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Differences in nutrient availability and mycorrhizal infectivity in soils invaded by an exotic plant negatively influence the development of indigenous *Acacia* species

Arsene Sanon [a,b,c,*], Thierry Beguiristain [c], Aurélie Cébron [c], Jacques Berthelin [c], Samba N. Sylla [a,b], Robin Duponnois [a,d]

[a] *Laboratoire Commun de Microbiologie IRD/ISRA/UCAD, BP 1386, CP 18524 Dakar, Senegal*
[b] *Université Cheikh Anta Diop, Département de Biologie Végétale, BP 5005, Dakar, Senegal*
[c] *LIMOS, Nancy Université, CNRS, UMR 7137, BP 70239, 54506 Vandoeuvre-lès-Nancy Cedex, France*
[d] *IRD, UMR 113 CIRAD/INRA/IRD/SupAgro/UM2, LSTM TA10/J 34398 Montpellier Cedex 5, France*

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ABSTRACT

Plant species (exotic invasive *vs* native non-invasive) colonization pattern and the relation with the soil nutrient availability and AM fungi abundance, was investigated. Soil samples were collected from two sites: one invaded by the exotic plant, *Amaranthus viridis*, and one uninvaded site for chemical and AM propagules density analyses. Additionally, we grew five Sahelian *Acacia* species in soil from the two sites, sterilized or not, to test the involvement of soil biota in the invasion process. While nutrient availability was significantly higher in soil samples from the invaded sites, a drastic reduction in AM fungal community density, was observed. Moreover, *Acacia* seedlings' growth was severely reduced in soils invaded by *Amaranthus* and this effect was similar to that of sterilized soil of both origins. The observed growth inhibition was accompanied by reduction of AM colonization and nodulation of the roots. Finally, the influence of soil chemistry and AM symbiosis on exotic plants' invasion processes is discussed.

1. Introduction

The large ecological and economic costs associated with invasion of terrestrial ecosystems by exotic plant species has stimulated great interest in elucidating how invasive plant species influence, and are influenced by, biotic and abiotic interactions (Mummey and Rillig, 2006). While many studies aimed to determine aboveground impacts of exotic plant invasion, it appeared that a wide range of belowground biotic interactions regulate plant distribution and ecosystem function (Bever et al., 1997; Stinson et al., 2006). Hence, understanding interactions between plant and soil microbes are required to fully understand the dynamic of plant community succession in the face of exotic invasive species development (Wolfe and Klironomos, 2005). Recent studies indicate that invasive plant species can impact soil microbial community composition and function, resulting from changes in plant-derivative inputs to the soil (Ehrenfeld et al., 2001; Kourtev et al., 2002; van der Putten et al., 2007), as well as phytochemistry interference (Vivanco et al., 2004; Stinson et al., 2006).

Among soil symbiotic microorganisms, Arbuscular Mycorrhizal (AM) fungi have been found to be essential components of sustainable soil-plant systems. Representing a key interface between the host plant and the soil mineral nutrients, AM fungi is also benefic by enhancing plant resistance to pathogens and other environmental stresses, and improving water relations (Smith and Read, 2008). More recently, evidence of detrimental impact of non-mycorrhizal invasive plants on AM communities has been documented (Vogelsang et al., 2004; Stinson et al., 2006). If persistent, altered microbial community composition and functioning in invaded areas may represent a limiting factor for restoration efforts even after removal of invasive species, i.e. there may be a soil ecological legacy of invasion (Mummey and Rillig, 2006).

Amaranthus viridis L. (Amaranthaceae) is an annual weed native from Central America, that is considered to be an invasive plant (USDA Plant Database), along with nine other *Amaranthus* species. In Senegal, *A. viridis* is found in agrosystems, and increasingly invades fallow lands, areas of pasture, domestic waste deposit areas and its growth is positively correlated to soil fertility (organic matter and nitrogen contents) (Le Bourgeois and Merlier, 1995). In *Amaranthus*-invaded large areas, the survival of native plants (grasses, shrubs and trees including *Acacia* species), is compromised (Sanon et al., 2009). The mechanism underlying *Amaranthus* capacity to enter and proliferate within intact Sahelian native plant

Abbreviation: IRD, Institut de Recherche pour le Développement.

* Corresponding author. Laboratoire Commun de Microbiologie IRD/ISRA/UCAD, BP 1386, CP 18524, Dakar, Senegal. Tel.: +221 33 849 33 28; fax: +221 33 849 33 02.
E-mail address: Arsene.Sanon@gmail.com (A. Sanon).

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communities has not been addressed yet. Moreover, much less is known about the impact of this invasive plant on soil microbiota, particularly AM fungi. *Acacia* species were selected as the bioassay test species because they are leguminous natives from Sahelian regions and are frequently used for soil rehabilitation programs as their rhizobial symbiosis improves soil fertility and, have high economical value.

The aims of this study were: 1) to investigate AM fungal community abundance and nutrient availability in soils invaded or not by *A. viridis*; 2) to study the effect of soil origin on the growth of native *Acacia* species; and 3) to better understand the mechanisms of growth inhibition of native plants by determining whether this inhibition is a microbially-mediated outcome. We hypothesized that *A. viridis* will colonize soil patches with specific properties and that post-alterations of soil properties by *A. viridis* development will ultimately affect the competitive performance of native *Acacia* species.

2. Material and methods

2.1. Field site and sampling design

The study was carried out in the region of Dakar (14°43′ N, 17°26′ W) in Senegal. The climate is sahelian influenced by maritime trade winds alleviating high temperatures and low moisture during dry season. The mean annual temperature is 24 °C and rainfall 300 mm (Gassama-Dia et al., 2003). The soil is sandy (>90% of soil) and representative of a Dior-type tropical ferruginous soil (Alfisol).

The sampling site was located at the IRD experimental station of Bel Air – Dakar. From this site, a sampling area (500 m^2) has been chosen in order to cover the diversity of non-invasive plant species and soil patches completely colonized by the invasive *A. viridis*. Most frequently non-invasive plants recorded were: *Alysicarpus ovalifolius* (Fabaceae; annual herb), *Boerhavia diffusa* L. (Nyctaginaceae; annual herb), *Commelina forskalaei* Vahl (Commelinaceae; annual herb), *Eragrostis tremula* L. (Poaceae; annual herb) with a canopy of hardwood trees including *Acacia* spp, *Leuceuna* spp, *Balanites aegyptiaca*. Six plots (1 m × 1 m each) were randomly chosen in sites entirely colonized by *Amaranthus* for *A. viridis*-invaded soil samples (further called invaded soils) and six other plots in sites dominated by non-invasive plants and without *A. viridis* (further called uninvaded soils). Soil samples (2 kg per plots) were collected from 1 to 15 cm depth layer of the 12 plots and they were sieved (mesh size < 2 mm) to remove coarse roots and debris.

2.2. Chemical properties and chitinase activity

For each type of soil, pH in a soil: water suspension (3/10) was determined. The total organic carbon was measured according to the ANNE method (Aubert, 1978) and the total nitrogen by the Kjeldahl method. The total phosphorus and soluble phosphorus were determined colorimetrically (Murphy and Riley, 1962).

Chitin, a polymer of N-acetyl glucosamine, is an important constituent of fungal structures and its dosage allows estimation of the amount of fungal mycelia in the soil, both viable and non-viable (Plassard et al., 1983), and is commonly used to assess mycorrhizal abundance in soil (Plassard et al., 1983). Enzymatic hydrolysis of chitin is mediated by two hydrolases (chitinase and chitobiase), chitinases being the most common in soil (Rodriguez-Kabana et al., 1983). Chitinase activity was measured following Beam (1971) method. Briefly, the hydrolysis of chitin substrates releases *p*-nitrophenol, which amount was determined by spectrophotometry (Ultraspec 3000, Pharmacia Biotech) at 420 nm and compared with standard curve.

2.3. Mycorrhizal propagules density measurement

Spores of AM fungi were extracted from the soil samples by wet sieving and decanting, followed by sucrose centrifugation (Sieverding, 1991) and recovery of the spores through 50 μm sieving of the supernatant. Spores were counted using a stereomicroscope and grouped according to morphological characteristics: size and color, wall structure and hyphal attachment (Walker, 1983; INVAM, 1997). The different morphotypes were identified to genus.

Hyphae were extracted from the soil samples by aqueous membrane-filtration, and subsequent microscopic examination. The total hyphal length was estimated using the Gridline intersect method (Hanssen et al., 1974). The AM fungi hyphae were distinguished from hyphae of other soil fungi following the morphological criteria described by Nicolson (1959).

2.4. Greenhouse experiments with Acacia species

Soils from the same origin site (invaded *vs* uninvaded) were pooled in the lab and, half of both soil types were sterilized (120 °C, 60 min, 2 cycles) by autoclaving to perform greenhouse experiments with sterile soil as well as native soil from the two origin types. On the four types of soils (invaded sterilized or not and, uninvaded sterilized or not), a single seedling of five different *Acacia* species: *Acacia albida*, *Acacia nilotica* var. *tomentosa*, *Acacia raddiana*, *Acacia senegal*, *Acacia seyal*, was grown in 250 mL PVC tubes. Six replicates for each treatment combination were done (4 × 5 × 6 = 120 tubes). Tubes were randomly placed in the greenhouse and were watered regularly with tap water without fertilizer. After 5 months of growth, shoots, roots, and root nodules were harvested, dried at 60 °C for one week, and weighed to determine biomass. Approximately 1-g subsample of roots from each seedling was extracted, cleared and stained (Phillips and Hayman, 1970) and analyzed for AM colonization percentage.

2.5. Statistical methods

Chemical and biological soil properties data were examined by one-way analysis of variance (ANOVA) and pairwise *t* tests corrected by Bonferroni adjustment method used to compare means (at $P < 0.05$). Computations were performed with the free R software (http://r-project.org).

3. Results

3.1. Soil chemical characteristics and AM inoculum potential

Invaded soils had higher pH, total organic carbon, nitrogen content and phosphorus content than non-invaded sites (Table 1).

Table 1
Chemical characteristics of the soil samples invaded or not by *Amaranthus viridis*.

	Soil origin		Significance of the relations		
	Uninvaded soil	Invaded soil	Df[b]	F value	*P* value
pH	7.8 a[a]	8.4 b	1	33.22	$P < 0.0001$
Total organic carbon (%)	1.2 a	2.5 b	1	247.82	$P < 0.0001$
Total nitrogen (%)	0.1 a	0.2 b	1	33.22	$P = 0.0001$
Total phosphorus (mg kg^{-1})	625.3 a	1675.7 b	1	247.82	$P < 0.0001$
Soluble phosphorus (mg kg^{-1})	107.6 a	211.6 b	1	235.02	$P < 0.0001$

[a] Data in the same line followed by the same letter are not significantly different according to the one-way analysis of variance ($P \leq 0.0001$).
[b] Degree of freedom.

Conversely, we observed significant decrease in all mycorrhizal parameters measured in the soil collected in *A. viridis* stands (Fig. 1). Compared to uninvaded soils, spore numbers were reduced 2.69 fold in invaded ones (Df = 1; F value = 64.25; *P* value = 0.000012). AM hyphal length decreased severely in the invaded soils compared to uninvaded ones, with values decreasing from 3.2 to 0.8 m g^{-1} dry soil for uninvaded and invaded sites, respectively (Df = 1; F value = 53.05; *P* value = 0.000027). The same pattern was observed for chitinase activity (Df = 1; F value = 39.87; *P* value = 0.000087) (Fig. 1).

Four AM species were detected in the soils: *Glomus* sp. strain 1 [81 and 83% of the total number of spores recorded for invaded and uninvaded soils, respectively]; *Glomus* sp. strain 2 [4 and 4.5% for invaded and uninvaded soils, respectively]; *Scutellospora* sp. strain 1 [10.5 and 8.9% for invaded and uninvaded soils, respectively]; and *Scutellospora* sp. strain 2 [5.1 and 3.6% for invaded and uninvaded soils, respectively]. Nevertheless, no significant differences were found between the distributions of AM species within the two soil origins ($\chi^2 = 28.7$ [$P = 0.3$]).

3.2. Acacia species growth in greenhouse experiment

Acacia species development (biomass), root AM colonization and nodulation were strongly affected by the soil origin. Growth of *Acacia albida*, *A. nilotica A. senegal* and *A. seyal* seedlings were significantly higher when plants were grown in uninvaded soils ($P < 0.05$), similarly root AM colonization and nodulation were higher. No significant difference was recorded for *A. raddiana* growth efficiency despite significantly higher AM colonization rates and nodulation for plants grown in uninvaded soil. The negative effect of invaded soil on the growth of these plants was similar to that observed when seedlings were grown in sterilized soil from both uninvaded and invaded soils (Table 2).

4. Discussion

4.1. Evidence for alterations in soil chemistry and AM fungal community

Our results clearly indicate that the exotic plant species, *A. viridis*, exerts a positive effect on soil nutrient content by increasing carbon, nitrogen and phosphorus concentrations. In the present study, changes in plant-derivative inputs and mineralization dynamic could have induced changes in nutrients cycling. Previous results have reported that invasion by exotic plant species could result in higher carbon and nutrient (N and P) pools in soil (Ehrenfeld et al., 2001; Kourtev et al., 2002; Ehrenfeld, 2003). Indeed, exotics have been described to increase standing crop biomass and net primary production (Ehrenfeld, 2003). Differences in the litterfall mass interact with differences in the decomposition rate to affect the net flux of C and nutrient into the soil. Also, the litter of many exotic plants decomposes more rapidly than litter of native plants (Ehrenfeld, 2003). In our experimental site, the similar pattern was observed when comparing decomposition rate (i.e. by comparing the mass of plant litter that remains on the soil surface) between *A. viridis* and other non-invasive plants (Duponnois R., unpublished data).

The higher pH recorded in soil samples collected from *A. viridis* stands could result from soil heterogeneity; but certain processes mediated by plants, including rapid uptake of nitrate (NO_3^-) and/or higher content of base cations in the litter returning to soil (Ehrenfeld et al., 2001) could also increase it. However, the mechanism driving the change remains unclear and further analyses regarding soil chemical properties that may affect soil pH such as [NO_3^-], [NH_4^+], nitrification rates or base cations concentration in the litter must be undertaken to support our hypothesis.

Additionally, important modifications have been recorded in soil bacterial community composition and enzyme activities in soils colonized by *A. viridis* (Sanon et al., 2009). These alterations in microbial functioning could also interact with nutrient cycling and might profoundly modify nutrient availability in soils.

Invasive plants affect the AM fungal community in ways that may create a plant-soil biota feedback facilitating invasion and altering native communities. It has been previously observed that mycorrhizal fungi could facilitate exotic plant invasions by increasing the competitive dominance of mycotrophic invasives (Richardson et al., 1994; Fumanal et al., 2006). Conversely, disruption of these mutualistic associations between native plants and AM fungi has been recorded as the main mechanism facilitating invasion of non-mycorrhizal plants (Mummey and Rillig, 2006; Stinson et al., 2006). In our study, a high reduction in mycorrhizal soil infectivity in soils collected from invaded areas was recorded as well as reduction of AM colonization of *Acacia* species roots grown in the same soil. Accordingly, the genus *Amaranthus* is generally thought as non-mycorrhizal (Vierheilig and Ocampo, 1990) and, in a greenhouse experiment where we assessed the mycorrhizal dependency of *A. viridis* following inoculation with different amounts of AM propagules (0; 3; 10; 30; 100), we observed a negative correlation between seedling growth and quantities of AM propagules inoculated (Sanon et al., 2009).

Therefore, the dominance of *A. viridis* may ultimately result in reduced densities of AM fungal community in invaded sites ('*The Degraded Mutualisms Hypothesis*'; Vogelsang et al., 2004) relative to sites covered by non-invasive mycotrophic plant species, as *A. viridis* may not contribute to multiplication of AM propagules. In addition, reduction in AM community could even result from high phosphorus content in soil (Smith and Read, 2008) as that recorded in invaded sites. AM fungal community degradation by

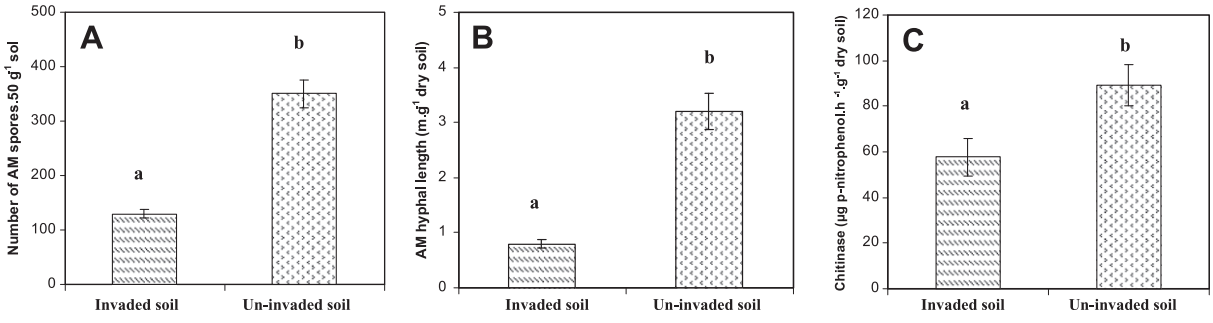

Fig. 1. AM spore density (A), AM hyphal length (B) and chitinase activity (C) in soils from invaded and uninvaded areas. For each soil property, bars indexed by different letters are significantly different ($P < 0.05$).

Table 2
Growth response, AM colonization and nodule biomass of *Acacia* species seedlings grown in soils invaded or uninvaded by *Amaranthus viridis* (adapted from Sanon et al., 2009).

	Invaded by *A. viridis*		Uninvaded by *A. viridis*	
	Sterilized	Un-sterilized	Sterilized	Un-sterilized
A. albida				
Plant total biomass (mg dry weight)	768.5 a[a]	847 a	891.8 a	1065.1 b
Root AM colonization (%)	–	29.8 a	–	83.7 b
Nodule biomass (mg dry weight)	–	6.9 a	–	17.5 b
A. nilotica				
Plant total biomass (mg dry weight)	2125 a	3131 b	2713.4 b	3548.4 c
Root AM colonization (%)	–	28.3 a	–	51.8 b
Nodule biomass (mg dry weight)	–	69.7 a	–	112.8 b
A. raddiana				
Plant total biomass (mg dry weight)	163 a	144.7 a	216.6 a	261.8 a
Root AM colonization (%)	–	9.67 a	–	20.8 b
Nodule biomass (mg dry weight)	–	0 a	–	8 b
A. senegal				
Plant total biomass (mg dry weight)	396.7 a	387.4 a	415.1 a	493.4 b
Root AM colonization (%)	–	33.1 a	–	75.5 b
Nodule biomass (mg dry weight)	–	2.3 a	–	8.8 b
A. seyal				
Plant total biomass (mg dry weight)	2150 a	3000 b	2720 b	3916.8 c
Root AM colonization (%)	–	28.3 a	–	51.8 b
Nodule biomass (mg dry weight)	–	69.7 a	–	112.8 b

[a] Data in the same line followed by the same letter are not significantly different according to the one-way analysis of variance ($P < 0.05$).

chemical inhibition might also be investigated as this pathway has ever been reported for other exotic invasives (Vivanco et al., 2004; Stinson et al., 2006).

Reductions in *Acacia* species nodulation were recorded in the greenhouse experiment. Importantly, when we studied in Petri dishes the effect of *A. viridis* aqueous extract on the growth of 30 strains of rhizobia originating from different areas of Africa, we observed drastic inhibition of rhizobial growth (Sanon et al., 2009). Such inhibition effect has also been observed on *Acacia sephorae* nodulation upon the invasion of bitou bush (*Chrysanthemoides monilifera* spp. *rotundata*) (Vranjic et al., 2000).

4.2. Implications for Acacia species growth reduction

Results of the greenhouse experiment indicated a significant growth reduction when seedlings were grown in invaded soil, sterilized or not, and in sterilized uninvaded soil. Additionally, these growth declines were accompanied by critical reductions of plant root colonization by AM fungi. The reduction in seedlings growth when they were grown in invaded soil is similar to that observed when seedlings were grown in sterilized soil from both invaded and uninvaded sites strongly supporting that the mechanism by which *A. viridis* suppresses the growth of native tree species is microbially-mediated. Our results thus corroborate the previous observations made by Stinson et al. (2006) who documented that the invasive plant, *Alliaria petiolata*, suppresses the growth of native tree seedlings through interference with soil biota.

The initial establishment of the exotic plant could therefore be facilitated by soil disturbance sufficient to reduce AM fungal density, thereby giving invasive species a competitive advantage over indigenous *Acacia* species (Vogelsang et al., 2004), which largely rely on mycorrhizal association for their development (Ducousso and Thoen, 1991).

Afterward, it could be expected that successive growth of *A. viridis* on certain soil patches during several rainy seasons could then generate a '*novel ecological niche*' on these sites, which might favor the exotic invasive plant's own fitness relative to that of native species (Bever et al., 1997; Klironomos, 2002). Additionally, the reduction in *Acacia* seedling nodulation induced by *A. viridis* might also contribute to reduce *Acacia* seedling growth.

These results support the evidence of additional mechanisms by which soil biota could shape plant invasion processes, in addition to the enemy-escape hypothesis, and in addition to other non-microbial mediators (e.g. direct plant–plant allelopathy interference, herbivory, etc.).

5. Conclusion

Our studies suggest that reduced dependence on the mycorrhizal mutualism might be one of the mechanisms underlying the success of the invasive plant, *A. viridis*, within the area studied. This invasive might preferentially colonize certain soil patches or transform soil attributes in such a way that native species are broadly disadvantaged. Importantly, our results suggest tight plant-mediated relationships between soil fertility, mutualistic AM fungi and, invasion processes in a Sahelian ecosystem where man-made disturbances (fertilization, tillage, pesticides, monocultures, …) ultimately result in an increase in nutrient availability and in AM inoculum degradation in ecosystems. These results might be of crucial importance for invaded areas' restoration because they highlight the necessity to protect mycorrhizal symbionts that could promote native plants performance and preserve biodiversity.

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