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Management of the mycorrhizal and rhizobial associations to mitigate the negative effects of Grevillea banksii on the development of *Dalbergia trichocarpa* an endemic tree species

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ABSTRACT. This study aims to improve the development of Dalbergia trichocarpa, a Malagasy native tree species, on a soil invaded by Grevillea banksii, an invasive plant species in eastern part of Madagascar, by inoculating seedlings with mycorrhizal fungal, Rhizophagus irregularis and AMFn strains or rhizobial STM609 and Rn strains, or a mixed rhizobial-mycorrhizal strains. After five months of growth, the results showed that single or dual inoculation boosted significantly the development of D. trichocarpa, compared to control treatments and all parameters measured were markedly different between the time periods of plant invasions. Indeed, the dry mass of aerial biomass was significantly higher in inoculated seedlings than in control seedlings. It was also observed that the number of nodules and the arbuscular mycorrhizal colonization rates of D. trichocarpa increased significantly with inoculated plantlets. However, soil inoculated with the rhizobial strain STM609 alone showed a significantly high global soil microbial activity and the dual inoculation has promoted the soil acid phosphatase activity. These results suggest that dual inoculation with rhizobial and arbuscular mycorrhizal strains was significantly beneficial to the growth, nodulation and mycorrhizal colonization rates of D. trichocarpa in the soil overgrown by G. banksii, an invasive exotic plant species. Thus, this biotechnology can be used for restoration of degraded ecosystems in Madagascar with native tree species.

Keywords : *Inoculation; Invasive plant; Mycorrhizae; Rhizobia; Soil microbes*

INTRODUCTION

The expansion of invasive plants species is threatening biodiversity, productivity, and ecosystem health throughout the world (Pejchar et al. 2009; Moles et al. 2012). *G. banksii*, an example of invasive plant species in the eastern part of Madagascar has disrupted dramatically the regeneration of native plants species (Andrianandrasana et al. 2014). For that reason, the dynamic of soil biota especially the associated microsymbionts (mycorrhizal fungi and phosphate solubilizing bacteria) with native plant species is greatly affected by these invasive plant species (Andrianandrasana 2015). This is one of the strategies of invasive plant species to spread rapidly in the invaded area (Kourtev et al. 2002, 2003; Li et al. 2006).

However, the artificial supply of effective microbial symbionts strains is an attractive alternative for reconstructing the vegetation in disturbed areas and facilitates the regeneration of native tree species. Some authors have already shown that the ability of a plant species to tolerate biotic and/or abiotic stress depends on the establishment and function of plant symbiont relationships (Odum 1959; Barea et al. 1997). Thus, the establishment of symbiotic structures promotes the release of root exudates that stimulate the development and activity of soil microorganisms (Altomare et al. 1999; Singh & Kapoor, 1999), especially the

mycorrhizal fungi and certain bacterial groups involved in the major biogeochemical cycles (N, P and C) (Frey-Klett et al. 2005; Smith & Read 1997). These effects affect both nutrients acquisition and improvement of nodulation, mycorrhizal colonization rates and development of the host plant (Della Cruz et al. 1988; Manjunath et al. 1984; Marques et al. 1997; Herrera et al. 1993). In addition, some authors have shown that the interaction between these two types of symbiosis association plays important roles in maintaining ecosystem functions (Duponnois et al. 2001a; Founoune et al. 2002; André et al. 2003). Ndoye et al. (2015) suggested that the success of dual inoculation with rhizobial and mycorrhizal strains to enhance the plant growth and soil bio-functioning depend on a careful selection of effective combinations of microsymbionts.

The main objective of this study was to improve the development of *D. trichocarpa*, a native tree species of Madagascar, in soil invaded by exotic species *G. banksii* in eastern part of the Island. We hypothesized that using native rhizobial and mycorrhizal fungal strains would improve the development of *D. trichocarpa* in soil invaded by *G. banksii*. We assessed the effects of single and dual inoculations with rhizobial and mycorrhizal strains or control in (i) the development of plantlets of *D. trichocarpa*, (ii) the microbial activities of soil culture, and (iii) the nodulation and mycorrhization colonization rates in roots system of *D. trichocarpa*.

MATERIALS AND METHODS

Soil culture. Two soil types were used in this experiment: (i) soil collected in the homogeneous stand of an invasive species *G. banksii* located in the eastern part of Madagascar in Vatomandry District (19° 10' 18.40"S 48°54' 37.50"E, 52m) where *G. banksii* was established for about five years according to the survey conducted among local populations. This soil was coded ***SI5*** (Soil Invaded during 5 years). This soil was constituted by composite sample collected in five replicates of soil from the Vatomandry district area; (ii) The second type of soil was collected under grassland or pseudo-steppe (19°10'10.58"S 48°54'48.91"E, 59m) located in the same district. However, this second type of soil was pre-colonized by *G. banksii* during 1 year on the greenhouse condition and this soil was coded ***SI1*** (Soil invaded for 1 year).

Experimental design. A split-plot design was set up with the SI1 and SI5 in main plots and the inoculation treatments in subplots (Steel et al. 1997). Two references strains STM609 (*Bradyrhizobium* spp from the Laboratoire des Symbioses Tropicales et Méditerranéennes) and the commercial strain of arbuscular mycorrhizal fungus *Rhizophagus irregularis* DAOM197198 (RI) (formerly named *Glomus irregulare*) and two native strains of the study site: Rhizobia native (Rn, isolated in this study and characterized in Institute for Integrative and Systems Biology laboratory- Canada) and native Arbuscular Mycorrhizal Fungi (AMFn, isolated on this study, was constituted by one spore mycorrhizal type), were used in this experiment, this two strains were selectionned with their capacity to increased *D. trichocarpa* development in the clean soil. The production of RI and AMFn was carried out in greenhouse condition with highly mycotrophic plant species (*Sorghum* spp.). The inoculum was prepared by cutting the roots of *Sorghum* into small fragments of about 1cm and mixed with rhizospheric soil. Five grams of this mixture was necessary for each strain and per seedling for inoculation. For the rhizobial inoculum, STM 609 and Rn were prepared from a pure colony of these bacteria using Yeast Extract Mannitol Agar culture medium (Vincent 1970). One milliliter of the inoculum (10^8cfu**.**ml^{-1}) was necessary for each strain and per seedling.

D. trichocarpa seeds were germinated and seedlings were transplanted individually in aseptic plastic bags (18 cm x 12 cm) containing about 800g of soil (SI1 and SI5). For each soil, nine treatments with 25 replicates were prepared with simple or dual inoculation using AM fungi and Rhizobia inoculum such as RI, STM609, Rn and AMFn were the simple inoculation treatments and STM609+RI, AMFn+Rn, STM609+AMFn and AMFn+Rn were the dual inoculation treatments. An uninoculated treatment was used as a control. The pots were arranged in a randomised complete block design.

Assessment of different treatment inoculation on the development of *D. trichocarpa*

Simple or dual inoculation effects were evaluated after 5 months of *D. trichocarpa* plastic bag culture. So, five plantlets per treatment were chosen randomly and removed from the plastic bags. The roots were washed carefully and the soil samples recovered. Root nodules per plant were counted and the dry weights of shoots and roots were determined after drying at 100°C for 24 h.

Five another plantlets were chosen and harvested. For each plant, roots were collected and gently washed. Roots were then cleared in KOH (10%) and stained with 0.05% Trypan blue following the method described by Phillips and Hayman (1970). Fine roots were then cut into 1 cm pieces and placed on slides for microscopic observation at 40X magnification. The intensity of mycorrhization (corresponding to the proportion of cortex colonized by the AMF) was assessed on about 50 roots pieces as described by Trouvelot et al. (1986).

Total microbial activity of each soil sample was measured by its ability to hydrolyze fluorescein diacetate (FDA) by their enzymes using the method described by Schnürer & Rosswall (1982) and Alef in 1998. This enzymatic conversion released a final product that can be determined colorimetrically at 490nm, after 1h of soil incubation. Total microbial activity was expressed as µg of hydrolysis product corrected for background fluorescence per hour and per gram of soil. Acid phosphatase activity of soil microorganisms was measured by their ability to hydrolyze a substrate p-Nitrophenol Phosphate (pNPP) and has a product p-Nitrophenol (p-NP) after enzymatic reaction measured by absorbance readings at 400nm according to the method described by Kuperman and Carreiro in 1979.

Data analysis All statistical analyses were done using XLSTAT 2008 software. Differences among the treatment means were assessed according to ANOVA test. Significant differences among the means were found through Newman Keuls significant difference test at $P < 0.05$. A principal component analysis (PCA) was carried out to assess correlation between inoculation treatments and measured parameters involved on the development of *D. trichocarpa* using the same software. The parameters with the treatments were projected on the first two axes of the factorial plane in order to group the treatments with their similar characters.

Results and Discussion

Results

Impacts of mycorrhizal and rhizobial inoculations on the growth of *D. trichocarpa* on invaded soil by *G. banksii*

After 5 months of culture, all treatment inoculation increased the total biomass dry weight of *D. trichocarpa* on soil SI1 and on soil SI5. The ANOVA analysis showed a clear significant difference between treatment inoculations on each soil type. For instance, plant

growth was dramatically influenced by the *R. irregularis* alone or associated with STM609 inoculation treatment (Fig.1A). Thus, RI and RI + STM609 inoculation enhanced respectively the total biomass dry weight of *D. trichocarpa* by 62.50% and 56.25%. In ***SI5*** soil type, simple inoculation of RI and dual inoculation of native strain Rn + MVAn had higher dry biomass weights of *D. trichocarpa* seedling than the other treatments (Fig.1B) and enhanced respectively the total dry weight of plant by 110% and 120%. Generally, *R. irregularis* strain treatment presented significantly height total biomass dry weight of *D. trichocarpa* in soil invaded during one or five years by *G. banksii*.

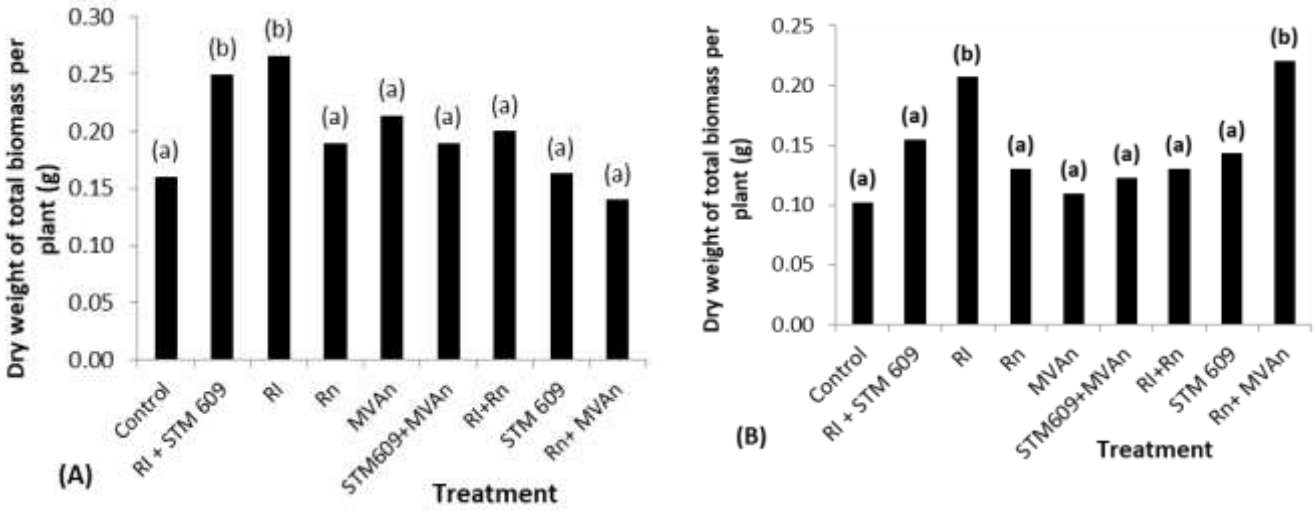

Figure 1. Impacts of mycorrhizal and rhizobial inoculation on the development of *D. trichocarpa* in soil invaded by *G. banksii* SI1 (A) and SI5 (B)

Means followed by the same letter are not significantly different according to the Newman-Keuls test ($p < 0.05$).
Control: No inoculation, **RI**: *Rhizophagus irregularis* strain, **STM 609**: rhizobial strain of LSTM Laboratory (Montpellier-France) collection, **Rn**: Rhizobia native strain, **AMFn**: native Arbuscular Mycorrhizal Fungi strain.

Impacts of mycorrhizal and rhizobial inoculation on nodulation and intensity of mycorrhization of *D. trichocarpa* in soil invaded by *G. banksii*

Nodule number per plant and intensity of mycorrhization of *D. trichocarpa* after inoculation with different treatment on two type soils invaded by *G. banksii* are presented in table 1. In SI5 soil type, the percentages of root colonization by arbuscular mycorrhizal fungi per seedling of *D. trichocarpa* for all inoculation treatments, except STM609, increased significantly compared to control plants. AMFn treatment showed the highest mycorrhizal colonization rate (98.17%) followed by RI combined with Rn treatment (89.67%). However, in SI1 soil type, RI alone and dual inoculation of native strain Rn + AMFn showed a high intensity of mycorrhization of 68.52% and 70%, respectively (Table 1).

For the number of nodules, a significant difference was noted in *D. trichocarpa* seedlings inoculated treatment compared a control plants for both soil type. The highest nodule numbers per plant were recorded in STM609 treatment followed by RI + Rn treatment. Between the two soils types, nodulation rate was more stimulated on SI1 soil type than SI5 (Table 1).

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Table 1. Impacts of mycorrhizal and rhizobia inoculation on nodulation and intensity of mycorrhization of *D. trichocarpa* in SI1 and SI5

Treatment	Nodule number per plant		Intensity of mycorrhizal (%)	
	SI1	SI5	SI1	SI5
Control	0.00[a]*	0.00[a]*	29.16[a]	25.05[a]
RI + STM 609	7.33[ab]	3.34[a]	59.59[a]	62.45[bc]
RI	7.33[ab]	3.00[a]	68.52[b]	64.11[bc]
Rn	4.66[ab]	1.34[a]	50.83[a]	67.24[bc]
AMFn	3.33[ab]	0.67[a]	38.33[a]	98.17[c]
STM609+AMFn	8.66[b]	3.00[a]	33.28[a]	84.85[bc]
RI + Rn	10.33[b]	3.67[a]	46.66[a]	89.67[bc]
STM 609	11.00[b]	3.67[a]	58.51[a]	13.30[a]
Rn+ AMFn	4.66[ab]	1.57[a]	70.00[b]	54.29[b]

* Means in the same column followed by the same letter are not significantly different according to the Newman–Keuls test ($p < 0.05$). **Control:** No inoculation, **RI**: *R. irregularis* strain, **STM 609**: rhizobial strain of LSTM Laboratory (Montpellier-France) collection, **Rn**: Rhizobia native strain, **AMFn**: native Arbuscular Mycorrhizal Fungi strain.

Impacts of mycorrhizal and rhizobial inoculations on microbes soil enzyme activities

The measurement of soil enzymatic activities would be crucial for a better understanding of the inoculation impact with any microorganism on soil. Our result indicates that the amount of p-Nitrophenol (hydrolysis result of pNPP by soil microorganisms) was significantly higher in RI+ STM609 treatment (31.90 µg $pN.h^{-1}.g^{-1}$soil) compared to the other treatments in SI5 soil type. However, RI and Rn+ RI treatments were very interesting in SI1 soil type, producing 154.36 and 121.66 µg $pN.h^{-1}.g^{-1}$soil, respectively. No significant difference was registered between the other treatments and the control (Table 2).

Microbial global soil activity, measured by fluorescein quantities per gram of soil, was dramatically increased with STM609 alone or combined with AMFn treatment (1069.28 and 970.15 $\mu g.h^{-1}.g^{-1}$soil in SI5 soil type, respectively). STM609 and GI+Rn treatments yielded 622.09 $\mu g.h^{-1}.g^{-1}$soil and 419.43$\mu g.h^{-1}.g^{-1}$soil in SI1 soil type, respectively (Table 2).

Table 2 Impacts of mycorrhizal and rhizobia inoculation on microbial enzymatic activities in soil invaded by *G. banksii*

	Acid phosphatase activity (µg p-Nitrophenol.h^{-1}.g^{-1}soil)		**Microbial global soil activity (µg fluorescein h^{-1}.g^{-1}soil)**	
	SI1	**SI5**	**SI1**	**SI5**
Control	44.44[a]*	163.09[a]*	70.93[a]	472.30[a]
RI + STM 609	50.31[a]	231.90[b]	84.59[a]	211.25[a]
RI	121.66[a]	171.11[a]	225.57[a]	173.80[a]
Rn	85.16[a]	160.08[a]	136.76[a]	156.18[a]
AMFn	44.12[a]	118.41[a]	98.91[a]	547.20[a]
STM609+AMFn	89.76[a]	152.54[a]	207.95[a]	1069.28[b]
RI+Rn	154.36[a]	143.73[a]	419.43[b]	231.08[a]
STM 609	97.46[a]	148.89[a]	622.09[b]	970.15[b]
Rn+ AMFn	52.14[a]	164.36[a]	69.17[a]	267.43[a]

*Means in the same column followed by the same letter are not significantly different according to the Newman–Keuls test ($p < 0.05$). **Control:** No inoculation, **RI**: *R. irregularis* strain, **STM 609**: rhizobial strain of LSTM Laboratory (Montpellier-France) collection, **Rn**: Rhizobia native strain, **AMFn**: native Arbuscular Mycorrhizal Fungi strain.

Correlation between inoculation treatments, plant growth and soils microbial properties

The Principal Component Analysis was performed on the correlation matrix of all data studied and treatments (Fig. 2). Results showed that the first two axes of PCA plane (fig. 2A:SI1) explained about 70.50% of the variability. Plant growth parameters (shoot and root weight), root mycorrhizal colonisation and rhizobia rate were positively correlated with simple inoculation by *G. intraradices*, STM609 and with co-inoculation by *G. intraradices* + rhizobia native, STM609 + MVA native, and linked to the first axis which explained 44.26% of the variability. However, acid phosphatase activity and global microbial activity of the soil were negatively influenced by the treatment above-mentioned. All parameters measured such as plant growth, root mycorrhizal colonisation, rhizobia rate, acid phosphatase activity and global microbial activity were positively correlated with simples inoculations by *G. intraradices*, rhizobia native, MVA native and by co-inoculation *G. intraradices*+STM609, and linked to the second axis which explained 26.24% of the variability.

On figure SI5, the first two axes of PCA explained about 61.91% of variability. Root biomasse, root mycorrhizal and acid phosphatase activity were positively correlated with simple inoculation by MVA native, rhizobia native, *G. intraradices* and with co-inoculation by *G. intraradices*+STM609, *G. intraradices* + rhizobia native, MVA native + rhizobia native and linked to the first axis which explained 39.13% of the variability. However, shoot biomass, microbial activity and rhizobia nodulation rate were positively correlated with the treatment STM 609, control and STM609+ MVA native wich explained 22.78% of the variability.

Generally, over the control treatment, all treatment inoculation increased *D. trichocarpa* plant's growth and microbial activities in soil invaded by invasive plant *G. banksii* during one or five years. Or, over the inoculation treatment, inocultion with GI alone or combined with STM609 were particularly improved microbial soil activity and plant growth.

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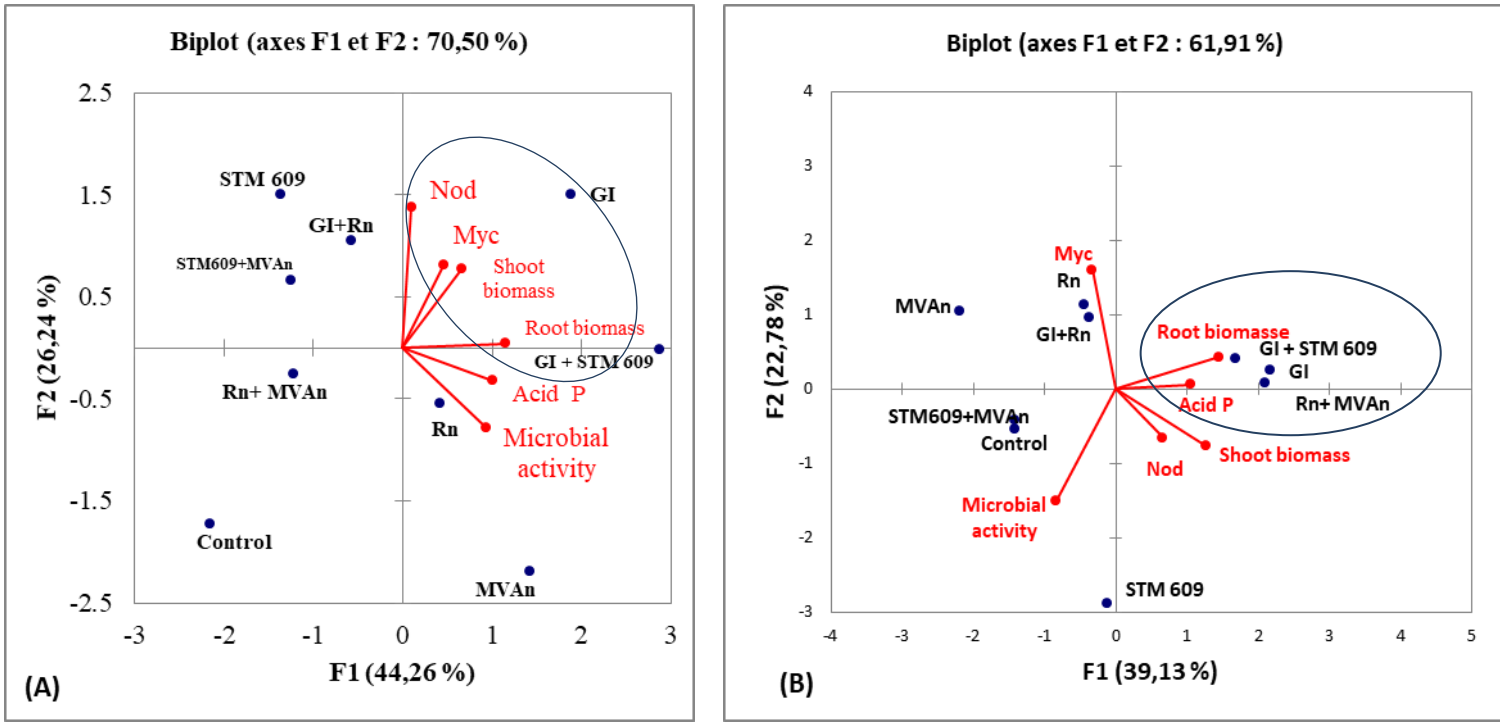

Figure 2. Correlation between inoculation treatments, plant growth and soils microbial properties cultivated on soil invaded by *G. banksii* during (A) one year and (B) 5 years. Myc: mycorrhizal colonisation rate, Nod: rhizobia nodulation rate, Acid P: acid phosphatase, Rn: Rhizobia native, MVAn: MVA native, GI: *Glomus irregular*,

Discussion

The interaction between host plants and their microsymbionts is important to re-establishing native plant communities in degraded landscapes (Smith *et al.* 1998; Requena *et al.* 2001; Caravaca 2003). Our results on invaded soil by *G. banksii* showed that certain treatments especially with simple inoculation of RI and dual inoculation of two native strains (AMFn and Rn) increased plant growth compared to the control treatment. It showed the importance of mycorrhizal and/or nitrogen-fixing symbiosis on the establishment and development of host plants in disturbed areas that some authors have already mentioned (Estaún *et al.* 1997; Duponnois *et al.* 2001b, 2005).

However, it was previously reported that the success of such a mechanism depends on several factors related to either soil (Slankis 1974) or symbiotic couples (Azcon *et al.* 1991). Indeed, our results showed that the effect of the inoculation on the development of *D. trichocarpa* and colonization of roots by microbial symbionts on the soil invaded by *G. banksii* varies greatly according to the duration of invasion by this exotic plant species. In this situation, the results of this study showed that native symbiotic strains of the study area have been particularly effective. For that reason, native rhizobium strain (Rn) alone or combined with native arbuscular mycorrhizal fungi of site (AMFn) improved both the development of *D. trichocarpa*, nodulation and mycorrhizal colonization rates of plants particularly in soil invaded more than five years. These results corroborate those of other studies in which native AMF or rhizobial strains contribute to the improvement of the development of native plants in disturbed areas (Caravaca *et al.* 2003; Tchabi *et al.* 2010; Ceccon *et al.* 2012). These

observations were also reported by Caravaca *et al*. (2003) with a native shrub *Rhamnus lycioides* and *Ceccon et al*. (2012) with *Acacia farnesiana* inoculated with *Sinorhizobium americanum*.

In certain soil types, the introduction of exotic AMF strain has altered the structure of the resident microbial communities and even disrupted the symbiotic association (Callaway & Walker 1997). However, in this study, a perfect synergy between the reference strain (RI) and native rhizobium (Rn) strain was observed. These results are congruent with those reported by other authors working on microbial strains from different origin (Azcon *et al.* 1991; Lal & Khanna 1993; Marques *et al.* 2001).

Conclusion

Our results show the positive effects of the inoculation technology using native microbial strains on stimulating the growth of a native plant species *D. trichocarpa* in invaded soil by *G. banksii*. The performance of microbial symbionts depends on the time period of establishment of invasive species, *G. banksii*. Indeed (i) on the soil invaded during one year, the two references strains *R. irregularis* and STM609 improve the development, nodulation and arbuscular mycorrhizal colonization of *D. trichocarpa*. These two strains have also increased the microbial global and acid phosphatase soil activities. But, (ii) on the soil invaded more than 5 years, development, nodulation and arbuscular mycorrhizal colonization rates of *D. trichocarpa* were especially improved by native strains (Rn and AMFn).

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