



Mycorrhizal associations in the Patagonian steppe, Argentina

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Abstract

The mycorrhizal status of plant species in north-west Patagonia was examined. Communities representative of Patagonian steppe and marshes were compared with respect to the mycorrhizal status of their species.

Most of both native and exotic plant species sampled were arbuscular mycorrhizal (AM). The percentage of species with mycorrhizal association was higher for perennial herbs and shrubs than for annual herbs. The higher ratio of mycorrhizal/nonmycorrhizal (NM) species found for dicotyledons than for monocotyledons, could reflect the presence of a considerable number of NM monocotyledons in the marsh. The mycorrhizal status of plants differed slightly between the steppe and the marsh. In the steppe, native AM species were more frequent than in the marsh. In contrast, in the marsh, the NM species were proportionally more represented than in the steppe. The Juncaceae and Cyperaceae, which include hydrohytic NM plants, accounted for many of these differences. Moreover, the dominant species in the marshes, *Juncus arcticus*, is a NM species.

In the present study, most of species belonging to the same taxonomic family tended to have the same mycorrhizal associations, in agreement with studies on plants from other regions. Exceptions to this general behaviour were observed in the families Cyperaceae, Scrophulariaceae, Berberidaceae and Amaryllidaceae. The most represented families in which mycorrhizal behaviour differed between species of the same family were Asteraceae, Fabaceae and Poaceae. *Senecio neaei* (Asteraceae) and *Boopis australis* (Calyceraceae) showed facultative mycorrhizal behaviour.

Introduction

The rhizosphere, the surface of plant roots, the space between root cells and the root cells themselves are habitats for micro-organisms. Among these, there is a group of filamentous fungi which form a symbiosis with the host plant root known as mycorrhizae (Harley and Smith, 1983). The benefits of mycorrhizal associations to plants include: Enhanced nutrient and water uptake, protection against pathogens, improved resistance to drought, higher tolerance to heavy metals and enlarged root system development (Allen, 1991; Perry et al., 1987). There is every indication that in such

communities a vigorous semi-permanent population of mycorrhizal symbionts with low host-specificity is involved in processes which effectively integrate species into extensive mycelial networks (Francis and Read, 1994). In species-rich natural communities, the colonisation of individual plants by mycorrhizal fungi occurs within a few days of the emergence of the radicle (Read and Birch, 1988), and can be important for the establishment and survival of compatible plant species (Francis and Read, 1994). Because of their effects on individual plant performance, mycorrhizae influence the productivity of plant communities, and can affect community composition, succession and species diversity (Janos, 1996). On the other hand, mycorrhizal fungi are influenced by the environment and age of the plant (Abbott and Robson, 1991).

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Mycorrhizae are widespread symbioses both geographically and in terms of the number of plant species involved. Numerous species, however, do not seem to develop mycorrhizae (Peterson and Bradbury, 1995; Schreiner and Koide, 1993; Tester et al., 1987; Trappe, 1987). In general, the ratio of mycorrhizal/nonmycorrhizal species tends to be similar in structurally similar communities, even though they may involve either geographically or taxonomically distant plant species. Nevertheless, generalisations about the mycorrhizal status of plants in one floristic region should not be indiscriminately applied to another; taxonomic and environmental attributes of each community may influence the mycorrhizal behaviour of each plant species (Brundrett, 1991). There are many reports of mycorrhizal plants in arid ecosystems, but within these habitats, gradients of decreasing soil moisture availability can be correlated with reductions in the population of mycorrhizal plants (Brundrett, 1991). The frequency and intensity of disturbance and availability of soil nutrients also affect the proportion of mycorrhizal/nonmycorrhizal species in a community (Brundrett, 1991). Minimal disturbance or low soil nutrient levels are correlated with a high proportion of plant species with mycorrhizal dependence. Moderate disturbance levels tend to favour facultative mycorrhizal species, whereas the combination of severe disturbance and high nutrient levels favours the establishment of nonmycorrhizal (NM) species (Miller, 1987).

There is also a significant phylogenetic component to the probability of mycorrhiza development by a particular plant species. In this respect, taxonomic families of vascular plants may be divided into three main groups based upon their mycorrhizal status (Brundrett, 1991; Harley and Smith, 1983): (i) families consisting predominantly of mycorrhizal plant species, which exhibit a strong fidelity to a particular mycorrhizal type, (ii) families which include a large majority of NM species and (iii) families in which both mycorrhizal and NM species are common.

The Patagonian steppe and the ecotone between this community and the Andean temperate forests have been subjected to desertification. Desertification results from a complex interaction between natural components (dry climate, strong winds and light soils) and human social factors (afforestation, intentional fires, overgrazing by sheep and cattle, and inappropriate agricultural techniques). It is self-sustained and self-intensified once it is triggered (Goergen, 1995; Peralta, 1995). The directly observable consequences of deser-

tification in Patagonia are a reduction in plant species number and plant cover, replacement of mesophyllous species by xerophyllous species, wind storms, root exposure, soil erosion, crevice development, salt crusting, increases in water table depth and a negative water balance (Goergen, 1995). Recent evaluations have determined that some areas in Patagonia have reached the stages of intermediate to intermediate-severe desertification (Ayesa et al., 1995). Particularly sensitive to the current scenario of desertification are the marshes, locally known as 'mallines', azonal communities developed in flat valleys with a high supply of water for most of the year. Because of the potentially high productivity of marshes in Patagonia, grazing pressure on them is indeed high (Becker, 1992).

The objectives of this work were to determine the mycorrhizal status of plant species in the north-west Patagonian region and to compare Patagonian steppe and marsh communities with respect to the plant mycorrhizal status. The relationships between mycorrhizal status and plant classification, plant growth form and species origin were also investigated.

Methods

Sampling region

Roots were sampled in two communities, the steppe (*sensu stricto*) and marshes, in north-west Patagonia. Phytogeographically, these communities are part of the Patagonian Province (Cabrera and Willink, 1980). The climate of this region is semi-arid to sub-humid (mean annual isotherm below 10° C; Muñoz and Garay, 1985; Soriano et al., 1983), characterised by the concentration of rain and snow in autumn and winter and a high frequency of strong, westerly winds. On average, springs and summers are cool, windy and dry. Temperature amplitude through the year is moderate, relative to that in regions in the northern hemisphere at approximately the same distance from the equator (Ayesa et al., 1995; Conti, 1998).

Steppe community

The steppe community is characterised by tussock grasses and cushion shrubs and half-shrubs. In some areas within this community, low or tall shrubs may dominate. To account for the variability in species composition, three areas within the steppe community were sampled (Table 1).

Table 1. Environmental and vegetation characteristics of north-west Patagonian study areas

Communities	Areas	Physiognomic characteristics	Cover %	Altitude m	Mean annual temperature °C (M–m)	Mean annual precipitation mm
Steppe	Area I PES	Low bushy steppe with tussock grasses and forbes	30–70% ^a	900–1300 ^a	7 (14–1) ^b	267 ^b
	Area II Airport	Low bushy steppe with tussock grasses	70% ^c	800 ^c	8 (14–2) ^c	700 ^c
	Area III Pampa de Huenuleo	High bushy steppe with tussock grasses	–	935 ^d	8 (13–2) ^d	1000 ^d
Marsh	Area IV PES	Centre: prairies of grasses and graminoids, (<i>Juncus arcticus</i>)	70–100% ^a	900–1050 ^a	7 (14–1) ^b	267 ^b
		Margin: prairies of <i>J. arcticus</i> with tussocks grasses (<i>Festuca pallescens</i>) and forbs	70–90% ^a	900–1050 ^a	7 (14–1) ^b	267 ^b

References: ^aLanciotti, 1994; Lores et al., 1983; ^bClimatic data between 1976 and 1995, from C. Bustos INTA-EEB (personal communication); ^cGhermandi, 1995; Grigera et al., 1989; ^dGrigera et al., 1996; Muñoz and Garay, 1985. PES: Pilcaniyeu Experimental Station of INTA-EEB. M: maximum, m: minimum.

Area I is in a research field within the Pilcaniyeu Experimental Station (PES) of INTA-EEB (Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Bariloche, Argentina), which extends over 70 km². It is 80 km east of S. C. de Bariloche city, well within the Patagonian steppe, close to the locality of Pilcaniyeu (41° S, 70° 43' W). (Tables 1 and 2; Lanciotti, 1994; Lores et al., 1983; climatic data between 1976 and 1995 from INTA-EEB¹). This area has a hilly topography and is characterised by a long history of grazing, including patches with moderate desertification and patches of the pre-desertification vegetation. A previous study (Lores et al., 1983) recognised several vegetation communities within this area. Among the dominant species in less degraded areas are the late-successional tussock grasses *Festuca pallescens*, *Festuca argentina* and *Poa ligularis*. The bushy species *Mulinum spinosum*, *Senecio bracteolatus*, *Senecio neaei* and *Adesmia campestris* and the tussock grass *Stipa speciosa* are more important in more degraded places (Roig, 1998). Sampling in area I was carried out within a 10 km² area.

Area II: An area approximately 4 km² within the wide valley known as Bariloche Airport valley (41° 09' S, 71° 13' W) was sampled (Tables 1 and 2; Ghermandi, 1995; Grigera et al., 1989). The vegetation of this valley has been grazed for at least a

century (Ghermandi, 1995). Plant species linked with human-related land degradation, such as *Stipa speciosa*, *Acaena splendens*, *Senecio bracteolatus* and *Baccharis* spp. (Roig, 1998) are dominant in this area. Less common species are *Bromus setifolius*, *Hordeum comosum*, *Festuca pallescens* and *Poa lanuginosa*.

Area III: A 5 km² sampling area was selected within the 12 km² area known as Pampa de Huenuleo, 3 km south-west of S. C. de Bariloche city centre (41° 09' S, 71° 21' W; Tables 1 and 2; Grigera et al., 1996; Muñoz and Garay, 1985). Its vegetation is intermediate between the Patagonian steppe and the woodland communities. It includes steppe species such as *Stipa speciosa* and *Poa ligularis* and typical woodland species such as *Austrocedrus chilensis*, *Lomatia hirsuta*, *Schinus patagonicus* and *Maytenus chubutensis*. The need for firewood by suburban settlements has increased the pressure on the latter group of plants in recent decades (Grigera et al., 1996). Today, the dominant species are typical of degraded communities: *Mulinum spinosum*, *Senecio bracteolatus*, *Acaena splendens*, *Rumex acetosella*, *Solidago chilensis*, *Discaria articulata* and *Mutisia spinosa* (Dimitri, 1962).

Marsh community

Area IV: This azonal community develops in permanently or temporarily flooded (especially in winter

¹ Bustos, C. INTA-EEB, Argentina: personal communication.

Table 2. Soil characteristics of north-west Patagonian communities and study areas

Communities	Areas ¹	Soil taxonomy ²	Soil characteristics	pH	OM%	N%
Steppe	Area I PES	xerosolic	Superficial soil with graded to moderate or deep soils.	neutral	1.5–1.3	0.20–0.04
		Haplargids	Loamy sand to sandy-loam texture, in some were loamy-clay-sand at the surface.			
	Area II Airport	mollic vitrixerands	Superficial soils developed on moraines, loamy-sand texture	6.5	2.5	0.10
	Area III Pampa de Huenuleo	typic Udivitrands	Soils developed on volcanic ashes covering glacial deposits.	5.6	0.7	0.12
Marsh	Area IV PES	Centre: typic	Deep soils with loamy texture	8.4–10.3	1.9–7.8	0.08–0.24
		Haplaquolls				
		Margin: typic Calcicquolls	Deep soils with loamy texture	7.2–8.8	0.5–2.9	0.03–0.10

References: 1: PES: Pilcaniyeu Experimental Station of INTA-EEB. 2: López C from INTA-EEB (personal communication). OM: organic matter, N: nitrogen.

and spring) flat valleys. Alkaline soil pH is common due to decreasing water content and subsequently increasing salinity (Becker, 1992). Five marshes were sampled at the Pilcaniyeu Experimental Station, covering an area of approximately 2 km² out of the 14 km² total marshland surface in the Pilcaniyeu Experimental Station (Tables 1 and 2; Lanciotti, 1994; Lores et al., 1983; climatic data between 1976 and 1995 from INTA-EEB). Marshes within this region are dominated by *Juncus arcticus*. Other common species are *Taraxacum officinale*, *Agrostis pyrogea*, *Carex* spp., *Trifolium repens* and *Pratia repens*. Degradation at the centre of each marsh is related to soil compaction, which is followed by salinization. Under such circumstances, marshes are invaded by the grass species *Distichlis* spp., *Festuca pallescens*, *Agrostis pyrogea*, *Hordeum comosum* and *Stipa speciosa* var. *major* and by graminoids (*Carex* spp., *Eleocharis* spp. and *Juncus* spp.).

Data collection

The following soil characteristics were determined for each site after soil sieving through a 2 mm mesh: pH in water (suspension 1:2.5; potentiometric method; USDA, 1982), nitrogen content (previous Kjeldahl digestion and colorimetric determination by blue indophenol; USDA, 1982) and organic matter content (OM; after soil sieving through a 0.5 mm mesh and

Walkley Black method; USDA, 1982). These analyses were carried out at the soil laboratory at INTA-EEB.

Species sampling was carried out several times during two consecutive years to permit collection and taxonomic classification of seasonally-representative plants. Because we intended to sample as many species as possible from each vegetation community, irrespective of their importance in terms of plant number or cover, all sample plants were selected by a random walk into the four areas. In the case of the more extensive area I, plants from several of the vegetation types recognised by Lores et al. (1983) were sampled. Some plant species, known as facultative mycorrhizal plants (Janos, 1980; Trappe, 1987), seem to change their mycorrhizal status under sharply different ecological conditions (Brundrett, 1991). For this reason, those species found both in area IV and in any of the three steppe areas were sampled from both sites.

The mycorrhizal status of each plant species was determined from fine-root samples (enough to fill a volume of 50 mL) of at least five individuals. Annual or biennial species with clear signs of senescence were avoided. Apparently, living roots <2 mm in diameter clearly attached to the sample plant were separated. In the case of small plants, the whole root system was collected. In the case of large plants or plants with deep root systems, soil was carefully excavated around each selected plant to confirm connection between root and shoot.

Roots were gently washed to remove free soil, carefully separated by morphological characteristics to avoid misinterpretations and then rinsed in water. All roots were preserved in vials with FAA (formalin-acetic acid-ethanol) and later cleared and stained for observation (Phillips and Hayman, 1970). The presence or absence of mycorrhizas and the mycorrhizal type were examined with dissecting and compound microscopes. The presence of arbuscules was used to designate arbuscular mycorrhizal (AM) associations (Brundrett, 1991). An AM association was considered doubtful whenever arbuscules were absent, but other typical structures such as external and internal hyphae and vesicles were present when colonisation was very scarce. The presence of typical intracellular coils or knots was used as a positive criterion for ericoid mycorrhizas (Harley and Smith, 1983). Those plants which did not represent any of the seven known mycorrhizal types in their roots (Harley and Smith, 1983) were considered NM. All plant species with a doubtful mycorrhizal status or with a status contrasting to that found for its taxonomic group in published studies, were newly sampled twice at different times of the year.

The growth form of each plant species was designated as tree, shrub, perennial herb, biennial herb and annual herb. Species known to occur in Patagonia only after European colonisation were considered exotic (Frenkel, 1970). All other species were considered native. Identification, growth form and origin of species were based on reports from Correa (1969, 1971, 1978, 1984a,b, 1988, 1998) and Dimitri (1972). Plant nomenclature follows Zuloaga et al. (1994) and Zuloaga and Morrone (1996, 1999a,b). The abundance of each species in the community where it was sampled was indicated by a classification adapted from Rønning (1979): rare (R, only occasionally and with low abundance), widespread (W, widely distributed but never abundant) and common (C, both widespread and abundant).

Results

Taxonomic groups

One hundred and fifty-eight samples were analysed (Table 3), including 1 pteridophyte, 2 gymnosperms in 2 families, and 155 angiosperms with 113 dicotyledons in 40 families and 42 monocotyledons in 6 families.

All species of Apiaceae, Onagraceae, Plantaginaceae, Ranunculaceae, Rhamnaceae, Rosaceae, Rubiaceae, Scrophulariaceae and Violaceae had AM (Table 3). Within the families Asteraceae, Berberidaceae, Fabaceae and Poaceae, both AM and NM species were found. AM were recorded in 14 out of 22 species of the Asteraceae. In the Berberidaceae, one species had AM and the other one was NM. All species of the Fabaceae, but *Adesmia lanata*, presented AM (Table 3). Some species of Poaceae in the genera *Agrostis*, *Hordeum*, *Poa* and *Stipa* found in the steppe were NM, but other members of these genera had AM (Table 3). All species in Brassicaceae, Caryophyllaceae, Chenopodiaceae, Juncaceae, Juncaginaceae and Portulacaceae found were NM. Among the Cyperaceae, all species but *Carex fuscata* (AM) were NM (Table 3). In the marsh, *Boopis australis* (Calyceae) and *Senecio neaei* (Asteraceae) contained AM, whereas in the steppe, both were either NM (*B. australis*) or had a infrequent and doubtful mycorrhizal development (*S. neaei*; Table 3). All other species both in the steppe and in the marshes were consistently mycorrhizal.

Growth form, origin, abundance and mycorrhizal status

At a regional scale, native species represented a high percentage of all species found (Tables 3 and 4). AM predominated when considering steppe and marsh plant species; about a quarter of all species were NM and only *Gaultheria mucronata* species had ericoid mycorrhizas (Tables 3 and 4). No species developed more than one kind of mycorrhizas. AM also predominated (Table 4) among native (74% of 131 species) and exotic plants (65% of 23 species). Most species were perennial herbs; shrubs and annual herbs were less represented. Only two biennial herb species and one tree species were included (Table 4). AM predominated in perennial herbs (72% of all perennials) and shrubs (84% of all shrubs), whereas the NM status was more common among annual herbs (50% of all annuals).

Steppe soils were xerolic or volcanic soils with acidic or neutral pH and normal to high organic matter content (Table 2). Plant cover in the steppe community areas varied between 30 and 70% (Table 1). Most species sampled in the steppe were perennial herbs; fewer were shrubs and annuals (Figure 1a) and still fewer biennial herb and tree species. In this community, AM predominated and the native species

Table 3. Mycorrhizal status of Patagonian plants by growth form, family, origin, area of collection and abundance

Plant species (growth form and family)	Origin ^a	Area ^b	Abundance ^c	Mycorrhizal status ^d
Trees				
Cupressaceae				
<i>Austrocedrus chilensis</i> (D.Don) Pic., Serm. & Bizzarri	N	III	R	AM
Shrubs				
Anacardiaceae				
<i>Schinus patagonicus</i> (Phil.) I.M. Johnst.	N	III	W	AM
Apiaceae				
<i>Mulinum microphyllum</i> (Cav.) Pers.	N	I	C	AM
<i>Mulinum spinosum</i> (Cav.) Pers.	N	I	C	AM
Asteraceae				
<i>Baccharis obovata</i> Hook. & Arn.	N	III	W	AM
<i>Chuquiraga oppositifolia</i> D. Don	N	I	W	AM
<i>Senecio bracteolatus</i> Hook. & Arn.	N	I, II, III, IV	C	AM
<i>Senecio neaei</i> DC.	N	I, IV	C	AM-D, AM
<i>Senecio subumbellatus</i> Phil.	N	II	W	AM
Berberidaceae				
<i>Berberis heterophylla</i> Just.	N	I	C	NM
<i>Berberis</i> aff. <i>buxifolia</i> Lam.	N	II	C	AM
Celastraceae				
<i>Maytenus chubutensis</i> (Speg.) Lourteig, O'Donell & Sleumer	N	III	W	AM
Ephedraceae				
<i>Ephedra frustillata</i> Miers	N	I	W	NM
Ericaceae				
<i>Gaultheria mucronata</i> (L.f.) Hook. & Arn.	N	III	W	ER
Euphorbiaceae				
<i>Stillingia patagonica</i> (Speg.) Pax & K. Hoffm.	N	I	R	AM
Fabaceae				
<i>Adesmia boronioides</i> Hook. f.	N	III	C	AM
<i>Adesmia volckmanni</i> Phil.	N	I	W	AM
<i>Anarthrophyllum rigidum</i> (Gillies) Hieron.	N	III	W	AM
Ledocarpaceae				
<i>Balbisia gracilis</i> (Meyen) Hunz. & Ariza Esp.	N	III	W	AM
Rhamnaceae				
<i>Discaria trinervis</i> (Gillies) Reiche	N	II, III	W	AM+F
<i>Discaria articulata</i> (Phil.) Miers	N	III	C	AM+F
Rosaceae				
<i>Tetraglochin caespitosum</i> Phil.	N	I	W	AM

Table 3. Continued

Plant species (growth form and family)	Origin ^a	Area ^b	Abundance ^c	Mycorrhizal status ^d
Santalaceae				
<i>Myoschilos oblongum</i> Ruiz & Pav.	N	III	W	NM
Saxifragaceae				
<i>Ribes cucullatum</i> Hook. & Arn.	N	III	W	AM
Solanaceae				
<i>Fabiana imbricata</i> Ruiz & Pav.	N	III	W	AM
Verbenaceae				
<i>Junellia succulentifolia</i> (Kuntze) Moldenke	N	I	W	AM
Perennial herbs				
Amaryllidaceae				
<i>Rhodophiala mendocina</i> (Phil.) Ravenna	N	I	W	NM
Apiaceae				
<i>Azorella ameghinoi</i> Speg.	N	I	W	AM
<i>Azorella trifurcata</i> (Gaertn.) Pers.	N	IV	W	AM
<i>Lilaeopsis macloviana</i> (Gand.) A.W. Hill	N	IV	R	AM
Asteraceae				
<i>Agoseris coronopifolia</i> (d'Urv.) K.L. Chambers	N	III	W	AM
<i>Gnaphalium psilophyllum</i> Meyen & Walp.	N	IV	W	AM
<i>Haploppapus glutinosus</i> Cass. f.	N	III	C	AM
<i>Hypochaeris</i> aff. <i>incana</i> (Hook. & Arn.) Macloskie	N	I	W	AM
<i>Hypochaeris radicata</i> L.	E	IV	W	AM
<i>Mutisia decurrens</i> Cav.	N	III	W	AM
<i>Mutisia spinosa</i> Ruiz & Pav.	N	III	W	AM
<i>Nassauvia aculeata</i> (Less.) Poepp. & Endl.	N	III	R	AM
<i>Nassauvia glomerulosa</i> (Lag.) D. Don	N	I	W	NM
<i>Perezia linearis</i> Less.	N	IV	R	AM
<i>Perezia recurvata</i> (Vahl) Less.	N	I, IV	R	AM
<i>Senecio gymnocaulos</i> Phil.	N	III	R	AM
<i>Senecio sericeo-nitens</i> Speg.	N	III	W	AM
<i>Taraxacum officinale</i> Weber	E	IV	W	NM
<i>Tragopogon dubius</i> Scop.	E	II	W	AM
Brassicaceae				
<i>Rorippa nasturtium-aquaticum</i> (L.) Hayek	E	III	W	NM
<i>Thlaspi magellanicum</i> Comm.	N	III	W	NM
Cactaceae				
<i>Maihuea patagonica</i> (Phil.) Britton & Rose	N	I	R	NM
Calyceraceae				
<i>Boopis australis</i> Decne.	N	I	R	NM
<i>Boopis australis</i> Decne.	N	IV	R	AM
<i>Nastanthus</i> aff. <i>patagonicus</i> Speg.	N	I	R	NM

Table 3. Continued

Plant species (growth form and family)	Origin ^a	Area ^b	Abundance ^c	Mycorrhizal status ^d
Campanulaceae				
<i>Pratia repens</i> Gaudich.	N	IV	W	AM
Caryophyllaceae				
<i>Cerastium arvense</i> L.	E	I	W	NM
Chenopodiaceae				
<i>Nitrophila australis</i> Chodat & Wilczek	N	IV	W	NM
Cyperaceae				
<i>Carex fuscata</i> d'Urv.	N	III	W	AM
<i>Carex gayana</i> E. Desv.	N	III	W	NM
<i>Carex macloviana</i> d'Urv.	N	III	W	NM
<i>Carex maritima</i> Gunn.	N	IV	W	NM
<i>Carex</i> aff. <i>subantarctica</i> Speg.	N	IV	W	NM
<i>Eleocharis</i> aff. <i>pachycarpa</i> E. Desv.	N	III	W	NM
<i>Eleocharis</i> sp. R. Br.	–	IV	W	NM
<i>Schoenus</i> sp. L.	–	IV	W	NM
<i>Scirpus</i> aff. <i>perpusillus</i> F. Phil.	N	IV	W	NM
Equisetaceae				
<i>Equisetum bogotense</i> H. B. K.	N	III	W	AM
Fabaceae				
<i>Adesmia</i> aff. <i>aucaensis</i> Burkart	N	III	R	AM
<i>Adesmia</i> aff. <i>corymbosa</i> Closs	N	I	W	AM
<i>Adesmia lanata</i> Hook. f.	N	IV	W	NM
<i>Lathyrus magellanicus</i> Lam.	N	III	W	AM
<i>Lotus pedunculatus</i> Cav.	E	III	W	AM
<i>Medicago lupulina</i> L.	E	IV	W	AM
<i>Trifolium repens</i> L. f.	E	IV	W	AM
<i>Vicia nigricans</i> Hook & Arn.	N	III	W	AM
Geraniaceae				
<i>Geranium magellanicum</i> Hook. f.	N	III	W	AM
Gunneraceae				
<i>Gunnera magellanica</i> Lam.	N	III	R	AM
Hydrophyllaceae				
<i>Phacelia secunda</i> J.F. Gmel.	N	III	C	AM
Iridaceae				
<i>Olsynium junceum</i> (E. Mey.) Goldblatt	N	III	C	AM
<i>Sisyrinchium arenarium</i> Poepp.	N	IV	C	AM-D
Juncaceae				
<i>Juncus arcticus</i> Willd.	N	IV	C	NM
<i>Juncus</i> aff. <i>stipulatus</i> Nees & Meyen	N	IV	W	NM
Juncaginaceae				
<i>Triglochin concinna</i> Burt Davy	N	IV	R	NM

Table 3. Continued

Plant species (growth form and family)	Origin ^a	Area ^b	Abundance ^c	Mycorrhizal status ^d
<i>Triglochin palustris</i> L.	N	IV	R	NM
Lamiaceae				
<i>Mentha piperita</i> L.	E	IV	R	AM
Loasaceae				
<i>Caiophora</i> aff. <i>patagonica</i> (Speg.) Urb. & Gilg	N	I	R	AM
Malvaceae				
<i>Tarasa humilis</i> (Gillies) Krapov.	N	III	R	AM
Onagraceae				
<i>Epilobium barbeyanum</i> H. Lév.	N	IV	R	AM
<i>Epilobium ciliatum</i> Raf.	N	IV	W	AM
<i>Oenothera odorata</i> Jacq.	N	II	C	AM
Plantaginaceae				
<i>Plantago</i> aff. <i>australis</i> Lam.	N	III	W	AM
<i>Plantago</i> aff. <i>barbata</i> G. Forst.	N	IV	W	AM
<i>Plantago lanceolata</i> L. (Mill.) Willd.	E	III	C	AM
Plumbaginaceae				
<i>Armeria maritima</i> (Mill.) Willd.	N	III	W	AM
Poaceae				
<i>Agrostis glabra</i> (J. Presl) Kunth	N	IV	W	AM
<i>Agrostis</i> sp. L.	–	IV	W	NM
<i>Bromus</i> aff. <i>caharticus</i> Vahl.	N	IV	C	AM
<i>Cortaderia araucana</i> Stapf	N	IV	W	AM
<i>Distichlis scoparia</i> (Kunth) Arechav.	N	I, IV	W	AM
<i>Festuca pallescens</i> (St. Yves) Parodi	N	I, IV	C	AM
<i>Holcus lanatus</i> L.	E	I, IV	C	AM
<i>Hordeum comosum</i> J. Presl	N	I	C	NM
<i>Hordeum</i> aff. <i>pubiflorum</i> Hook. f.	N	IV	W	AM
<i>Poa lanuginosa</i> Poir.	N	I	C	AM
<i>Poa ligularis</i> Nees ap. Steud.	N	I	C	AM
<i>Poa</i> aff. <i>holciformis</i> J. Presl	N	IV	–	NM
<i>Rytidosperma</i> aff. <i>sorianoi</i> Nicora	N	IV	W	AM
<i>Rytidosperma virescens</i> (Desv.) Nicora	N	III	W	AM
<i>Stipa chrysophylla</i> Desv.	N	IV	W	NM
<i>Stipa neaei</i> Nees.	N	I	W	NM
<i>Stipa poeppigiana</i> Trin. & Rupr.	N	III	W	AM
<i>Stipa speciosa</i> Trin. & Rupr. var. <i>major</i> (Speg.) Parodi	N	I, IV	C	AM-D
<i>Stipa speciosa</i> Trin. & Rupr. var. <i>speciosa</i>	N	I, IV	C	AM-D
Polygalaceae				
<i>Polygala salasiana</i> Gay	N	IV	W	AM

Table 3. Continued

Plant species (growth form and family)	Origin ^a	Area ^b	Abundance ^c	Mycorrhizal status ^d
Polygonaceae				
<i>Rumex acetosella</i> L.	E	II	C	AM-D
Portulacaceae				
<i>Montiopsis gayana</i> (Barnéoud) D.I. Ford	N	III	W	NM
Ranunculaceae				
<i>Anemone multifida</i> Poir.	N	II	C	AM
<i>Ranunculus cymbalaria</i> Pursh	N	IV	W	AM
Rosaceae				
<i>Acaena</i> aff. <i>antarctica</i> Hook. f.	N	IV	W	AM
<i>Acaena magellanica</i> (Lam.) Vahl	N	III	W	AM
<i>Acaena pinnatifida</i> Ruiz & Pav.	N	III	C	AM
<i>Acaena</i> aff. <i>platyacantha</i> Speg.	N	I, IV	W	AM
<i>Acaena splendens</i> Gillies	N	IV	C	AM
<i>Fragaria chiloensis</i> (L.) Duchesne f.	N	III	W	AM
<i>Geum magellanicum</i> Pers.	N	III	W	AM
Rubiaceae				
<i>Galium richardianum</i> (Gillies ex Hook. & Arn.) Endl.	N	I	W	AM
<i>Oreopolus glacialis</i> (Poepp.) Ricardi	N	III	W	AM
Santalaceae				
<i>Arjona pusilla</i> Hook. f.	N	IV	R	NM
<i>Arjona tuberosa</i> Cav.	N	I	R	NM
<i>Quinchamalium chilense</i> Molina	N	III	W	AM
Scrophulariaceae				
<i>Calceolaria biflora</i> Lam.	N	IV	C	AM
<i>Calceolaria polyrrhiza</i> Cav.	N	III	C	AM
<i>Limosella australis</i> R. Br.	N	IV	W	AM
<i>Mimulus glabratus</i> Kunth	N	IV	W	AM
<i>Veronica anagallis-aquatica</i> L.	E	IV	W	AM
Valerianaceae				
<i>Valeriana carnosa</i> Sm.	N	III	W	AM
Violaceae				
<i>Viola</i> aff. <i>cotyledon</i> Ging.	N	III	R	AM
<i>Viola maculata</i> Cav. var. <i>maculata</i>	N	III	C	AM
<i>Viola maculata</i> Cav. var. <i>microphyllos</i> (Poir.) Ging.	N	I	C	AM
Biennial herbs				
Apiaceae				
<i>Osmorhiza chilensis</i> Hook. & Arn.	N	III	W	AM
Geraniaceae				
<i>Erodium cicutarium</i> (L.) L'Hér.	E	I	C	AM

Table 3. Continued

Plant species (growth form and family)	Origin ^a	Area ^b	Abundance ^c	Mycorrhizal status ^d
Annual herbs				
Asteraceae				
<i>Lactuca serriola</i> L.	E	IV	W	AM
<i>Triptilion achilleae</i> DC.	N	I	C	NM
Boraginaceae				
<i>Heliotropium</i> sp. L.	N	I	C	NM
<i>Plagiobothrys verrucosus</i> (Phil.) I.M. Johnston	N	II	W	AM
Brassicaceae				
<i>Descurainia pimpinellifolia</i> (Barnéoud) O.E. Schulz	N	IV	W	NM
<i>Erophila verna</i> (L.) Chevall.	E	II	C	NM
Calyceraceae				
<i>Boopis gracilis</i> Phil.	N	IV	W	NM
Caryophyllaceae				
<i>Arenaria serpyllifolia</i> L.	E	III	C	NM
<i>Holosteum umbellatum</i> L.	E	II	C	NM
<i>Scleranthus annuus</i> L.	E	III	C	NM
Onagraceae				
<i>Clarkia tenella</i> (Cav.) H.F. Lewis & M.R. Lewis	N	III	W	AM
Poaceae				
<i>Bromus</i> aff. <i>setifolius</i> J. Presl	N	I, IV	W	AM
<i>Bromus tectorum</i> L.	E	IV	C	AM
<i>Bromus</i> sp. L.	–	II	–	AM
<i>Hordeum murinum</i> L.	E	I	C	NM
<i>Polypogon</i> aff. <i>monspeliensis</i> (L.) Desf.	E	IV	W	AM
<i>Vulpia australis</i> (Nees) Blom	N	II	W	AM
<i>Vulpia bromoides</i> (L.) S.F. Gray	E	III	W	AM
Polemoniaceae				
<i>Collomia linearis</i> Nutt.	N	II	C	AM
Portulacaceae				
<i>Montiopsis polycarpoides</i> Phil.	N	IV	W	NM

Note: ^aN= native, E= exotic, ^bI: Pilcaniyeu Experimental Station; II: Bariloche Airport; III: Pampa de Huenuleo; IV: marsh. ^cR=rare, W=widespread but uncommon and C=common. ^dAM=arbuscular mycorrhizal, D=doubtful arbuscular mycorrhizal, ER=ericoid mycorrhizal, NM=nonmycorrhizal, AM+F=symbiosis tripartite between *Frankia* sp., AM and host plant.

Table 4. Percentage of plant species at regional scale, corresponding to different taxonomic groups, growth forms, origins and mycorrhizal status

Taxonomic group	Growth form ^a	Origin and mycorrhizal status ^b							Total
		Native			Exotic		ND		
		AM	NM	Ericoid	AM	NM	AM	NM	
Pteridophytes	PH	0.6	0	0	0	0	0	0	0.6
	Subtotal 4	0.6	0	0	0	0	0	0	0.6
Gymnosperms	Trees	0.6	0	0	0	0	0	0	0.6
	Shrubs	0	0.6	0	0	0	0	0	0.6
	Subtotal 1	0.6	0.6	0	0	0	0	0	1.2
Angiosperms									
Monocotyledons	PH	10.2	9.5	0	0.6	0	0	1.9	22.2
	AH	1.3	0	0	1.9	0.6	0.6	0	4.4
	Subtotal 2	11.5	9.5	0	2.5	0.6	0.6	1.9	26.6
Dicotyledons	Shrubs	13.4	1.3	0.6	0	0	0	0	15.3
	PH	32.9	6.3	0	5.8	1.9	0	0	46.9
	BH	0.6	0	0	0.6	0	0	0	1.2
	AH	1.9	3.2	0	0.6	2.5	0.0	0	8.2
	Subtotal 3	48.8	10.8	0.6	7.0	4.4	0.0	0	71.6
Total		61.5	20.9	0.6	9.5	5.0	0.6	1.9	100

^aPH=perennial herbs; BH=biennial herbs; AH=annual herbs. ^bAM=arbuscular mycorrhizal fungi; NM=nonmycorrhizal associations.

exceeded exotics (Figure 1a). The plant species dominating this community, among them *Stipa speciosa*, *Poa ligularis*, *Festuca pallescens*, *Mulinum spinosum*, *Senecio* spp. and *Berberis* aff. *buxifolia*, had AM mycorrhizas (Table 3). The most abundant NM species in this community (e.g. *Nassauvia glomerulosa*, *Hordeum comosum* and *Taraxacum officinale*) were far less important than abundant AM species. Most native species had AM; the AM species–NM species ratio was higher for widespread and common species than for rare species (Figure 2a). Among exotic species in the steppe, there was a similar proportion of AM and NM species (54 and 46%), and none were rare (Figure 2a).

Marshes have hydromorphic soils with high to normal values of organic matter and an alkaline pH (Table 2). Plant cover in this community was higher than 70%. Seventy-one percent of all marsh species presented AM (Figures 1b and 2b). Most species in the marsh community were perennial herbs; the rest were annual herbs or shrubs (Figure 1b). The native NM species *Juncus arcticus* was, by far, the most dominant in marshes, both in terms of density and cover. Other native species, either AM (e.g. *Senecio neaei*, *Stipa*

speciosa, *Festuca pallescens* and *Bromus* aff. *catharticus*) or NM (*Carex* spp. and *Juncus* aff. *stipulatus*), were common or widespread. The majority of exotics in this community were widespread AM species (e.g. *Medicago lupulina*, *Trifolium repens* and *Hypochaeris radicata*; Figure 2b).

Discussion

Mycorrhizal status of plants in north-west Patagonia

In general, most plants in warm or dry wild grasslands develop AM mycorrhizae and other types of mycorrhizae (such as the ericoid mycorrhizae) are present but poorly represented in most communities (Brundrett, 1991). Our study supports this trend. The proportion of species with AM found here for the Patagonian region was similar to those found for temperate and semi-arid natural grasslands of North America and Europe and for the Russian steppe (Brundrett, 1991), a xeric woodland of *Austrocedrus chilensis* in north-western Patagonia in Argentina (Fontenla et al.,

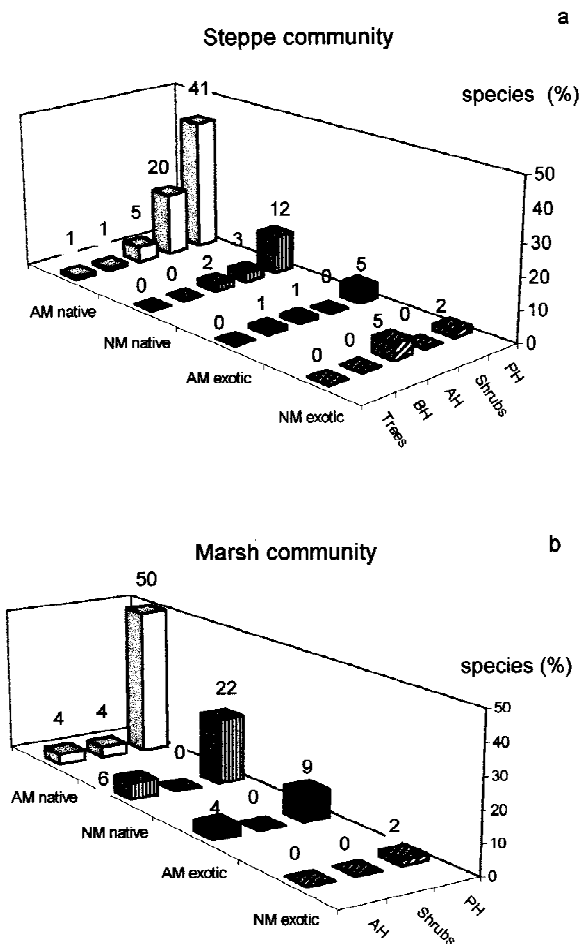


Figure 1. North-west Patagonian plant species in steppe (a) and marsh (b) communities discriminated by growth form (trees, shrubs, PH=perennial herbs, BH=biennial herbs and AH=annual herbs), origin (native, exotic) and mycorrhizal status (AM=arbuscular mycorrhizal, NM=nonmycorrhizal); ericoid mycorrhizal in steppe communities are not illustrated.

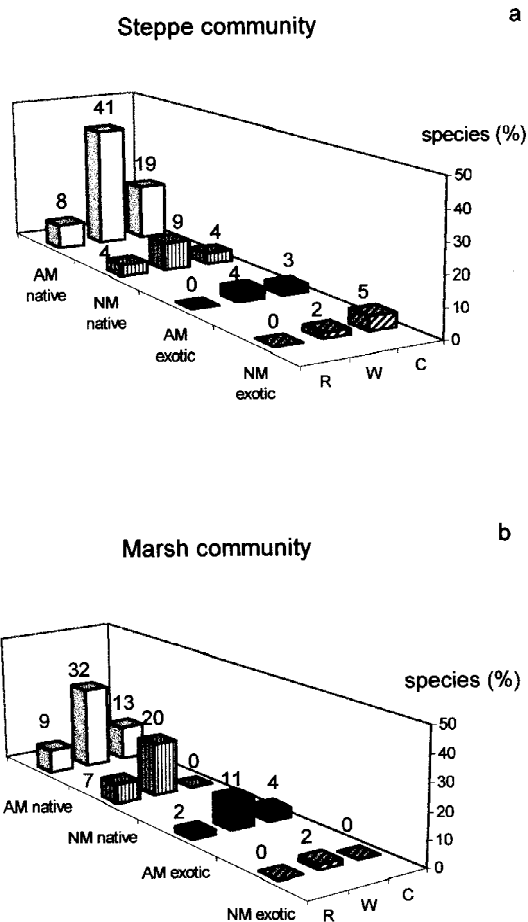


Figure 2. North-west Patagonian plant species in steppe (a) and marsh (b) communities discriminated by abundance (R=rare, W=widespread but uncommon and C=common, origin (native, exotic) and mycorrhizal status (AM=arbuscular mycorrhizal, NM=nonmycorrhizal); ericoid mycorrhizal in steppe communities are not illustrated.

1989), and a temperate conifer forest in south-western Chile (Carrillo et al., 1992; Godoy et al., 1994).

The predominance of AM species found here is also comparable with those obtained for other regions of the Southern Hemisphere, such as savannas of South Africa (Thomazini, 1973), temperate forests of New Zealand (Johnson, 1977) and forests of western Australia (Brundrett et al., 1995, 1996). However, the Patagonian steppe region differs in having very low numbers of other mycorrhizal types (including the absence of ectomycorrhizal species) and the absence of individuals with dual ectomycorrhizal-AM association. The absence of species with ectomycorrhizal symbiosis is consistent with the type of communities

studied. Both the steppe and the marsh communities consist mostly of herb species. The number of woody species is very low; most of them have AM (e.g. *Austrocedrus chilensis*, Cupressaceae) and none has ectomycorrhizae. In closely located forests of north-western Patagonia, not included in the present study, ectomycorrhizal (*Nothofagus* spp.) or AM (e.g. *Austrocedrus chilensis* and *Araucaria araucana*) woody species are present (Fontenla et al., 1989, 1991; Fontenla, pers. comm.).

The NM status was more common among annual herbs than shrubs and perennial herbs. Previous studies have indicated that annual NM plants would occupy recently disturbed or degraded habitats (Grime, 1979; Janos, 1980). Our results show that some of the

annual species acting as ruderals in Patagonia, such as *Lactuca serriola*, *Plagiobothrys verrucosus* and *Bromus tectorum* (Chancellor, 1966; Matthei, 1995), are AM.

Trappe (1987) found AM/NM ratios of 4.9 for dicotyledons and 3.8 for monocotyledons (6500 species analysed, mostly from northern temperate regions). The ratios in our study indicated higher proportions of NM: 4.2 for dicotyledons and 1.1 for monocotyledons. This could result from the marshes in the steppe, which added a considerable number of hydrophytes to our samples. Hydrophytes are more likely to be NM than strict land plants (Brundrett, 1991; Khan, 1974; Khan and Belik, 1995).

In the present study, species belonging to the same family tended to have the same mycorrhizal behaviour, as found in other studies (Carrillo et al., 1992; Fontenla et al., 1998; Harley and Smith, 1983; Trappe, 1987). Several exceptions to this general behaviour were observed. For instance, the AM species *Carex fuscua* belongs to a typically NM family (Newman and Reddell, 1987; Tester et al., 1987). Another case was that of the predominantly AM family Asteraceae, three of the most profuse species of which were NM (two natives and one exotic), e.g. *Taraxacum officinale*, (cited as an AM or as a NM plant in Harley and Harley, 1987a,b, 1990). Cases of species contrasting in their mycorrhizal status with taxonomically and phylogenetically closely related species (including members of the Cyperaceae) have been pointed out in other studies (Francis and Read, 1994; Lovera and Cuenca, 1996; Meney et al., 1993; Tester et al. 1987).

The AM status of all five species of Scrophulariaceae found here contrasts with the predominantly NM status recorded previously for this family (Brundrett, 1991, 1995; Harley and Harley, 1987a,b). The NM status of *Rhodophiala mendocina* (Amaryllidaceae) sampled in the present study contrasts with the overall mycorrhizal status of the genus (Fontenla et al., 1998; Harley and Harley, 1987a,b, 1990). The NM status recorded here for one of the two *Berberis* species in the present study is at odds with the previously published mycorrhizal status of *Berberis* spp. (Carrillo et al., 1992; Fontenla et al., 1998) and other Berberidaceae (Harley and Harley, 1987a,b, 1990). Contrasting mycorrhizal status in species of the same genus has been reported for Fabaceae and Poaceae (Harley 1987a,b, 1990).

A number of plant species, known as facultative mycorrhizal species, vary in their mycorrhizal status according to environmental conditions (Trappe, 1987).

Senecio neaei (Asteraceae) and *Boopis australis* (Calyceae) showed facultative mycorrhizal behaviour in the present study.

Mycorrhizal status of plants in steppe and marsh communities

The mycorrhizal status of plants of different origin and growth form differed slightly between the steppe and the marsh communities. In the Patagonian steppe community, the AM status prevails among native species and among the most representative species of this community in terms of cover and abundance. The NM status is far more important in marshes than in the steppe, more notably so with respect to plant cover. The Juncaceae and Cyperaceae, which include predominantly hydrophytic NM species, such as the marsh dominant *Juncus arcticus*, accounted for much of influence on this difference between marshes and steppe.

The prevalence of AM species found here for the Patagonian steppe complies with results for other arid areas (Brundrett, 1991; Varma, 1995). NM plants are better represented in wetlands than in dry lands in Patagonia and elsewhere (Brundrett, 1991; Varma, 1995). The different mycorrhizal behaviour or the relative prevalence of NM species in marshes could result from fluctuations in soil water availability, aeration and water table depth, which could affect survival of plants and mycorrhizal associations (Khan and Belik, 1995).

The relative proportion of AM plants to NM plants among exotic species was higher in the marsh than in the steppe, contrary to what was found for native species. This difference between the steppe and the marsh in the mycorrhizal behaviour of exotic species may be ascribed to (1) the presence in the steppe of annual NM species of worldwide distribution (*Erophila verna*, *Arenaria serpyllifolia*, *Scleranthus annuus* and *Hordeum murinum*; Correa, 1978, 1984a, 1988), and (2) the fact that most of the exotic species found in the marshes are terrestrial (though capable of withstanding seasonal water-logging) rather than typical wetland species (Correa, 1971, 1978, 1984a, 1988). Our results, together with the contrasting soil features of the steppe and the marsh, support the general conclusion that edaphic variations within an ecosystem may affect the representation of different plant growth forms and the mycorrhizal behaviour of the community (Brundrett, 1991; Gregory, 1987).

Studies in agriculture, forestry, horticulture and restoration ecology emphasize that mycorrhizal management improves plant survival and growth (Barea and Jeffries, 1995; Varma, 1995). Desertification in Patagonia is reaching alarming proportions (Peralta, 1995) that call for urgent measures to control erosion and promote revegetation (Ayesa et al., 1995; Goergen, 1995). Since most species in the Patagonian steppe develop AM associations, the planting of already infected seedlings could be considered a viable option in landscape restoration programs. A better knowledge of the fungal species involved in these symbioses would, in this case, be necessary. AM inoculation or management of indigenous AM plant species may improve conditions for plant establishment.

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