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Ectomycorrhization of six *Acacia auriculiformis* provenances from Australia, Papua New Guinea and Senegal in glasshouse conditions: effect on the plant growth and on the multiplication of plant parasitic nematodes

R. Duponnois[A], *H. Founoune*[A], *D. Lesueur*[B], *J. Thioulouse*[C] *and M. Neyra*[D]

[A]IRD, Laboratoire de Biopédologie, BP 1386, Dakar, Sénégal.
[B]CIRAD, Programme Arbres et Plantation du CIRAD - Forêt, Laboratoire de Microbiologie, IRD, BP 1386, Dakar, Sénégal.
[C]CNRS, Laboratoire de Biométrie et Biologie Evolutive, Université Lyon 1, 69622 Villeurbanne Cedex, France.
[D]IRD, Laboratoire de Microbiologie, BP 1386, Dakar, Sénégal.

Abstract. Six provenances of *Acacia auriculformis* have been tested for their ectomycorrhizal dependency with 2 indigenous strains of *Pisolithus* sp. Moreover, the endomycorrhizal and rhizobial symbiosis, the multiplication of plant parasitic nematodes have been quantified. The results showed significant variations in plant development between provenances. Both the compatibility with and dependency on the ectomycorrhizal strains were different among the provenances. Three main genera of nematodes have been identified, in particular *S. cavenessi*, which is one of the most pathogenic nematodes of soudano-sahelian crops. Endomycorrhizal structures were sometimes detected on the root systems. These results suggest that provenances of *A. auriculiformis* that are well adapted to the indigenous environmental conditions (pedoclimatic, soil borne pathogens) must be selected for their mycorrhizal dependency and for their resistance to plant parasitic nematodes. Moreover, the ectomycorrhizal symbiosis has to be considered as an important component of the cultural system.

Additional keywords: provenance variation, reforestation, plant parasitic nematodes, mycorrhizae, Sénégal.

Introduction

Although trees are essential for protection of the environment and for the local economy, a dramatic deforestation has occurred in dry tropical Africa following an over-exploitation of the natural resources. Among the most useful plants of the soudano sahelian areas, indigenous leguminous trees, in particular *Acacia* species, are well adapted to these poor climatic and soil conditions. Their positive impacts on the soil, erosion and local economies are well documented (Michon 1968; Giffard 1975; Cossalter 1986). These indigenous *Acacia* species are represented by about 30 species (Cossalter 1986), which form a small part of the *Acacia* genus including nearly 1200 species (Pedley 1986). Other species originating from tropical Australia, north-east Brazil, Indian and Pakistani deserts also have the genetic material for their introduction in dry tropical Africa. The performances of these exotic acacias have usually been evaluated by the plant growth in field trials (Cossalter 1986; Khasa *et al.* 1995) but the interactions between these tree species and the indigenous microflora and mesofauna have often been neglected. More recently, it has been shown that controlled rhizobial symbiosis could enhance the development of Australian acacias such as *A. mangium* (Galiana *et al.* 1994). This symbiosis is of great interest in agroforestry systems since the continuous replacement of leaves and roots ensures transfer of nitrogen (N) to the soil (Zakra 1994). As both ecto and endomycorrhizas have been reported on *Acacia* species, these symbiotic fungi have been used in controlled mycorrhization experiments under field conditions (Cornet *et al.* 1982) and acacias have greatly responded to endomycorrhizal inoculations (Cornet *et al.* 1982). All this research has focussed on promoting

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Table 1. Geographical origins of the *Acacia auriculiformis* provenances

Provenance	Seedlot	Region	Seed collection site	Altitude (m)
P 1	95/10265N	Australia	12°47'S, 142°49'E	100
P 2	95/10266N	Australia	15°59'S, 145°3'E	200
P 3	95/10262N	Australia	15°52'S, 144°53'E	240
P 4	95/10263N	Australia	12°34'S, 143°10'E	20
P 5	89/08718N	Papua New Guinea	8°52'S, 142°2'E	10
P 6	n.d.	Sénégal	14°36'N, 17°1'W	5

n.d., not determined.

microorganisms but the influence of exotic acacias on the development of pathogenic microorganisms such as plant parasitic nematodes is largely unknown excepted for the root-knot nematodes (Duponnois *et al.* 1997*a*, 1997*b*).

The purposes of this study were therefore (i) to measure the early growth of 6 provenances of *A. auriculiformis* in a natural Senegalese soil, (ii) to evaluate the impact of the ectomycorrhizal symbiosis on plant development using 2 isolates of *Pisolithus* sp. and (iii) determinate the interactions between plant-parasitic nematodes, *A. auriculiformis* provenances and fungal isolates.

Materials and methods

Plant

The provenances of *A. auriculiformis* are indicated in Table 1. The seeds were surface sterilised with concentrated sulfuric acid for 60 min. The acid solution was then decanted off and the seeds rinsed and imbibed for 12 h in 4 changes of sterile distilled water. Seeds were then transferred aseptically in Petri dishes filled with 1% (w:v) water agar medium. These plates were incubated for 4 days at 25°C. The germinating seeds were used when rootlets were 1–2 cm long.

Fungus

The ectomycorrhizal fungus *Pisolithus* sp., isolates COI 007 and COI 024, was maintained on MNM agar medium (Marx 1969). The solid inoculum was prepared in 1.6-L glass jars containing 1.3 L vermiculite:peat mixture (4:1, v:v) moistened with liquid MNM medium. This substrate was inoculated with fungal plugs taken from the margin of the fungal colonies and incubated for 6 weeks at 28°C in the dark.

Glasshouse experiment

Seedlings of *A. auriculiformis* provenances were grown in 1 dm^3 pots filled with autoclaved soil (140°C, 40 min). This soil has been sampled from a 17-year-old plantation of *A. holosericea* at Sangalkam (50 km from Dakar), was hightly infected with rhizobia but without ectomycorrhizal fungi (Duponnois unpublished data). Its physicochemical characteristics were as follows: pH H_2O 6.5; fine silt 7.4%; coarse silt 25.4%; fine sand 36.6%; coarse sand 21.5%; total carbon 0.54%, total nitrogen 0.06% and Olsen phosphorus 8.8 mg/kg . This soil was mixed with 10% (v:v) fungal inoculum or 10% vermiculite–peat mixture (4:1, v:v) for the treatments without fungus. The seedlings were placed in a glasshouse (32°C day, 28°C night, 12-h photoperiod) and watered twice weekly without fertiliser addition. After 3 months' culture, the plants were transferred into 10-L pots filled with the same soil but non autoclaved and put outside the glasshouse. The experimental design was a complete 2-way factorial with 6 *A. auriculiformis* provenances and 3 fungal treatments (control without fungal inoculation, COI 007 and COI 024). Treatments were replicated 10 times.

After 6 months' culture, the height and the root collar diameter of the plants were measured. Then they were uprooted and the root systems gently washed. The soil from each pot was mixed, a 250-g subsample was taken and the nematodes were extracted using Seinhorst's (1962) elutriation technique. The leaves and the stems of each plant were separated and their oven-dried weights (2 weeks at 65°C) were measured.

Root nodules induced by indigenous rhizobia were searched and counted. Subsamples of root systems (about 2 g fresh weight) were collected to assess the intensity of mycorrhizal symbiosis and kept in alcohol (70% v/v). The root samples were observed under a stereomicroscope (magnification: x120) to determine the ectomycorrhizal rates (number of ectomycorrhizal short roots/total number of short roots) from at least 100 short roots. Then the same samples were used to quantify the internal colonisation of arbuscular mycorrhizal fungi in the roots. The roots were clarified and stained according to the method of Phillips and Hayman (1970). The extent of colonisation was estimated in terms of percentage of mycorrhizal root pieces. The roots were segmented into about 1-cm pieces which were placed on a slide for microscopic observation (Brundrett *et al.* 1985). About 100, 1-cm root pieces were observed per plant. Then the entire root systems were washed, cut into short pieces and placed in a mist chamber for 2 weeks to recover nematodes (Seinhorst 1950). The nematodes were counted and identified under a stereomicroscope (magnification: x120). The root systems were oven dried (1 week, 60°C) and weighed. Mycorrhizal dependency (MD) was calculated according to Plenchette *et al.* (1983).

Statistical analyses

Data were subjected to a 2-way analysis of variance using the Super ANOVA Computer program and means were compared with the Newman–Keuls multiple range test ($P = 0.05$). For the mycorrhizal rate, the data were transformed by arcsine ($\sqrt{x}$) before statistical analysis while for nematode populations data were transformed by $\log_{10}(x+1)$ before analysis.

Table 2. Growth of *Acacia auriculiformis* provenances in a non-disinfected soil after 6 months in culture
Values in each column followed by the same letter are not significantly different at $P = 0.05$ (1-way ANOVA)

Provenance	Height (cm)	Root collar diam. (mm)	Leaf biomass (g)	Stem biomass (g)	Total shoot biomass (g)	Root biomass (g)
P1	46.8abc	7.7ab	5.4b	3.7ab	9.1a	5.7ab
P2	57.6bc	8.7b	2.9a	6.8b	9.7a	7.0b
P3	61.1c	8.5b	2.8a	5.3ab	8.1a	5.6ab
P4	41.1ab	8.6b	3.5ab	3.5ab	6.7a	4.2ab
P5	31.2a	6.7ab	2.4a	3.4ab	5.8a	2.7a
P6	34.9a	5.7a	3.3ab	2.3a	5.6a	2.2a

Results

Growth and susceptibility to plant parasitic nematodes of A. auriculiformis *provenances*

The 6 provenances tested showed significant differences in growth at 6 months. One provenance, P3, showed superior height compared to P4, P5 and P6 but was not significant compared to P1 and P2 (Table 2). The root collar diameter was higher for P2, P3 and P4 provenances than for P6. For this parameter, no significant differences were observed between these provenances and P1 and P5 (Table 2). The shoot biomass was not significantly different among the provenances (Table 2). However, P1 showed the highest leaf biomass and P2 the highest stem biomass. The root biomass was significantly more important for P2 than for the P5 and P6 provenances. No significant differences were calculated between P2, P5, P6 and P1, P3 and P4 (Table 2).

Three genera of plant parasitic nematodes have been identified in the cultured soil: *Scutellonema cavenessi*, *Tylenchorynchus germanii* and *Hoplolaimus pararobustus* (Table 3). The number of *S. cavenessi* was significantly higher for P1 than for the other provenances. For *T. germanii*, the larger population was recorded for P3, significantly different from P4 and P6 but not from P1, P2 and P5 (Table 3). The population of *H. pararobustus* was significantly larger for P1 than for P4 and P6 (Table 3). For this nematode genus, no significant differences were recorded between the 3 provenances P1, P4, P6 and P2, P3, P5. The total number of plant parasitic nematodes was significantly higher for P3 compared to P4 and P6 (Table 3). However, the data recorded for this provenance (P3) was not significantly different from P1, P2 and P5 (Table 3).

Influence of the fungal strain and A. auriculiformis *provenance factors on fungal and rhizobial symbiosis*

No nodules were detected along the root systems among all the seedlings of all provenances (Table 4). The uninoculated controls (all provenances combined) showed a low level of contamination from *Pisolithus* ectomycorrhizae. The ectomycorrhizal symbiosis was well established and the ectomycorrhizal rates were significantly higher for COI 007 than for COI 024 (Table 4). The fungal strain factor had no significant effect on the endomycorrhizal rates (Table 4). There was also no

Table 3. Plant parasitic nematode communities on *Acacia auriculiformis* provenances in a non-disinfected soil after 6 months in culture
Values in each column followed by the same letter are not significantly different at $P = 0.05$ (1-way ANOVA)

Provenance	Number of plant parasitic nematodes (no. per pot)			
	S. cavenessi	*T. germanii*	*H. pararobustus*	Total
P1	22981b	34808ab	1249b	59039bc
P2	12619a	28275ab	840ab	41734abc
P3	8641a	54794b	521ab	64033c
P4	6018a	16019a	280a	22548ab
P5	8710a	29609ab	500ab	38889abc
P6	4567a	10322a	400a	15370a

Table 4. Effects of fungal strain and *Acacia auriculiformis* provenance on fungal establishment (percentage ectomycorrhizal and endomycorrhizal short roots) and on rhizobial symbiosis after 6 months in culture

Values followed by the same letter are not significantly different at $P = 0.05$ (Newman–Keuls test)

Factor[A]	Number of nodules per plant	Ectomycorrhizal roots (%)	Endomycorrhizal roots (%)
Fungal strain			
Uninoculated[B]	0	6.8a	1.4a
COI 007	0	73.1c	2.1a
COI 024	0	65.5b	0.6a
Provenance			
P1	0	55.5a	0.0a
P2	0	47.1a	5.4b
P3	0	44.4a	0.6a
P4	0	49.0a	0.0a
P5	0	49.7a	0.0a
P6	0	41.7a	1.9a

[A]Fungal strain factor is for all provenances combined; the provenance factor is for all fungal strains combined. Values are means of 60 replicates for fungal strain effect and 30 replicates for provenance effect.
[B]Uninoculated control plants were initially grown in disinfected soil.

significant effect of the provenance factor on the ectomycorrhizal rates (Table 4). On the contrary, a significant positive influence of P2 on the endomycorrhizal rate was recorded. No endomycorrhizal structures were associated with P1, P4 and P5 (Table 4).

Influence of the fungal strain and A. auriculiformis *provenance factors on plant growth*

For all provenances combined, both fungal strains significantly increased the root collar diameter, stem biomass and total shoot biomass (Table 5). Only

Table 5. Effects of fungal strain and *Acacia auriculiformis* provenance on plant growth in a non-disinfected soil after 6 months in culture

Values in each column followed by the same letter are not significantly different at $P = 0.05$ (Newman–Keuls test)

Factor[A]	Height (cm)	Root collar diameter (cm)	Leaves biomass (g)	Stem biomass (g)	Total shoot biomass (g)	Root biomass (g)
Fungal strain						
Uninoculated[B]	45.9a	0.76a	3.4a	4.2a	7.6a	4.7a
COI 007	54.9a	1.02b	4.0a	7.5b	11.5b	7.4b
COI 024	65.4b	1.05b	4.3a	9.6b	13.9b	9.8c
Provenance						
P1	69.9c	1.04b	4.3a	10.5b	14.8b	10.7c
P2	58.1abc	0.95ab	3.1a	7.3ab	10.4a	7.4b
P3	59.3bc	0.92ab	3.2a	5.9a	9.1a	6.6ab
P4	47.8ab	1.00b	4.9a	6.9ab	11.8ab	7.8bc
P5	52.1ab	0.95ab	4.4a	7.1ab	11.5ab	7.1ab
P6	44.9a	0.80a	3.5a	4.8a	8.3a	3.9a

[A]Values are means of 60 replicates for fungal strain effect and 30 replicates for provenance effect. Fungal strain factor is for all provenances combined; the provenance factor is for all fungal strains combined.
[B]Uninoculated control plants were initially grown in disinfected soil.

Table 6. Effects of fungal strain and *Acacia auriculiformis* provenance on ectomycorrhizal dependency of plants after 6 months in culture

Values followed by the same letter are not significantly different at $P = 0.05$ (Newman–Keuls test)

Factor[A]	Mycorrhizal dependency (%)
Fungal strain	
COI 007	41.1a
COI 024	58.1b
Provenance	
P1	60.7c
P2	28.0a
P3	33.4ab
P4	56.0c
P5	71.5c
P6	54.9bc

[A]Values are means of 60 replicates for fungal strain effect and 30 replicates for provenance effect. Fungal strain factor is for all provenances combined; the provenance factor is for all fungal strains combined.

COI 024 increased the plant height. For the root biomass, the positive effect of COI 024 was significantly higher than that for COI 007 (Table 5). No significant differences were recorded for the leaf biomass (Table 5).

Table 5 shows that the provenance factor had no significant effect on height growth. For the other parameters, P1 showed a greater height (significantly different from P4, P5 and P6), root collar diameter (significantly different from P6), stem biomass (significantly different from P3 and P6), total shoot biomass and root biomass (significantly different from P2, P3, P6 and P2, P3, P5, P6, respectively) (Table 5). The lowest values were recorded for P6.

The ectomycorrhizal dependency (MD) was significantly higher for COI 024 than for COI 007 when all provenances were combined (Table 6). Significant differences also occurred among the provenances. P1 and P5 showed the highest mycorrhizal dependencies which were significantly different from P2 and P3. The lowest dependency was measured for P2.

Influence of fungal strain and A. auriculiformis *provenance factors on nematode populations*

The fungal inoculation had a significant effect on the population of *H. pararobustus* and on the total number of nematodes (Table 7). The numbers of nematodes (*H. pararobustus* and the total populations) were significantly greater than in the not inoculated treatments. In the same way the provenance factor involved some significant differences (Table 7). The numbers of *S. cavenessi* and *T. germanii* were significantly greater with P1 than for the other provenances (Table 7). For *H. pararobustus*, the greater population was associated with P5. The total number of nematodes was significantly higher with P5 than for P1, P2, P3 and P6 (Table 7).

Table 7. Effects of fungal strain and *Acacia auriculiformis* provenance on structure of the nematode community in a non-disinfected soil after 6 months in culture

Values in each column followed by the same letter are not significantly different at $P = 0.05$ (Newman–Keuls test)

Factor[A]	Number of plant parasitic nematodes (no. per pot)			
	S. cavenessi	*T. germanii*	*H. pararobustus*	Total
Fungal strain				
Uninoculated[B]	4589a	12669a	23152a	40410a
COI 007	4099a	24787a	37800ab	66687ab
COI 024	3505a	23876a	56779b	84161b
Provenance				
P1	16909b	68219b	1053a	86182cd
P2	1477a	12865a	26027ab	40369ab
P3	1329a	9134a	51314bc	61777bc
P4	1561a	12139a	60133c	73833bcd
P5	1429a	12202a	97327d	111000d
P6	792a	4576a	16093a	21462a

[A]Values are means of 60 replicates for fungal strains effect and 30 replicates for provenance effect. Fungal strain factor is for all provenances combined; the provenance factor is for all fungal strains combined.
[B]Uninoculated control plants were initially grown in disinfected soil.

Discussion

The results showed distinct variation in the growth, the mycorrhizal dependency and the nematode populations between provenances. It has been shown already that provenances of *A. auriculiformis* exhibited a high level of variability in growth and morphological characteristics (Boland *et al.* 1990; Pinyopusarerk *et al.* 1991). In field conditions, the tree development could be influenced by the environment. Genotype x environment (G x E) interaction usually exists resulting from changes in performance genotype. It is necessary to identify the origins of G x E interactions before making decisions about plantation programs (Kremer 1986). These environmental conditions could inhibit the growth of woody legumes (pathogenic microorganisms such as plant parasitic nematodes) or, on the contrary, improve their development (bacterial or fungal symbionts).

Among these pathogenic microorganisms, plant parasitic nematodes are a cosmopolitan and important problem affecting the production of subtropical and tropical crops (Johnson and Fassuliotis 1984). In this experiment, 3 main nematode genera parasitising *A. auriculiformis* provenances have been identified: *S. cavenessi*, *T. germanii* and *H. pararobustus*. The *Hoplolaimus* genus has been recorded in particular in sugarcane fields (Spaull and Cadet 1990). *S. cavenessi* is considered to be the most pathogenic species of the soudano-sahelian crops (Germani 1981). However, in our experiment, the susceptibility of *A. auriculiformis* provenances to *S. cavenessi* has not been assessed. Moreover, the multiplication rates of this nematode have not been calculated with each provenance. This information could be of great interest in order to predict the growth of these provenances in an infected soil by *S. cavenessi*.

Acacia species are widely planted in agroforestry systems. Their capacity to reduce inert gazeous N_2 to organic forms through rhizobial symbiosis allows woody legume development in poor soil, deprived of nitrogen. Moreover, much of the nitrogen fixed by rhizobia in the nodules of acacia roots is returned to the soil where the natural loss of leaves and the resulting humus improves the fertility of the soil and its physical properties. Our results show that no bacterial strains formed nodules along the root systems of all *A. auriculiformis* provenances. However, it is usually assumed that *A. auriculiformis* is a promiscuous host because of its ability to nodulate effectively with a wide range of *Bradyrhizobium* spp. strains (Galiana *et al.* 1990). These authors concluded that *A. auriculiformis* clearly belong to the first group of *Acacia* spp. according to the classification of Dreyfus and Dommergues (1981). This species can nodulate effectively with *Bradyrhizobium* spp. strains but their association with *Rhizobium* spp. was ineffective. These conclusions are supported by the fact that only *Bradyrhizobium* spp. strains were isolated in the field from this *Acacia* species. A lack of *Bradyrhizobium* spp. strains in this Senegalese soil could explain the absence of nodules along the root systems. These observations suggest that the introduction of *A. auriculiformis* to Senegal may require some microbiological studies in order to characterise the indigenous populations of *Rhizobium* spp. and *Bradyrhizobium* spp.

The endomycorrhizal symbiosis is also poorly established in the control treatments. It has been established that in P-deficient soils the formation of VA mycorrhizas is an important factor in the successfull establishment of *Acacia* spp. (Jasper *et al.* 1989). This symbiotic association enhances the growth and the mineral nutrition of the host plant (Guissou *et al.* 1998). However, after 6 months in culture, endomycorrhizal structures have not been recorded with 3 provenances (P1, P4 and P5). This loss in infectivity of the indigenous endomycorrhizal fungi suggests that the soil is deficient in infective fungal propagules. This conclusion is supported by the low numbers of endomycorrhizal spores extracted from this area (R. Duponnois unpublished data).

The importance of ectomycorrhizae for Australian *Acacia* growth has been neglected compared to the numerous reports of endomycorrhizal fungi stimulating the growth of tree species both in pot experiments (Cornet and Diem 1982; Jasper *et al.* 1987, 1988) and under field conditions (Cornet *et al.* 1982). Duponnois and Bâ (1999) showed that the ectomycorrhization of *A. mangium* with 1 strain of *Pisolithus* in several different Senegalese soils significantly improved plant growth under nursery conditions. More recently, it has been demonstrated that 1 strain of *Pisolithus* enhanced the growth of *A. holosericea* in glasshouse conditions (Duponnois *et al.* 2000). However, there was no information on the effect of the ectomycorrhizal symbiosis on *A. auriculiformis* development. The experiment shows that all the provenances can contract ectomycorrhizal symbiosis with the 2 strains of *Pisolithus*. However, the fungal effects are very different among the provenances which also influence fungal establishment. It has already been established that both host species and fungal genotype influence mycorrhizal

development and subsequent seedling growth (Malajczuk *et al.* 1990). It appears that both fungal strains can promote the growth of *A. auriculiformis* provenances but at various levels. These results confirm the large variation between *Pisolithus* isolates in their ability to promote the growth of the host plants such as *Eucalyptus grandis* (Burgess *et al.* 1994) or pine (Lamhamedi *et al.* 1990).

One of the objectives of this study was to evaluate the interactions between the plant parasitic nematodes and the ectomycorrhizal symbiosis. The endomycorrhizal symbiosis could act against nematodes such as root-knot nematodes (Duponnois and Cadet 1994). More recently, it has been shown that the ectomycorrhizal strain COI 007 can decrease the multiplication of a root knot nematode *Meloidogyne javanica* (Duponnois *et al.* 2000). In our experiment, the number of nematodes was not decreased by these fungi but, on the contrary, increased in some cases. It appears that these fungi do not have an inhibiting effect against these nematodes and, moreover, through their beneficial effect on root development, offer more feeding sites for these ectoparasitic nematodes.

This study has outlined the importance of the rhizospheric microorganisms (pathogenic or symbiotic) associated with several provenances of a woody legume species, *A. auriculiformis*. It is the first time that the effect of ectomycorrhizae during the early stages of plant growth has been measured in West Africa.

In conclusion, there is a need to select the most appropriate provenances of a woody legume species, well adapted to indigenous environmental conditions (pedoclimatic, soil borne pathogens). Moreover, the ectomycorrhizal fungi must be screened for their efficiency on the development of the host plant and considered as one component of the cultural system, together with tree genotypes, soil microbial populations and cultural techniques.

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