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Biodiversity of arbuscular mycorrhizas in three vegetational types from the semiarid of Ceará State, Brazil

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ABSTRACT

Semiarid lands are the object of a limited number of studies, very few among them aimed at characterizing root-associated fungal communities. The diverse vegetation occurring in the tropical dry forest from the Ceará State, Brazil, core area of the Brazilian tropical semiarid, has been attributed to its soil, topography and climatic variation. However, the arbuscular mycorrhizal (AM) symbiosis may have an important role in the function of these ecosystems. We examined AM association in 29 semiarid Brazilian species from three different locations: thorny dry woody savanna vegetation, known as caatinga; non-thorny dry forest and closed, non thorny dry tall-shrubby vegetation, known as carrasco. AM fungal diversity was also compared among the different sites. Twenty of the 22 trees and two of the seven herbs examined had AM association. *Arum*-type AM morphology was the dominant association occurring in 19 trees and in 3 hemicryptophyte plants. AM morphology is reported for the first time in 21 trees and two herbaceous species. Over the different sites, spore densities in the soil ranged from 5 to 32 per 100 g air-dried soil. Spores of 32 AM fungal taxa were isolated from the soil samples of trees of which twelve belonged to *Acaulospora*, two to *Scutellospora*, three to *Gigaspora*, four to *Racocetra*, three to *Glomus*, one to *Clareoideoglomus*, one to *Ambispora*, one to *Pacispora*, one to *Sclerocystis*, one to *Dentiscutata*, one to *Orbispora*, one to *Quatunica* and one to *Entrophospora*. Species richness was high in woody caatinga and *Glomus macrocarpum*, *Gigaspora gigantea* and *Cetraspora pellucida* were the most frequent species at different sites. Species diversity (Shannon–Weaver index) did not differ significantly among sites. Water content and phosphorus availability was found to influence the AMF species composition at the plant community level, providing information about the caatinga dominium biodiversity, mainly for its conservation.

1. Introduction

Arbuscular mycorrhiza (AM) is supported by both terrestrial and aquatic plants and are the predominant type of mycorrhizal fungi in tropical soils that associate with a wide range of plant species (Smith and Read, 2008). Most plants in natural ecosystems depend to various extents on the mycorrhizal fungi for the uptake of phosphorus (P), nitrogen (N) and other nutrients; consequently, they are of high interest for restoration of degraded lands and conservation of natural ecosystems. Some of the benefit of AM for plants are: increase in tree biomass (Pagano et al., 2008; Zandavalli et al., 2004) and seed production (Koide and Lu, 1992), both contributing to modify their competitive ability (Moora and Zobel, 1996, 1998). As nutrient mobility is limited under drought conditions, AM may have a more significant impact on plant growth and development in dry relative to well-watered conditions (Sanchez-Diaz and Honrubia, 1994) increasing tolerance to hydric stress (Mathur and Vyas, 2000; Subramanian et al., 1995). Thus the non-nutritional effects of this symbiosis, such as modifying water relationships or stabilizing soil structure, hence physical soil quality (Rillig and Mummey, 2006) and reducing plant diseases (Calvet et al., 1993; Fusconi et al., 1999; Liu et al., 2007; Wehner et al., 2010), are of special importance. Bioprotection may be then the primary role for AM in some natural ecosystems rather than nutrient acquisition (Dodd, 2000).

AM are diverse, both systematically and functionally, with abundant ecological differentiation and specialization to both their biotic and abiotic environments (Fitter et al., 2004; Thonar et al., 2011).

Reports from dry Deciduous Forest of northern Ethiopia (Birhane et al., 2010) showed a high root colonization in the dry season; and, from arid ecosystems of Namibia, a high AM spore diversity (Uhlmann et al., 2006).

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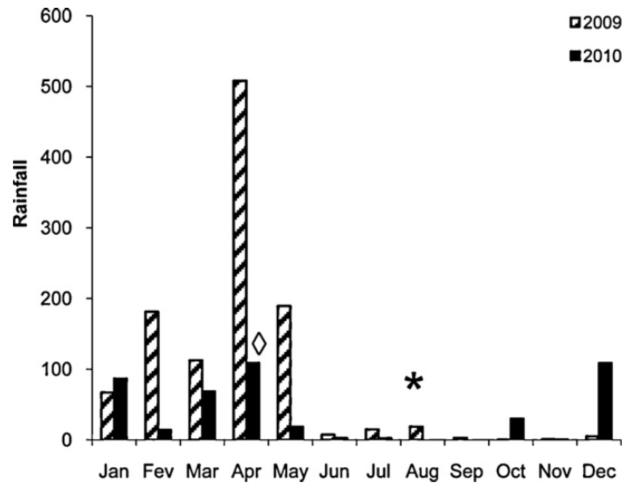

Fig. 1. Regional precipitations for the period 2009–2010 in WCA. Meteorological data from INMET, Estação Climatológica Principal de Crateús, Ceará, Lat: 05°10′S, Long: 40°40′W, Altitude: 296.82 m. Jan, January; Feb, February; Mar, March; Apr, April; May, May; Jun, June; Jul, July; Aug, August; Sep, September; Oct, October; Nov, November; Dec, December. Also shown are dates when mycorrhizal samples were obtained (2009 = star, 2010 = diamond).

It is known that in the Brazilian semiarid zone the main limiting factor is water availability as the annual rainfall is concentrated in just three or four consecutive months. The seasonally dry tropical vegetation belongs to one of the most threatened tropical ecosystems, where Leguminosae, Myrtaceae, Meliaceae and Euphorbiaceae are commonly found (Araújo et al., 2011). Some studies have revealed that AM are well represented in tropical dry forests from Brazil (See checklist by Goto et al., 2010); however, the different physiognomies on different soil classes of the Brazilian tropical semiarid have been poorly investigated (Araújo et al., 2011), and little is known about their root symbioses.

In the State of Ceará, core area of the Brazilian tropical semiarid zone, different vegetation, such as the thorny dry woody savanna (caatinga), the non-thorny dry forest (presenting trees higher than 7 m height) and the closed, non thorny dry tall-shrubby vegetation (namely carrasco) have just begun to be studied. Some perennial evergreen and most deciduous species are dominant members of tree communities throughout the semiarid; however the lack of long-term data on the dynamics of the vegetation constrains their understanding as plant functional groups. Benefits from studies would then accrue, thus improving our knowledge of AM biology and biodiversity. The aim of the present study was to assess the functional relationships of AM and the vegetation cover in its natural habitat in the Ceará State, Brazil. Our hypothesis is that the distribution of plant species may be associated to its relationship with AM, and a higher spore density must be observed during the dry season but higher root colonization during the rainy season. No previous studies have characterized the root-associated fungal community of this important natural site.

2. Materials and methods

2.1. Study sites and characteristics

This study was carried out on three natural sites in Serra das Almas Natural Reserve (05°15′–5°00′S and 40°15′–41°00′W), State of Ceará, Brazil. The climate is tropical semi-arid (type of Koeppen's BSh) with an annual average temperature of approximately 26 °C. The total rainfall in Woody caatinga is often less than 750 mm/year, mostly occurring between November and June, followed by a prolonged dry season (Fig. 1) (INMET, Crateús Main Climatologic Station, L: 05°10′S, L: 40°40′W, Altitude: 296.82 m).

Table 1
Location and forest type characteristics of the three study sites.

Locality	Melancias	Croatá	Grajaú
Location	5°09′S 40°54′W	5°09′S 40°55′W	5°07′S 40°52′W
Altitude (m)	600–750	650–700	300–400
Annual rainfall (mm)	1365	1365	632.2
Soil types (FAO/WRB)	Podzols	Arenosols	Solonetz, leptosols
Area Size in unit	27.93 km^2	11.79 km^2	17.10 km^2
Vegetational types	Deciduous Forest	Carrasco	Woody caatinga

Adapted from Araújo et al. (2005, 2011).

The different vegetation types are: (1) non thorny dry forest (presenting trees higher than 7 m high) 662 m.a.s.l.; (2) an adjacent closed, non thorny dry tall-shrubby vegetation (known as carrasco) 700–900 m.a.s.l.; and (3) thorny dry woody savanna (known as caatinga) 300 m.a.s.l. The plant community composition and soil type differ (Table 1). The floristics and life-forms along a topographic gradient of those physiognomies in this State Reserve were recently showed by Araújo et al. (2011). Species from families with the most frequently occurring species as well as many representatives of the families that are commonly encountered in plant surveys at each site were sampled.

2.2. Field sampling

Soils and roots were sampled in the beginning of the dry (on August 24–26, 2009) and middle of the rainy (on April 26–28, 2010) seasons (Fig. 1), in order to check for seasonality in the AM populations.

Soil samples were collected from the top 20 cm at each rhizospheric soil from 7 plants of each species within the canopy, using simple digging and measuring the depth with a ruler. Soils were air-dried and stored until processing, totalizing 154 soil samples for each season. Soils were used for extracting spores and soil characteristics. One set of soil samples were collected from each sampling tree at each season, which was used for spore analysis (100 g). For physical and chemical soil analysis a composite sample from soil of each vegetation type at each season was prepared. In total 308 soil samples from 22 species weighing about 250–500 kg each were transported to the laboratory using sealed plastic bags. The soil samples were air-dried, passed through a 2 mm sieve and stored at 4 °C until analysis.

Twenty two plant species of arboreous strata distributed in nine families were randomly sampled at both dry and rainy seasons: Fabaceae (8 species), Euphorbiaceae (3 species), Apocynaceae (3 species), Myrtaceae (2 species), Combretaceae (2 species), and Rutaceae, Malpighiaceae, Boraginaceae and Flacourtiaceae (one species). The most frequent plant species (unique to each vegetational type and easily sampled) were selected; however when the dry season begins, the percentage of the herbaceous component decreases. In the herbaceous cover, seven species were sampled during the rainy season in order to check their mycorrhizal colonization.

2.3. Determination of soil properties

Soils from a composite sample of the trees from each area (Deciduous Forest, Carrasco and Woody caatinga) were transported to the laboratory for analysis (chemical and physical properties). The soil analysis was performed by the Soil-Water Laboratory — Foundation of Meteorology and Water Resources (FUNCEME) — Federal University of Ceará, according to EMBRAPA (1979). Soil pH was determined in 1:1, soil: water (v/v) using a digital pH meter.

The total N, total P, and exchangeable potassium (K) after extraction with ammonium acetate were determined according to Jackson (1971). Soil organic matter (SOM) was determined by the Walkley and Black method.

Water content was determined gravimetrically after oven-drying for 24 h at 105 °C. Soil humidity (gravimetric soil moisture) was measured by a drying method (percent soil humidity = fraction of total evaporable moisture content of sample/mass of dried sample × 100). All soils types were stony in their surface and within the soil profile. Soil aggregate stability was evaluated according to the procedure described by Lax et al. (1994), which measures the percentage of soil aggregates between 0.5 and 2 mm that remain stable after being submitted to a simulated rainfall of 150 ml.

2.4. AM fungal assessment

The roots were collected by excavating from the trunk to the lateral root system of each tree, and were fixed in FAA solution in tightly sealed plastic pots and stored at room temperature until they were transported to the laboratory, and until samples could be processed. Samples were collected from seven individual trees for each species at each vegetation type. Roots were stained and assessed for mycorrhizal infection (Phillips and Hayman, 1970). Roots that were pigmented after clearing were bleached in alkaline hydrogen peroxide (0.5% NH_4OH and 0.5% H_2O_2 v/v in water) to remove any phenolic compounds (Kormanik and McGraw, 1982) before acidification. The time required for roots to discolor in this solution varied between samples.

2.5. Quantification of root diameter and colonization

Fine roots (<2 mm) were separated manually and the diameters were measured using a digital micrometer. Fine roots were cut into 1 cm segments, and thirty one-cm-root fragments were examined per sample for their AM status under a microscope. If at least one root segment was found to contain fungal mycelia, arbuscules or vesicles, then the sample was considered as an AM plant, recorded as "+". Plants were recorded as non-mycorrhizal ("−") when neither arbuscules/vesicles, nor fungal mycelia were detected in their root cortical cells of 30 fragments. The percentage of root colonization was estimated according to McGonigle et al. (1990) procedure, separately quantifying arbuscules, vesicles and extraradical hyphae with the formula: $F\% = 100\ [(q + r + s + t)/N]$, where *F*%, frequency of mycorrhizal colonization; *q*, arbuscules, *r*, vesicles, *s*, mycorrhizal hyphae, *t*, external hyphae and *N*, number of fine root centimeters observed. Results were expressed as percentage of colonized segments.

The AM intensity was assessed by the method of Trouvelot et al. (1986) in which %*M* indicates the intensity of mycorrhization according to an arbitrary scale of 1–5 (1 – trace of AM colonization; 5 – >90% of the root cortex colonized). Then %*M* is calculated as the proportion of root centimeters colonized by AM, but weighted by the intensity of the colonization: $\%M = (95n5 + 70n4 + 30n3 + 5n2 + n1)/N$, where $n5, n4, \ldots n1$ indicate the number of root centimeters with an intensity 5, 4,. . .1, and *N* is the number of fine root centimeters observed.

Rate of colonization was 1: 0–5%; 2: 6–25%; 3: 26–50%; 4: 51–75%; and 5: 76–100% according to Kormanick and McGraw (1982). Colonization pattern was observed and the AM morphology was classified as *Arum*- or *Paris* type based on whether the fungal hyphae were present mainly as hyphae running through intercellular spaces or within cells as coils, respectively, following the description by Dickson (2004).

2.6. Isolation, enumeration and characterization of AM fungal spores

AM spores extracted from 100 g soil were analyzed for spore identification. AM spores were recovered from soil samples of each vegetal species in the field, separated by wet sieving (Gerdeman and Nicolson, 1963), decanting and sucrose centrifugation (Walker et al., 1982), and analyzed data were expressed as number of spores/100 g of dry soil. Intact AM fungal spores (non-collapsed spores with cytoplasmic contents and free from parasitic attack) were transferred to a glass slide containing PVLG with or without Melzer's reagent (1:1, v/v) using a wet needle (Morton et al., 1993). Spores were identified based on spore morphology and subcellular characters. Identification was done with reference to the original species descriptions. The frequency of occurrence of each species from AM was calculated as the ratio of a particular spore morphotype to the total number of AM fungal spores × 100 with the formula: $X_i/X_0 \times 100$, where X_i, the population density for an individual species and X_0, the total population. Species richness was calculated as the number of identified AM species per soil sample.

2.7. Diversity of AM fungal community

The frequency of occurrence of each species from AM was computed with the formula: $x_i/x_0 \times 100$, where x_i = the population density for an individual species and x_0 = the total population. The frequency of occurrence of each species was used to calculate the Shannon–Weaver biodiversity index (H′) and species richness, according to Magurran (1988). Differences in AM diversity among plant species were determined by ANOVA, and means were compared by the Tukey test ($P < 0.05$). The Shannon–Weaver index (H′) was calculated from the equation $H = -\sum pi \ln pi$, where *pi* is the relative abundance of the species compared to all the species in a sample.

2.8. Plant and AM fungal nomenclature

Plant nomenclature and authorities are used by APG III (2009) and for AM fungi are those of IMA Fungus (Oehl et al., 2011) and mycobank (www.mycobank.org).

2.9. Statistical analysis

One-way analysis of variance (ANOVA) was used to test the significance of variation within AM fungal variables. Pearson's correlation was used to assess the relationship between AM and soil variables. Spore numbers were log transformed and percentage data on root colonization was arcsin transformed prior to analysis. Differences in AM spore number and diversity were determined with ANOVA using MINITAB® version 16.2.0 (2010), and means were compared by the Tukey test ($P < 0.05$). The data of root colonization were arcsin $(x/100)^{1/2}$ transformed. The data were subjected to one-way ANOVA, and means were compared by the Tukey test ($P < 0.05$). The differences among AMF communities in the three vegetational types were depicted as a dendrogram constructed by the unweighted pair group with mathematical average method (UPGMA) with a Manhattan distance coefficient using the software MINITAB® 16.2.0 (2010).

3. Results

3.1. Soil properties

The soil characteristics of the study sites are presented in Table 2. Some basic properties of the soils were as follows: acid pH and high organic matter content, but P content was moderated to low. With

Table 2
Soil characteristics of study sites in Serra das Almas Reserve, Ceará (dry and wet season).

Soil property	Deciduous forest[a]		Carrasco		Woody caatinga	
	D	R	D	R	D	R
pH (H_2O)	4.0bB	4.6aB	4.1aB	4.3aC	5.2bA	5.8aA
Soil organic matter (%)	26.61aAB	20.62aB	22.13aB	17.41bC	32.75aA	28.93aA
C (g kg soil^{-1})	15.44aNS	11.96a	12.84a	9.66b	19.62a	16.78a
N (g kg soil^{-1})	1.53aNS	1.10b	1.3a	1.04b	1.93a	1.66a
C/N	10.09nsNS	11	9.87	9.66	10.16	16.78
P (mg dm^{-3})	4aB	1.53bB	3aC	2.33aB	15.33aA	17aA
K^+(cmol (+) kg^{-1})	0.13a	0.13aB	0.05a	0.04bC	0.39a	0.22bA
Al^{3+} (cmol (+) kg^{-1})	1.25b	1.53a	1.08a	1.88b	0.13a	0.16a
Ca^{2+} (cmol (+) kg^{-1})	1aB	0.9a	0.8aB	0.36b	4.5aA	4.33a
Mg^{2+} (cmol (+) kg^{-1})	0.8aB	0.76aB	0.7aB	0.4bC	2.03aA	2.1aA
CEC (cmol (+) kg^{-1})	6.3aB	6.9aB	7.9aB	5.6bB	8.6aA	10.3aA
Base saturation (%)	32aB	27aB	24aB	15.6bC	71aA	65.33aA
Soil humidity (%)	2.35bA	7.67aAB	1.55bA	5.37aB	0.55bB	10.72aA
WSA	62.03ns	59.96AB	56.83ns	75.4A	41.45ns	26.20B

[a] Vegetational type; D, dry season; R, rainy season. Data are means of three composite samples. mg L^{-1}, milligram per litter, CEC, cation exchange capacity, WSA, Percentage of water stable aggregates. Different lowercase letters (compare means in row between D and R) or capital letter (compare means in row of different vegetational types at the same season) indicate significant differences as determined by Tukey's HSD test ($^*P < 0.05$). NS, not significantly different.

regard to chemical properties, there were significant differences in soil pH, N, P, K and SOM between forest types. Nutrient contents were maximal in Woody caatinga and least in Carrasco. The soils were more acidic in Deciduous Forest and Carrasco (pH 4) and less acidic in Woody caatinga (pH 5). P content was very low in both Carrasco and Deciduous Forest, except for Woody caatinga, which present a medium P content. P was five times more concentrated and more than three times in Woody caatinga than in Carrasco and Deciduous Forest, respectively. The soil in Woody caatinga site had the highest organic C content.

Soil texture was as follows: coarse sand = 13–39%, fine sand = 32–71%, silt = 2–8% and clay = 6–9% (0–25 cm depth). Clay content was higher in Woody caatinga soils than in the other sites. SOM content was high in the three sites but C/N relation was lower in Carrasco. As expected, soil humidity at sampling was higher in: Deciduous Forest ≥ Carrasco > Woody caatinga (dry season); however, in the rainy season Woody caatinga ≥ Deciduous Forest ≥ Carrasco ($P < 0.05$) (Table 2). With regard to percentage of water stable aggregates, only in the rainy period significant differences among vegetational types were observed (Woody caatinga presented lower values followed by Deciduous Forest and Carrasco) (Table 2).

3.2. Root diameter and AM colonization

Average fine root diameters were higher in the Carrasco than in other vegetational types; however, Carrasco only differed significantly from herbs root diameter following the order: Carrasco ≥ Woody caatinga ≥ Deciduous Forest ≥ Herbs.

AM associations were the only form of mycorrhiza found in all vegetational types. AM colonization was evident in most roots collected at the three sites and AM structures were observed in 23 plant species (Table 3). Plants lacking AM were *Zanthoxylum stelligerum* (Rubiaceae), *Urochloa fasciculata* (Poaceae), *Chamaecrista duckeneana* (Fabaceae), *Alternanthera brasiliana* and *Cuphea circaeoides* (Lythraceae). Only two hemicryptophytes showed mycorrhizal colonization (*C. erecta*, 19.6 and *C. surinamensis*, 33%) in the Woody caatinga (rainy period).

AM fungal structures were observed in 21 (95%) of 22 tree species, and the colonization rate varied among them. As generally found, aseptate hyphae (>37%) and vesicles (>32%) were the most frequent structures present in the studied plants in the dry period, roots did not present root-hair incidence. No AM fungal structures were observed in one tree species (*Z. stelligerum*) associated to remnant Carrasco. Two (dry season) and seven (rainy season) tree species did not present colonization (Table 3).

In general, the roots showed medium to high mycorrhizal colonization in most species especially in the dry season (Fig. 2), but low arbuscular formation. Aseptate intra and intercellular hyphae and vesicles were observed in the majority of the plant samples. In general, the extent of AM colonization varied from about 2% to 79% (root colonization = 1–5). Total root colonization and hyphae ranged from >1% (root colonization = 1) (*Aspidosperma subincanum*) to 79% (root colonization = 5) (*Byrsonima gardneriana*) (Table 3). Root with vesicles ranged from 3.5% (*Poincianella bracteosa*, *Eugenia* sp.) to 70% (*Hymenaea velutina*) and arbuscules ranged from 16% (*Xylosma ciliatifolium*) to 41% (*Ephedranthus pisocarpus*). Vesicles were absent in two tree species. Significant variations were found to exist among trees (dry season) for hyphae ($F = 4.65$; $P < 0.001$), vesicles ($F = 5.04$; $P < 0.001$), arbuscules ($F = 31.44$; $P < 0.05$) and extraradical hyphae ($F = 2.23$; $P < 0.05$). Extraradical hyphae in the dry period (13.4%) was over 27% that averaged in rainy (3.6%). With regard to herbaceous species, two of them presented only hyphae and vesicles but intensity of colonization was low (<2%).

3.3. AMF spore numbers

The AMF spore numbers were consistently higher in the Deciduous Forest than in the other studied sites. Spore number of each AM

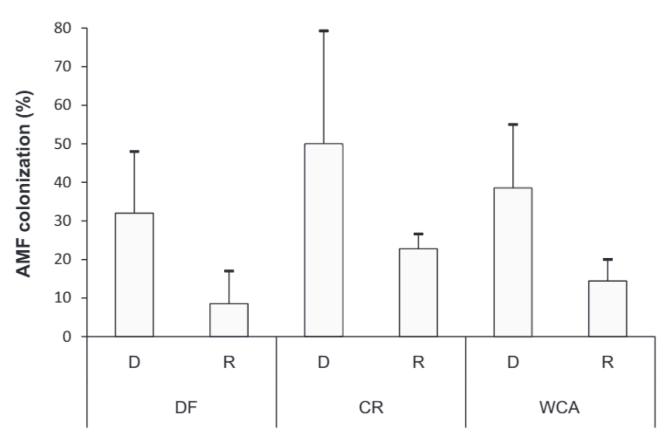

Fig. 2. Variation of AMF colonization among different vegetation types at the two seasons at Serra das Almas Reserve, Ceará. Bars = standard deviation. Vegetational type: Dry Forest (DF), Carrasco (CR) and Woody caatinga (WCA); D, dry season; R, rainy season.

Table 3
Plant species studied and their root colonization at Serra das Almas Reserve, Ceará, Brazil.

VT[a]	Functional group	Family	LF	Species	MT	RC	
						D	R
DF	Legumes	Mimosaceae	PH	*Pytirocarpa moniliformis* (Benth.) Luckow & Jobson	AM-*Arum*	3	0
		Caesalpiniaceae	PH	*Bauhinia* cf. *pulchella* Benth.	AM-*Arum*	2	2
		Caesalpiniaceae	PH	*Hymenaea velutina* Ducke	AM-*Arum*	4	2
		Caesalpiniaceae	PH	*Copaifera martii* Hayne	AM-*Arum*	2	0
	Non legumes	Apocynaceae	PH	*Aspidosperma subincanum* Mart. ex A. DC.	ND	1	0
		Euphorbiaceae	PH	*Croton argirophyloides* Müll Arg.	AM-*Arum*	0	2
		Combretaceae	PH	*Buchenavia capitata* (Vahl) Eichler	AM-*Arum*	3	2
		Flacourtiaceae	PH	*Xylosma ciliatifolia* (Clos) Eichler	ND	3	0
CR	Legumes	Caesalpiniaceae	PH	*Bauhinia acuruana* Moric.	AM-*Arum*	4	3
	Non legumes	Myrtaceae	PH	*Eugenia* sp.	AM-*Arum*	2	2
		Myrtaceae	PH	*Eugenia* aff. *dysenterica* DC.	AM-*Arum*	3	2
		Malpighiaceae	PH	*Byrsonima gardneriana* A. Juss.	AM-*Arum*	5	0
		Euphorbiaceae	PH	*Sapium* cf. *lanceolatum* (Müll. Arg.) Huber	AM-*Arum*	4	3
		Rutaceae	PH	*Zanthoxylum stelligerum* Turcz.	NF	0	0
		Combretaceae	PH	*Combretum glaucocarpum* Mart.	AM-*Arum*	2	2
		Apocynaceae	PH	*Ephedranthus pisocarpus* R. E. Fr.	AM-*Paris*	3	4
WCA	Legumes	Mimosaceae	PH	*Mimosa caesalpiniifolia* Benth.‡	AM-*Arum*	3	2
		Mimosaceae	PH	*Mimosa tenuiflora* (Willd.) Poir.	AM-*Arum*	3	2
		Caesalpiniaceae	PH	*Poincianella bracteosa* (Tul.) L.P.Queiroz	AM-*Arum*	2	2
		Fabaceae	HM	*Chamaecrista duckeneana (P.Bezerra & Afr.Fern.)* H.S. Irwin & Barneby	NF	ND	0
	Non legumes	Euphorbiaceae	PH	*Croton blanchetianus* Baill.	AM-*Arum*	4	3
		Apocynaceae	PH	*Aspidosperma pyrifolium* Mart.	AM-*Arum*	2	0
		Boraginaceae	PH	*Cordia oncocalyx* Allemão[b]	AM-*Arum*	4	2
		Poaceae	TR	*Urochloa fasciculata* (Sw.) R.D. Webster	NF	ND	0
		Commenilaceae	HM	*Commelina nudiflora* L.	AM-*Arum*	ND	2
		Cyperaceae	HM	*Cyperus surinamensis* Rottb.	AM-*Arum*	ND	2
		Oxalidaceae	HM	*Oxalis divaricata* Mart. ex Zucc.	NF	ND	0
		Lythraceae	TR	*Alternanthera brasiliana* (L.) Kuntze	NF	ND	0
			TR	*Cuphea circaeoides* Sm. ex Sims	NF	ND	0

[a] Vegetational types: deciduous forest (DF), Carrasco (CR) and woody caatinga (WCA); D, dry season; R, rainy season; LF, life form: P, phanerophyte, H, hemicryptophyte, T, therophyte; MT, Mycorrhizal type; RC: root colonization rate by AMF (1: 0–5%; 2: 6–25%; 3: 26–50%; 4: 51–75%; and 5: 76–100%); NF: no fungal association; ND: not determined.
[b] Endangered or near threatened plant species.

family varied between vegetational types (Fig. 3). Deciduous Forest and Carrasco presented higher spore number of Gigasporales, followed by Glomeraceae and Acaulosporaceae. On the other hand, Woody caatinga showed lower spore numbers of Gigasporales.

3.4. AM diversity

In total, 32 AM species were identified in the samples taken from the three vegetational types in Serra das Almas (Table 4). The average species richness found in the Woody caatinga was higher when

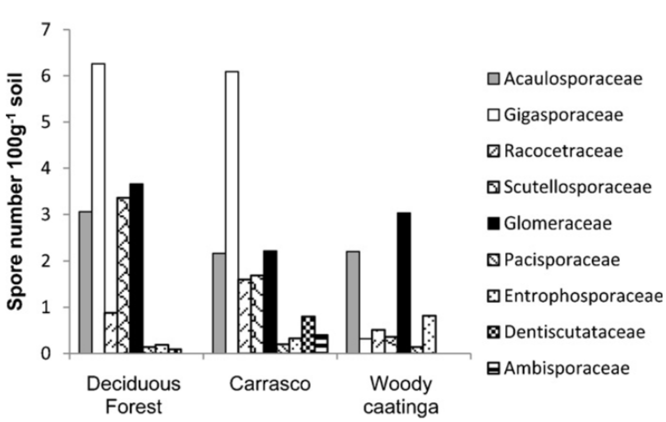

Fig. 3. Variation of AMF spore numbers of different AMF families in the Vegetational types at Serra das Almas Reserve, Ceará, at dry period.

compared with the other vegetational types. *Acaulospora* was the genus with the highest number of species recovered (12), followed by *Racocetra* (4), *Scutellospora* (3), *Glomus* (3), among others. The AM diversity of the different vegetational types showed no statistical differences based upon the Shannon diversity index (Table 4). However, the AM communities showed different species compositions: only 9 out the 32 species found were common to all of the studied vegetational types (*Acaulospora laevis*, *Claroideoglomus etunicatum*, *Gigaspora margarita*, *Gigaspora gigantea*, *Glomus macrocarpum*, *Pacispora franciscana*, *Scutellospora calospora*, *Cetraspora pellucida* and *Dentiscutata biornata*), while other species were found only in one or two habitats.

Spores belonging to *Acaulospora*, *Glomus*, *Gigaspora* and *Scutellospora* were the most frequent in the three vegetational types, whereas *Ambispora* and *Entrophospora* were observed with less frequency. The sporocarpic species *Sclerocystis taiwanensis* was unique to native caatinga; however, *Glo glomerulatum* was common in the three vegetational types.

The AM species richness was higher at the dry season. The Shannon diversity index calculated for the different areas sampled was 3.4 in the case of Woody caatinga, 2.4 for Deciduous Forest and Carrasco. The Shannon index calculated for the whole study was 2.73. The Shannon index decreased from the highest value of 3.4 to the lowest value of 2.4 in the order of succession Woody caatinga > Deciduous Forest ≥ Carrasco (dry season) and Carrasco > Deciduous Forest > Woody caatinga (rainy season) (Table 4); however the differences were not significant due to the variability in AM associated to each plant species.

Table 4
Distribution of AMF species associated with different vegetational types at Serra das Almas Reserve, Ceará, at dry and rainy periods (+, presence; –, absence) ($n = 7$).

AMF species	DF[a]		CR		WCA	
	D	R	D	R	D	R
Acaulosporaceae						
Acaulospora bireticulata F.M. Rothwell & Trappe	–	–	–	–	+	+
A. delicata C. Walker, Pfeiffer & Bloss	–	–	–	–	–	+
A. excavata Ingleby & C. Walker	–	–	–	–	+	–
A. foveata Trappe & Janos	–	+	+	–	–	–
A. lacunosa J.B. Morton	–	–	–	–	+	–
A. laevis Gerdemann & Trappe	+	+	+	+	+	+
A. mellea Spain & Schenck	–	+	–	–	–	–
A. rhemii Sieverding & S. Toro	+	–	–	–	+	–
A. scrobiculata Trappe	+	+	–	–	+	–
A. spinosa C. Walker & Trappe	–	+	–	–	+	–
A. tuberculata Janos & Trappe	–	–	–	–	+	–
A. aff. *bireticulata* F.M. Rothwell & Trappe	–	–	–	–	+	–
Ambisporaceae						
Ambispora appendicula (Spain, Sieverd. & N.C. Schenck) C. Walker	–	–	+	+	–	–
Entrophosporaceae						
Claroideoglomus etunicatum (W.N. Becker & Gerd.) C. Walker & A. Schüβler	+	–	+	–	+	–
Entrophospora infrequens (I.R. Hall) R.N. Ames & R.W. Schneid.	–	–	–	–	+	–
Gigasporaceae						
Gigaspora decipiens I.R. Hall & L.K. Abbott	–	–	–	+	–	–
G. gigantea (T.H. Nicolson & Gerd.) Gerd. & Trappe	+	+	+	+	–	+
G. margarita W.N. Becker & I.R. Hall	+	+	+	+	+	+
Racocetraceae						
Cetraspora pellucida (T.H. Nicolson & N.C. Schenck) Oehl, F.A. Souza & Sieverding	+	–	+	+	+	+
Racocetra fulgida (Koske & C. Walker) Oehl, F.A. Souza & Sieverd.	–	–	–	+	–	–
R. gregaria (N.C. Schenck & T.H. Nicolson) Oehl, F.A. Souza & Sieverd	–	–	–	+	–	–
R. verrucosa (Koske & C. Walker) Oehl, F.A. Souza & Sieverd.	–	–	+	–	–	–
Scutellosporaceae						
Orbispora pernambucana (Oehl, D.K. Silva, N. Freitas, L.C. Maia) Oehl, G.A. Silva & D.K. Silva	+	–	–	–	–	–
Scutellospora calospora (T.H. Nicolson & Gerd.) C. Walker & F.E. Sanders	+	+	+	+	+	–
S. scutata C. Walker & Dieder.	+	–	–	–	+	–
Dentiscutataceae						
Dentiscutata biornata Spain, Sieverd. & S. Toro	+	–	+	+	+	+
Quatunica erythropa (Koske & C. Walker) F.A. Souza, Sieverd. & Oehl	–	–	+	–	–	–
Glomeraceae						
Glomus macrocarpum Tul. & C. Tul.	+	+	+	+	+	+
Glo glomerulatum Sieverd.	–	–	+	+	+	–
Glo multicaule Gerd. & B.K. Bakshi	–	–	+	–	–	–
Glomus sp. 1	–	+	+	+	+	+
Glomus sp. 2	+	+	+	+	–	–
Glomus sp. 3	–	–	–	–	+	–
Sclerocystis taiwanensis C.G. Wu & Z.C. Chen	–	–	–	–	+	–
Pacisporaceae	+	+	+	+	+	–
Pacispora franciscana Sieverd. & Oehl	+	+	+	+	+	–
Species richness	15	13	18	16	23	9
Diversity[b]	2.4	2.3	2.4	2.4	3.4	2.1

[a] Vegetational type: deciduous forest (DF), Carrasco (CR) and woody caatinga (WCA); D, dry season; R, rainy season.
[b] Maximal AM diversity found in each VT.

Potential undescribed species were found in the present study (species with acaulosporoid morphologies and *Glomus* species). The identity of *Acaulospora* aff. *bireticulata* could not be confirmed.

The dendrogram constructed by UPGMA using the AM species showed that the AM community from Woody caatinga was more distant than Deciduous Forest and Carrasco (Fig. 4).

3.5. Correlation of biotic and abiotic factors

In Serra das Almas Reserve, mycorrhization of trees (extraradical hyphae) was significantly correlated (Table 5) with total-P content (−0.451, $P = 0.024$). Moreover, the number of AM species recorded was significantly correlated with soil moisture (−0.394, $P = 0.016$).

4. Discussion

4.1. Soil properties

The Woody caatinga is located in the crystalline basement relief, at low altitudes. Herbs account for the highest species richness,

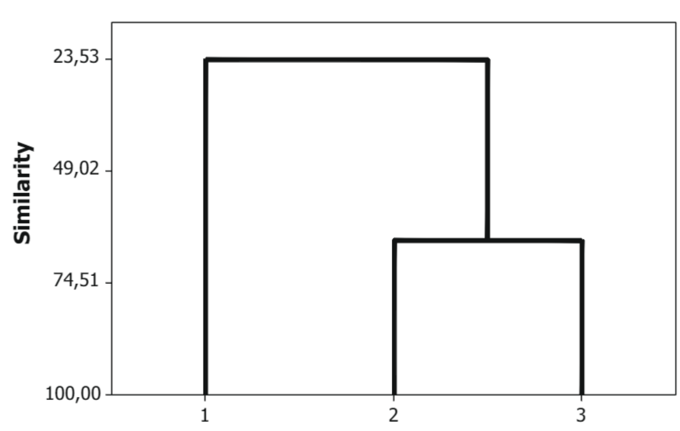

Fig. 4. Dendrogram constructed by UPGMA using the AMF species present in the three VT at Serra das Almas, Ceará, Brazil. 1, WCA; 2, DF; 3, CR.

Table 5
Correlation coefficients between biotic and abiotic factors. Statistically significant ($^*P < 0.05$) correlations are printed in bold.

Correlation between	
Mycorrhization of trees (Hyphae)/P	0.10
Mycorrhization of trees (Hyphae)/species number	0.26
Mycorrhization of trees (Vesicles)/P	−0.12
Mycorrhization of trees (Extradical hyphae)/P	**−0.45***
Mycorrhization of trees (Hyphae)/soil moisture	−0.18
Mycorrhization of trees (Hyphae)/base saturation	0.29
Mycorrhization of trees (Hyphae)/fine root diameter	0.18
Species number/P	−0.12
Species number/Soil moisture	**−0.39***

and the presence of Cyperaceae (known as sedges) indicates water saturation. Base saturation is higher than in Deciduous Forest and Carrasco. Thus Woody caatinga can be considered an accumulation zone for nutrients and water retention. The higher soil humidity found in Woody caatinga (rainy season) is in agreement with this.

On the other hand, the Deciduous Forest (on the eastern hogback of the Ibiapaba plateau, on Podzols (FAO/WRB) and at higher altitudes than Woody caatinga) presents the highest tree species richness, which is more related to the Carrasco vegetation (Araújo et al., 2011; Lima et al., 2009). The Carrasco (on the backside of the plateau at altitudes of ca. 700 m with smooth declivity) presenting more quartz sand content (89%), showed lower humidity (rainy season), probably related with higher water infiltration and shorter tree occurrence. As expected, water content at sampling varied according to the site and was usually higher in those with more-dense vegetation (Deciduous Forest and Carrasco) in the dry period, but lowest at Carrasco in the rainy period.

The percentage of water stable aggregates obtained for Woody caatinga in the present study agrees with values (∼66) reported by Maia et al. (2006a) for native forest sites also in the semi-arid region of Ceará. However, no reports for Deciduous Forest and Carrasco were previously registered.

4.2. Root AM colonization

In this study, the mycorrhizal status of most trees, which belong to the Combretaceae, Euphorbiaceae and Fabaceae families, on the semiarid vegetation of Ceará is reported for the first time. There is no previous report (Wang and Qiu, 2006) on the mycorrhizal status of the sampled species in the present study except for *Cyperus surinamensis* (Silva et al., 2001) and *Mimosa caesalpiniifolia*. *M. caesalpiniifolia*, a fast growth tree legume, tolerant to dry conditions with enormous potential for reforestation in semiarid zone of Brazil, was previously studied by Burity et al. (2000), who showed higher seedling growth, leaf area, height and colonization when inoculated (AM and *Rhizobium*) in greenhouse. In the present study a medium root colonization was found for this species, with "h"-shape anastomosis pattern on intraradical hyphae and ellipsoid to round vesicles (*Glomus*-type colonization).

Moreover, *A. brasiliana* (plant with medicinal use) did not present AM symbioses; however, it was reported by Rodrigues-Filho (personal communication) to contain endophytic fungi and a related species of *Commelina* aff. *erecta* was reported as AM by Corkidi and Rincón (1997). With regard to the other herbs, related species such as *Chamaecrista chamaecristoides*, *Cuphea carthagenensis* and seven species of *Oxalis* were reported as AM (see Wang and Qiu, 2006); however, in the present study species of the same genera did not present symbioses. With regard to the representative of Poaceae, other species such as *Urochloa decumbens* and *Urochloa humidicola* were reported as AM for sclerophyllous shrubland in Venezuela by Cuenca and Lovera (1992) and Lovera and Cuenca (1996); however, in the present study *U. fasciculata* did not present symbioses.

The results obtained showed that most species present colonization of the *Arum*-type, which was seen to be dominant in most plants that usually grow in the sunlight. The spreading rate of colonization was also reported to be faster than the *Paris*-type (Brundrett and Kendrick, 1990; Yamato and Iwasaki, 2002), which suggests that prevailing environmental conditions can influence AM morphology. Additionally, roots frequently had *Scutellospora* like auxiliary cells in extraradical hyphae associated with them, which is associated with P reserves.

We found intercellular hyphae and vesicles with no arbuscules in most tree species; however, only two herbaceous species present those fungal structures. Few tree species (non legumes) presented arbuscules in their root samples, and these were located in the vegetation types presenting low soil P content. This agrees with common findings regarding the presence of arbuscules as indicating allocation of this element (Smith and Read, 2008).

We found intercellular hyphae and vesicles with no arbuscules in 16 tree species, mostly in the dry period. It has been pointed out that drought increased root colonization more often than it decreased it (Augé, 2001; Apple et al., 2005). However, some reports (Clark et al., 2009; Pagano et al., 2009) showed the opposite. In this regard, Birhane et al. (2010) also found higher root colonization in the dry period in dry woodland areas of Ethiopia (two sites with 647 and 800 mm rainfall), suggesting a temporal uncoupling of C fixation by plant and AM. This is in line with our predictions that other functions of AM are prevailing in our study sites.

In contrast, extraradical hyphae are often (though not always) reduced when water is limited (Augé, 2001; Lutgen et al., 2003; Querejeta et al., 2007; Staddon et al., 2003). In the present study higher extraradical hyphae were found in the dry period in vegetational types (Deciduous Forest ≥ Carrasco ≥ Woody caatinga) presenting higher soil humidity, which was also observed by Clark et al. (2009). Otherwise, in the rainy period the percent of extraradical hyphae (lower than in the dry period) decreased in the following order: Carrasco ≥ Woody caatinga ≥ Deciduous Forest. The percent of extraradical hyphae was negatively correlated with total-P content; thus, it can be concluded that low extraradical hyphae was found in Woody caatinga (presenting higher P content) and high extraradical hyphae was observed in Carrasco (low P content). However, correlation between AM species richness and soil moisture as well as extraradical hyphae and P content are weaker. Although it is important to understand the AM patterns of individual plant species, it is equally important to identify AM patterns among plant functional types. In the present work, a high number of non AM dependent plant species was found in Woody caatinga. This is in agreement with Allen and Allen (1990), who showed low environmental water availability related to a high number of plant species with low or intermediate AM dependency. Muthukumar and Udaiyan (2000) also found low AM colonization in herbaceous species in Southern India. Additionally, Çakan and Karatas (2006) found that major functional groups (therophytes and cryptophytes) were little or non-colonized by AM, while phanerophytes and hemicryptophytes presented a high AMF dependence in the semiarid of Turkey.

4.3. AM fungal spores communities

A conspicuous diversity of AM spores was present in rhizospheric soils, which indicates that AM symbiosis plays an important role in the studied vegetational types. All the species present AM spores in their rizospheres, and this might be helpful in modeling the changes in AM characteristics that influence the standing vegetation, as well as nutrient availability and dynamics.

In the present study, the AM spore densities recovered from soils were generally low (32 per 100 g dry wt. soil) and depended on the plant host. For instance, spores were most numerous in the *Bauhinia* cf. *pulchella* (Deciduous Forest), *B. gardneriana* and *Combretum glaucocarpum* (Carrasco) rhizospheres and least numerous in the *Mimosa tenuiflora* (Woody caatinga) rhizosphere. The AM spore densities recovered in the present study agree with reports of caatinga formation (Maia et al., 2010). However, other studies in the same biome showed a higher spore density (∼84 spores from the rhizosphere of *Aspidosperma pyrifolium* and ∼44 spores from *Poincianella pyramidalis* (Tul.) L.P. Queiroz) (Souza et al., 2003). In the present study, the high number of non-viable spores observed in Woody caatinga is in agreement with Lima et al. (2007) who detected ∼5–9 spores/100 g soil using iodonitrotetrazolium chloride technique (Walley and Germida, 1995) in soils from native caatinga. In the present study, the vegetational types presented low spore densities in spite of high colonization recorded; showing that spores may be relatively unimportant as propagules (hyphae networks being crucial).

In general, the dry season shows the highest AM species richness detected (Caproni et al., 2003; Souza et al., 2003; Tchabi et al., 2008). Moisture along with the growth of plants favors vegetative growth of the fungus, resulting in root colonization and reduction of the number of spores present in the soil (Guadarrama and Álvarez-Sánchez, 1999). In the present study the number of AM species recorded was also negatively correlated with soil moisture.

Thirty one distinct species of AM fungi were detected in field; however, two to three *Acaulospora* and *Glomus* species could not be identified at species level, these possibly being new species (Blaszcowsky personal communication). Thus, the diversity reported in the present study (evaluated only with field samples) can be increased with the help of a trap crop. This revealed that the vegetational types from Ceará harbors more than 13% AMF species described all over the world (Oehl et al., 2011) and ∼29% of identified species in Brazilian ecosystems (Stürmer and Siqueira, 2006).

In the present work, the presence of AM families agrees with other reports from the Brazilian semiarid, and some AM species were also identified from caatinga (Maia et al., 2006b). However, some AM species found in our study had not been previously recorded (Goto et al., 2010) in the Brazilian semiarid (*Acaulospora* aff. *bireticulata*, *P. franciscana* and *S. taiwanensis*).

Previous reports posit that some AM have specific preference toward host species (Pagano et al., 2011) or ecological types (Bever, 2002; Sýkorová et al., 2007; Davison et al., 2011). In the present study *Acaulospora paulinae*, *Acaulospora tuberculata*, *Entrophospora infrequens* and *S. taiwanensis* were recovered from *A. pyrifolium* and/or *Cordia oncocalyx* in the Woody caatinga. Moreover, *Ambispora appendicula* were recovered only in Carrasco. In this sense, it has been shown that differences in AM species distributions are caused by habitat preferences of taxa, for example differences in tolerance to high nutrient availability (Egerton-Warburton et al., 2007; Porras-Alfaro et al., 2007), pH and soil type (Lekberg et al., 2007; Oehl et al., 2010; Carvalho et al., 2012), and others report no effect of plant community composition on AM communities (Santos et al., 2006; Urcelay et al., 2009; Dumbrell et al., 2010).

With regard to AM biodiversity, *Glomus*, *Acaulospora*, *Racocetra* and *Gigaspora*, as well as sporocarpic species of *Glomus* were common in native caatinga, which is in agreement with other reports in the semiarid zone (Souza et al., 2003; Maia et al., 2006a,b). Furthermore, the association seems to be multifunctional, as most plant species studied presented AM species belonging to different families in their rhizospheres. The presence of different families of Glomeromycota, having different life strategies (de Souza et al., 2005), indicates that AM could have different functions in these vegetational types, besides AM species complementarity.

Our data indicate that some AM species (*A. appendicula*, *Gigaspora decipiens* and *E. infrequens*) seem to show strong preference for only one vegetational type, since they were found mainly in this area. In other studies, environmental factors, such as sampling season and soil N content, influenced the composition of the AM community in the roots of some plant species. If we compare our data with the AM detected by Lekberg et al. (2007), who analyzed the effects of soil characteristics on AM communities of maize in sand and clay soils, we can see that the predominance of Glomeraceae in clay soils as well as Gigasporaceae in sand soils, agree with our results.

4.4. AM significance for conservation and ecology

All the tree species examined (except for one species of Rutaceae, which remains uncertain) were colonized by AM, which was expected in these vegetational types. Among 29 plants, 2 have endangered or threatened status.

The results of this study suggest that the diversity of AM is related to the heterogeneity of habitats and that the soil properties (moisture and P content) are more clearly related to the structure of the AM communities than to other attributes. Our survey provides information to expand our knowledge about AM biodiversity from the Ceará State, thus contributing information for its conservation.

5. Conclusions

The results of this study clearly indicate that the three vegetational types (Deciduous Forest and Carrasco presenting more related AM communities) are an AM biodiversity reservoir and this brings interesting features for conservation of the Biota of Ceará State. The AM diversity is related to the variability among those habitats (plants and soils). Among the variabilities, the soil moisture and P content, which is more related to AM richness and extraradical hyphae respectively, than the other chemical attributes of soil, should be highlighted. This study has shown new reports of mycotrophic species from Brazil. Moreover, the association of AM with endangered plants may play a significant role in the reestablishment and conservation of them. Notably, the AM diversity is well represented in the tree vegetation types, and Gigasporales appears to have a wide distribution and might have a wide range of ecological adaptations.

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