	$y = 1252.8 - 3.89$	0.22	0.077
Amides	$y = 124.1 + 4.82x$	0.19	0.10
Organic acids	$y = -205.9 + 75.5x$	0.82	<0.0001
Soil microbial biomass	$y = 2.2 + 30x$	0.89	<0.0001
Hyphal length	$y = 14.1 - 2.8x$	0.74	<0.0001
qCO_2	$y = 0.353 - 0.022x$	0.55	0.0015
MBC/TOC	$y = 0.179 + 0.437x$	0.89	<0.0001

on the functions of soil microbial communities was not root growth-dependent but resulted from the presence of the AM fungus and more particularly from the extraradical mycelium that is thought to be the main source of AM inoculums in arid and semi-arid ecosystems (Sylvia and Jarstfer 1992). AM inoculation has increased soil soluble P content and soil N content as well as P and N leaf contents. AM fungi are known to solubilize mineral phosphates and to improve phosphorus nutrition (Caravaca et al. 2004). The presence and effects of phosphatases of AM extraradical hyphae have been previously reported (Joner et al. 1995; Joner and Johansen 2000), and it has been clearly demonstrated that AM hyphae mainly contributed to phosphatase activity in the root-free soil by direct exudation of phosphatases into the soil (Joner and Johansen 2000). Since AM inoculation has improved P uptake, a higher amount of organic P could be mineralized under *G. intraradices*-inoculated trees. More recently, it has been demonstrated that P solubilizing ability of AM fungi could result from a multitrophic microbial association including hyphosphere and mycorrhizosphere communities which were selected by AM fungi and potentially beneficial to the plant growth and the fungal symbiosis (Ouahmane et al. 2007). This multitrophic microbial association could be also involved in the process of mineralization of P from organic material. In the literature, there is no evidence of organic breakdown by AM fungi to take up N from soil and transport it to the host plant (Frey and Schüepp 1993). It is usually admitted that organic N has to be mineralized first by other microorganisms before it becomes available to extraradical hyphae of AM fungi. It confirms that mycorrhizal symbiosis takes place in the microbial complex functioning where AM symbiosis has a direct effect on the plant growth and also an indirect effect though its selective pressure on soil microbial functionalities.

The lowest MBC to TOC ratio was found for the AM inoculation treatment. The C_{mic}-to-C_{org} is considered as a good index of the changes in soil organic matter (Insam and Domsch 1988). According to Anderson and Domsch (1989), it suggests a lower C organic matter accumulation in the soil under AM-inoculated trees. Diallo et al. (2006) have demonstrated that amendment with naturally senesced leaves of *A. holosericea* decreased soil microbial biomass, and the rate of its decomposition was very low due to its chemical composition. In addition, since AM inoculation decreased the C_{mic}-to-C_{org} ratio, it indicates that mycorrhizal treatment did not favor soil organic matter dynamics. On the other hand, the specific respiration rate of soil microbial biomass (qCO_2) under AM-inoculated trees was significantly higher than those recorded in the other soil treatments. The values of qCO2 were higher than those found by Insam (1990) and Garcia et al. (2005). This could be due to the arid conditions encountered in the experimental area since the metabolic quotient values are influenced by climate and increase with temperature (Insam 1990). This index has been previously used to evaluate the status of soil microbial communities in reclamation studies (Insam and Merschak 1997). It has been found that this index increased when a semiarid soil was subjected to stress (Garcia and Hernandez 1996). Hence and according to our data, the introduction of the exotic tree species previously mycorrhized, has implied a stress for the soil. This result is corroborated with the highest catabolic evenness recorded in the *G. intraradices* treatment. It has been previously reported that stress and disturbance caused much greater changes in soils with low catabolic evenness than in soils with high catabolic evenness (Degens et al. 2001). Microbial catabolic diversity generally followed the classical "humpback" responses of diversity in response to increasing stress and disturbance (Degens et al. 2001; Remigi et al. 2008). In the present study, the increase of catabolic evenness in the stressed soil (*G. intraradices–A. holosericea* treatment) may be attributed to this humpback pattern previously reported in plant communities (Austin 1987). This theory predicts that evenness would increase with stress as a result of smaller population and reduced competition (Drobner et al. 1998). This type of soil response can be adapted to stress induced by the exotic plant introduction, as microbial biomass has been significantly reduced and as it has been demonstrated that AM or ectomycorrhizal inoculation associated with an exotic tree species significantly reduced the soil microbial diversity (Kisa et al. 2007; Remigi et al. 2008) and consequently reduced the competition between soil microbial components.

Conclusion

The results from the present study clearly showed that exotic plant species may be directly responsible for important changes in soil microbiota with great disturbances in the functions of microbial communities. In addition, the present study reports some significant effects of fertilizer amendments on soil microbial functions that need further researches to determine their potential impacts on sustainable soil biofunctioning. Data from the present study highlight the importance of AM symbiosis and more particularly the mycorrhizal soil potential in the functioning of soils and its relevance in sustainable agriculture. Since it has been clearly demonstrated that this forestry practice induced significant stresses to the soil, further researches have to be undertaken to determine the potential effects of these exotic tree species on soil functioning at a larger temporal and geographical scale and to determine the real role of AM symbiosis in soil biofunctioning since it remains contradictory results regarding the influence of AMF communities on plant cover development (productivity, stability, composition, etc.). In addition, further researches should be focused on the selection of the most appropriate native AM symbionts (e.g., multipartners inoculum) to maximize their mitigation effects.

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