Mycologia, 105(3), 2013, pp. 509–520. DOI: 10.3852/11-353

Issued 17 May 2013

Composition and structure of arbuscular-mycorrhizal communities in El Palmar National Park, Argentina

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Abstract: The arbuscular-mycorrhizal-fungal (AMF) communities from the El Palmar National Park of Entre Ríos Province, Argentina, were investigated and characterized. The species of AMF present in five distinct vegetation types—gallery forest, grassland, marsh, palm forest, and scrubland—were isolated, identified and quantified over 2 y. Forty-six AMF morphotaxa were found. The composition of the AMF communities differed between the seasons, soil and vegetation types. Seasonal variations were observed in members of the Acaulosporaceae, Archaeosporaceae, Claroideoglomeraceae, Gigasporaceae and Pacisporaceae. Depending on soil type, the AMF-spore communities were dominated by members of one of the two main orders of the Glomeromycota. AMF communities from grassland and palm forest, which occur on sandy soils, comprised primarily members of the Diversisporales, with a high percentage of species of *Acaulospora* and of Gigasporaceae. Communities from the gallery forest, marsh and scrubland, which occur on loam-clay soils, were composed of members of the Glomerales, with a high percentage of spores from species of *Glomus*. Thus, both AMF and plant communities would appear to be strongly and similarly influenced by edaphic conditions.

Key words: biodiversity conservation, Glomeromycota, palm forests, seasonality, vegetation types

Submitted 25 Oct 2011; accepted for publication 3 Oct 2012.
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Introduction

Arbuscular-mycorrhizal fungi (AMF) form symbioses with the majority of vascular plants and as such are considered essential components of natural plant-soil systems. AMF can enhance plant fitness, community composition and structure, and ecosystem functioning (van der Heijden et al. 1998a, Millner and Wright 2002).

AMF show little host specificity, in that the roots of a given host species can be associated with different species of AMF (Eom et al. 2000, Helgason et al. 2002, Lovelock et al. 2003). Nevertheless, host preference for certain AMF has been suggested (Vandenkoornhuyse et al. 2002, Gollote et al. 2004). AMF have been shown to influence plant community structure and diversity (van der Heijden et al. 1998b, O'Connor et al. 2002), but plant communities also have been shown to affect the diversity and composition of the AMF communities (Johnson et al. 2004). Thus, van de Voorde et al. (2010) demonstrated in a long-term field experiment that AMF communities in plant roots were not dissimilar when collected from sown instead of nonsown plant communities. Moreover, results from studies on natural and seminatural ecosystems have indicated that AMF diversity and species composition are affected by abiotic ecological conditions, for example light, moisture, phosphorus (P) and nitrogen (N) supplies (Börstler et al. 2006).

At present, 234 AMF species have been described (www.amf-phylogeny.com) within the Glomeromycota. Conserving AMF biodiversity appears crucial for the natural functioning of plant communities (van der Heijden 2003). Safeguarding AMF biodiversity may be achieved best via protection of their ecosystems and habitats. The Convention on Biological Diversity (www.cbd.int) established in Article 8 that protected areas are propitious places for the in situ conservation of biological diversity and the recovery of viable populations of species within their natural environments.

El Palmar National Park (PNP), one of the most floristically diverse national parks in Argentina, covering 8500 hectares, was established in 1965 with the purpose of preserving the endemic palm *Butia yatay* (Mart.) Becc., an endangered species (Chebez 1994). PNP comprises different edaphic conditions and hosts, as well as one of the last remnants of *B. yatay* forest within the region. Such protected areas are useful to conserve floristic biodiversity and

TABLE I. Characteristics of the vegetation types in El Palmar National Park, Argentina

Vegetation type	Description	Dominant plant species
Gallery forest (GF)	Closed forest frequently flooded along permanent streams and rivers	*Guetarda urugüensis* Cham. & Schltdl., *Ligustrum lucidum* Aiton, *Melia azedarach* L., *Nothoscordum gracile* (Dryand. ex Aiton) Stearn, *Pavonia hastata* Cav., *Phyllantus niruri* L.
Grassland (GRA)	Short grassy vegetation up to 50 cm tall on sandy soils	*Agrostis alba* L., *Aster squamatus* (Spreng.) Hieron, *Briza calotheca* (Trin.) Hack, *Bromus auleticus* Trin., *Capsella bursa pastoris* L., *Lippia alba* (Mill.) Br., *Paspalum exaltatum* Presl., *Plantago brasiliensis* Sims
Marsh (MAR)	Tall grasses and sedges on intermittent streams and ponds	*Cyperus reflexus* Vahl., *C. virens* Michx., *Juncus bufonius* L., *J. capillaceus* Lam., *J. densiflorus* Kunth
Palm forest (PF)	Savanna-like physiognomy with tall *Butia yatay* palms (> 12 m) and sparse trees	*Bidens pilosa* L., *B. yatay, Daphnopsis racemosa* Griseb., *G. urugüensis*, *Microgramma vacciniifolia* (Langsd. & Fisch) Copel., *Smilax campestris* Griseb
Scrubland (SCR)	Open vegetation with continuous shrubby cover up to 3 m tall	*Acacia* sp., *Acacia atramentaria* Benth, *Baccharis dracunculifolia* DC., Prodr., *Eupatorium buniifolium* Hook. et Arn., *Prosopis nigra* (Griseb.) Hieron.

associated microorganisms (Hawksworth 1991, Velázquez et al. 2008). The park contains plant communities such as gallery forest, grassland, marsh, palm forest and scrubland, ideal for the study of differences in the abundance and diversity of AMF, which have not yet been characterized.

The aim of the present study was to determine: (i) AMF-spore communities in the five vegetation types present in PNP, (ii) the seasonal variation in the AMF families in the five vegetation types, (iii) the main edaphic characteristics that influence AMF spore communities in the PNP, (iv) the interaction between season and soil in structuring AMF communities.

MATERIALS AND METHODS

Study area.—PNP, Entre Ríos (31°50′S, 58°17′W), is in the Argentine phytogeographical region referred to as the Espinal Province (Cabrera and Willink 1980). The climate is temperate with a mean annual temperature of 18.9 C. The mean annual rainfall is about 1300 mm, and a deficit of water usually occurs in summer (Goveto 2005). Entisol and Inceptisol soils with little vertical soil structure and pedogenic processes predominate the park. All soils in the area are of fluvial origin (van der Sluijs 1971, Bertolini 1995). Based on physiographic and floristic characteristics, five distinct vegetation types were identified in the PNP (Velázquez et al. 2008, 2010): gallery forest (GF), grassland (GRA), marsh (MAR), palm forest (PF) and scrubland (SCR) (TABLE I).

Sampling design.—Three sites were sampled (FIG. 1) and at each site five vegetation types were identified: GF, GRA, MAR, PF and SCR. Composite random (Dick et al. 1996) soil samples were collected seasonally (four per year) from all five vegetation types throughout 2004 and 2005. In those places where each sample was collected, five to six subsamples from square areas of approx. 3 m^2 were pooled. Per sampling date, therefore, 15 (= 3 sites × 5 vegetation types) such composite samples were collected and stored at 4 C until processed, totaling 120 samples (= 3 sites × 5 vegetation types × 4 seasons × 2 y) over the 2 y period.

Physical and chemical properties of the soil.—The analysis of soil texture involved a particle-size fractionation by means of the hydrometer method (Bouyocus 1962). Electrical conductivity and pH were measured with a glass-electrode pH meter at a 1 : 2.5 (w/v) ratio of soil to water. The percentage of organic carbon (C) was determined by the wet-oxidation method of Walkley and Black (1934), while the percent total N was measured by the micro-Kjedahl method (Jackson 1967). Organic matter was estimated as the carbon content multiplied by the factor 1.72. The available P was assayed by the method of Bray and Kurtz (1945).

AMF-spore isolation and identification.—Spores of AMF were extracted from aliquot of 100 g dry weight of rhizosphere soil. The soil samples were wet-sieved and decanted (Gerdemann and Nicolson 1963), and the supernatant centrifuged in a sucrose gradient (Walker et al. 1982). Only apparently healthy spores were counted in a 9 cm Petri dish by direct observation under a stereomicroscope. For identification, each spore type was mounted in polyvinyl-lactic acid-glycerine (PVLG) (Koske and Tessier 1983) and PVLG and 1 : 1 (v/v) Melzer's reagent mixture (Brundrett et al. 1994). The identification was based on the currently accepted taxonomic criteria for spore size, color, surface ornamentation and wall structure (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/). Spores from the Acaulosporaceae, Archaeosporaceae, Claroideoglomeraceae, Entrophosporaceae, Gigasporaceae, Glomeraceae, Pacisporaceae and Paraglomeraceae were identified. Non-identified specimens were named with their genus name followed by a specification number.

Analysis of AMF species and communities.—On the basis of the above data, these calculations were made: (i) spore

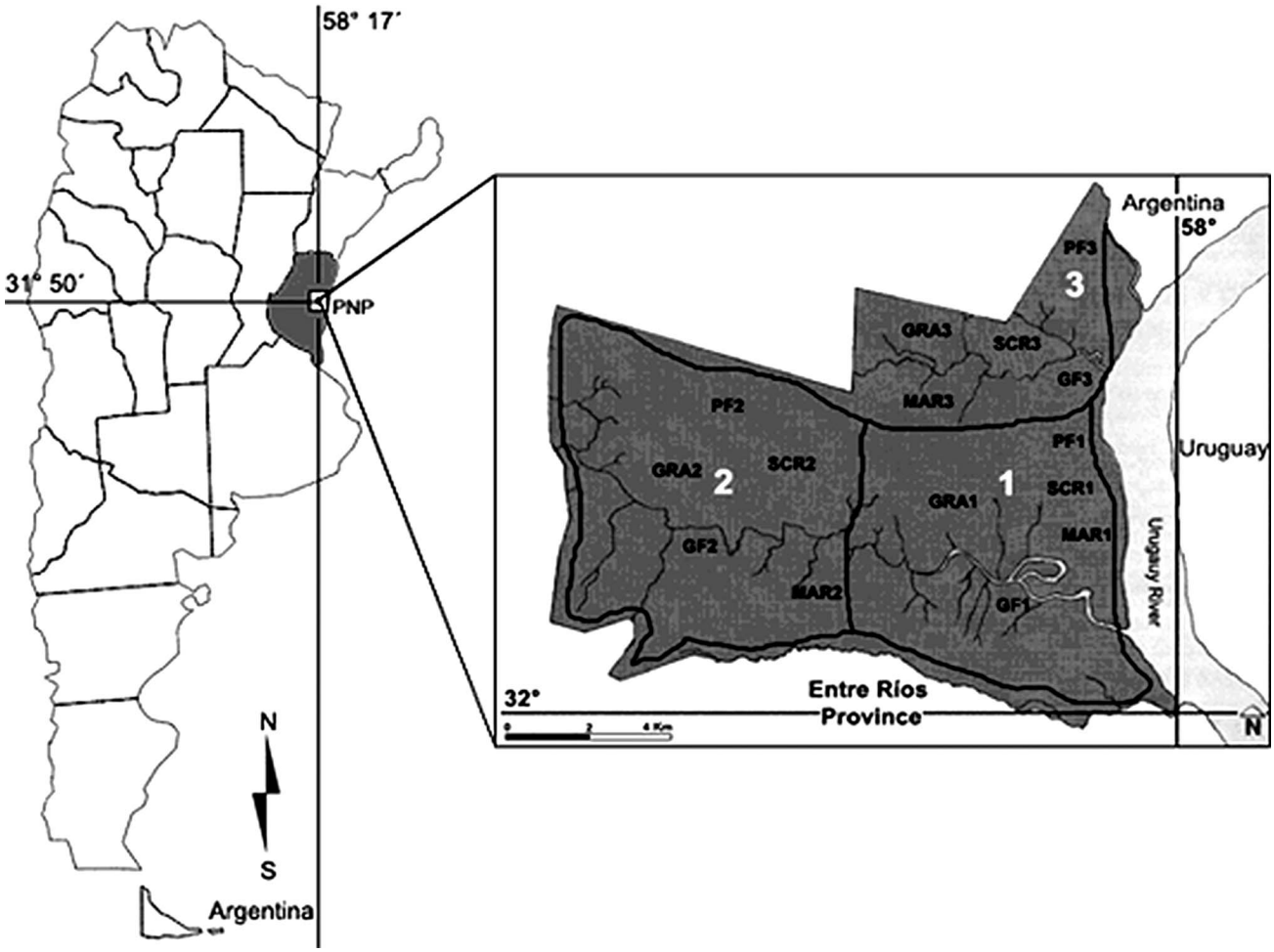

FIG. 1. Location of the three sampling sites in the El Palmar National Park (PNP) Argentina. Five vegetation types, gallery forest (GF), grassland (GRA), marsh (MAR), palm forest (PF) and scrubland (SCR), were sampled at each.

number = total number of spores found in 100 g dry weight of soil; (ii) AMF species richness (S) = total number of different AMF-spore taxa recorded in 100 g dry weight of soil; (iii) the frequency of occurrence (FC) = percentage of samples from which a particular AMF taxon was isolated; and (iv) Shannon diversity index (H′), $H' = -\sum p_i \ln p$, where p is the relative abundance of the ith species compared to all identified species per sample (Magurran 1988).

Statistical analysis.—The spore number of each Glomeromycota family in the vegetation types were transformed to [($\log_2$ spore number) + 1] values. To determine the correlation of the species spore numbers from the five vegetation types (n = 8) with the edaphic factor, a canonical correspondence analysis (CCA), a unimodal model for nonlinear-multivariate-gradient analysis, was employed (Ter Braak 1986). Organic matter and lime were excluded from the

TABLE II. Mean (n = 3) values of the physicochemical properties of the soils in the five studied vegetation types in El Palmar National Park: gallery forest (GF), grassland (GRA), marsh (MAR), palm forest (PF), scrubland (SCR)

VT	OM (%)	C_{ox} (%)	N (%)	C:N	P (ppm)	pH	EC (ds/m)	Clay (%)	Lime (%)	Sand (%)	Texture
GF	$1.12^{a, b}$	$0.56^{a, b}$	0.04^{a}	12.84^{a}	7.30^{a}	6.38^{a}	$0.21^{a, b}$	2.89^{a}	$5.33^{a, b}$	80.18^{a}	Sandy-loamy
GRA	0.47^{b}	0.24^{b}	0.02^{a}	10.52^{a}	9.12^{a}	5.45^{a}	0.08^{b}	$3.35^{a, b}$	3.59^{a}	93.06^{a}	Sandy
MAR	$1.31^{a, b}$	$0.66^{a, b}$	0.07^{a}	9.68^{a}	8.58^{a}	5.10^{a}	$0.11^{a, b}$	20.55^{b}	$8.57^{a, b}$	70.88^{a}	Sandy-clayey-loamy
PF	$1.23^{a, b}$	$0.62^{a, b}$	0.04^{a}	13.03^{a}	9.71^{a}	5.37^{a}	$0.16^{a, b}$	$5.12^{a, b}$	$10.34^{a, b}$	84.55^{a}	Sandy
SCR	2.35^{a}	1.18^{a}	0.10^{a}	12.69^{a}	8.84^{a}	5.77^{a}	0.36^{a}	$12.16^{a, b}$	17.33^{b}	70.51^{a}	Sandy-loamy

[a] VT = vegetation type; Cox = oxidizable carbon; OM = organic matter; N = nitrogen; P = phosphorus; EC = electrical conductivity.

[a, b] = results of statistical mean comparison test among sites. Values with the same superscript letter are not significantly different ($P > 0.05$).

TABLE III. Mean spore density (n = 8) and frequency of occurrence (FC) of the identified taxa of Glomeromycota recovered in the 15 composite soil samples from different vegetation types

AMF species	Gallery Forest			Grassland			Marsh			Palm forest			Scrubland			
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	FC%
Acaulosporaceae																
Acaulospora dilatata Morton	40	3	0.7	20	22	13.2	2.5	23.7	23.2	8.7	95.2	10	40.5	13	2.2	100
A. mellea Spain & Schenck	4	12	2	13.2	3.5	14.7	13.5	1.75	9.3	7	4.2	1.5	34.2	26.7	26	100
A. scrobiculata Trappe	17.7	10.2	0.5	15	35.7	6.7	10.2	6.2	17.2	40	23.2	27	16	14.2	11	100
A. delicata Walker, Pfeiff. & Bloss	12.7	44.7	3.7	4.5	1	12.5	74.7	8	28.7	6.2	7.2	4	14.7	10	0	93.3
A. spinosa Walker & Trappe	1.7	0	0	0.5	0	0.5	2.5	7.7	0	3.5	0.5	3.2	1.2	6.2	3.7	73.3
Acaulospora sp. 1	0	0	0.7	0.5	1.5	2	4.2	0	2.2	0.5	2.5	1.7	12.5	1.7	0	73.3
Acaulospora sp. 2	1	0	0.7	2	0	0.5	2.5	0.7	2	3.7	0	1.7	1.7	4.7	0	73.3
A. bireticulata Rothwell & Trappe	0	0	0	14.2	0.5	0	0	1	0.5	1.7	3.7	7.2	0	0.5	0	53.3
A. laevis Gerd. & Trappe	0	0.5	0	0	0	4	4.2	1.5	2	0	0	1	1.2	0	0	46.6
A. nicolsonii Walker, Reed & Sanders	0	0.75	0	0	0	0	0	44	2.5	1.5	0	0.5	0	0.5	0	40
A. excavata Ingleby & Walker	0	0	0	0	0	0	0	1	4.25	0	0.5	0	0	0	1.75	26.6
A. lacunosa Morton	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	6.6
A. tuberculata Janos & Trappe	0	0	0	0	0	0	0	0	0	3.5	0	0	0	0	0	6.6
A. denticulata Sieverd. & Toro	0	0	0	0	0	0	0	0	0.5	0.5	0	0	0.5	0.7	0	3.3
Archaeosporaceae																
Archaeospora trappei (Ames&Lind) Morton&Redecker emd Spain	0	0	0	0	0	0	0	0	0	0	0	0	0.7	0	0	6.6
Entrophosporaceae																
Entrophospora infrequens (Hall) Ames & Schneid.	1	3	1.5	0	1.5	0	2	0	7.2	0.5	0	3.7	2	0.5	0.5	73.3
Gigasporaceae																
Gigaspora candida Bhattacharjee, Mukerji, Tewari & Skoropad	0	0	0	1	9.7	5.5	0	0	0.5	0.5	1.2	1.7	0	1.7	1.7	60
Gi. gigantea (Nicolson & Gerd.) Gerd. & Trappe	0	0	0	0	0	0	0	0	0	2.7	0	0	0	0	0	6.6
Gi. margarita Becker & May	0	0	0	0	0	0	0	0	0	0	1.7	0	0	0	0	6.6
Gigaspora sp. 1	0	0	0	0	1.7	0	0	0	0	0	0	0	0	0	0	6.6
Gigaspora sp. 2	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0	6.6
Racocetra coralloidea(Trappe, Gerd. & Ho) Oehl, Souza & Sieverd.	0	0	0	0	0	0	0	0	0	0	1.7	0	0	0	0	6.6
R. fulgida (Koske & Walker) Oehl, Souza & Sieverd.	0	0	0	0	0	0	0	0	0	0	1.2	0	0	0	0	6.6
Scutellospora gilmorei (Trappe & Gerd.) Walker & Sanders	0	0	0	5.5	6.2	8.5	1.2	2.5	0.5	5	0.5	5.5	4	4	1.7	80
S. dipapillosa (Walker & Koske) Walker & Sanders	0	0	0	5	2	3.5	1	2.7	1.4	1.7	7.5	0	0	1.7	0	60
S. biornata Spain, Sieverd. & Toro	0	0	0	0	3.2	1	0.7	0	0	0.5	0	2.7	6	0.7	0	40
S. calospora (Nicolson & Gerd.) Walker & Sanders	0	0	0	3.5	13.2	7	0	0	0	1.5	0	0.5	2.5	0	0	40

TABLE III. Continued

AMF species	Gallery Forest			Grassland			Marsh			Palm forest			Scrubland			FC%
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	
S. heterogama (Nicolson & Gerd.) Walker & Sanders	0	0	0	0	3.2	0	0	0	0	0	0	0	5.2	0	2.5	20
Scutellospora sp.	0	0	0	0	0	0.5	0	0	0	0	0	0	0.5	2.2	0	20
Claroideoglomeraceae																
Claroideoglomus etunicatum (Becker & Gerd.) Walker & Schuessler	12.2	42.5	78.2	10.5	3.2	3.2	58	19.5	90.5	9.5	6.7	6.7	7.5	9.5	9	100
C. claroideum (Schenck & Sm) Walker & Schuessler	7.2	6.5	7.5	0	0	0.5	23.7	8	12.2	0	0	0.5	7.2	6.5	7.5	93.3
Glomeraceae																
Funneliformis coronatum (Giovann.) Walker & Schuessler	0.5	0.7	4.2	0	0	0.5	58	19.5	0.7	0	0	0.5	12.7	1.2	3.7	66.6
F. mosseae (Nicolson & Gerd.) Walker & Schuessler	2.2	60	4.2	6	4.7	10.7	18.5	3.2	10.7	7	26.5	19.2	0.7	0	0	66.6
Glomus sp.	3.7	2.5	0	6	4.7	10.7	18.5	3.2	1.2	7	26.5	19.2	20.7	3.5	3.2	93.3
G. microaggregatum Koske, Gemma & Olexia	0.5	0.5	0.5	0	0	1	12.2	2	2.2	1	0.5	1.5	1.7	0	0	73.3
G. dimorphicum Boyetchko & Tewari	10.2	0.5	1.2	0	0	0	0	0	6	0	0	0	0	0	0.5	40
G. aggregatum Schenck & Sm.	0.5	0	0	0	0	0	0.7	0.7	0	0	0	0	2	0	0	26.6
G. glomerulatum Sieverd.	0	0	0	0	0	3.5	0.7	0	0	4	0	5.2	0	0	0	26.6
G. ambisporum Sm. & Schenck	0	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	6.6
Rhizophagus clarus (Nicolson & Schenck) Walker & Schuessler	13.7	3.2	13.2	2	0	7	29	2.2	2.2	24	7	44	10.2	2	10	73.3
R. intraradices (Schenck & Sm.) Walker & Schuessler	1	4	0.5	0	0	0	0	0	1	0	0	0	0	0	0.5	26.6
R. diaphanus (Morton & Walker) Walker & Schuessler	0	0.7	0	0	0	0	0	0	0	0	0	0.5	0	0	0	13.3
R. fasciculatum (Thaxt.) Walker & Schuessler	0	0	0	0	0	0	0	0	0	0	0	0	0	34.5	0	6.6
Septoglomus constrictum (Trappe) Walker & Schuessler	0	0.7	0	0	0	0	1.2	0.7	8.5	0	0	0	0	2	3	33.3
Pacisporaceae																
Pacispora sp.	0	0	4.5	0	0.5	0	1.2	0	0	0	0	0	0	2.5	0	26.6
Paraglomeraceae																
Paraglomus laccatum Renker, Błaszk. & Buscot	0	0	0	0	0	1.5	0	0	0	0	0	0	1.2	0	0	13.3

analysis because of collinearity. An analysis of the community data on the basis of the spore-number values for all given AMF taxa recovered from the five vegetation types was carried out by means of the two-way indicator species analysis (TWINSPAN). CCA was performed with the Multivariate Statistical Package (MVSP 3.1) and TWINSPAN with PC-ORD 4.25.

Species richness, diversity index and soil physicochemical variables were analyzed by the one-way analysis of variance (ANOVA). Mean comparison were made, using Fisher's least significant difference (LSD) test (5% and 1%). A mixed model ANOVA (Pinhero and Bates 2000) was performed to test for differences in the spore number in vegetation types and seasons. The vegetation types and seasons were treated as fixed effects and sites and years as random effects.

RESULTS

Soil properties.—The soil physicochemical parameters for each vegetation type are summarized (TABLE II). Mean soil pH did not differ significantly ($P > 0.05$), being slightly acidic. The soil texture was sandy in the GRA and PF, but sandy-clayey-loamy in the MAR and sandy-loamy in the SCR and GF. Organic matter was higher in SCR than in GRA but did not differ significantly ($P > 0.05$) from GF, MAR and PF.

AMF-spore number.—Forty-six different AMF morphotaxa belonging to the Acaulosporaceae, Archaeosporaceae, Claroideoglomeraceae, Entrophosporaceae, Gigasporaceae, Glomeraceae, Pacisporaceae and Paraglomeraceae were identified to genus and to species whenever possible; seven taxa could not be clearly identified to species (TABLE III). Fourteen taxa were from the Acaulosporaceae, 13 each from the Glomeraceae and the Gigasporaceae, two from the Claroideoglomeraceae, and one taxon each from the Archaeosporaceae, the Entrophosporaceae, the Pacisporaceae and the Paraglomeraceae.

The relative abundances of members of families of AMF fungi varied among vegetation types. The mean spore number was highest in MAR (2755 spores), somewhat lower in GF, PF, and SCR (1867, 1809, 1709 spores respectively), and lowest in GRA (1314 spores).

The relative abundances of AMF species differed across the five vegetation types (TABLE III). Claroideoglomeraceae, Glomeraceae and Acaulosporaceae were dominant in all five vegetation types. *Acaulospora dilatata*, *A. mellea*, *A. scrobiculata* and *Claroideoglomus etunicatum* were the dominant species with a 100% FC, followed by *A. delicata*, *C. claroideum* and *Glomus* sp. with a 93.3% FC plus *Scutellospora gilmorei* with an 80% FC. Some taxa with intermediate FC values were *A. spinosa*, *Acaulospora* sp. 1, *Acaulospora* sp. 2, *Entrophospora infrequens*, *Rhizophagus clarus* and *G. microaggregatum* with a 73.3% FC along with *Gigaspora candida* and *S. dipapillosa* with a 60% FC. Other species occurred in only a single vegetation type; *Archaeospora trappei* was present in SCR; *A. tuberculata*, *Gi. gigantea*, *Gi. margarita* and *Racocetra fulgida* in PF; *Gigaspora* sp. 1, *Gigaspora* sp. 2, *A. lacunosa* and *R. coralloidea* in GRA; and *G. ambisporum* in GF.

AMF family seasonality.—Relative abundances of spores of Acaulosporaceae, Archaeosporaceae, Claroideoglomeraceae, Entrophosporaceae, Gigasporaceae, Glomeraceae, Pacisporaceae and Paraglomeraceae in the five vegetation types varied by season (FIG. 2). The number of AMF families in the GF, GRA, PF and SCR was greater during the summer, while in the MAR equal numbers of families were detected throughout the year. Spores belonging to the Acaulosporaceae, Gigasporaceae and Glomeraceae were present in one or more of the vegetation types during all four seasons, whereas Claroideoglomeraceae were detected in only the SCR and MAR all year long. The Entrophosporaceae and Pacisporaceae had a low representation with their abundances varying seasonally (FIG. 2). Two families were present only in the SCR: the Archaeosporaceae (recorded during the autumn) and the Paraglomeraceae during the summer.

Significant differences in the total numbers of spores of Glomeromycota families were found in the different vegetation types and seasons. The abundance of members of the Claroideoglomeraceae, Gigasporaceae and Glomeraceae differed among the vegetation types (TABLE IV). Abundance of the Acaulosporaceae, Archaeosporaceae, Entrophosporaceae, Pacisporaceae and Paraglomeraceae did not differ significantly among the vegetation types. Seasonally the abundance of Acaulosporaceae, Archaeosporaceae, Claroideoglomeraceae, Gigasporaceae and Pacisporaceae spores varied throughout the year; whereas the Entrophosporaceae, Glomeraceae and Paraglomeraceae did not (TABLE IV). A significant interaction between the vegetation types and the seasons also was found for members of the Archaeosporaceae, Claroideoglomeraceae and Entrophosporaceae.

AMF communities.—The total number of AMF species (S) did not differ significantly among the vegetation types (FIG. 3). However, most morphospecies were found in the SCR vegetation type (S = 33), followed by PF (S = 32), GRA (S = 31) and MAR (S = 30), with the fewest being recorded in GF (S = 25). AMF diversity did not differ significantly between the vegetation types. The diversity index (FIG. 3) was greatest in GRA (H = 3.29) and lowest in GF (H = 2.73).

Total first and second axes of the CCA analysis (FIG. 4) accounted for 68% of the variance. The vegetation types GF and MAR were separated from

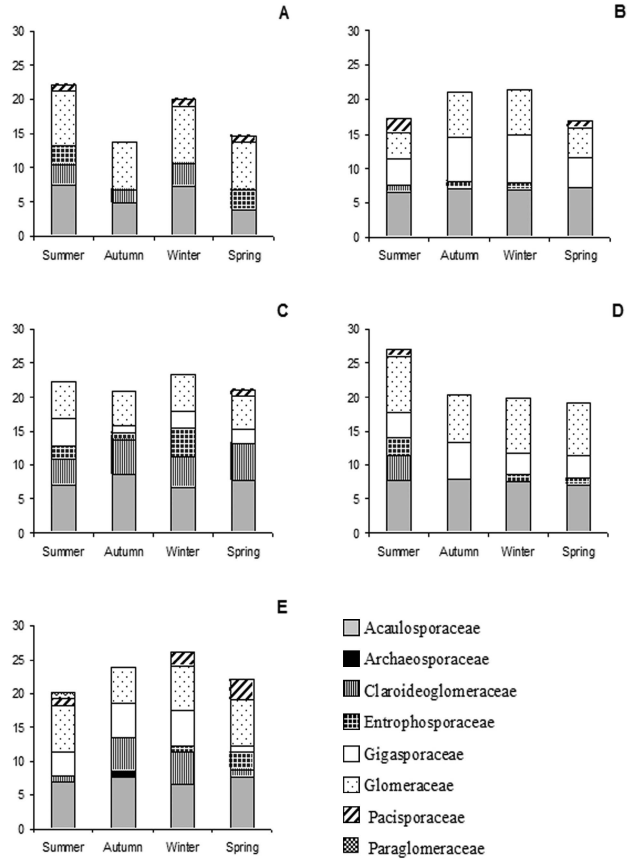

FIG. 2. Spore number of each family of Glomeromycota in the vegetation types (mean values, n = 8) for members of the families Acaulosporaceae, Archaeosporaceae, Claroideoglomeraceae, Entrophosporaceae, Gigasporaceae, Glomeraceae, Pacisporaceae and Paraglomeraceae obtained over two years within the vegetation types. Data were transformed to [($\log_2$ spore density) + 1]. A. Gallery forest (GF). B. Grassland (GRA). C. Marsh (MAR). D. Palm forest (PF). E. Scrubland (SCR).

GRA, SCR and PF. Clay soil was the highest correlation with canonical axis 1 (−0.52), while EC (0,69), N (0.63) and C (0.50) were the most prominent factors correlated with axis 2.

The TWISPAN analysis grouped the AMF communities from the 15 samples (3 sites × 5 vegetation types) into two main groups (FIG. 5). This form of analysis grouped the AMF communities between the group containing GRA and PF and the one comprising the GF, MAR and SCR vegetation types. The spore abundance of *C. claroideum* was identified as an indicator for the GF, MAR and SCR vegetation types, whereas that of *Gi. candida* was indicative of PF and GRA. In contrast, the spore abundance of *S. heterogama* was a marker for SCR1 and SCR3. Finally, although the GF samples all were characterized by the lack of *S. gilmorei*, the vegetation types MAR1 and MAR3 were separated from MAR2 and SCR2 on the basis of differences in the sporulation of that same species (TABLE III). Moreover, AMF similarities in site II for SCR2 and MAR2 could be related to distance from the Uruguay River. The AMF communities in MAR and GF were more similar to each other than to those of the SCR (FIG. 5).

DISCUSSION

The roles of AMF have been well described for several terrestrial ecosystems, however ecological data on these microorganisms in protected environments such as wildlife reserves and national parks are still scarce. Such information has a high socioecological value that is enhanced by the presence of rare or endangered plant species (Mota et al. 2002, Fuchs and Haselwandter 2004), because those niches could constitute vital repositories for the conservation of AMF diversity (Turrini et al. 2010).

In the present study, we extracted AMF directly from soil samples in five vegetation types and identified a total of 46 morphotaxa representing 12 genera. This number was relatively high compared to the numbers that have been reported before for Argentina (Lugo and Cabello 2002, Irrazabal et al. 2004, Becerra et al. 2011). The high species number could be explained as follows. First, environmental heterogeneity with scrubland, marsh, palm forest, grassland and gallery forest communities occurring close to each other could have contributed to a high diversity of AMF host plant species. PNP is one of the floristically most diverse national parks in Argentina with more than 700 species of vascular plants (Biganzoli et al. 2001). This plant diversity should increase the probability of an AMF species encountering a suitable host. Second, undisturbed natural environments have a greater diversity of AMF compared to disturbed areas, as reported by Öpik et al. (2006), who found the species richness decreased in anthropogenically disturbed environments.

In this investigation, the Acaulosporaceae were the most widespread and abundant (49% of spores) Glomeromycota, followed by the Glomeraceae (40%) and Gigasporaceae (6%). *Acaulospora* species have been reported to be dominant in natural ecosystems (Li et al. 2003, Zhao et al. 2003, Tao et al. 2004), whereas *Glomus* species have proven more abundant in agricultural soils (Zhang et al. 1988, 1994; Vestberg 1995; Oehl et al. 2003; Gai et al. 2004; Schalamuk et al. 2006). Other studies, however, indicated co-occurrence of both genera in the same environments (Trufem and Viriato 1990, Zhao 2000, Zhao et al. 2001, Muthukumar et al. 2003, Tawaraya et al. 2003). Indeed, assessments of AMF communities, based on spores, can be biased towards taxa that

TABLE IV. Results of analyses of variance (ANOVA) for the total numbers of the members of the AMF families present in the vegetation types and seasons along with the interactions among these variables

	Acaulosporaceae			Archaeosporaceae			Claroideoglomeraceae			Entrophosporaceae		
Effect	df	*F* value	*P*	df	*F* value	*P*	df	*F* value	*P*	df	*F* value	*P*
Vegetation type (VT)	2.53	4,10	ns	1.00	4,10	ns	37.8	4,10	< 0.001	0.25	4,10	ns
Season (S)	2.71	3,90	< 0.01	2.90	3,90	< 0.01	4.8	3,90	< 0.01	2.38	3,90	ns
VT X S	1.57	12.90	ns	2.90	12.90	< 0.001	4.4	12.90	< 0.001	2.92	12.90	< 0.001

ns = not significant.

sporulate more abundantly under certain environmental conditions. Trap culturing can reveal further AMF taxa (Oehl et al. 2003, Velázquez and Cabello 2011).

Seasonal variation influences AMF distribution (McGee 1989, Oehl et al. 2009) and may or may not be significant depending on the Glomeromycota families in question. A different pattern of sporulation in different AMF over time may explain the seasonal variation in the frequency of detecting different AMF families. In our study at PNP we found that AMF families could be separated into three groups: (i) those that sporulate throughout the year (members of the Acaulosporaceae, Claroideoglomeraceae, Gigasporaceae and Glomeraceae); (ii) those that, at a low representation and abundance, varied seasonally (the Entrophosporaceae and Pacisporaceae); and (iii) those that sporulated in only a single season (the Archaeosporaceae in autumn and Paraglomeraceae in summer). These seasonal differences in sporulation are characteristic of AMF-community dynamics, which may be explained by fungal substitutions determined by the differing life strategies of each AMF, the seasonal variation of environmental conditions and host phenology (Merryweather and Fitter 1998, Eom et al. 2000, Pringle and Bever 2002).

In addition, we observed strong AMF-community differentiation in response to the different vegetation types and edaphic conditions in the PNP. Cluster analysis of AMF communities revealed effects of the five vegetation types. *C. claroideum* played the role of an indicator species separating the AMF communities of the GF, MAR and SCR from the other two vegetation types. We consider *C. claroideum* a generalist species that preferentially sporulates under disturbance. Turnau et al. (2001) and Börstler et al. (2006) indicated that *C. claroideum* is cosmopolitan with no particular host specificity, thus suggesting a high tolerance toward different ecological conditions. The species-wide distribution has been documented in Argentina (Cabello 2001, Irrazabal et al. 2004, Schalamuk et al. 2006).

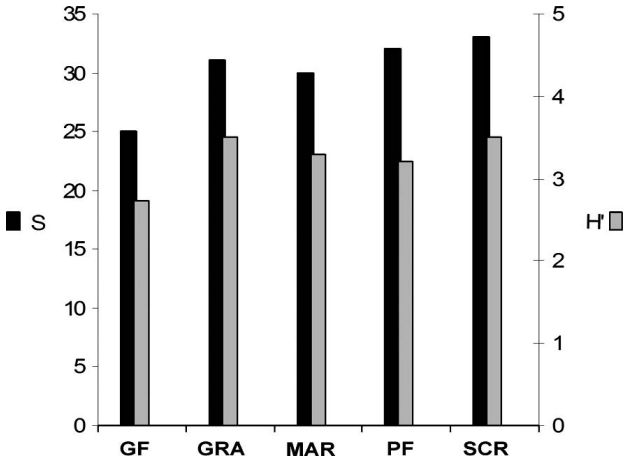

FIG. 3. Species richness (S) and biodiversity (H′) for gallery forest (GF), grassland (GRA), marsh (MAR), palm forest (PF) and scrubland (SCR). Data are the means of spore counts over 2 y with four seasonal assessments at three replicate study sites.

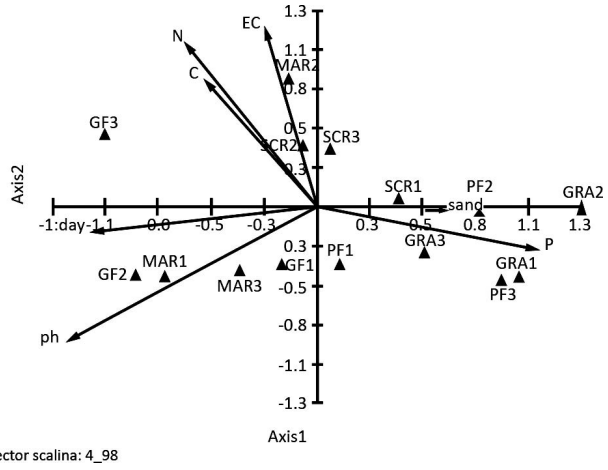

FIG. 4. Canonical correspondence analysis (CCA) of the diversity indicated, as calculated from the relative AMF-species abundances within the spore communities assessed seasonally over 2 y. Indices 1–3 refer to the replicate vegetation types in three tudy sites. Gallery forest (GF), grassland (GRA), marsh (MAR), palm forest (PF), scrubland (SCR).

TABLE IV. Extended

Gigasporaceae			Glomeraceae			Pacisporaceae			Paraglomeraceae		
df	*F* value	*P*	df	*F* value	*P*	df	*F* value	*P*	df	*F* value	*P*
15.67	4,10	< 0.001	5.64	4,10	< 0.01	0.37	4,10	ns	0,75	4,10	ns
13.11	3,90	< 0.001	2.09	3,90	ns	2.90	3,90	< 0.01	0,75	3,90	ns
7.86	12.90	ns	1.05	12.90	ns	1.03	12.90	ns	1,08	12.90	ns

The Gigasporaceae characterized samples from both the GRA and the PF which are subject to less disturbance than the other vegetation types. *Scutellospora heterogama* was found exclusively under SCR vegetation and previously was reported from Argentina once (Menéndez et al. 2001). Spores from *Gi. candida* were abundant from samples from the GRA, and this species has not been reported previously in Argentina.

Palm forest and the GRA exhibited similar AMF-community compositions; in these two vegetation types Gigasporaceae were found to be the most abundant (e.g. six species from *Scutellospora*, five species from *Gigaspora* and two species from *Racocetra*). Indeed in sandy soils such as in sand-dune ecosystems, Gigasporaceae have been found dominant (Bergen and Koske 1984, Gemma et al. 1989, Stürmer and Bellei 1994, Beene et al. 2000). On the contrary, occurrence of *Glomus* was correlated with the vegetation and soil of the GF, MAR and SCR. These vegetation types are characterized by sandy-loamy soils in the GF and the SCR and sandy-clay-loam in the MAR. A preference of *Glomus* species for loamy and clay soils had also been reported by Egerton-Warburton and Allen (2000), Treseder and Allen (2002) and Landis et al. (2004).

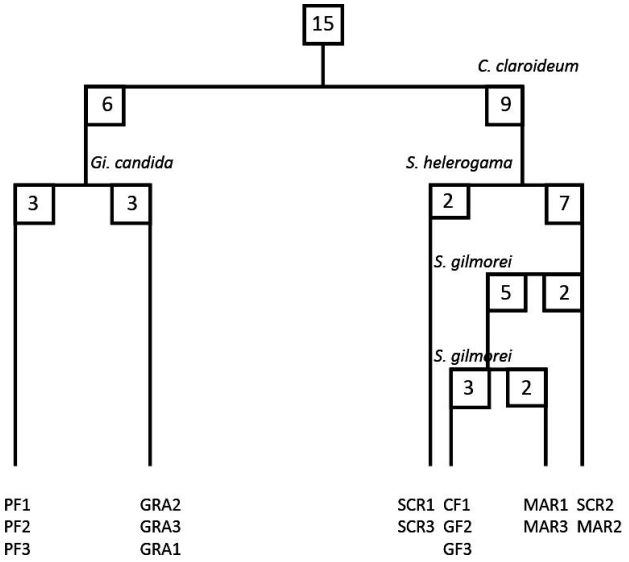

FIG. 5. TWINSPAN dendrogram for quantitative separation of vegetation type-specific AMF spore communities. Numbers in boxes indicate the number of samples per division. Gallery forest (GF), grassland (GRA), marsh (MAR), palm forest (PF), scrubland (SCR). Indices 1–3 refer to replicate vegetation types in three study areas.

Thus, variation in both vegetation and soil types and season are possible drivers of shifts in AMF communities within the PNP. This present study constitutes the first report of glomeromycotan diversity in a national park of Argentina and demonstrates strong interrelationships among vegetation type and associated AMF-species richness and diversity. Our findings here thus underscore the need to preserve both of these natural assets, the diverse vegetation types and the symbiotic fungi that optimize their well being.

ACKNOWLEDGMENTS

The authors thank Dr Donald F. Haggerty, a retired career investigator and native English speaker, for editing the final version of the manuscript and Dr M. Arturi for statistical assistance. The National Parks authorities provided permits to do this study in El Palmar National Parks. This research was supported by grants from UNLP (11/N651) Project, CICPBA, Agencia de Promoción Científica y Tecnológica (PICT 2007-01233). The constructive reviews of the two anonymous reviewers and Dr D. Taylor and Dr J. Stone have greatly improved the quality of the paper.

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