Arbuscular mycorrhizas in the *Larrea divaricata* scrubland of the arid "Chaco", Central Argentina

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Arbuscular mycorrhizal root colonization and spore diversity were analyzed, in terms of seasons, dry and wet period and host species, in an arid secondary scrubland ecosystem ("Jarillal") in Central Argentina. *Larrea divaricata*, dominant in this plant community, was the most colonized species followed by the grass *Trichloris crinita* ("herbaceous stratum fitness indicator") whereas the lowest values were found in *Sporobolus pyramidatus* and *Neobouteloua lophostachya* (both of them "disturbance indicators"). Root colonization was closely related to host role in the community. The AMF diversity was low because of the disturbed features of "Jarillal" and arid conditions. Spore total density, specific spore density and spore richness were more related to the seasons and water availability than to the host species.

Key words: AM colonization, AM fungal spore diversity, bushland, grassland, seasonality, soil moisture.

Introduction

Arbuscular mycorrhizal (AM) fungi are found in nearly all soils where plants grow, and they are expected to have their greatest impact when plants are exposed to growth-limiting environmental stress (Allen, 1991; Sylvia and Williams, 1992; Smith and Read, 1997; Varma, 1999). They also affect plant-plant interactions and communities in most terrestrial plant ecosystems (Allen, 1996; Francis and Read, 1994; Grime *et al*., 1987). They are widespread from tropical to Arctic and Antarctic regions (Cabello *et al*., 1994; Vestberg, 1995) and associated with a great number of plant species (Harley, 1989).

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Vegetation systems dominated by AM herbaceous plants progressively become more extensive on a global scale with decreasing latitude, mean annual temperature, soil organic contents and phosphorus availability and with increasing evapo-transpiration rates and soil pH. Under these conditions, plants with AM become dominant (Read, 1991); thus they predominate in grasslands and bush lands of arid and semiarid areas. Currently, AM fungi are believed to improve resistance of plants to water stress in the field. In arid soils, erosion results in detrimental effects on the chemical, physical and microbial properties of soil and mycorrhizal propagules are not abundant (Sylvia and Williams, 1992). AMF are fundamental for host survival in harsh conditions (Cabello, 2001). Investigations on mycorrhiza have been carried out in arid natural ecosystems worldwide (Khan, 1974; Miller, 1979; Reeves *et al*., 1979; McGee, 1986), though AM studies in South American arid regions are scarce (Dhillon *et al*., 1995).

The *Zygophyllaceae* is often considered as a non-host family (Khan, 1974; Pond *et al*., 1984; Sieverding, 1991; Varma, 1999), but colonization has been found by Staffeldt and Vogt (1974). Poaceous species form arbuscular mycorrhiza (Newsham and Watkinson, 1998).

This study was carried out in a South American natural arid secondary community named the "*Larrea divaricata* scrubland" or “Jarillal” where this zygophyllaceous plant is dominant with other poaceous species; all of them play specific roles in this ecosystem. Root colonization and fungal diversity (density and richness) of AMF spores were analyzed taking into account host species, soil moisture, season and dry-wet period.

Materials and methods

Sampling site

This research was carried out in Central Argentina, Córdoba Province, in an area located between Jaime Peter and Cruz del Eje towns, in Ischilín Department. This region belongs to the NW Argentinean Semidesertic Plains Dominion, in the arid "Chaco" Phytogeographical Province, where water availability is scarce, temperatures are uniform throughout the year, and annual mean rainfall is around 400 mm. The dry period is from April to September (autumn-winter) and the wet period from October to March (spring-summer). We studied the *Larrea divaricata* scrubland or “Jarillal” (Cabido *et al*., 1992) which is a secondary community appearing after devastation of Chaco forest caused by felling, overgrazing and burning (Cabido and Zak, 1999). The community was characterized by tree stratum which covers up to 10-15% of

the area, 5-7 m, height; shrub stratum covering 60-70%, 1-4 m, height, and grass stratum covering 30-40% (Cabido unpublished data). Three sampling sites of 20 ×150 m, each, separated by ca. 300 m, were selected.

Hosts

The species studied, all perennial, were *Poaceae*: *Neobouteloua lophostachya* (Griseb.) Gould, *Sporobolus pyramidatus* (Lam.) Hitchc. and *Trichloris crinita* (Lag.) Parodi and *Zygophyllaceae*: *Larrea divaricata* Cav.). In the "Jarillal" *L. divaricata* is the dominant species (coverage: 25-50%) followed by the grasses *Neobouteloua lophostachya* (coverage: 5-25%) and *Sporobolus pyramidatus* (coverage: 1-5%) as "disturbance indicators" and *Trichloris crinita* (coverage: 5-25%) as "herbaceous stratum fitness indicator" (Cabido *et al*., 1992).

Experimental design

In each sites, samples were collected in autumn (24-VI-99 and 15-IV-2000), winter (30-VIII-99), spring (4-XI-99), and summer (8-II-2000). Five whole (stem and root) individuals with the complete root system per host species and their rhizospheric soil were randomly collected from each site. The root system of the grasses were gathered from a depth of 10-15 cm; root system of *L. divaricata* (shrub with 20-30 cm, shoot height) with the soil adjacent were carefully dug to a depth of 30-40 cm. Samples were kept in plastic bags, at 4ºC until root samples were separated from soil, washed and fixed in FAA solution. Soil samples were kept in a refrigerator for about 1 week before processing.

Roots were cleared and stained (Grace and Stribley, 1991). Three subsamples of 100 root segments (each 1 cm, long) for each host species were analyzed at each site, for each season. Percentage of root length colonized (% RL) was quantified according to the method of Biermann and Linderman (1981). From each host species 100 colonized root fragments from each of the 3 subsamples (n = 300) were placed onto slides, and the number of fungal intraradical structures such as arbuscules, vesicles, coils and entry points was estimated following the method of Ocampo *et al*. (1980).

The rhizospheric soil from 5 host individuals for each species from the same sample site was mixed, and 100 g, wet weight was separated and dried to give constant weight. Water loss was expressed as percent gravimetric soil moisture for each sample site. Physico-chemical analysis was performed using a fraction of rhizospheric soil. For the spore and sporocarps extraction, 100 g, dry weight soil were treated by the wet sieving and decanting method

(Gerdemann and Nicolson, 1963). The resulting material was centrifuged with 80% sucrose (Walker *et al*., 1982). Quantification was carried out in 9-cm-diameter Petri dishes with a 1 cm square gridline under a stereoscopic microscope at 50×. In the major fractions (500 and 250 µm sieves) the total divisions were counted, while only 10 divisions were counted in the minor one (45 µm). These 10 divisions were related to the total number of spores, using the method modified by McKenney and Lindsey (1987). Sporocarps were counted as one spore. For the taxonomic identification, fungal spores and sporocarps were mounted onto slides using PVA (Omar *et al*., 1979) with and without Melzer reagent (Morton, 1988). Vouchers were deposited at the LPS Herbarium (Instituto Spegazzini, La Plata), Argentina.

The total fungal density was considered as total spore number per 100 g, of dried soil, and spore density of each fungal species as the spore number of a specific fungal species per 100 g, of dried soil. Spore richness was counted as total number of fungal species per 100 g, of dried soil, and it was used as the absolute value of richness.

Table 1. Characteristics of rhizospheric soil from different host species.

Rhizospheric soil	pH	Electrical conductivity (mmhos/cm)	OM	C_{ox} %	N total	$P_{extract.}$ (ppm)	Ca	Mg	Na	K	CEC (cmolc/kg)
Larrea divaricata	7.8	0.38	3.9	1.3	0.13	18.2	5.5	1.6	0.2	1.0	7.3
Neobouteloua lophostachya	7.8	0.34	3.6	0.9	0.12	12.7	4.7	1.3	0.3	1.0	6.6
Sporobolus pyramidatus	7.0	0.36	3.8	1.2	0.14	21.8	3.8	1.4	0.3	0.9	7.9
Trichloris crinita	7.1	0.38	4.1	1.2	0.14	23.3	4.4	4.7	0.2	0.9	8.8

OM: organic matter; CEC: cation exchange capacity.

Data analysis

None of the variables analyzed (percentage of root length colonized; percentage intraradical structures; total and specific spore density; spore richness; percent gravimetric soil moisture) was normally distributed, and data transformation was not suitable for parametric analysis. Data were compared using ranks when the factors had more than two levels (season and host species) by Kruskall-Wallis one-way analysis, and Mann-Whitney U-test when factors had only two levels (dry-wet periods) using SPSS (Systat Co.). When Kruskall Wallis showed significant differences, data were analyzed by *a*

posteriori test of the post-hoc multiple comparison method (Marascuilo and McSweeney, 1977) using the Infostat statistic program (Infostat Beta Version, Department of Statistics and Biometry, Faculty of Agronomic Sciences, National University of Córdoba, Córdoba, Argentina). All factors were analyzed at $\alpha = 0.05$ and $P \leq 0.005$ significance. Spearman rank correlation was used to examine the relationship between percent gravimetric soil moisture and spore total density with a 2-tailed *a posteriori* test.

Results

Soil characteristics

Texture varied from loamy to sandy loam. Soils had neutral to basic pH, mean to high degradation velocity and low organic matter, with a large amount of available phosphorus (Kurtz and Bray 1) and N (Table 1).

Root colonization

Root colonization varied significantly with seasons and host species. The highest values of colonization were found in summer-spring, followed by autumn and winter. Periods (dry and wet) did not influence colonization values. Among host species, the highest values were found in *Larrea*. *divaricata* followed by *Trichloris crinita*, *Sporobolus pyramidatus* and *Neobouteloua lophostachya*.

Table 2. Seasonal percent root length colonization from different host species.

Host	Autumn	Winter	Spring	Summer
Larrea divaricata	2.29 ± 1.29^{ab}	wfr	17.40 ± 4.80^{c}	23.12 ± 5.13^{c}
Neobouteloua lophostachya	4.44 ± 0.90^{b}	0.17 ± 0.73^{a}	1.72 ± 0.51^{a}	1.04 ± 0.23^{a}
Sporobolus pyramidatus	1.20 ± 0.39^{a}	1.03 ± 0.51^{a}	2.67 ± 0.84^{ab}	1.38 ± 0.43^{a}
Trichloris crinita	5.24 ± 1.28^{b}	1.90 ± 0.80^{a}	3.62 ± 1.62^{b}	6.72 ± 1.69^{b}

Values are mean ± standard error. Data were analyzed by nonparametric statistical methods (Kruskal Wallis and Mann Whitney tests). Different letters indicate significant differences according with *a posteriori* test of post-hoc multiple comparison method. (wfr: without fine roots)

Seasonal variations in the colonization are showed in Table 2. In autumn, root length colonization showed significant differences among host species. *Trichloris crinita* showed the highest percentages followed by *Neobouteloua lophostachya*, *Larrea divaricata* and *Sporobolus pyramidatus*. In winter, *L. divaricata* could not be quantified due to the absence of thin roots; thus, only

grass roots were analyzed. In this season, the percentages did not vary significantly with host species. In spring and summer, host species strongly affected colonization which showed the highest value in *Larrea divaricata,* followed by *Trichloris crinita*, *Sporobolus pyramidatus* and *Neobouteloua lophostachya*.

Intraradical fungal structures

Table 3 shows the intraradical fungal structures analyzed according to seasons and host species. Vesicles showed significant differences among host in all seasons. The highest values were found in *Larrea divaricata* in summer. Arbuscles showed significant differences among species only in summer. Entry points and coils showed significant differences among host species in autumn and summer.

Rhizospheric spores

In the rhizospheric soil, total spore density and percent gravimetric soil moisture were related; the correlation was significant, negative and modest (r = -0.498, P = 0.013) in dry period -autumn and winter- and not significant, positive and weak (r = 0.027, P = 0.901) in wet period -spring and summer-. When data were analyzed in each season separately, these variables showed a significant, negative and strong correlation (r = -0.747, P = 0.003) only in autumn, whereas in winter there was no correlation. In spring, correlation was very weak and negative (r = -0.117, P = 0.359), and in summer it was weak and positive (r = 0.257, P = 0.21); neither spring nor summer correlation was significant.

Rhizospheric percent gravimetric soil moisture

This variable (Table 4) showed significant differences according to seasons and periods; host species did not influence it. Percent gravimetric soil moisture was higher in summer and spring (wet period); its values were nearly zero in autumn as well as in winter (dry period).

Total spore density

Total spore density (Table 4) was not influenced by seasons and periods, but it was modified by host species. Thus, *Trichloris crinita, Sporobolus*

Table 3. Seasonal variation of percentage of vesicules, arbuscules, entry points and coils analysed in different host species.

	Host	% Vesicules	% Arbuscules	% Entry points	% Coils
Autumn	*Larrea divaricata*	0.26±0.15[d]	0.008±0.008[a]	0.11±0.05[b]	wd
	Neobouteloua lophostachya	2.86±1.07[a]	0±0[a]	0.08±0.03[c]	0.01±0.009[b]
	Sporobolus pyramidatus	1.20±0.63[c]	0.008±0.006[a]	0.23±0.07[a]	0.005±0.004[c]
	Trichloris crinita	2.40±0.80[b]	0.006±0.005[a]	1.90±0.61[a]	0.11±0.05[a]
Winter	*Larrea divaricata*	wfr	wfr	wfr	wfr
	Neobouteloua lophostachya	0.07±0.04[c]	0.011±0.007[a]	0±0[a]	wd
	Sporobolus pyramidatus	0.42±0.17[b]	0.20±0.07[a]	0±0[a]	0.007±0.007[a]
	Trichloris crinita	1.30±0.50[a]	0.40±0.22[a]	0±0[a]	0.006±0.003[a]
Spring	*Larrea divaricata*	3.41±1.50[a]	0.40±0.40[a]	0.60±0.40[a]	0±0[a]
	Neobouteloua lophostachya	0.13±0.06[d]	0±0[a]	0.02±0.01[a]	0±0[a]
	Sporobolus pyramidatus	0.41±0.14[b]	0±0[a]	0.01±0.01[a]	0±0[a]
	Trichloris crinita	0.23±0.12[c]	0.007±0.007[a]	0.11±0.07[a]	0.03±0.02[a]
Summer	*Larrea divaricata*	7.90±1.73[a]	0.00±0.005[c]	3.30±0.72[a]	0±0[c]
	Neobouteloua lophostachya	0.53±0.40[d]	0±0[d]	0.13±0.05[d]	0±0[c]
	Sporobolus pyramidatus	0.61±0.20[c]	0.01±0.01[b]	0.23±0.005[c]	0.003±0.002[b]
	Trichloris crinita	1.80±0.44[b]	0.24±0.07[a]	2.40±0.71[b]	0.08±0.04[a]

Data followed by de same letter are not significantly different from each other ($P \geq 0.05$) according to *a posteriori* test of the multiple comparison of Kruskall-Wallis one-way analysis.
[wfr] Without fine roots
[wd] Without data

pyramidatus and *Larrea divaricata* showed the highest total spore density, whereas *Neobouteloua lophostachya* showed the lowest density.

Spore richness

In the "Jarillal" a total of 7 AMF entities were found: *Entrophospora infrequens* (Hall) Ames & Schneider, *Gigaspora* sp., *Glomus* sp., *Glomus aggregatum* Schenck & Smith emend. Koske, *Glomus ambisporum* Smith & Schenck, *Glomus mosseae* (Nicolson & Gerd.) & Trappe and *Glomus sinuosum* (Gerd. & Bakshi) Almeida & Schenck. Spore richness (Table 4) was found to be affected by seasons and periods; however, it was not modified by host

species. The highest spore richness values were found in autumn and winter (dry period).

Table 4. Percent gravimetric soil moisture, total spore density/100 g, of dry soil and spore richness/100 g, of dry soil related to seasons, periods (dry and wet) and host species.

		Percent gravimetric soil moisture	Total spore density	Spore richness
Season	Autumn	2.46±1.16[b]	115.42±28.09[a]	3.75±0.30[ab]
	Winter	0[a]	162.92±46.27[a]	4.08±0.19[b]
	Spring	9.92±0.58[c]	122.33±25.76[a]	3.25±0.35[a]
	Summer	10.83±0.49[c]	142.50±28.84[a]	3.03±0.19[a]
Period	Dry	1.23±0.62[a]	139.17±26.93 [a]	3.92±0.18[b]
	Wet	10.37±0.38[b]	132.42±19.03 [a]	3.17±0.19[a]
Host	*Larrea divaricata*	5.00±1.53[a]	158.92±29.79[b]	3.50±0.26[a]
	Neobouteloua lophostachya	6.96±1.26[a]	69.75±20.36[a]	3.33±0.22[a]
	Sporobolus pyramidatus	5.00±1.41[a]	168.58±43.55[b]	3.67±0.31[a]
	Trichloris crinita	6.25±1.92[a]	145.92±28.27[b]	3.67±0.35[a]

Values are mean ± standard error. Data were analyzed by non parametric statistical tests (Kruskal Wallis and Mann Whitney tests). Different letters indicate significant differences according with *a posteriori* test of post-hoc multiple comparison method.

Specific spore density

Table 5 shows data for specific spore density throughout the seasons, dry-wet periods and host species. *Entrophospora infrequens* and *Glomus* sp. were influenced by seasons but each one showed a different pattern. *Entrophospora infrequens* had low density with higher values in winter decreasing in autumn, summer and spring; *Glomus* sp., was higher in autumn than in spring, and its spores could not be found in summer and winter. The most abundant species was *Glomus ambisporum*, although its spore density was not influenced by seasons as it was in *Gigaspora* sp., *Glomus aggregatum*, *Glomus mosseae* and *G. sinuosum*. *Entrophospora infrequens* and *Glomus aggregatum* were positively influenced by dry period, whereas *G. ambisporum* showed the opposite; *Gigaspora* sp., *Glomus* sp., *G. mosseae* and *G. sinuosum* did not present differences between periods. *Glomus ambisporum* was the only AMF species influenced by host species. This species produced the highest number of spores in the rhizosphere of *Sporobolus pyramidatus*, *Trichloris crinita* and *Larrea divaricata*, the lowest value was found in *Neobouteloua*

lophostachya. On the other hand, *Entrophospora infrequens*, *Gigaspora* sp., *Glomus mosseae*, *G. aggregatum*, *Glomus* sp. and *G. sinuosum* were not modified by host species.

Table 5. AMF spores density related to seasons, period and host species.

		Entrophospora ***infrequens***	***Gigaspora*** sp	***Glomus ambisporum***	***Glomus mosseae***	***Glomus aggregatum***	***Glomus*** sp.	***Glomus sinuosum***
Season	Autumn	32.17± 16.45^{c}	0^{a}	40.33± 13.77^{a}	7.75 ± 5.81^{a}	6.08± 3.61^{a}	17.83± 7.77^{b}	10.00± 2.28^{a}
	Winter	32.75± 6.70^{c}	10.42 ± 6.97^{a}	96.33 ± 44.36^{a}	0^{a}	11.83 ± 4.22^{a}	0^{a}	13.33± 2.95^{a}
	Spring	4.17 ± 4.17^{a}	3.67 ± 2.13^{a}	84.42 ± 21.76^{a}	0.17 ± 0.11^{a}	5.42 ± 3.05^{a}	13.33 ± 6.09^{b}	11.25 ± 1.87^{a}
	Summer	12.25± 7.49^{b}	1.83 ± 0.96^{a}	114.00 ± 27.33^{a}	1.00 ± 0.66^{a}	2.17 ± 1.15^{a}	0^{a}	11.25 ± 1.51^{a}
Period	Dry	32.46 ± 8.69^{b}	5.21 ± 3.57^{a}	68.33 ± 23.45^{a}	3.87 ± 2.95^{a}	8.96 ± 2.78^{b}	8.92 ± 4.23^{a}	11.67 ± 1.86^{a}
	Wet	8.21± 4.27^{a}	2.75 ±1.16^{a}	99.21 ± 17.36^{b}	0.58 ± 0.34^{a}	3.79 ± 1.63^{a}	6.67± 3.29^{a}	11.25 ± 1.18^{a}
Host	*Larrea divaricata*	33.33 ± 16.17^{a}	2.17 ± 1.64^{a}	82.25 ± 22.13^{b}	0.75 ± 0.66^{a}	8.08 ± 3.99^{a}	21.25 ± 9.16^{a}	9.75 ± 1.34^{a}
	Neobouteloua lophostachya	7.42± 2.77^{a}	2.08 ± 1.62^{a}	35.33 ± 20.99^{a}	6.17 ± 5.89^{a}	6.08 ± 3.8^{a}	4.00 ± 2.69^{a}	8.67 ± 1.46^{a}
	Sporobolus pyramidatus	22.67 ± 9.89^{a}	2.00 ± 1.09^{a}	121.25 ± 43.29^{b}	1.25 ± 0.79^{a}	4.17 ± 2.43^{a}	4.75 ± 0.64^{a}	14.33 ± 2.79^{a}
	Trichloris crinita	17.92± 6.86^{a}	9.67 ± 6.86^{a}	96.25 ± 22.11^{b}	0.75 ± 0.51^{a}	7.17 ± 2.97^{a}	1.17± 0.82^{a}	13.08± 2.54^{a}

Values are mean ± standard error. Data were analyzed by non parametric statistical methods (Kruskal Wallis and Mann Whitney tests). Different letters indicate significant differences.

Discussion

The family *Zygophyllaceae* is regarded as a non-mycorrhizal arbuscular host family by some authors (e.g. Varma, 1999; Sieverding, 1991). Some species of the genera *Fagonia, Pegenum, Tribulus* and *Zygophyllum* have been reported without AM colonization in arid regions of Pakistan (Khan, 1974), whereas *Larrea tridentata* has been found to have mycorrhizal associations in certain regions of the United States (Staffeldt and Vogt, 1974), although this is not always the case (Pond *et al*., 1984). In the area studied here, *Larrea divaricata (Zygophyllaceae*) is the dominant plant species with high levels of mycorrhizal colonization, thus supporting the hypothesis that dominant species are closely related to AM fungi (Grime *et al*., 1987; Sanders and Fitter, 1992a; Gange *et al*., 1993; Wilson and Hartnell, 1997). The “Jarillal” is a community formed secondarily after “W Chaco Forest” felling, overgrazing or burning

(Cabido and Zak, 1999). *Larrea divaricata* plays an important role as a wet nurse plant in soils disturbed by fire (Rossi and Villagra, 2001), allowing the growth of other species within the community. *Larrea divaricata* exerts beneficial effects at early successive stages after strong disturbance.

The other hosts studied here belong in the family *Poaceae*. *Trichloris crinita* is an indicator of the "goodness herbaceous stratum", and *Sporobolus pyramidatus* and *Neobouteloua Iophostachya* are closely related to the "Jarillal" and "disturbance indicators" (Cabido *et al*., 1992). Mycorrhizal fungi not only affect the nutritional aspects of plants but they also determine the vegetal composition of the community they are associated with (Francis and Read, 1994). It is important to take into account the role-played by each host within the community; in the "Jarillal", *Trichloris crinita* was found to be the second most colonized host, whereas *Sporobolus pyramidatus* and *Neobouteloua lophostachya* showed lowest values; both of them were clearly related to major perturbation within the system. It is well known that perturbation negatively affects the mycorrhizal association in these environments (Miller, 1979; Moorman and Reeves, 1979; Reeves *et al*., 1979), and that the structure of the vegetal community depends, in part, on the structure of the AMF community (van der Heijden *et al*., 1998).

Seasonality had a significant affect on root colonization by mycorrhizal fungi (Lugo *et al*., 2003). The greatest percentage of colonization was recorded in the summer, followed by the spring, autumn and winter. It must be noted that, in this community without thermal winter, two periods are strongly marked by water availability in the soil. One of them is the wet period (spring – summer) and the other is the dry season (autumn – winter). Water availability influences root colonization with percent gravimetric moisture being significantly higher during the wet period.

In arid regions, AMF spore germination is slow (Varma, 1999), and the percent gravimetric moisture could even decrease spore germination rates. This occurrence would favor a greater availability of mycelium in the soil. Hence, the major root colonization occurs during the wet period since water is essential for the fungal mycelium growth (Smith and Read, 1997). Our observations concerning seasonal changes with root colonization, and its relationship to the host phenology and water availability in soil, were similar to those results reported by other authors (Ebbers *et al*., 1987; Bentivenga and Hetrick, 1992; Rosendahl and Rosendahl, 1992; Sanders and Fitter, 1992a; De Mars and Boerner, 1995; Sigüenza *et al*., 1996; Wilson and Hartnett, 1997; Lugo, 1999).

Among the intraradical structures fluctuating with seasons and host species, following a similar pattern to that of root colonization, only arbuscles

were influenced by the wet period due to the fact that water is indispensable for their formation. Some authors argue that arbuscules are important in mycorrhizal symbiosis in spite of the fact that they were absent in *Neobouteloua lophostachya* and scarcely found in *Sporobolus pyramidatus*, indicating their role in perturbation. Vesicles were abundant in *Larrea divaricata* whereas coils could be detected only in *poaceous* hosts. The absence of coils in *L. divaricata* could be attributed to their particular root anatomy which may have affected the colonization morphology. *Entrophospora infrequens* and *Gigaspora* sp. may be AMF species involved in the formation of intraradical coils, but these taxa were not found associated with any host.

The percent gravimetric soil moisture was negatively correlated to the total spore density in the dry period. The result was consistent with Anderson *et al*. (1983), but differed from those of Dickman et al. (1984); these data, however, come from ecosystems markedly different to the "Jarillal". This negative correlation based on samples from rhizospheric soil might indicate that the increased sporulation could be a mechanism of resistance or adaptation, enabling the AMF to survive during an unfavorable season. The total spore density was found to be low when compared to that obtained by other authors (e.g. Rathore and Singh, 1995) from similar soils. In this regard, the community studied may be considered as one of substitution or healing after the cutting down of trees, overgrazing, or fires in the "Chaco" forest; these occurrences cause strong perturbation in the AMF community, leading to subsequent biodiversity loss.

Although the percent gravimetric soil moisture changed significantly with seasons and different periods, the total spore density was not modified by any of the above factors, but the large amount of spores was counterbalanced by soil moisture. The abundance of spores, almost constant over the year could be due to, either the thermal uniformity of the "Jarillal" or to the differential spore supply of different species which would sporulate more or less, according to soil moisture. It is clearly shown that the spore specific density in *Entrophospora infrequens, Glomus mosseae and Glomus* sp. is related to seasonal changes. Certain AMF species such as *Entrophospora infrequens* and *Glomus aggregatum* are strongly influenced by the season; they sporulate more during the dry period. However, *Glomus ambisporum* produces more spores in the wet period; a fact that would clarify the differences in their abundance, although the total spore density did not alter. However, it was strongly affected by the host species, showing the highest values in the rhizosphere of *Trichloris crinita, Sporobolus pyramidatus*, and *Larrea divaricata* whereas the lowest value was found in *Neobouteloua Iophostachya*. The behavior of the spore specific density in *Glomus ambisporum* showed the same pattern; this species

yielded the largest amount of spores throughout the year. Then, we think that fluctuations between total spore density and the host largely depend on this fungal symbiont. Concerning specific density, the second abundant species was *Glomus sinuosum*. It is a sporocarpic species like *Glomus ambisporum*, and quite common in other non- secondary "Jarillal" forests in the province of Mendoza where it was found to be associated to *Trichloris crinita*, and to that of other *Poaceae* (Lugo *et al*. 1995). Both fungal species give rise to sporocarps featured by the peridium as a protecting structure. For this reason, their growth may have been favored in arid regions.

It must be pointed out that, of all factors studied, the season markedly influenced the abundance and diversity of AMF spores whereas the host species had no correlation to rhizospheric spore production in most AMF species in the "Jarillal".

As noted, water is a key factor in the composition and functioning of the plant-fungus community. Healing or secondary stage plant communities have low fungal diversity as compared to permanent "long term" plant communities, a fact in agreement with the low physiological specificity or differential association hypothesis (Hetrick *et al*., 1990; Sanders and Fitter, 1992b; Hartnett *et al*., 1993; Bever *et al*., 1996; Read, 1998; van der Heijden *et al*., 1998; Lugo and Cabello, 2002). It is well-known that the number of spores present does not always represent the AMF community (Clapp *et al*., 1995), but the seasonal survey was designed to show a direct cause and effect relationship between them.

In the last few years, important contributions have been made in order to understand the behavior of AMF communities, and their effect upon plant communities (Grime *et al*., 1987; Francis and Read, 1994; Newsham *et al*., 1995; Wilson and Hartnett, 1997; van der Heijden *et al*., 1998; Hart *et al*., 2001). We are in agreement with Hart *et al*. (2001) in that "natural communities may function at some intermediate level between the extremes – passenger or driver". In the secondary community of "Jarillal" of arid "Chaco" we found the features of a disturbed system with low AMF diversity and relatively low root colonization, but these results come from a low diversity plant community. Also, chronological changes should be taken into account, the AMF low diversity possibly being related to the successive stages of the system as proposed by Johnson *et al*. (1991). Considering Hart *et al*. (2001) proposal, the AMF community in this "Jarillal" would be formed by one passenger and some drivers. But, which one is the first? The passenger or the driver? Taking into account this theoretical hypothesis we could analyze the AMF community in the undisturbed "Chaco" forest where greater plant community diversity is found. Then, we are able to compare this undisturbed

forest to the secondary “Jarillal” in order to get a better insight into the community plant-AMF associations.

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