Mycologia, 103(2), 2011, pp. 273–279. DOI: 10.3852/10-193

Native arbuscular mycorrhizal fungi in the Yungas forests, Argentina

Alejandra G. Becerra[1]

Instituto Multidisciplinario de Biología Vegetal (CONICET), Cátedra de Diversidad Vegetal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, C.C. 495, 5000 Córdoba, República Argentina

Marta N. Cabello

Instituto Spegazzini, Facultad de Ciencias Naturales y Museo, Avenida 53, No. 477, 1900 La Plata, República Argentina

Norberto J. Bartoloni

Cátedra de Métodos Cuantitativos Aplicados, Facultad de Agronomía, UBA, República Argentina

Abstract: The arbuscular mycorrhizal fungal (AMF) communities from the Yungas forests of Argentina were studied. The AMF species present in the rhizosphere of some dominant native plants (one tree: *Alnus acuminata*; three herbaceous species: *Duchesnea indica*, *Oxalis conorrhiza*, *Trifolium* aff. *repens*; and one shrub: *Sambucus peruviana*) from two sites (Quebrada del Portugués and Narváez Range) of the Yungas forests were isolated, identified and quantified during the four seasons of the year. Twenty-two AMF morphotaxa were found. Spore density of some AMF species at each site varied among seasons. The genera that most contributed to the biodiversity index were *Acaulospora* for Quebrada del Portugués and *Glomus* for Narváez Range. High diversity values were observed in the Yungas forests, particularly in the spring (rainy season). We concluded AMF differed in species composition and seasonal sporulation dynamics in the Yungas forests.

Key words: *Alnus* forests, AM fungal diversity, *Glomeromycota*, montane cloud forest, seasonality

INTRODUCTION

The Yungas or Tucumán-Bolivian forests (Cabrera 1976, Hueck 1978), which belong to the humid subtropical South American ecosystems, are among the environmental units of the Montane Cloud Forest. The Yungas are of great regional importance due to their high biodiversity (Brown et al. 1993), one of the most important plant communities being the forest of *Alnus acuminata* Kunth (Betulaceae) (Cabrera 1976), a pioneer species that colonizes disturbed areas (Grau 1985, Aceñolaza 1995).

Submitted 11 Jun 2010; accepted for publication 8 Sep 2010.
[1] Corresponding author. E-mail: abecerra@efn.uncor.edu

Alnus acuminata (Andean alder) forms ectomycorrhizal (Becerra et al. 2002, 2005a–d), arbuscular mycorrhizal (AM) (Becerra and Cabello 2007, Becerra et al. 2007, Becerra et al. 2009) and actinorrhizal relationships with *Frankia* (Carú et al. 2000). Through these highly efficient symbioses, in which microsymbionts benefit from plant photosynthates, actinorrhizal plants such as alders colonize poor substrates, enrich the soil and initiate plant succession (Roy et al. 2007).

Arbuscular mycorrhizae are the most widespread plant symbiosis in nature, mycorrhizal fungi being key components of natural ecosystems. The presence of arbuscular mycorrhizal fungi (AMF) has been shown to have a great influence on the structure of plant populations (Lu and Koide 1994, Philip et al. 2001) and communities (Hart et al. 2001) as well as on ecosystem processes (Rillig 2004), such as soil aggregation (Tisdall and Oades 1982) and nutrient cycling (Read and Perez-Moreno 2003). Most natural plant communities contain AMF communities that vary in composition and species numbers (Helgason et al. 1998, 2002).

Although AM fungi are not host specific, different fungal isolates are more beneficial to some hosts than to others (Gange et al. 1993, Kiers et al. 2000) and AM fungal communities have been observed to vary significantly with different host species (Sieverding 1989, Eom et al. 2000, Lovelock et al. 2003).

We recently studied the AM colonization and AMF spore density associated with the dominant plant species (one tree: *Alnus acuminata* Kuthn; three herbaceous species: *Duchesnea indica* (Andrews) Focke, *Oxalis conorrhiza* Jacq., *Trifolium* aff. *repens* L.; and one shrub: *Sambucus peruviana* Kunth) present in soils from the Yungas forest (Becerra et al. 2009) and found that these mycorrhizal variables varied among plant species depending on phenological, climatic and edaphic conditions. In the present study we focused further on the seasonal changes of the AMF spore community present in the rhizosphere soils of the dominant plant species from two sites of the Yungas forests. These sites differ in mean annual precipitation and soil type, but mean annual temperatures and understory vegetation are similar at both locations.

MATERIALS AND METHODS

Study area.—We worked at two sites of the Yungas, in northwestern Argentina (NWA). One is Quebrada del Portugués (QP), Tafí del Valle (Tucumán Province), which

is at 26°58′S, 65°45′W, 2187 m, with average yearly precipitation of 1200–1500 mm. Soil at QP is characterized as lithic ustorthent, a sandy loam (Vargas Gil and Bianchi 1981). The other is Narváez Range (NR), (Catamarca Province), at 27°43′S 65°54′W, 1820 m, with yearly average precipitation of 698 mm. Soil at NR is characterized as typic ustorthent, a coarse loam (Vargas Gil and Bianchi 1981). The soils from NR have higher contents of organic matter, total N and water-holding capacity than soil at QP, which had slightly higher P (Becerra et al. 2009). Mean annual temperatures are 5.8–24 C for both locations. The vegetation at both sites is a nearly homogeneous *A. acuminata* forest (6–15 m tall, 20–30 y old) with few herbaceous mycorrhizal understory plants, such as *Duschesnea* sp., *Conyza* sp., *Axonopus* sp., *Selaginella* sp. and *Prunella* sp. (Aceñolaza 1995, Becerra et al. 2007).

Host species.—Hosts were selected with the Braun-Blanquet (1965) method (abundance scale of + to 5). The dominant species were the tree *Alnus acuminata* (Braun-Blanquet: 4/5), the herbaceous understory species *Duchesnea indica* (Rosaceae) (Braun-Blanquet: 2), *Oxalis conorrhiza* (Oxalidaceae) (Braun-Blanquet: 2) and *Trifolium* aff. *repens* (Fabaceae) (Braun-Blanquet: 2), and the shrub *Sambucus peruviana* (Caprifoliaceae) (Braun-Blanquet: 1). The most common plant species at these sites are listed in Becerra et al. (2007).

Sample collection.—Soil sampling was conducted at both locations in autumn (May 2001, dry season), winter (Jul 2002, dry season), spring (Nov 2002, rainy season) and summer (Mar 2002, rainy season). Plots of 30 × 30 m were selected at each site (QP and NR) taking into account the same floristic composition. Ten soil samples from each of the dominant plant species (*A. acuminata*, *D. indica*, *O. conorrhiza*, *T.* aff. *repens* and *S. peruviana*) were collected at each site during each season. Samples were collected by carefully digging around selected plants. Soil sample size for *A. acuminata* trees and *S. peruviana* shrubs was 15 × 15 × 25 deep cm excavated at 15–50 cm from the trunk of trees and shrubs. Most *A. acuminata* and *S. peruviana* roots occurred in the top 20 cm of soil. For herbs (*D. indica*, *O. conorrhiza* and *T.* aff. *repens*) the whole root system was sampled. Samples were placed in plastic bags and stored at 4 C.

Extraction and counting of AMF spores.—Ten soil samples representing each plant species at each site and sample date were pooled and thoroughly mixed. Three aliquots of 100 g (dry weight) soil were processed for each pooled sample. Spores were extracted from the soil by wet-sieving and decanting (Gerdemann and Nicholson 1963), followed by centrifugation in sucrose (Walker et al. 1982). A sieve (38 μm) was used to collect small spores, and the coarse material remaining on the top sieve (500 μm) was checked for sporocarps and large spores. Only apparently healthy spores were counted in a 9 cm Petri dish by direct observation under a stereoscope at 40–100× magnification. Sporocarps were counted as a single spore.

Each spore type was mounted in polyvinyl alcohol-lactic acid-glycerin (PVLG) and PVLG + Melzer's reagent for identification. The identification was based on spore color, size, surface ornamentation and wall structure, following the current taxonomic criteria (Schenck and Perez 1990, International Culture Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi, http://invam.caf.wvu.edu, Blaszkowski AMF site www.agro.ar.szczecin.pl/~jblaszkowski/). Further details of AM fungal spore identification in this study can be found in Becerra and Cabello (2008). Specimens not identified were maintained in culture and named with the genera followed by an identification number. Spore density for each fungal species (specific spore density) are reported as the number of spores per 100 g dry soil. Soil moisture content was calculated for each soil sample as percent oven-dry weight of soil by drying at 80 C for 48 h.

Ecological measures of diversity.—The fungal specific spore density was used to calculate the biodiversity index Shannon-Weaver biodiversity index (H), species richness (S) and evenness (E). Species richness (S) was estimated as the number of different species found in all samples. Species diversity (H), which encompasses both S and E, was calculated according to Magurran (1988) with the equation:

$$H = \sum pi \ln pi$$

where *pi* is the proportion of individuals found in the *i* species, estimated as *ni/N*; *ni* is the number of individuals in the *i* species; and *N* is the total number of individuals.

Species evenness (E) measures the presence of each species in all samples, as follows:

$$E = H/\log_2 S$$

The species contribution to H index was calculated as:

$$pi(\log_2 pi)$$

Statistical analysis.—The mean values of three aliquots of the rhizosphere soil of each plant species (*A. acuminata*, *S. peruviana*, *D. indica*, *O. conorrhiza* and *T.* aff. *repens*) were considered as one replicate, making a total of five replicates per site and season. These data were used to calculate the AMF species spore density, species contribution to diversity (H), total diversity (H), richness (S) and evenness (E) at each site and season without considering the host plant. Spore densities, species richness, evenness and diversity were not normally distributed, according to Kolmogorov-Smirnov and Shapiro-Wilks normality tests, and variances were not homogeneous (Levene's test). Therefore data were compared by Kruskal-Wallis one-way analysis of variance by ranks and multiple comparisons between the samples with Conover test. Spearman's correlation analyses were used to test correlations between AMF diversity (H), fungal richness (S) and evenness (E). All statistical analyses were performed with Infostat (2001).

RESULTS

Twenty-two species of AMF spores were common to both sites. Spores belonged to orders Glomerales, Diversisporales and Archaeosporales and were represented by families Acaulosporaceae, Ambisporaceae,

Entrophosporaceae, Glomeraceae, Pacisporaceae and Gigasporaceae. The AMF found in Narváez Range were *Acaulospora denticulata* Sieverd. & Toro, *A. excavata* Ingleby & Walker, *A. laevis* Gerd. & Trappe, *A. mellea* Spain & Schenck, *A. rehmii* Sieverd. & Toro, *A. scrobiculata* Trappe, *A. spinosa* Walker & Trappe, *Ambispora leptoticha* Walker, Vestberg & Schuessler, *Pacispora chimonobambusae* (Wu & Liu) Sieverd. & Oehl, *Glomus claroideum* Schenck & Smith, *G. clarum* Nicolson & Schenck, *G. fuegianum* (Speg.) Trappe & Gerd., *G. geosporum* (Nicolson & Gerd.) Walker, *G. intraradices* Schenck & Smith, *G. lacteum* Rose & Trappe, *Glomus* sp., *Entrophospora infrequens* (Hall) Ames & Schneider, *Scutellospora biornata* Spain, Sieverd. & Toro, *Scutellospora* sp., *Scutellospora dipapilosa* (Walker & Koske) Walker & Sanders. The same AMF species were found in Quebrada del Portugués, although two additional undescribed species of *Acaulospora* (*Acaulospora* sp. 1 and *Acaulospora* sp. 2) also were found at QP.

Specific spore density.—The density of some AM fungal species showed significant seasonal variations. At NR (TABLE I) *Acaulospora excavata*, *A. mellea*, *Glomus fuegianum*, *G. geosporum*, *G. intraradices*, *Glomus* sp. and *P. chimonobambusae* had the highest density in spring (rainy season). At QP (TABLE I) highest density values were recorded as *A. laevis* and *G. fuegianum* in autumn (dry season) and spring, *Scutellospora* sp. in spring. The remaining fungal species were not influenced by seasons.

Species contribution to H index.—Biodiversity index, considering all four seasons, in NR was 1.17. The contribution of genus *Glomus* was 52% (H = 0.604) (*Glomus fuegianum* = 0.19, *G. geosporum* = 0.15, *Glomus* sp. = 0.12, *G. claroideum* = 0.08, *G. intraradices* = 0.05, *G. lacteum* = 0.02, *G. clarum* = 0.01), whereas the contribution of genus *Acaulospora* was 31% (H = 0.36) (*Acaulospora laevis* = 0.12, *A. excavata* = 0.09, *A. mellea* = 0.08, *A. scrobiculata* = 0.05, *A. rehmii* = 0.02, *A. spinosa* = 0.01, *A. denticulata* = 0.0004). The contribution of genus *Scutellospora* was 2.6% (H = 0.03) (*Scutellospora biornata* = 0.02, *Scutellospora* sp. = 0.01).

The site QP had a biodiversity index, considering all four seasons, of 1.11. Genus *Acaulospora* accounted for 45% of biodiversity (H = 0.50) (*Acaulospora laevis* = 0.25, *A. scrobiculata* = 0.08, *A. mellea* = 0.07, *A. excavata* = 0.05, *A. rehmii* = 0.02, *A. spinosa* = 0.012, *Acaulospora* sp. 1 = 0.01, *Acaulospora* sp. 2 = 0.001, *A. denticulata* = 0.001), whereas genus *Glomus* contributed with 38% (H = 0.42) (*Glomus fuegianum* = 0.17, *G. geosporum* = 0.10, *G. claroideum* = 0.07, *G. intraradices* = 0.03, *Glomus* sp.= 0.02, *G. lacteum* = 0.02, *G. clarum* = 0.001). The contribution of genus *Scutellospora* was 3.6% (H = 0.04) (*Scutellospora biornata* = 0.03; *Scutellospora* sp. = 0.01).

Diversity, richness and evenness.—The biodiversity index (H), richness (S) and evenness (E) of the AMF spore community at both forest sites per season are provided (TABLE II). The diversity index and species richness varied significantly between seasons at each site. In general for both sites higher diversity and richness were observed in spring (rainy season). Species richness and evenness were positively correlated with the biodiversity index ($r = 0.74$, $P < 0.0001$, $r = 0.59$, $P < 0.001$ respectively), but richness was more important than evenness in explaining changes in the diversity index.

DISCUSSION

The Yungas forests, which belong to humid subtropical South American ecosystems, are among the ecosystems most affected by human activity in Argentina, with a consequent loss of biodiversity. Some previous arbuscular mycorrhizal studies have been conducted in the Yungas forest (Becerra et al. 2007, 2009; Becerra and Cabello 2008), and this study provides a baseline of data to allow for future comparisons.

Specific spore density.—AMF sporulation is seasonal (McGee 1989, Oehl et al. 2009). Specific spore density varied among seasons at each site examined here. At NR AMF species could be separated into two groups: (i) those that sporulated in spring (rainy season) (*Acaulospora excavata*, *A. mellea*, *Glomus fuegianum*, *G. geosporum*, *G. intraradices*, *Glomus* sp. and *P. chimonobambusae*) and (ii) those that sporulated throughout the year (the remaining species found). At QP only *Scutellospora* sp. preferentially sporulated in spring, while *A. laevis* and *G. fuegianum* sporulated in both autumn (dry) and spring (rainy), and the remaining species sporulated throughout the year. These differences in the time of sporulation are characteristic of AMF community dynamics, which may be explained by fungal substitution determined by different life strategies of each AMF, seasonal variation of environmental conditions and host phenology (Merryweather and Fitter 1998, Eom et al. 2000, Pringle and Bever 2002).

Species contribution to H index.—The genus that most contributed to the biodiversity index at QP was *Acaulospora* (45%), whereas *Glomus* (52%) made the greatest contribution at NR. At both sites species within Acaulosporaceae and Glomeraceae were dominant. Similar results were observed in the tropical forests of China (Zhao 1999, Zhao et al. 2001) and

TABLE I. Seasonality of specific spore density/100 g soil in Narváez Range (NR) and Quebrada del Portugués (QP). Data are means of five replicates for each site and season ± SE. Values within a row followed by a different letter were significantly different for each AMF and each site among seasons by Kruskal-Wallis non-parametric test ($P < 0.05$)

AMF species	Sites	Autumn (dry season)	Winter (dry season)	Spring (rainy season)	Summer (rainy season)
Acaulospora denticulata	NR	0 a	0 a	0.53 ± 1.2 a	0 a
	QP	0 a	4 ± 8.9 a	0.9 ± 2.1 a	0 a
A. excavata	NR	48.7 ± 45.4 ab	22 ± 6.4 abc	68 ± 74 a	1.9 ± 3.1 d
	QP	13.8 ± 14.9 abc	47.4 ± 81.7 abcd	32.1 ± 19.7 ab	5.2 ± 7.8 ab
A. laevis	NR	46 ± 12.7 a	26.7 ± 22 c	87.7 ± 14.9 ab	27 ± 7.4 c
	QP	154 ± 59.2 bc	76.6 ± 64.1 abc	126.2 ± 33.3 a	51.7 ± 39.5 bc
A. mellea	NR	55.5 ± 105.7 abc	5.7 ± 12.7 c	96.3 ± 84.2 a	5.4 ± 8.1 bc
	QP	3.7 ± 4.6 bc	10.2 ± 16 bc	86.9 ± 52.7 ab	8.7 ± 10.6 bc
A. rehmii	NR	3.7 ± 7.1 a	5.6 ± 7.8 a	1 ± 1.5 a	2.5 ± 3.1 a
	QP	0.5 ± 1 a	3.3 ± 5.4 a	24.9 ± 55.6 a	0 a
A. scrobiculata	NR	38.6 ± 77.1 a	5.4 ± 5.5 a	11.5 ± 8.8 a	5.5 ± 8.2 a
	QP	20.2 ± 13.7 a	9.2 ± 9.8 a	26.3 ± 18.2 a	30.7 ± 26.4 a
A. spinosa	NR	2 ± 4.5 a	0.5 ± 1 a	3.9 ± 3.9 a	1 ± 2.2 a
	QP	3 ± 6.7 a	3.6 ± 5.8 a	2.7 ± 3.1 a	2.8 ± 5.1 a
Acaulospora sp.1	NR	0 a	0 a	0 a	0 a
	QP	0 a	3.1 ± 4.7 a	0 a	0 a
Acaulospora sp.2	NR	0 a	0 a	0 a	0 a
	QP	0.5 ± 1 a	0 a	0.5 ± 1 a	0 a
Ambispora leptoticha	NR	50.6 ± 54.4 a	34.2 ± 27.5 a	41.5 ± 58.4 a	20.1 ± 6.9 a
	QP	31.7 ± 18.2 a	20.8 ± 16.8 a	27.0 ± 10.2 a	38.4 ± 21.5 a
Entrophospora infrequens	NR	5 ± 5.9 a	0 a	4.5 ± 4.3 a	1.9 ± 3.2 a
	QP	5.1 ± 3.2 a	3.6 ± 6.8 a	1.8 ± 3 a	0.5 ± 1 a
Glomus claroideum	NR	4.3 ± 3 a	17.6 ± 10.6 a	36.1 ± 32.3 a	25.7 ± 23 a
	QP	2.8 ± 2.6 a	16.1 ± 11.3 a	27.9 ± 15.5 a	22.3 ± 8.7 a
G. clarum	NR	0 a	0 a	0.5 ± 1 a	4.8 ± 10.7a
	QP	0 a	3.5 ± 6.7 a	0 a	0.5 ± 1 a
G. fuegianum	NR	85.9 ± 104.1 abc	14.1 ± 5.5 c	289 ± 259.1 a	53.5 ± 29.9 abc
	QP	77 ± 41.8 ab	42.5 ± 69.3 bc	131.9 ± 70.4 a	33.6 ± 28.7 bc
G. geosporum	NR	167.4 ± 221.4 ab	29.1 ± 31.4 c	91.7 ± 47.7 a	7.7 ± 7.6 c
	QP	44.8 ± 37.1 abc	26.2 ± 24.8 c	31.9 ± 18.1 bc	21.1 ± 23.4 c
G. intraradices	NR	11.3 ± 11.8 bc	5 ± 5.4 bc	42.5 ± 24.8 a	13.5 ± 14.2 abc
	QP	3.8 ± 4.3 c	5.5 ± 6 bc	21.4 ± 14.2 ab	6.1 ± 5 bc
G. lacteum	NR	8.9 ± 19.8 a	2.7 ± 3.9 a	0.5 ± 1.2 a	1.9 ± 2.6 a
	QP	16.9 ± 22.6 a	2.2 ± 3.6 a	0.5 ± 1 a	0 a
Glomus sp.	NR	58.8 ± 20.3 ab	15 ± 12.4 bcd	69.6 ± 23.9 a	42 ± 27.6 abc
	QP	10 ± 17.2 c	0.5 ± 1 c	10.7 ± 14.4 cd	3.3 ± 2.8 c
Pacispora chimonobambusae	NR	3.4 ± 6.4 c	6 ± 8.2 c	89.5 ± 60 a	6.5 ± 8 c
	QP	12.6 ± 10.3 bc	7.1 ± 9 bc	26.3 ± 19 ab	8.7 ± 5.7 bc
Scutellospora biornata	NR	3 ± 5.3 a	2.9 ± 4 a	12.1 ± 7.4 a	2.5 ± 3.7 a
	QP	4.3 ± 2.6 a	3.2 ± 2.1 a	12.4 ± 15.3 a	5.7 ± 5 a
Scutellospora sp.	NR	0 b	0 b	12.9 ± 15.6 ab	0 b
	QP	0 b	1.9 ± 3 ab	11.7 ± 9.9 a	0 b
Scutellospora dipapilosa	NR	0 a	0 a	0.5 ± 1 a	0.5 ± 1 a
	QP	0 a	0.4 ± 1 a	0.4 ± 0.9 a	1.5 ± 3.3 a

Mexico (Guadarrama and Alvarez-Sánchez 1999) as well as in temperate and tropical regions of the south and west coasts of China (Zhang et al. 1998, Shi et al. 2006). It is known that species of these families have multiple propagules (e.g. spores, hyphal fragments and mycelia within roots) that can initiate colonization (Jasper et al. 1989).

Diversity, richness and evenness.—High diversity was observed in the Yungas forests. AMF diversity values recorded in this study are higher than those found in soils under agricultural management in Minnesota (H = 0.57–0.64) (Kurle and Pfleger 1996) and in soils under cocoa production in Venezuela (H = 0.6–0.78) (Cuenca and Meneses 1996), whereas high values of

TABLE II. Biodiversity index, evenness and species richness values for AMF morphotypes found in Narváez Range and Quebrada del Portugués. Data are means of five replicates for each site and season. Values within a column followed by the same letter were not significantly different for each site among seasons ($P < 0.05$)

Seasons	Biodiversity index (H)		Evenness (E)		Richness (S)	
	QP	NR	QP	NR	QP	NR
Autumn (dry season)	2.41 ab	2.52 a	0.75 a	0.81 a	9.4 abc	9 ab
Winter (dry season)	2.32 a	2.79 ab	0.73 a	0.89 a	9 ab	9.2 abc
Spring (rainy season)	2.95 d	3.03 b	0.83 a	0.83 a	12 c	12.8 d
Summer (rainy season)	2.46 abc	2.58 ab	0.82 a	0.86 a	8.4 a	8.4 a

diversity were reported under agricultural management in Argentina (H > 2.5) (Schalamuk et al. 2006) and in unmanaged soils from Poland (H = 1.91–2.2) (Blaszkowski 1995). The latter values were similar to those found here in the Yungas and in temperate forests (Louis and Lim 1987, Morton et al. 2004).

The biodiversity index often shows a higher correlation with richness than evenness (Magurran 1988). Richness was more important than evenness in explaining the high diversity values in the AMF spore communities at both sites examined here. Richness values were 4–16, with an average of 9.8 species for the two sites. Species richness can vary between samples (Walker et al. 1982) because numerous ecological variables, such as seasonality and host dependence, influence sporulation by AMF (Morton et al. 2004). In addition the Yungas soils studied here had relatively high fertility, few AMF spores (Becerra et al. 2009) but high species richness, in agreement with observations reported by Hetrick and Bloom (1983) for grassland soils.

In conclusion this study showed that the species composition of AMF spores varied across seasons at two sites in the Yungas forest and that the overall diversity of the AMF community was highest during the spring (rainy season). Genus *Acaulospora* contributed most to the biodiversity index at QP, while *Glomus* contributed most at NR. Further long-term studies are necessary to elucidate the ecological role of different AMF in Yungas forests of Argentina.

ACKNOWLEDGMENTS

AGB is researcher of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). MNC is researcher from the Comisión de Investigaciones Científicas (CIC). We are very grateful for the aid of three anonymous reviewers who provided constructive suggestions.

LITERATURE CITED

Aceñolaza PG. 1995. Estructura y dinámica de bosques de aliso (*Alnus acuminata* HBK subsp. *acuminata*) de la Provincia de Tucumán [doctoral thesis]. Fac. de Ciencias Naturales e Instituto Miguel Lillo. Natl. Univ. Tucumán. 286 p.

Becerra A, Beenken L, Pritsch K, Daniele G, Schloter M, Agerer R. 2005c. Anatomical and molecular characterization of *Lactarius aff. omphaliformis*, *Russula alnijorullensis* and *Cortinarius tucumanensis* ectomycorrhizae on *Alnus acuminata*. Mycologia 97:1047–1057, doi:10.3852/mycologia.97.5.1047

———, Cabello M. 2007. Arbuscular mycorrhizas in *Alnus acuminata* (Betulaceae) seedlings inoculated with *Glomus intraradices* (Glomaceae). Bol Soc Arg Bot 42: 155–158.

———, ———. 2008. Arbuscular mycorrhizal fungi in the Yungas forests of *Alnus acuminata* (Betulaceae) Argentina. Bol Soc Arg Bot 43:197–203.

———, Cabello MN, Chiarini F. 2007. Arbuscular mycorrhizal colonization of vascular plants from the Yungas forests, Argentina. Ann For Sci 64:765–772, doi: 10.1051/forest:2007056

———, ———, Zak MR, Bartoloni N. 2009. Arbuscular mycorrhizae of dominant plant species in the Yungas forests, Argentina. Mycologia 101:612–621, doi:10.3852/08-176

———, Daniele G, Domínguez L, Nouhra E, Horton T. 2002. Ectomycorrhizae between *Alnus acuminata* H.B.K. and *Naucoria escharoides* (Fr.:Fr.) Kummer from Argentina. Mycorrhiza 12:61–66, doi:10.1007/s00572-001-0148-3

———, Nouhra E, Daniele G, Domínguez L, McKay D. 2005a. Ectomycorrhizas of *Cortinarius helodes* and *Gyrodon monticola* with *Alnus acuminata* from Argentina. Mycorrhiza 15:7–15, doi:10.1007/s00572-003-0278-x

———, Pritsch K, Arrigo N, Palma M, Bartoloni N. 2005d. Ectomycorrhizal colonization of *Alnus acuminata* Kunth in northwestern Argentina in relation to season and soil parameters. Ann For Sci 62:325–332, doi:10.1051/forest:2005027

———, Zak MR, Horton T, Micolini J. 2005b. Ectomycorrhizal and arbuscular mycorrhizal colonization of *Alnus acuminata* from Calilegua National Park (Argentina). Mycorrhiza 15:525–531, doi:10.1007/s00572-005-0360-7

Blaszkowski J. 1995. The influence of pre-crop plants on the occurrence of arbuscular mycorrhizal fungi (Glomales)

and *Phialophora graminicola* associated with roots of winter XTriticosecale. Acta Mycol 30:213–222.

Braun-Blanquet J. 1965. Plant sociology: the study of plant communities. (Translated and edited by Fuller GD, Conard HS.) London: Hafner. 439 p.

Brown A, Placci G, Grau HR. 1993. Ecología y biodiversidad de las selvas subtropicales de Argentina. In: Goñi F, Goin C, eds. Principios de política ambiental. Buenos Aires: Cámara Diputados Provincia Buenos Aires. p 215–222.

Cabrera AL. 1976. Fitogeografía de la República Argentina. Enciclopedia Argent Agron Jard 2:74.

Carú M, Becerra A, Sepúlveda D, Cabello A. 2000. Isolation of infective and effective *Frankia* strains from root nodules of *Alnus acuminata* (Betulaceae). WJ Microbiol Biotech 16:647–651, doi:10.1023/A:1008929520571

Cuenca G, Meneses E. 1996. Diversity patterns of arbuscular mycorrhizal fungi associated with cacao in Venezuela. Plant Soil 183:315–322, doi:10.1007/BF00011447

Eom A-H, Hatnett DC, Wilson GWY. 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. Oecologia 122:435–444, doi:10.1007/s004420050050

Gange AC, Brown VK, Sinclair GS. 1993. Vesicular-arbuscular mycorrhizal fungi: a determinant of plant community structure in early succession. Funct Ecol 7:616–622, doi:10.2307/2390139

Gerdemann JW, Nicolson TH. 1963. Spores of mycorrhizal Endogone species extracted from soil by wet sieving and decanting. Trans Brit Mycol Soc 84:679–684.

Grau A. 1985. La expansión del aliso del cerro (*Alnus acuminata* H.B.K. subsp. *acuminata*) en el noroeste de Argentina. Lilloa 36:237–247.

Guadarrama P, Álvarez-Sánchez FJ. 1999. Abundance of arbuscular mycorrhizal fungi spores in different environments in a tropical rain forest, Veracruz, México. Mycorrhiza 8:267–270, doi:10.1007/s005720050244

Hart MM, Reader RJ, Klironomos JM. 2001. Life strategies of arbuscular mycorrhizal fungi in relation to their successional dynamics. Mycologia 93:1186–1194, doi:10.2307/3761678

Helgason T, Daniell TJ, Husband R, Fitter AH, Young BD. 1998. Ploughing up the wood-wide web. Nature 394:431, doi:10.1038/28764

———, Merryweather JW, Denison J, Wilson P, Young JPW, Fitter AH. 2002. Selectivity and functional diversity in arbuscular mycorrhizas of co-ocurring fungi and plants from a temperature of deciduous woodland. J Ecol 90:371–384, doi:10.1046/j.1365-2745.2001.00674.x

Hetrick BAD, Bloom J. 1983. Vesicular-arbuscular mycorrhizal fungi associated with native tall grass prairie and cultivated winter wheat. Can J Bot 61:2140–2146.

Hueck K. 1978. *Los bosques de Sudamérica*. Soc. Alem. Coop. Tec., Eschborn.

Infostat. 2001, Programa de análisis estadísticos. Cordoba: Cátedra de Estadística. Facultad de Ciencias Agropecuarias. Natl. Univ. Cordoba.

Jasper DA, Abbott LK, Robson AD. 1989. Soil disturbance reduces the infectivity of external hyphae of vesicular-arbuscular mycorrhizal fungi. New Phytol 112:93–99, doi:10.1111/j.1469-8137.1989.tb00313.x

Kiers ET, Lovelock CE, Krueger EL, Herre EA. 2000. Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: implications for tropical forest diversity. Ecol Lett 3:106–113, doi:10.1046/j.1461-0248.2000.00126.x

Kurle JE, Pfleger FL. 1996. Management influences on arbuscular mycorrhizal fungal species composition in a corn-soybean rotation. Agron J 88:155–161, doi:10.2134/agronj1996.00021962008800020007x

Louis I, Lim G. 1987. Spore density and root colonization of vesicular-arbuscular mycorrhizas in tropical soil. Trans Brit Mycol Soc 88:207–212, doi:10.1016/S0007-1536(87)80216-4

Lovelock CE, Andersen K, Morton JB. 2003. Arbuscular mycorrhizal communities in tropical forests are affected by host tree species and environment. Oecologia 135:268–279.

Lu X, Koide RT. 1994. The effects of mycorrhizal infection on components of plant growth and reproduction. New Phytol 128:211–218, doi:10.1111/j.1469-8137.1994.tb04004.x

Magurran AE. 1988. Ecological diversity and its measurement. Princeton, New Jersey: Princeton Univ. Press. 179 p.

McGee PA. 1989. Variation in propagule numbers of vesicular-arbuscular mycorrhizal fungi in a semi-arid soil. Mycol Res 92:28–33, doi:10.1016/S0953-7562(89)80092-9

Merryweather JW, Fitter AH. 1998. The arbuscular mycorrhizal fungi of *Hyacinthoides non-scripta*. I. Seasonal and spatial patterns of fungal populations. New Phytol 138:131–142, doi:10.1046/j.1469-8137.1998.00889.x

Morton JB, Koske RE, Stümer SL, Bentivenga SP. 2004. Mutualistic arbuscular endomycorrhizal fungi. In: Mueller GM, Bills GF, Foster MS, eds. Biodiversity of fungi inventory and monitoring methods. Elsevier Academic Press. p 317–342.

Oehl F, Sieverding E, Ineichen K, Mäder P, Wiemken A, Boller T. 2009. Distinct sporulation dynamics of arbuscular mycorrhizal fungal communities from different agroecosystems in long-term microcosms. Agric Ecosyst Environ 134:257–268, doi:10.1016/j.agee.2009.07.008

Philip LJ, Posluszny U, Klironomos JN. 2001. The influence of mycorrhizal colonization on the vegetative growth and sexual reproductive potential of *Lythrum salicara* L. Can J Bot 79:381–388, doi:10.1139/cjb-79-4-381

Pringle A, Bever JD. 2002. Divergent phenologies may facilitate the coexistence of arbuscular mycorrhizal fungi in a North Carolina grassland. Am J Bot 89:1439–1446, doi:10.3732/ajb.89.9.1439

Read DJ, Pérez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? New Phytol 157:475–492, doi:10.1046/j.1469-8137.2003.00704.x

Rillig MC. 2004. Arbuscular mycorrhizae, glomalin and soil quality. Can J Soil Sci 84:355–363.

Roy S, Khasa DP, Greer CW. 2007. Combining alders, frankiae and mycorrhizae for the revegetation and remediation of contaminated ecosystems. Can J Bot 85:237–251, doi:10.1139/B07-017

Schalamuk S, Velázquez S, Chidichimo H, Cabello M. 2006. Fungal spore diversity of arbuscular mycorrhizal fungi associated with spring wheat: effect of tillage. Mycologia 98:22–28, doi:10.3852/mycologia.98.1.16

Schenck NC, Pérez Y. 1990. Manual for the identification of Mycorrhizal Fungi. Gainesville, Florida: Synergistic Publications. 286 p.

Shi ZY, Chen YL, Feng G, Liu RJ, Chrisite P, Li XL. 2006. Arbuscular mycorrhizal fungi associated with the Melicaceae on Hainan Island, China. Mycorrhiza 16: 81–87, doi:10.1007/s00572-005-0017-6

Sieverding E. 1989. Ecology of VAM fungi in tropical agrosystems. Agric Ecosyst Environ 29:369–390, doi:10.1016/0167-8809(90)90303-U

Tisdall JM, Oades JM. 1982. Organic matter and water-stable aggregates in soils. J Soil Sci 33:141–163, doi:10.1111/j.1365-2389.1982.tb01755.x

Vargas Gil JR, Bianchi AR. 1981. Regiones Naturales del NOA. Memoria Anual de Información Técnica para productores, INTA, Salta.

Walker C, Mize W, McNabb HS. 1982. Populations of endogonaceous fungi at two populations in central Iowa. Can J Bot 60:2518–2529, doi:10.1139/b82-305

Zhang MQ, Wang YS, Xing LJ. 1998. The ecological distribution of AM fungal community in south and east coast of China. Mycosystema 17:274–277.

Zhao ZW. 1999. Population composition and seasonal variation of VA mycorrhizal fungi spores in the rhizosphere soil of four pteridophytes. Acta Bot Yunn 21:437–441.

———, Xia YM, Qin XZ, Li XW, Chen LZ, Sha T, Wang GH. 2001. Arbuscular mycorrhizal status of plants and the spore density of arbuscular mycorrhizal fungi in tropical rain forest of Xishuangbanna, southwest China. Mycorrhiza 11:159–162, doi:10.1007/s005720100117