

Colonization of native Andean grasses by arbuscular mycorrhizal fungi in Puna: a matter of altitude, host photosynthetic pathway and host life cycles

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Abstract

The relationships of altitude, host life cycle (annual or perennial) and photosynthetic pathway (C₃ or C₄) with arbuscular mycorrhiza (AM) root colonization were analysed in 35 species of Andean grasses. The study area is located in north-western Argentina along altitudinal sites within the Puna biogeographical region. Twenty-one sites from 3320 to 4314 m were sampled. Thirty-five grasses were collected, and the AM root colonization was quantified. We used multivariate analyses to test emerging patterns in these species by considering the plant traits and variables of AM colonization. Pearson's correlations were carried out to evaluate the specific relationships between some variables. Most grasses were associated with AM, but the colonization percentages were low in both C₃ and C₄ grasses. Nevertheless, the AM root colonization clearly decreased as the altitude increased. This distinctive pattern among different species was also observed between some of the populations of the same species sampled throughout the sites. An inverse relationship between altitude and AM colonization was found in this Southern Hemisphere Andean system. The effect of altitude on AM colonization seems to be more related to the grasses' photosynthetic pathway than to life cycles. This study represents the first report for this biogeographical region.

Introduction

Arbuscular mycorrhizas (AM) are distributed from the Equator to the Antarctic and Arctic regions (Trappe, 1987; Smith & Read, 2008) and are even found at high altitudes up to 5250 m in the Andes (Schmidt *et al.*, 2008). The majority of angiosperms are associated with symbiotic fungi forming AM. In the *Poaceae*, 99.6% of the species studied are AM symbionts (Wang & Qiu, 2006), constituting an AM group in Poales (Brundrett, 2009). Most of the studied species are mainly from the Northern Hemisphere and Eurasia, and only few of them are from South America.

In general, AM occur in environments with soils that have low organic material content, high nitrogen content and low phosphorous availability (Allen, 1991; Read, 1991). However, AM are also present in phosphorous-

polluted soils where other factors are at limiting concentrations (Blanke *et al.*, 2005) or AM could be dominant in the organic soil of montane cloud forests (Kottke *et al.*, 2004). Ericoids and ectomycorrhizas are absolutely essential for their host plants (obligate mycotrophs); in contrast, arbuscular mycorrhizal fungi (AMF) can form associations with plant species that can live with or without mycorrhizal fungi (facultative mycotrophs) (Trappe, 1987). The degree of association with AMF depends on the photosynthetic pathway of the grass, and either C₃ or C₄. C₃ grasses are considered to be facultative mycotrophs, while C₄ species are obligate mycotrophs (Hetrick *et al.*, 1990). In the Northern Hemisphere, cool-season (C₃) grasses and warm-season (C₄) grasses coexist. Considering the root systems, the C₃ grasses have highly fibrous roots and are less dependent on mycorrhizal symbiosis despite the low phosphorus level available in the

soil, and could develop an extensive root architecture as a strategy for nutrient acquisition (Hetrick *et al.*, 1988). The C_4 grasses have coarse root systems and are obligate mycotrophs and use mycorrhizal association as their main nutritional strategy (Hetrick *et al.*, 1988, 1990, 1991). In South American mountain grasslands, C_3 and C_4 native grasses display comparable mycorrhizal patterns (Lugo *et al.*, 2003) to those described for the Northern Hemisphere (Hetrick *et al.*, 1988, 1990, 1992).

The host's life cycle (annual and perennial) also has an influence on the characteristics of the plant–mycorrhizal association. Annual grasses can avoid environmental stress, such as seasonal heating, cold, drought or flooding, by the production of large quantities of small seeds that have a dormancy period and are capable of long-distance dispersal. Species with a perennial life cycle usually experience competition and avoid stressed environments. Trappe (1987) reported that annuals are less associated with AM (about 15%) in contrast to perennials (85%) 'possibly because they often occur in disturbed habitats'. Furthermore, when metabolic types and life cycles are considered, some trends emerge: while the C_4 perennial grasses are notably benefited by the AM, the annual C_4 and perennial C_3 grasses are less influenced (Wilson & Hartnett, 1998; Hartnett & Wilson, 2002).

Along with elevation gradients, changes in important factors such as precipitation, temperature and soil conditions can affect the structure of plant communities and, consequently, may determine the shifts in plant–mycorrhiza associations (Körner, 1999; Smith & Read, 2008). In alpine environments of the Northern Hemisphere, as altitude increases, (1) coverage of mycorrhizal plant species decreases (Väre *et al.*, 1997), (2) mycorrhizal types change and AM plants are replaced by ectomycorrhizal, ericoid or nonmycorrhizal species and (3) mycorrhizal colonization decreases (Read & Haselwandter, 1981; Trappe, 1988; Kohn & Stasovski, 1990; Routsalainen *et al.*, 2004). In spite of the fact that mycorrhizal associations have been studied in relation to altitude in northern environments, data on AM 'colonization patterns along altitudinal gradients at species-level generally is lacking' (Routsalainen *et al.*, 2004).

Puna is an arid biogeographical province of the 'Andina' Region of South America (Morrone, 2001). The Puna Region is a plateau located between 2000- and 4400-m altitude from north-west Argentina to southern Perú. The climatic conditions are predominantly continental; this arid region is characterized by a dry and cold climate throughout the year, a wide daily temperature range, low annual precipitation mainly during the summer and intense solar radiation. The soils of the Puna are shallow and immature, very poor in organic matter, sandy and stony (Cabrera, 1976) and of the Entisol and Aridisol type (Martínez Carretero, 1995). Although the Puna is a

unique biogeographical region, it was considered to be an alpine environment because of its altitude (Ruthsatz, 1977), but it shows particular features such as climatic condition, flora and fauna that differ greatly from alpine regions.

The aim of this study is to analyse the influence of altitude, host life cycle (annual or perennial) and photosynthetic pathway (C_3 or C_4) on AM colonization in native grasses from the Argentinean Puna. Consequently, the distribution of species along these sites, their photosynthetic pathways, life cycles and AM colonization are reported for the Puna area studied. We expect altitude, plant photosynthetic pathway and grass life cycle are important factors influencing AM colonization; specifically, we suppose that an inverse relationship exists between AM colonization and altitude, a higher AM colonization in perennial than in annual grasses and in C_4 than in C_3 grasses. Therefore, altitude will show the strongest relationship with AM colonization on annual C_3 grasses, followed by perennial C_3 grasses and annual C_4 , and the weakest one will be with perennial C_4 .

Materials and methods

Study area

Puna is a harsh biogeographical province that contains varied floristic districts, and the vegetation is predominantly xerophytic, constituted of shrub steppes, low shrubs and mountain grasslands with only one tree species and few herbs (Cabrera & Willink, 1980; Morrone, 2001). The study area is located in north-western Argentina and experiences a dry season in winter and an annual precipitation of 100–400 mm in summer. Specifically, available data showed a monthly mean precipitation at Iturbe – nearly the lowest point of the gradient – of 88, 63 and 41 mm for January, February and March, respectively, and values of 95, 96 and 32 mm, respectively, for these months at Mina El Aguilar, the highest point (Ruthsatz, 1977). The solar radiation is intense, and the relative air humidity is low (10–15%), with large temperature differences between the maximum and the minimum during the day (16–20 °C). The resulting climate is of a desert type. The annual mean temperature oscillates between 8.5 and 9.5 °C (Cabrera & Willink, 1980). During the summer, the monthly mean temperatures at Mina El Aguilar were 6.3, 6.6 and 5.7 °C for January, February and March, respectively; no records exist for Iturbe.

Sampling design

Samples were collected during the summer growing season along the road that connects the town of Iturbe

(Jujuy) with Iruya (Salta) heading up to Mina El Aguilar, Jujuy, the highest point considered. Thus, altitudinal sites were established between 3320 and 4314 m. Along the sites, 21 (30 × 40 m) sampling sites were established (at 3220, 3370, 3390, 3450, 3520, 3560, 3620, 3650, two at 3700, two at 3770, 3800, 3820, 3860, 3870, 3950, 4000, 4050, 4300 and 4314 m) with an interval of ≥ 50 m between them. However, in some instances, these elevation steps were ≤ 40 m because of perceived changes in the community composition of the grasses. No replicates were carried out within sites because of the changing conditions of the grasses composition, slope and exposition at each site.

Hosts

A total of 35 native species of annual and perennial *Poaceae* were sampled in the 21 sites (Supporting Information, Table S1). Twenty-two species of the 35 had a C_3 photosynthetic pathway (three annual and 19 perennial), and 13 had a C_4 pathway (seven annual and six perennial). Fifteen of these 35 species were sampled 2–6 times along the altitudinal sites. The remaining species were sampled only once.

Root colonization

For each of the studied species, four or five complete individuals were collected at each sampling site (i.e. if a species grew along the altitudinal sites, it was sampled at each altitudinal point) and stored in plastic bags that were refrigerated at 4 °C. At the laboratory, the roots were washed and set in formalin–acetic acid–alcohol solution for their subsequent clarification and staining (Grace & Stribley, 1991). The finest roots of each individual in each species were cut into approximately 1-cm segments, mixed and randomly selected for mounting on one or two slides in polyvinyl-lactic acid-glycerol. For each preparation, the roots were quantified in 100 intersections under the microscope (McGonigle *et al.*, 1990) at 50× to determine the percentages of arbuscules (A%), hyphae (H%), vesicles (V%) and total root colonization (RC%).

Statistical analyses

The variables considered to characterize AM colonization were the percentages of arbuscules (A%), hyphae (H%), vesicles (V%) and total root colonization (RC%). To determine the relationships between these variables and altitude, Pearson's correlations were performed with the data for all species. Additionally, to analyse the effects of life cycles and photosynthetic pathways, linear regressions

were conducted. To analyse the interspecific differences in each of the variables, we considered a whole data set ($N = 69$ samples corresponding to the 35 species studied, some of which were sampled in 2–6 sites) and a restricted data set ($N = 35$, the 35 species studied considered from only one site each; the selected site was the midpoint in the altitudinal sites for each of the species that were sampled at many sites). To analyse intraspecific patterns, regression lines were plotted for those species sampled four or more times within the altitudinal sites; rare species were not included.

We used multivariate analyses to generate hypotheses about the relationship between the AM colonization of 35 grass species and factors related to the environment (altitude) and those related to the plants (photosynthetic pathway and life cycle). Principal coordinate analysis (PCoA) and principal component analysis (PCA) were conducted according to Digby & Kempton (1996). Data were standardized prior to the analyses, with Gower distance in the case of PCoA. We carried out the statistical analyses and plotted the figures using SPSS Inc (2006) and InfoStat (2008).

Results

Grass species composition along the studied gradient

Grass species were considered rare (found at only one sampling site), mean rare (in two or three sites), less common (four or five sites) and common (six sites) depending on the number of occurrences in the 21 sites sampled along the altitudinal sites. The site at 3700 m had the highest number of rare grass species. Five C_3 grasses were found only at this site; eight grasses were mean rare species; and six were less common species (Table S1). Along the studied sites, the proportion of annual and perennial grasses did not show a clear pattern. The proportion was equal at some points (3320, 3370 and 3450 m) but differed in most of the sampling sites (Table S1). For example, the perennial grasses were absent or less represented at some altitudinal points (sites 3390, 3520 and 3620 m), more frequent at other sites (sites 3700 and 3870 m) and 100% predominant over the annual grasses at most of the sites (3560, 3770, 3800, 3820, 3860, 3950, 4000, 4050, 4300 and 4314 m; Table S1).

In contrast, the distribution of species according to their photosynthetic pathways (C_3 and C_4) showed a clear pattern with the altitudinal sites (Table S1). At low altitudes (from 3320 to 3620 m), the C_4 grasses were predominant over the C_3 grasses in a proportion of 83–100%. At higher altitudes (above 3650 m), the

predominance changed, and C₃ grasses prevailed over C₄ from 75% to 100% when the altitude was higher than 3900 m (Table S1).

Interspecific patterns of AM colonization along the altitudinal sites

As the altitude increased, inverse relationships were found with the different variables that quantified AM colonization. There were statistically significant trends between altitude and the percentages of hyphae, vesicles and total root colonization values but no significant trend with arbuscules (Table 1). These trends were similar considering the whole data set and the restricted data set ($N = 35$, 35 species studied that were sampled at only one site or, for those species that were repeatedly sampled, the intermediate site within the altitudinal sites) (Table 1; Fig. 1). The general patterns are consistent in both the C₃ and C₄ grasses with a general decrease in AM colonization as the altitude increases (Fig. 1a–d). In contrast, when the relationship between altitude and AM colonization was considered for each life cycle, no clear patterns emerged (results not shown, but see Fig. 3).

Most grasses formed AM except for the perennial grasses *Calamagrostis* sp. (C₃), *Chascolytrium subaristatum* (C₃), *Poa pratensis* (C₃) and *Eragrostis lugens* (C₄). In general, the AM colonization values were low (Tables 2 and 3). The percentages of arbuscules among the C₃ annual grasses were higher than in the C₃ perennial or than in the annual or perennial C₄ grasses (Tables 2 and 3). Hyphal colonization and total root colonization were always observed in C₃ annual grasses but not always in perennial C₃/C₄ plants (Tables 2 and 3). The percentages of vesicles were lower in C₃ annual grasses than in C₃ perennial or C₄ species (Tables 2 and 3).

Table 1. Pearson's correlation analyses of AM root colonization vs. altitude of sites

Data set	Statistics	AM root colonization (%)			
		Arbuscules	Vesicles	Hyphae	Root colonization
Extended ($N = 69$)	r	-0.054	-0.275	-0.271	-0.267
	P	0.661	0.022	0.024	0.027
Reduced ($N = 35$)	r	-0.127	-0.402	-0.343	-0.351
	P	0.466	0.017	0.044	0.039

Pearson's correlation analyses of AM root colonization vs. altitude considering all data (i.e. 69 data corresponding to all the collected samples along the altitudinal sites) or a reduced data set (i.e. 35 data corresponding to each species, independently if some of them were sampled at many sites; the selected site was the midpoint among the altitudinal sites for each of the species sampled at many sites). References: r = Pearson's correlation coefficient, P = probability.

Intraspecific patterns of AM colonization along the altitudinal sites

The total root colonization percentages were plotted to analyse the general tendencies for the C₄ species sampled four or more times within the altitudinal sites (*Aristida asplundii*, *Bouteloua barbata*, *Bouteloua simplex* and *Microchloa indica*; Fig. 2). A pattern emerged, with an inverse relationship between the AM colonization and altitude (Fig. 2). The same patterns were observed for the other two variables of AM colonization, the percentages of hyphae and vesicles (results not shown). In contrast, the trends are not clear for the C₃ species sampled at more than four sites (*Bromus catharticus*, *Poa calchacquiensis* and *Poa lilloi*; results not shown). However, the reduced sample size used for the observation of intraspecific tendencies does not allow for generalizations.

Multivariate analyses

PCoA showed that the principal two axes provide a clear ordination of the species into two separate groups. The two principal axes together account for 62.9% of the variability in AM colonization, with 39.4% and 23.5% accounted for by the first and second axes, respectively (Fig. 3a). There is a clear distinction between the photosynthetic pathway of the species, with C₃ on the upper-left part of the figure and C₄ species on the lower-right side (Fig. 3a and Table S1 for the identification of the species' photosynthetic pathway). PCA showed that the main two factors related to the separation of the two groups of species are altitude and the photosynthetic pathway of the species, especially on the second axis (Fig. 1b). In the PCoA figure, the C₄ species are on the upper part and the C₃ species on the lower one (Fig. 3b). The plant life cycle seems to be of minor importance in the distinction between the two groups of species (Fig. 3b). PCA explained a comparable proportion of the total variation in the AM colonization, with the first two axes accounting for 74.8% of the variability (47.1% and 27.7% for the first and second axes, respectively; Fig. 3b). In brief, the PCoA and PCA showed a clear distribution of AM colonization of C₃/C₄ grasses in this altitudinal sites in the Puna.

Discussion

Photosynthetic pathway distribution of grasses

C₄ plants are more competitive under limited water stress, while C₃ plants are better adapted to cool and shady conditions (e.g. Ehleringer & Monson, 1993 and

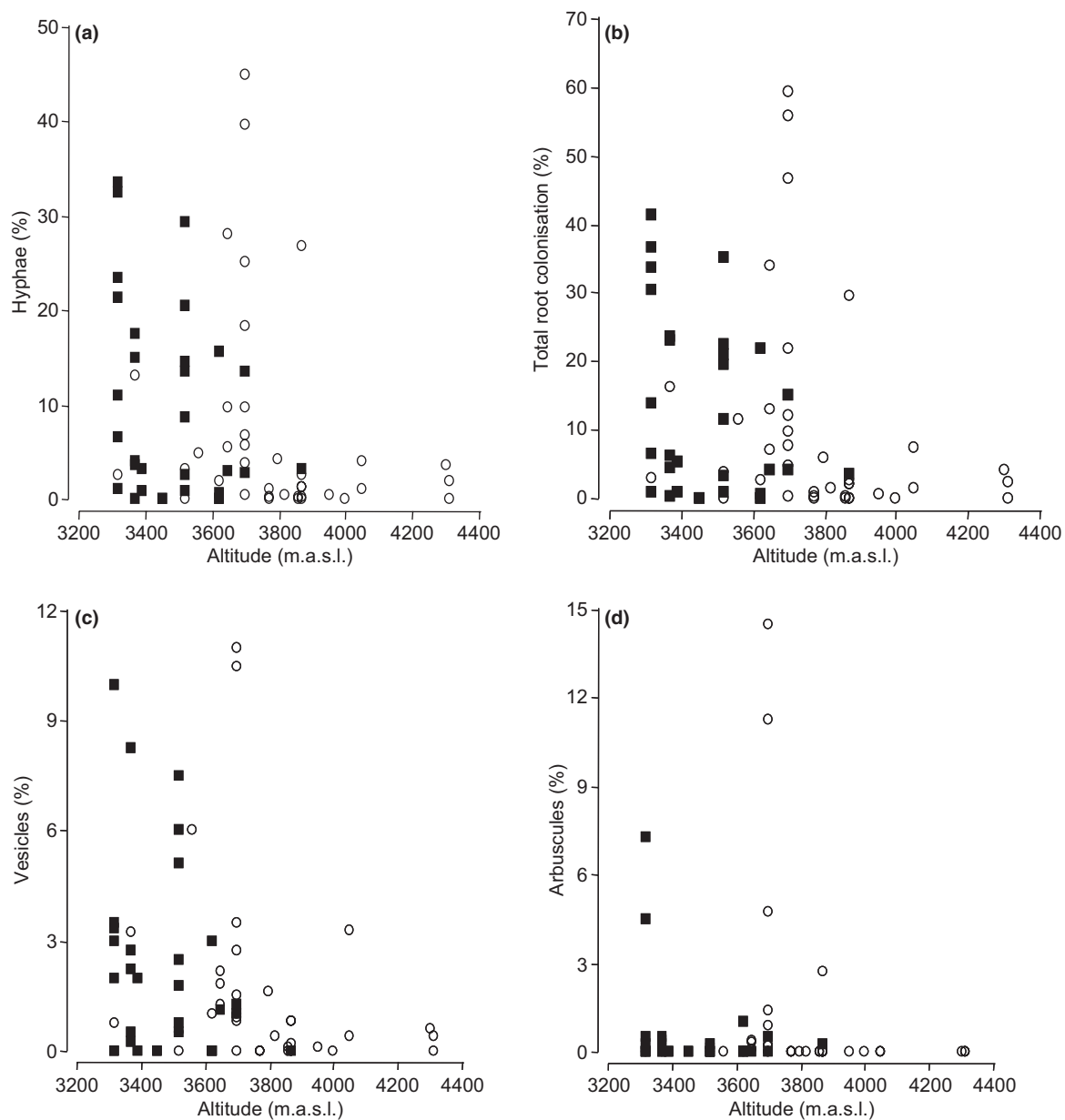


Fig. 1. Dispersion diagrams of AM colonization vs. altitude along altitudinal sites of the Puna (Argentina) using the whole data set (69 samples of 35 species). (a) hyphae, (b) total root colonization, (c) vesicles, (d) arbuscules. Filled squares = C₄ species; open circles = C₃ species; m.a.s.l. = metres above sea level.

references therein). However, some exceptions were found considering altitude, temperature and C₄ and C₃ grass distribution (Pittermann & Sage, 2000, 2001; Sage, 2001a). The proportion of C₃/C₄ grasses changed along the studied altitudinal sites in the Puna. The C₄ grasses were common at the lowest altitudes and decreased in abundance up to 3870 m, and C₃ was the unique photosynthetic pathway found above this altitude up to 4314 m. The C₄ grass distribution could be predicted by

temperatures warmer than 8 °C corresponding to the minimum temperature of the warmest month and the mean minimum temperature of the rainy season (Teeri & Stowes, 1976; Ehleringer & Monson, 1993). In the Puna sites studied, the historic reported mean minimum temperatures for rainy season were 0.7–4.8 °C above 4000 m (Ruthsatz, 1977). These temperatures can explain the absence of C₄ grasses above this altitude. It has been proposed that a species transition between C₃/C₄ grasses

Table 2. AM root colonization data for 15 *Poaceae* species sampled along altitudinal sites (2–6) of the Puna (Argentina)

Host	<i>Poaceae</i>	AM Root colonization (%)			
		Arbuscules	Vesicles	Hyphae	Root colonization
Annual C ₃	<i>Bromus catharticus</i> Vahl	1.43 ± 0.51	2.91 ± 0.93	17.09 ± 3.58	21.70 ± 4.70
	<i>Vulpia myuros</i> (L.) Gmel. f. <i>megalura</i> (Nutt.) Stace et Cotton	7.25 ± 3.05	0.75 ± 0.62	19.88 ± 7.83	27.88 ± 10.73
Perennial C ₃	<i>Danthonia annableae</i> P. M. Peterson et Rúgolo	0	0.77 ± 0.30	1.69 ± 0.52	2.40 ± 0.65
	<i>Festuca rigescens</i> (J. Presl) Kunth	0.03 ± 0.03	0.83 ± 0.37	3.67 ± 1.10	4.73 ± 1.48
	<i>Jarava plumosula</i> (Nees ex Steud) F. Rojas	0.13 ± 0.13	1.88 ± 0.95	8.13 ± 3.54	10.00 ± 3.96
	<i>Koeleria praeandina</i> A. M. Molina	5.00 ± 2.03	4.67 ± 1.86	11.11 ± 4.50	20.80 ± 8.31
	<i>Poa calchaquiensis</i> Hack.	0	0.16 ± 0.07	0.56 ± 0.14	0.71 ± 0.21
	<i>Poa lilloi</i> Hack.	0	1.20 ± 0.94	2.27 ± 0.85	3.50 ± 1.72
Annual C ₄	<i>Aristida adscensionis</i> L.	1.67 ± 0.93	2.75 ± 0.91	15.29 ± 4.30	19.70 ± 5.04
	<i>Bouteloua barbata</i> Lag.	0.53 ± 0.15	1.53 ± 0.41	13.35 ± 1.90	16.12 ± 2.41
	<i>Bouteloua simplex</i> Lag.	1.82 ± 0.96	2.53 ± 0.71	16.00 ± 3.10	20.32 ± 3.92
	<i>Microchloa indica</i> (L. f.) P. Beauv.	0	0.94 ± 0.34	3.71 ± 1.23	4.59 ± 1.51
Perennial C ₄	<i>Aristida asplundii</i> Henrard	0.09 ± 0.07	3.87 ± 0.87	8.91 ± 1.94	12.85 ± 2.71
	<i>Cynodon dactylon</i> (L.) Pers. var. <i>biflorus</i> Merino	0	0.75 ± 0.22	1.75 ± 0.48	2.50 ± 0.63
	<i>Eragrostis</i> sp ₁	0.25 ± 0.25	5.43 ± 0.89	22.94 ± 4.22	28.81 ± 3.90

Host photosynthetic pathways (C₃, C₄) and life cycle (annual, perennial) for each species are indicated. Data correspond to mean ± standard error of the different populations sampled at many sites (previously, data for individual plants were used to characterize each population).

Table 3. AM root colonization data for 20 *Poaceae* species sampled only at one site along altitudinal gradient of the Puna (Argentina)

Host	<i>Poaceae</i>	AM Root colonization (%)			
		Arbuscules	Vesicles	Hyphae	Root colonization
Annual C ₃	<i>Polypogon interruptus</i> Kunth	1.44 ± 0.67	1.00 ± 0.33	9.78 ± 3.40	12.22 ± 4.20
Perennial C ₃	<i>Calamagrostis</i> sp.	0	0	0	0
	<i>Calamagrostis breviaristata</i> (Wedd.) Pilg.	0	0.40 ± 0.22	1.10 ± 0.66	1.50 ± 0.86
	<i>Calamagrostis trichodonta</i> (Wedd.) Soreng	0.40 ± 0.24	2.20 ± 0.37	28.00 ± 0.55	34.00 ± 0.55
	<i>Chascolytrum subaristatum</i> (Lam.) Desv.	0	0	0	0
	<i>Danthonia boliviensis</i> Renvoize	0	0.22 ± 0.15	2.56 ± 1.20	2.80 ± 1.20
	<i>Festuca humilior</i> Nees et Meyen	0	3.50 ± 0.29	18.25 ± 2.59	21.75 ± 2.75
	<i>Hordeum muticum</i> J. Presl	0.89 ± 0.51	0.89 ± 0.42	5.78 ± 1.78	7.56 ± 2.37
	<i>Nassella meyeriana</i> (Trin. & Rupr.) Parodi	0	0.40 ± 0.22	1.90 ± 0.91	2.30 ± 1.11
	<i>Piptochaetium indutum</i> Parodi	0	0.80 ± 0.37	1.20 ± 0.58	2.00 ± 0.89
	<i>Poa laetevirens</i> R. E. Fries	0.25 ± 0.25	2.75 ± 0.85	6.75 ± 1.89	9.75 ± 2.75
	<i>Poa pratensis</i> L.	0	0	0	0
	<i>Poa superata</i> Hack.	0	6.00 ± 3.35	4.80 ± 2.40	11.60 ± 5.54
Annual C ₄	<i>Trisetum spicatum</i> (L.) K. Rich	0.20 ± 0.20	0.80 ± 0.58	3.80 ± 1.36	4.80 ± 1.66
	<i>Eragrostis nigricans</i> (Kunth) Steud. var. <i>nigricans</i>	0	2.00 ± 0.91	3.25 ± 1.49	5.25 ± 2.29
	<i>Eragrostis nigricans</i> var. <i>punensis</i> Nicora	0	0	0.75 ± 0.48	0.75 ± 0.48
	<i>Eragrostis mexicana</i> (Hornem.) Link ssp. <i>virescens</i> J. Presl.	0	0	6.63 ± 3.12	6.63 ± 3.12
Perennial C ₄	<i>Cynodon dactylon</i> (L.) Pers.	0	0	0.60 ± 0.24	0.60 ± 0.24
	<i>Eragrostis lugens</i> Nees	0	0	0	0
	<i>Muhlenbergia rigida</i> (Kunth) Kunth	0	0	1.00 ± 0.71	1.00 ± 0.71

Host photosynthetic pathways (C₃, C₄) and life cycle (annual, perennial) for each species are indicated. Data correspond to mean ± standard error of a sample of plant individuals of each species at the sampled site.

occurs at similar altitudes around the world regardless of the phytogeographic region (Rundel, 1980). Nevertheless, in the South American semi-arid and arid Monte and Prepuna biogeographical provinces, Cavagnaro (1988) found a transition between C₃ and C₄ grasses at 1500 m and that C₄ grasses were absent above 2200 m. Also, in

the arid Chaco province, Cabido *et al.* (1997) met the same transitional trend, and C₄ grasses were rare above 1000 m but were found up to 2100 m. In the studied Puna altitudinal sites, the transition between C₃ and C₄ grasses was higher (at 3650 m) than in other arid and semi-arid South American biogeographical provinces, and

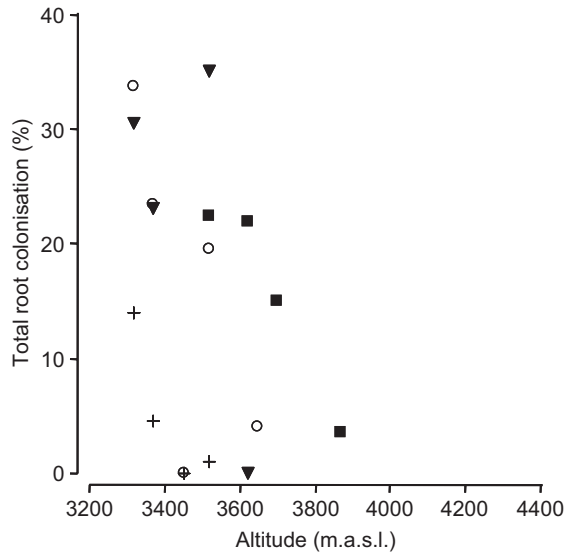


Fig. 2. Dispersion diagram showing intraspecific relationships between AM colonization (percentage of total root colonization) and altitude for four C_4 species sampled at many sites along altitudinal sites of the Puna (Argentina). Open circles = *Aristida asplundii*; filled squares = *Bouteloua barbata*; filled triangles = *Bouteloua simplex*; crosses = *Microchloa indica*; m.a.s.l. = metres above sea level.

C_4 grasses were found up to 3870 m (e.g. *Bouteloua barbata*), although C_4 species became rare above 3520 m. Moreover, some of the Puna environmental characteristics such as the occurrence of open sites, arid zones with low CO_2 partial pressure, large amounts of animal disturbance and high soil salinity create excellent conditions for C_4 grass establishment (Pittermann & Sage, 2000, 2001; Sage, 2001a, b).

AM colonization, altitude and host's photosynthetic pathway

Altitude has been recognized as an important factor in European alpine ecosystems affecting the distribution of many organisms (e.g. Körner, 2007). Although autotrophy is the norm for alpine plants at the highest elevations (Trappe, 1987; Brundrett, 2009), mycotrophy also can be found at high altitudes as in the Alps (Nespiak, 1953; Read & Haselwandter, 1981), Bolivian Andean highlands (Urcelay *et al.*, 2011), Peruvian Andes (Schmidt *et al.*, 2008), western North America mountains (Trappe, 1988) and the Puna (this work). Gardes & Dahlberg (1996) found similar associations in arctic and alpine tundra. In high mountain grasslands, AM are common and well documented (Read & Haselwandter, 1981; Mullen & Schmidt, 1993; Onipchenko & Zobel, 2000). In general, our results showed a clear pattern of a decrease in the

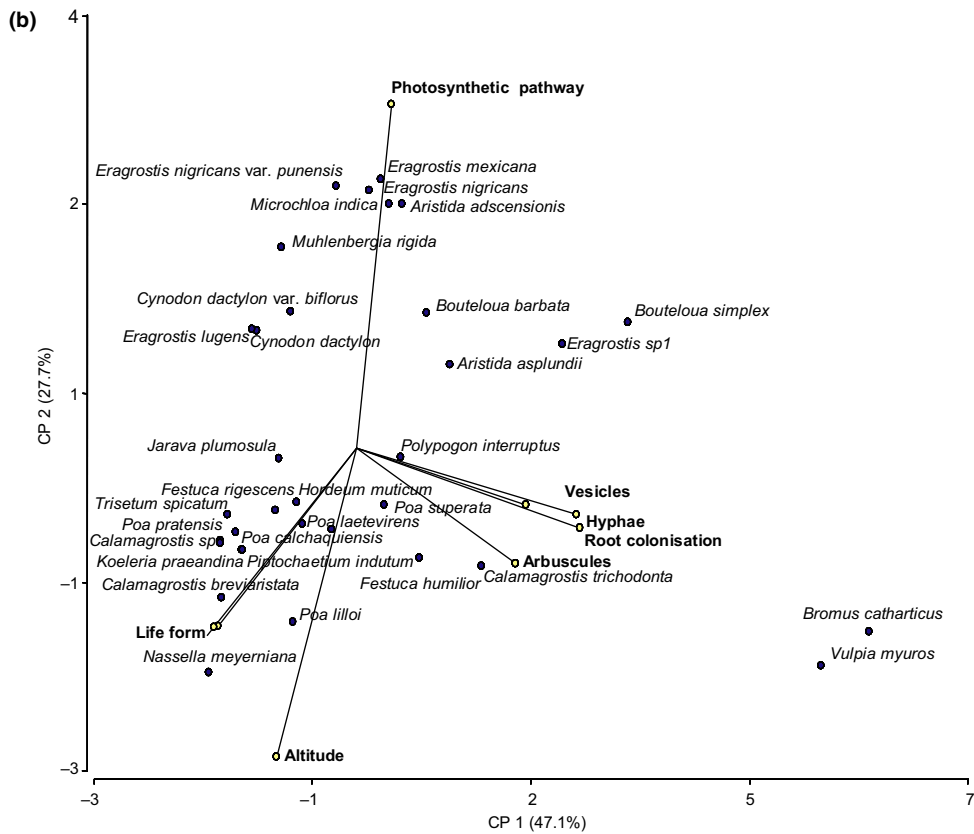
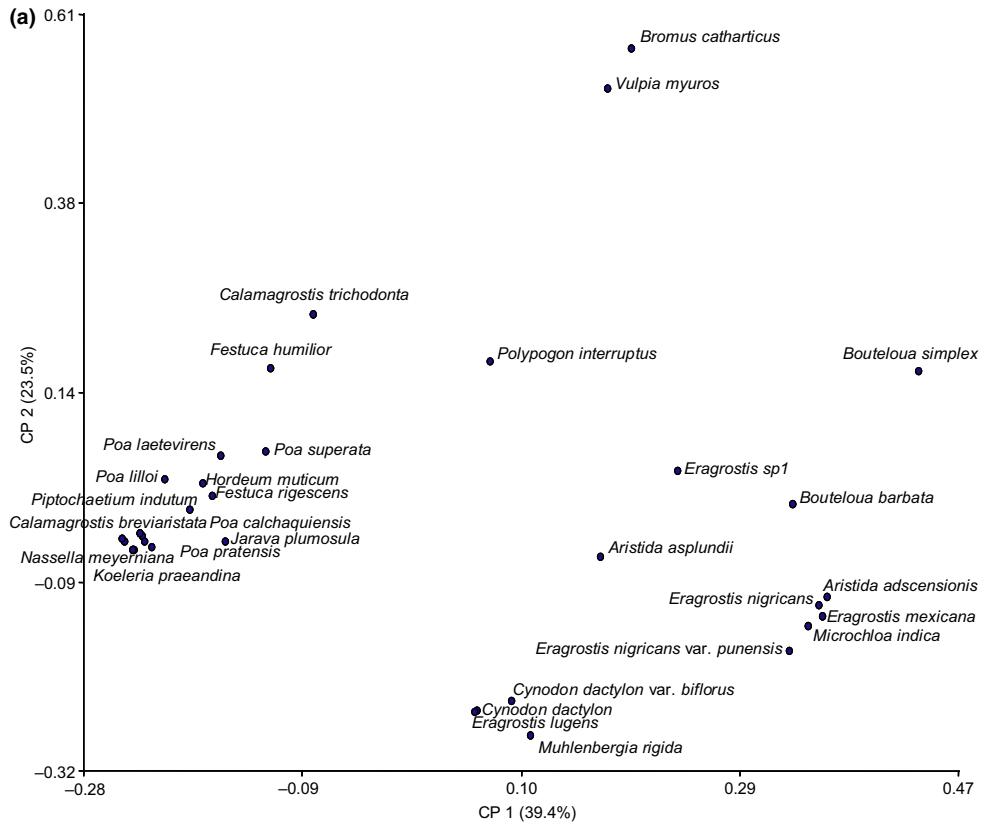
AM colonization in the roots of Puna grasses with an increase in altitude. This trend could be related to a mean temperature decrease as the altitude is increased and consequently to a reduction in soil fungal diversity as well as in fungal growth rate (Koske, 1987; Entry *et al.*, 2002), which negatively influence the AM colonization capacity (Smith & Read, 2008). In fact, along Puna sites, the diversity of AM fungi (richness and density of spores) decreased with the altitudinal increase (Lugo *et al.*, 2008). Although spores constitute only a part of the propagules of AMF, their decline along the sites would imply a lower availability of AMF in soil and therefore a decrease in root colonization with increasing altitude. Thus, the decrease in spore diversity could be related to the diminishing pattern of the root colonization along the Puna sites studied.

A decrease in arbuscular mycorrhizal colonization along altitudinal gradients had been found when the altitudes were stretched out over 1245–1300 m (Haselwandter, 1979; Haselwandter & Read, 1980; Routsalainen *et al.*, 2004) but the colonization showed intermediate trends when the altitude gradients were smaller (Read & Haselwandter, 1981). However, Väre *et al.* (1997) reported that AM colonization decreased along a gradient of 300 m. Although the Puna altitudinal difference was shorter (994 m) than most gradients studied in the Northern Hemisphere, the decrease in root colonization in the grasses agrees with the patterns found for larger gradients in alpine environments (Haselwandter & Read, 1980; Routsalainen *et al.*, 2004).

The general trends among different species of the Puna grasses were also observed at the intraspecific level. Intraspecific colonization in four Puna C_4 species showed a decreasing trend with altitude. In contrast, the C_3 species did not show a consistent pattern. Although these are preliminary results because of the low sample size and the sampling design (without replications), this is the first field report from the Puna Region for native grasses. Experimental mycorrhizal influence within a single species and among different species was previously reported from grasses of North American tallgrass prairie. The competitive advantage of the dominant prairie C_4 host was strongly reduced during the absence of mycorrhiza, and the mycorrhizal effect on competition for the C_3 host was smaller (Hartnett *et al.*, 1993).

AM colonization and life cycle

In the Puna grassland, both annual and perennial grasses had mycorrhizal colonization; however, the life cycle was a subordinate factor compared to the photosynthetic pathways, according to the results of the multivariate analyses. The presence of AM in grasses with both life



cycles is striking because in the Northern Hemisphere, annual species are frequently nonmycorrhizal, while the perennial forms are predominantly mycorrhizal (Trappe, 1987). This difference could be related to environmental conditions because the reported nonmycorrhizal annual plants in the Northern Hemisphere come from disturbed areas and behave as ruderal weeds, while annual grasses in the Puna differ functionally because they are native and well established in this biogeographical region.

The mycorrhizal root colonization of the Puna grasses had opposite characteristics to Northern tallgrass prairie grasses. In North American tallgrass prairie, annual grasses of both C₃ and C₄ photosynthetic pathways showed a low responsiveness to mycorrhizal colonization (Wilson & Hartnett, 1998). Thus, although the roots of annual and perennial C₄ grasses in the Puna were less colonized than those from Northern tallgrass prairie, the annual and perennial C₃ colonization was higher in the Puna. The higher root colonization of C₄ grasses in tallgrass prairies could be explained by the lower altitudes at which these species grow, and the higher mycorrhizal colonization in the perennial C₃ Puna grasses could indicate that these grass species were able to acclimate to the low temperatures of the highest sites in the Puna.

AM colonization: linking altitude, photosynthetic pathway and life cycle

Our results are the first field report showing complex shifts in arbuscular mycorrhizal colonization in a sample of 35 species of Andean grasses along 21 altitudinal sites at high elevation. Results suggest that altitude is the most important factor, the host photosynthetic pathway is the second most relevant and the plant life cycle seems to be subordinated. Routsalainen *et al.* (2002) proposed a model for optimal mycorrhizal colonization along altitudinal gradients that considered photosynthetic nutrient use efficiency (PNUE) as the driver of altitudinal mycorrhizal trends and suggested that associations cannot always be favoured at low PNUE. Furthermore, PNUE is related to photosynthetic pathways; C₃ plants have a lower PNUE than C₄ plants, and consequently, a lower root colonization in C₃ than in C₄ grasses would be expected. Besides, different PNUE values among C₃ plant species occur, and interspecific differences are also related to root activity (Hikosaka, 2010); that is, species with higher PNUE have higher root activity to maintain higher leaf nitrogen concentration.

Arbuscular mycorrhizas are considered to be ubiquitous symbiotic associations because of their broad host spectrum (approximately 80% of land plants) in spite of the scant number of fungi forming this type of association (only *c.* 230 species of Glomeromycota) (Smith & Read, 2008; Krüger *et al.*, 2011). However, glomalean fungi have been shown to select their host based on ecological factors (Sanders & Fitter, 1992a, b; Eon *et al.*, 2000; Helgason *et al.*, 2002; Husband *et al.*, 2002), and this selection may partly explain the interspecific differences found experimentally in root colonization in grasses from the Northern Hemisphere (Hartnett *et al.*, 1993; Wilson & Hartnett, 1998). Moreover, when the AMF community was analysed in the grasses' rhizosphere at five sites in Puna (Lugo *et al.*, 2008), the AMF diversity was not related to the grasses' photosynthetic pathway, although AM root colonization along the 21 sites was associated with the pathway. In microcosm experiments, AMF from a mown grassland showed host dependence of sporulation rates and diversity (Bever *et al.*, 1996); also AMF identity rather than AMF diversity affected the plant community diversity and productivity in North American tallgrass prairie (Vogelsang *et al.*, 2006). Besides, AMF community can present spatial patterns at a local scale, and this spatial heterogeneity of AMF communities might have an impact on plant communities in structure and processes (Pringle & Bever, 2002). Therefore, AMF communities in the 21 sites sampled in this work, instead of five sites (Lugo *et al.*, 2008), possibly include new AMF communities with spatial heterogeneity that may involve different AMF species with their specific host dependence, affecting the plant community composition. Furthermore, AMF sporulation host dependence (Bever *et al.*, 1996) could suggest a host preference effect and therefore interspecific differences in root colonization as were found in grasses of Puna and that represent a first field report from the Southern Hemisphere of this variation in AM colonization. All of the factors studied here, including altitude, host photosynthetic pathway and host life cycle, confirm an interesting pattern in the variability of hyphae, vesicles and root colonization percentages that is not evident in arbuscules. The lack of a clear pattern for arbuscules may occur because their presence is usually related to other factors such as the soil phosphorus content (Smith & Read, 2008). Additionally, the proportion of annual mycorrhizal species seems to be related to the type of habitat; that is, in dry, mesophytic and calcareous grasslands, a large proportion of the species are annual

Fig. 3. (a) PCoA and (b) PCA for 35 grasses species growing along altitudinal sites of the Puna (Argentina). The variables of AM colonization were percentages of hyphae, vesicles, arbuscules and total root colonization. Altitude, photosynthetic pathways (C₃ and C₄), and life cycle (annual and perennials) for each species can be seen in Table S1.

mycorrhized grasses (Peat & Fitter, 1993). The different amount of colonization observed by Newsham *et al.* (1995) could be due to the differential effect of AM on the host: in perennial grasses, phosphorus recovery is more efficient, while in the annuals, phosphorus recovery is not affected, although their resistance to pathogens is increased. Newsham & Watkinson (1998) found that some grass species that are normally nonmycorrhizal or slightly colonized when the soil is fertile are strongly infected when the soil is poor. Furthermore, according to Fitter & Merryweather (1992), the level of mycorrhizal colonization of roots is a characteristic that plants may regulate depending on the benefit they receive. In the Puna grasses, the slight or subordinate influence of the host life cycle on root colonization could be a result of the low nutrient availability in the soil, which would favour an association with annual as well as with perennial hosts (Entry *et al.*, 2002) and could also be compelled by a cost–benefit trade-off that varies with the characteristics of the hosts, such as their photosynthetic pathways or life cycle, at different altitudes.

Although AM–plant interactions in grasses were mostly driven by the altitude, more questions result if we consider that ‘altitude’ is conceptually more than a single factor and includes a reduction in the land area along with many climatic trends such as decreasing total atmospheric pressure, decreasing partial pressures of O₂ and CO₂ (among other atmospheric gases), reduction in atmospheric temperature and following implications for ambient humidity, increasing radiation under a cloudless sky, incoming increasing solar radiation and outgoing night-time thermal radiation and higher UV-B radiation (Körner, 2007). Moreover, it has been shown that in grasslands, root production, turnover and respiration also decrease along altitudinal gradients, while solar radiation increases and the resource availability remains low (Fitter *et al.*, 1998). This trend of root traits would result in a diminishing of the AM colonization along the Puna sites because of a decreasing availability of roots to colonize. Therefore, this trend of decreasing AM colonization with altitude could be considered to be a general pattern regardless of the geographical location of the biome considered. Moreover, different relationships between AM and plants can be understood along the altitudinal gradient as complex strategies depending on the characteristics of the hosts at different altitudes, including their photosynthetic pathways or life cycles.

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References

- Allen MF (1991) *The Ecology of Mycorrhizae* (Barnes RSK, Birks HJB, Connor EF, Harper JL & Paine RL, eds). Cambridge University Press, Cambridge.
- Bever JD, Morton JB, Antonovics J & Schultz PA (1996) Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *J Ecol* **84**: 71–82.
- Blanke V, Renker C, Wagner M, Füllner K, Held M, Kuhn AJ & Buscot F (2005) Nitrogen supply affects arbuscular mycorrhizal colonization of *Artemisia vulgaris* in a phosphate-polluted field site. *New Phytol* **166**: 981–992.
- Brundrett MC (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant Soil* **320**: 37–77.
- Cabido M, Ateca N, Astegiano ME & Anton AM (1997) Distribution of C₃ and C₄ grasses along an altitudinal gradient in Central Argentina. *J Biogeogr* **24**: 197–204.
- Cabrera AL (1976) Territorios fitogeográficos de la República Argentina. *Enciclopedia Argentina de Agricultura y Jardinería, 2da. Edición, II (1)*. ACME, Argentina.
- Cabrera AL & Willink A (1980) *Biogeografía de América Latina*. OEA, Washington, DC.
- Cavagnaro JB (1988) Distribution of C₃ and C₄ grasses at different altitudes in a temperate arid region of Argentina. *Oecologia* **76**: 273–277.
- Digby PGN & Kempton RA (1996) *Multivariate Analysis of Ecological Communities*. Chapman and Hall, London.
- Ehleringer JR & Monson RK (1993) Evolutionary and ecological aspects of photosynthetic pathway variation. *Annu Rev Ecol Syst* **24**: 411–439.
- Entry JA, Rygielwicz PT, Watrud LS & Donnelly PK (2002) Influence of adverse soil conditions on the formation and function of arbuscular mycorrhizas. *Adv Environ Res* **7**: 123–138.
- Eon A-H, Hartnett DC & Wilson GWT (2000) Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. *Oecologia* **122**: 435–444.
- Fitter AH & Merryweather JW (1992) Why are some plants more mycorrhizal than others? An ecological inquiry. *Mycorrhizas in Ecosystems* (Read DJ, Lewis DH, Fitter AH & Alexander IJ, eds), pp. 23–37. CAB International University Press, Cambridge.
- Fitter AH, Graves JD, Self GK, Brown TK, Bogie DS & Taylor K (1998) Root production, turnover and respiration under two grassland types along an altitudinal gradient: influence of temperature and solar radiation. *Oecologia* **114**: 20–30.

- Gardes M & Dahlberg A (1996) Mycorrhizal diversity in arctic and alpine tundra: an open question. *New Phytol* **133**: 147–157.
- Grace C & Stribley DP (1991) A safer procedure for routine staining of vesicular arbuscular mycorrhizal fungi. *Mycol Res* **95**: 1160–1162.
- Hartnett DC & Wilson GW (2002) The role of mycorrhizas in plant community structure and dynamics: lessons from de grasslands. *Plant Soil* **244**: 319–331.
- Hartnett DC, Hetrick BAD, Wilson GW & Gibson DJ (1993) Mycorrhizal influence on intra- and interspecific neighbour interactions among co-occurring prairie grasses. *J Ecol* **81**: 787–795.
- Haselwandter K (1979) Mycorrhizal status of ericaceous plants in alpine and subalpine areas. *New Phytol* **83**: 427–431.
- Haselwandter K & Read DJ (1980) Fungal associations of roots of dominant and subdominant plants in high-alpine vegetation systems with special reference to mycorrhiza. *Oecologia* **45**: 57–62.
- Helgason T, Merryweather JW, Denison J, Wilson P, Young JPW & Fitter AH (2002) Selectivity and functional diversity in arbuscular mycorrhizas of co-existing fungi and plants from a temperate deciduous woodland. *J Ecol* **90**: 371–384.
- Hetrick BAD, Kitt DG & Wilson GWT (1988) Mycorrhizal dependence and growth habit of warm-season and cool-season tallgrass prairie plants. *Can J Bot* **66**: 1376–1380.
- Hetrick BAD, Wilson GWT & Todd TC (1990) Differential responses of C₃ and C₄ grasses to mycorrhizal symbiosis, phosphorus fertilization, and soil microorganisms. *Can J Bot* **68**: 461–467.
- Hetrick BAD, Wilson GWT & Leslie JF (1991) Root architecture to warm- and cool-season grasses: relationship to mycorrhizal dependence. *Can J Bot* **69**: 112–118.
- Hetrick BAD, Wilson GWT & Todd TC (1992) Relationships of mycorrhizal symbiosis, rooting strategy, and phenology among tallgrass prairie forbs. *Can J Bot* **70**: 1521–1528.
- Hikosaka K (2010) Mechanisms underlying interspecific variation in photosynthetic capacity across wild plant species. *Plant Biotechnol* **27**: 223–229.
- Husband R, Herre EA, Turner SL, Gallery R & Young PW (2002) Molecular diversity of arbuscular mycorrhizal fungi and patterns of host association over time and space in a tropical forest. *Mol Ecol* **11**: 2669–2678.
- InfoStat (2008) *INFOSTAT version 2008*. Grupo InfoStat, Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba, Córdoba, Argentina.
- Kohn LM & Stasovski E (1990) The mycorrhizal status of plants at Alexandra Fiord, Ellesmere Island, Canada, a High Arctic site. *Mycologia* **82**: 23–35.
- Körner C (1999) *Alpine Plant Life*. Springer, New York.
- Körner C (2007) The use of “altitude” in ecological research. *Trends Ecol Evol* **22**: 569–574.
- Koske RE (1987) Distribution of VA mycorrhizal fungi along a latitudinal temperature gradient. *Mycologia* **79**: 55–68.
- Kottke I, Beck A, Oberwinkler F, Homeier J & Neill D (2004) Arbuscular endomycorrhizas are dominant in the organic soil of a neotropical montane cloud forest. *J Trop Ecol* **20**: 125–129.
- Krüger M, Krüger C, Walker C, Stockinger H & Schüssler A (2011) Phylogenetic reference data for systematics and phylotaxonomy of arbuscular mycorrhizal fungi from phylum to species level. *New Phytol* **193**: 970–984.
- Lugo MA, González Maza ME & Cabello MN (2003) Arbuscular mycorrhizal fungi (AMF) from native Argentinian -South American- mountain grassland II. Seasonal variation of colonization and its relation with grazing and metabolic host type. *Mycologia* **95**: 407–415.
- Lugo MA, Ferrero M, Menoyo E, Estévez MC, Siñeriz F & Anton AM (2008) Arbuscular mycorrhizal fungi and rhizospheric bacteria diversity along an altitudinal gradient in South American Puna grassland. *Microbial Ecol* **55**: 705–713.
- Martínez Carretero E (1995) La Puna Argentina: delimitación general y división en distritos florísticos. *Bol Soc Argent Bot* **31**: 27–40.
- McGonigle TP, Miller MH, Evans DG, Fairchild DL & Swam JA (1990) A new methods which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytol* **115**: 495–501.
- Morrone JJ (2001) *Biogeografía de América Latina y el Caribe*. Manuales y Tesis SEA. Vol. 3 SEA (Sociedad Entomológica Aragonesa), CYTED (Cooperación Iberoamericana Subprograma II, Diversidad Biológica) & UNESCO (ORCYT), México.
- Mullen RB & Schmidt SK (1993) Mycorrhizal infection, phosphorus uptake, and phenology in *Ranunculus adoneus*: implications for the functioning of mycorrhizae in alpine systems. *Oecologia* **94**: 229–234.
- Nespiak A (1953) Mycotropy of the alpine vegetation of the Tatra Mountains. *Acta Soc Bot Pol* **22**: 97–125.
- Newsham KK & Watkinson AR (1998) Arbuscular mycorrhizas and the population biology of grasses. *Population Biology of Grasses* (Cheplick GP, ed), pp. 286–312. Cambridge University Press, Cambridge.
- Newsham KK, Fitter AH & Watkinson AR (1995) Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends Ecol Evol* **10**: 407–411.
- Onipchenko VG & Zobel M (2000) Mycorrhiza, vegetative mobility and responses to disturbance of alpine plants in the Northwestern Caucasus. *Folia Geobot* **35**: 1–11.
- Peat HJ & Fitter AH (1993) The distribution of arbuscular mycorrhizas in the British Flora. *New Phytol* **125**: 845–854.
- Pittermann J & Sage RF (2000) Photosynthetic performance at low temperature of *Bouteloua gracilis* Lag., a high-altitude C₄ grass from the Rocky Mountains, USA. *Plant, Cell Environ* **23**: 811–823.
- Pittermann J & Sage RF (2001) The response of the high altitude C₄ grass *Muhlenbergia montana* (Nutt.) A. S. Hitchc. to long- and short-term chilling. *J Exp Bot* **52**: 829–838.

- Pringle A & Bever JD (2002) Divergent phenologies may facilitate the coexistence of arbuscular mycorrhizal fungi in North Carolina grassland. *Am J Bot* **89**: 1439–1446.
- Read DJ (1991) Mycorrhizas in ecosystems. *Experientia* **47**: 376–391.
- Read DJ & Haselwandter K (1981) Observations on the mycorrhizal status of some alpine plant communities. *New Phytol* **88**: 341–352.
- Routsalainen AL, Tuomi J & Väre H (2002) A model for optimal mycorrhizal colonization along altitudinal gradients. *Silva Fenn* **36**: 681–694.
- Routsalainen AL, Väre H, Oksanen J & Tuomi J (2004) Root fungus colonization along an altitudinal gradient in North Norway. *Arct Antarct Alp Res* **36**: 239–243.
- Rundel PW (1980) The ecological distribution of C₄ and C₃ grasses in the Hawaiian Islands. *Oecologia* **45**: 354–359.
- Ruthsatz B (1977) *Pflanzengesellschaften und ihre Lebensbedingungen in den Andinen Halbwüsten Nordwest Argentiniens*. Dissertationes Botanicae. Band 39. J. Cramer Fl 9490 Vaduz.
- Sage RF (2001a) C₄ plants. *Encyclopedia of Biodiversity* (Levin SA, ed), pp. 575–598. Vol 1. Academic Press, London.
- Sage RF (2001b) Environmental and evolutionary preconditions for the origin and diversification of the C₄ photosynthetic syndrome. *Plant Biol* **3**: 202–213.
- Sanders IR & Fitter AH (1992a) Evidence for differential responses between host–fungus combinations of vesicular-arbuscular mycorrhizas from a grassland. *Mycol Res* **96**: 415–419.
- Sanders IR & Fitter AH (1992b) The ecology and functioning of vesicular-arbuscular mycorrhizas in co-existing grassland species. I Seasonal pattern of mycorrhizal occurrence and morphology. *New Phytol* **120**: 517–524.
- Schmidt SK, Sobieniak-Wiseman LC, Kageyama SA, Halloy SRP & Schadt CW (2008) Mycorrhizal and dark-septate fungi in plant roots above 4270 meters elevation in the Andes and Rocky Mountains. *Arct Antarct Alp Res* **40**: 576–583.
- Smith SE & Read DJ (2008) *Mycorrhizal Symbiosis*. Academic Press, London.
- SPSS Inc. (2006), *SPSS Version 15.0*. Chicago, IL.
- Teeri JA & Stowes LG (1976) Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia* **23**: 1–12.
- Trappe JM (1987) Phylogenetic and ecologic aspects of mycotrophy in the Angiosperms from an Evolutionary standpoint. *Ecophysiology of VA Mycorrhizal Plants* (Safir GR, ed), pp. 5–25. CRC Press, Boca Raton, FL.
- Trappe JM (1988) Lessons from alpine fungi. *Mycologia* **80**: 1–10.
- Urcelay C, Acho J & Joffre R (2011) Fungal root symbionts and their relationship with fine root proportion in native plants from the Bolivian Andean highlands above 3700 m elevation. *Mycorrhiza* **21**: 323–330.
- Väre H, Vestberg M & Ohtonen R (1997) Shifts in mycorrhizal activity along an Oroarctic altitudinal gradient in Northern Fennoscandia. *Arct Antarct Alp Res* **29**: 93–104.
- Vogelsang KM, Reynolds HL & Bever JD (2006) Mycorrhizal fungal identity and richness determine the diversity and productivity of a tallgrass prairie system. *New Phytol* **172**: 554–562.
- Wang B & Qiu Y-L (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* **16**: 299–363.
- Wilson GTW & Hartnett DC (1998) Inter-specific variation in plant responses to mycorrhizal colonization in prairie grasses and forbs. *Am J Bot* **85**: 1732–1738.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Grasses species distribution along altitudinal sites of the Puna (Argentina).

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