

# Vertical Distribution of Mycorrhizal Colonization, Root Hairs, and Belowground Biomass in Three Contrasting Sites from the Tropical High Mountains, Mérida, Venezuela

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## Abstract

Very little is known about the distribution and abundance of mycorrhizae in the high Tropical mountains. The objective of the present study was to determine whether soil drainage and soil depth in a toposequence in a Venezuelan páramo affect the extent of mycorrhizal colonization, percentage root hairs, and belowground biomass of unknown species randomly sampled from the study sites. Well-drained soils in the shrub-rosette site (SR) during the dry season were less fertile and mycorrhizal colonization was the highest ( $69.4 \pm 2.5\%$ ) compared to the more poorly drained pasture soils, located in topographically low situations, which were more fertile but with a lower mycorrhizal colonization and more root hairs. A low diffusion of oxygen in the poorly drained soils of the humid pasture (HP), which remained wet throughout the year, may explain the abrupt decline in mycorrhizal colonization. Vertical distribution of belowground biomass and mycorrhizal colonization suggest that nutrients are mainly distributed in the surface soil layer.

## Introduction

Mycorrhizae have been defined as a mutualistic symbiosis between plant and fungus characterized by a net movement of energy and inorganic resources from plant to fungus and inorganic resources from fungus to plant (Allen, 1991). Despite the fact that mycorrhizae are the most important and durable symbiosis on earth, its functional relationship cannot be demonstrated in all cases (Allen, 1996). Read (1991) has outlined the main climatic and edaphic characteristics that determine the dominance of distinctive types of mycorrhizas in a defined biome. However, this pattern may not be so simple and the establishment of a more diverse mixture of mycorrhizal types is actually controlled by different characteristics at the microhabitat level (Allen, 1991).

The distribution of arbuscular mycorrhizae (AM) in both vertical and horizontal gradients may vary depending on the local conditions. Several authors have suggested that AM are located near the soil surface where labile nutrients are released but this is not true of all cases. The vertical distribution of AM would depend on the availability of soil resources and in some cases, AM roots can extend deep into the soil profile (Allen, 1991). The horizontal patchy distribution of AM in undisturbed areas seems to relate with the allocation of resources associated with individual plants (Allen, 1991) which also supports the notion of a shifting mosaic for vegetation—across any landscape—where multiple AM species can distribute within a community associated with specific plant species (Allen, 1996). Differences in topographical position, organic matter accumulation, and soil drainage may also play an important role in the distribution of AM fungi spores in soils (Khalil and Loynachan, 1994).

The Andean páramo is a natural area of the Tropical High Mountains, located between 3000 m and the snowline (4500–4800 m). The soils are young with a very low nutrient avail-

ability, which limits plant distribution (Monasterio and Sarmiento, 1991). Other characteristics of the Venezuelan páramo soils include acidity ranges from acid to very acid; very low available phosphorus; and a notable accumulation of organic matter (Malagón, 1982). Extreme temperature fluctuations on a daily basis are typical of this area (Monasterio, 1980a) but changes in soil temperature are far less extreme (Azócar and Monasterio, 1980). Smith and Klingner (1985) suggested that tropical alpine vegetation, and particularly some Venezuelan páramos, are normally under a high total annual stress (including grazing pressure) but slight seasonality. As a consequence, there is not a high proportion of belowground phytomass accumulation either for anchorage (support) or storage of food reserves, showing the highest aboveground:belowground (A:B) ratios (Smith and Klingner, 1985).

Very little is known about the occurrence of mycorrhizae in the Andean páramo. Read (1991) suggested that ericoid mycorrhizae predominate on mor humus soils of high latitudes and altitudes. Highly organic and wet soils at high altitudes tend also to be dominated by ectomycorrhizae, but in drier alpine habitats AM grasses and herbs dominate (Allen, 1991). Dark-septate fungi have been commonly found in the Austrian Alps associated with plant roots (e.g. Haselwandter and Read, 1980; Blaschke, 1991). This association differs from ericoid mycorrhizae and may be congeneric with *Phialocephala fortinii*, obtained from alpine habitats of the Alberta Rocky Mountains (Stoyke and Currah, 1991, 1993).

The specific aim of this study was to compare three contrasting sites of the Andean páramo in order to determine whether topographical differences actually affect root biomass and the extent of both mycorrhizal colonization and root hairs in a particular toposequence. Samples were collected during the dry and wet seasons at three different depths in this  $3 \times 3 \times 2$  factorial experiment.

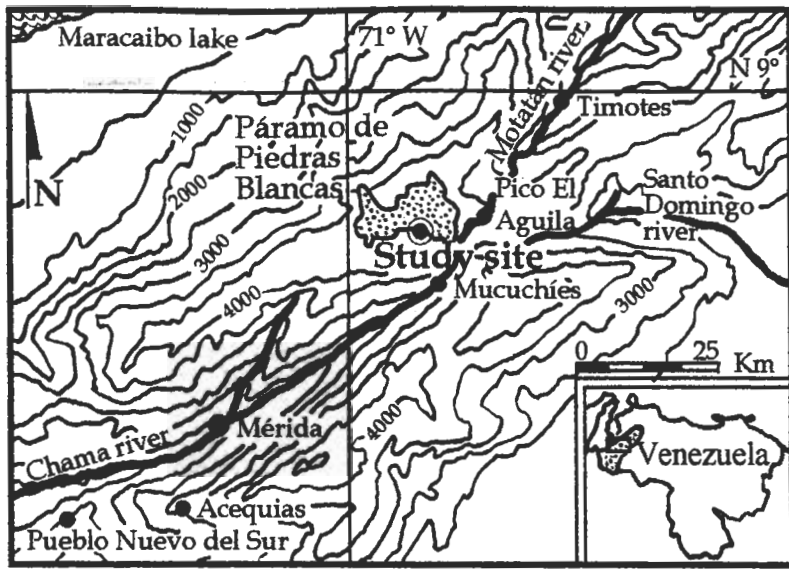


FIGURE 1. Location map of the study area (páramo Piedras Blancas, adjacent to El Banco).

### Study Area

The area of study was located in the páramo El Banco (8°45'N, 70°52'W, 3800 m, Fig. 1), situated in Sierra de la Culata (Mérida, Venezuela) between the Andean and Altiandean ecological belts (Monasterio, 1980b). The selected area is a toposequence on a steep hill that stands out above a small deposition plain. It has a bedrock of Precambrian gneiss originated by a massive sedimentation (Malagón, 1982).

The selected study sites were chosen in relation to the relative topographic condition, which in turn determined a clear difference in their respective characteristics. The first site was the shrub-rosette (SR) association of *Espeletia shultzii* and *Hypericum laricifolium* (defined by Monasterio, 1980b) situated on a slope (25–30%) with a well-drained soil. The other two sites were in topographically low situations, receiving runoff from the surrounding slope: the seasonal pasture (SP) and the humid pasture (HP). They both were situated on a slight slope (0–5%) and were representative of the Páramo Pasture formation defined by Monasterio (1980b). The seasonal pasture (SP), with a somewhat poorly drained soil (the water table was at the surface during the wet season), was dominated by small herbs (*Eleocharis acicularis*, *Muehlenbergia ligularis* and *Calamagrostis mulleri*) while the humid pasture (HP), with a poorly drained soil, remained wet throughout the year. Monasterio (1980b) described the humid pasture, which is commonly distributed in two layers accordingly to the soil drainage regime: The taller layer is composed by some Cyperaceae or other small herbs and a ground layer, composed by some monocots (like *Altensteinia palacea*) and mosses.

Annual precipitation and air temperature at the Mucuchíes Meteorological Station (8°46'N, 70°54'W, 3100 m) average 676.7 mm and 11.3°C, respectively. The rainfall has a unimodal distribution with a wet season from May to October and a marked dry season from December to March (Monasterio and Reyes, 1980). A notable concentration of frosts occur during the dry season due to clear skies and a high nocturnal re-irradiation (Azócar and Monasterio, 1980). These soils are therefore subjected to daily freezing cycles that determine the typical characteristics of periglacial morphology. The area of study is also under extensive cattle grazing, especially during the dry season.

### Methods

A list of species was made from the shrub-rosette (SR) and the seasonal pasture (SP) and the relative cover was measured with the point-intercept method as described by Fariñas (1975). Three individuals of the dominant species from these two sites (SR and SP) were excavated and their roots checked for mycorrhizal presence. A list of species from the humid pasture (HP) was not made because most of the plants sampled in this site were not properly identified.

Belowground biomass, percentage of root hairs, and mycorrhizal colonization from unknown plant species were estimated from quadrangular soil cores of 10 × 10 cm at each site, in both the dry (February 1991) and the wet (September 1991) seasons. In total, 10 cores were randomly sampled at each site (5 per season). Soil cores were carefully separated at the following depths: 0–5, 5–10, and 10–30 cm (sometimes the excavation was stopped by rock or stones), soaked in water and then washed through a 0.425-mm mesh sieve. Dead roots were discarded and a small sample of live roots from each soil core depth—unknown species—were randomly taken to quantify mycorrhizal colonization and root hairs. The rest of the roots were oven-dried at 100°C for 24 h and then weighed. Biomass results were expressed in grams per square meter. Five more topsoil samples (0–15 cm) were collected randomly from each site and sampling date. The following parameters were estimated: soil pH (water 1:2), organic carbon (Walkley-Black), total N (micro-Kjeldahl), available P (Olsen), cation exchange capacity (ammonium acetate extraction), K, Na, and Ca (atomic absorption).

The roots were cleared in 10% KOH, acidified in 10% HCl, and stained in 0.05% trypan blue (Phillips and Hayman, 1970). One hundred root segments from each soil core were scored for presence or absence of mycorrhizal colonization and root hairs using the grid-line intercept method (50 ×) described by Giovanetti and Mosse (1980). The data of mycorrhizal colonization was assessed using three-way ANOVA with the 3 sites nested into the 3 sampling depths and 2 sampling dates, respectively. Pairs of means were compared using least significant difference multiple comparisons at a 95% confidence level. Prior to statistical analysis, AM colonization and root hairs were arcsine-transformed. Analyses were performed with SAS (SAS, 1988). The Spearman nonlinear correlation test (Siegel, 1970) was used to

TABLE 1  
Soil characteristics of the study sites during the dry and wet seasons

Soil factor	Shrub-rosette (SR)		Seasonal pasture (SP)		Humid pasture (HP)	
	Dry season <sup>a</sup>	Wet season <sup>b</sup>	Dry season <sup>a</sup>	Wet season <sup>b</sup>	Dry season <sup>a</sup>	Wet season <sup>b</sup>
pH <sup>c</sup>	4.10 ± 0.06	4.14 ± 0.15	4.82 ± 0.29	5.14 ± 0.21	4.28 ± 0.27	5.36 ± 0.38
Organic matter <sup>d</sup> (%)	4.41 ± 0.79	5.61 ± 0.92	9.10 ± 1.11	9.95 ± 0.13	10.48 ± 0.14	10.27 ± 0.23
Total N (%)	0.29 ± 0.11	0.31 ± 0.05	0.71 ± 0.13	1.24 ± 0.45	2.00 ± 0.33	1.83 ± 0.57
C/N	15.96 ± 2.57	18.02 ± 0.44	13.06 ± 0.91	9.22 ± 3.25	5.42 ± 1.03	6.58 ± 3.11
P <sup>e</sup> (mg kg <sup>-1</sup> )	3.20 ± 0.70	3.40 ± 1.20	3.60 ± 0.50	5.20 ± 5.80	6.40 ± 3.00	8.60 ± 4.90
CEC <sup>f</sup> (meq·100 <sup>-1</sup> )	9.86 ± 1.21	10.42 ± 1.57	37.38 ± 11.9	31.38 ± 4.74	59.44 ± 3.00	54.36 ± 7.03
K (meq·100 <sup>-1</sup> )	0.17 ± 0.02	0.27 ± 0.07	0.26 ± 0.06	0.45 ± 0.11	0.36 ± 0.04	0.81 ± 0.30
Na (meq·100 <sup>-1</sup> )	0.11 ± 0.02	0.08 ± 0.01	0.22 ± 0.02	0.22 ± 0.04	0.73 ± 0.26	0.78 ± 0.19
Ca (meq·100 <sup>-1</sup> )	1.63 ± 1.43	0.45 ± 0.42	9.27 ± 0.63	9.97 ± 2.54	20.55 ± 7.61	26.28 ± 6.14

Values with typical error at 95% confidence level ( $n = 5$ ).

<sup>a</sup> February 1991.

<sup>b</sup> September 1991.

<sup>c</sup> pH (water 1:2).

<sup>d</sup> Organic matter (Walkey-Black).

<sup>e</sup> Available P (Olsen).

<sup>f</sup> CEC = Cation Exchange Capacity (ammonium acetate extraction).

assess the association degree between the percentage of root hairs and mycorrhizal colonization data pairs regardless of site, depth and sampling date.

## Results

There were differences in edaphic factors among the areas. The increase of soil water contents in the low positioned soils across the landscape was significant (data not shown). As a consequence, organic matter and total nitrogen contents increase as soils become more poorly drained in both the seasonal and humid pastures (Table 1). The cation exchange capacity as well as sodium, potassium, and calcium contents significantly increased in the more poorly drained soils and this could relate to the

increase of organic matter contents in the same soils (Table 1). The study sites ranged from extremely acid (shrub-rosette) to slightly acid (humid pasture) and these values significantly increased during the wet season (Table 1).

The average belowground biomass in the humid pasture (208.4 g m<sup>-2</sup>) was the lowest compared with the mean belowground biomass for the shrub-rosette (397.5 g m<sup>-2</sup>) and the seasonal pasture (396.1 g m<sup>-2</sup>, Fig. 2). ANOVA test shows that depth effect on belowground biomass was significant ( $P \leq 0.001$ , Table 2) and the average value of the 0 to 5 cm layer (559.8 g m<sup>-2</sup>), regardless of the site or sampling date, was the highest and it provides some information on the root distribution.

The average percentage of root hairs in the humid pasture (36.9%) was significantly higher than those measured in the shrub-rosette and seasonal pasture (8.8 and 13.5%, respectively) regardless of depth and sampling date (Fig. 3). The calculated Spearman correlation coefficient ( $\tau_s$ ) for all the percentage of root hairs and mycorrhizal colonization data pairs, regardless of site, depth, and sampling date, was  $-0.5904$ . The calculated Student's  $t$  was 6.862 with 88 degrees of freedom ( $P < 0.001$ ).

Arbuscular mycorrhizae were the only type of mycorrhizae observed in root samples from soil cores and individual plants but no further identification of either genera or species of the involved fungi was done. Table 3 shows the relative cover and mycorrhizal status of the dominant species of the shrub-rosette. *Hypericum laricifolium* (relative cover = 42.4%) were colonized and showed profuse mycelium and vesicles. This suggests the importance of the symbiosis within the shrub-rosette. *Conyza lasseriana* (Asteraceae) and *Rumex acetosella* (Polygonaceae) collected in the shrub-rosette did not form mycorrhizae (Table 3). Montilla et al. (1992) did not observe mycorrhizae in *R. acetosella* sampled in a succession-regeneration agro-ecosystem in the Andean páramo.

Plant species from the seasonal pasture, mainly composed by short grasses, were mycorrhizal and showed large amounts of AM hyphae, with the exception of root samples of *Carex albolutescens* (Cyperaceae) (Table 4). Allen et al. (1987) report that some species in this family generally do not form mycorrhizae in flooded soils, although *Eleocharis acicularis* (Cyperaceae), sampled in the seasonal pasture, formed mycorrhizae. It

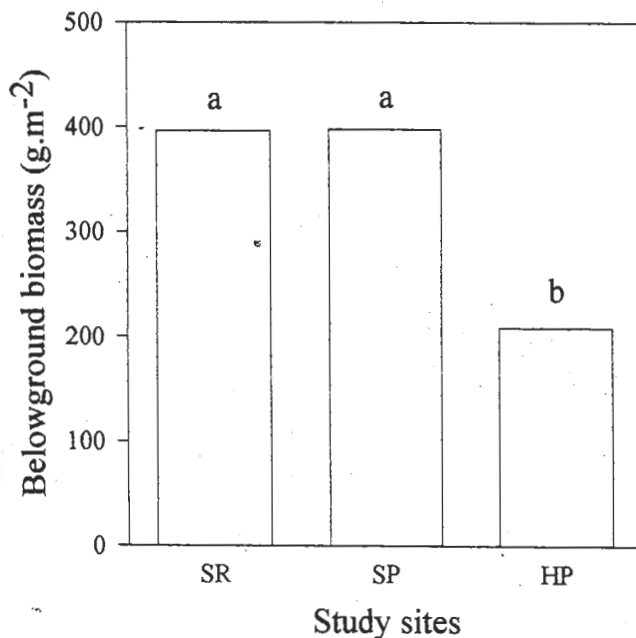


FIGURE 2. Average values of belowground biomass (g m<sup>-2</sup>,  $n = 30$ ) in shrub-rosette (SR), seasonal pasture (SP), and humid pasture (HP). Bars with different letters differ at 0.05 level.

TABLE 2

*F* ratios from ANOVA tests of study site (SR, SP, and HP), depth (0–5, 5–10, and 10–30 cm) and sampling date (dry and wet seasons) effects on belowground biomass, root hairs, and mycorrhizal colonization

Response variable	Source of variation					
	Main effects			Interactions <sup>a</sup>		
	Site (SI)	Depth (DE)	Sampling date (SD)	SI × DE	SI × SD	DE × SD
Belowground biomass	5.18**	18.99***	7.11**	2.13	1.27	1.84
% Root hairs	34.90***	2.87	0.07	1.47	0.82	0.91
% Mycorrhizal colonization	193.25***	56.05***	172.43***	6.76***	15.81***	7.35**

\*, \*\*, \*\*\*, indicate that *F* ratios were significant at  $P \leq 0.05$ ,  $0.01$ ,  $0.001$ , respectively.

<sup>a</sup> None of the three-way interactions was significant at  $P \leq 0.05$ .

should be noted that *R. Acetosella* sampled in the seasonal pasture formed mycorrhizae but only very few roots were colonized (Table 4).

The average mycorrhizal colonization during the dry season on the shrub-rosette (69.4%), regardless of soil depth, was the highest and the extent of mycorrhizal colonization significantly decreased in all sites during the wet season (Fig. 4A). The average mycorrhizal colonization of the 0 to 5 cm layer on the shrub-rosette (70.6%), regardless of the sampling date, was the highest and the extent of mycorrhizal colonization significantly decreased according to soil depth (Fig. 4B).

## Discussion

Belowground biomass values are comparable to those reported by Smith and Klinger (1985), who obtained an average value of  $181.7 \text{ g m}^{-2}$  for live belowground phytomass, sampled during the dry season in Piedras Blancas, a Venezuelan páramo similar to the seasonal pasture described in this paper. The be-

lowground biomass of the 0 to 5 cm layer contains the largest proportion of the total root mass in all the study-sites. Hofstede and Rossenaar (1995) also obtained the same distribution of roots in different areas from a Colombian páramo.

Smith and Klinger (1985) calculated an aboveground-belowground ratio (A:B) of 1:1.4 for the above mentioned area. They suggested that tropicalpine vegetation is characterized by a high (A:B) ratio due to a lesser proportion of belowground phytomass compared with other nontropical high mountain environments, where seasonal variation is significantly higher (Smith and Klinger, 1985). Molinillo (1992) obtained an average aboveground biomass of  $10.6 \text{ g m}^{-2}$  during the dry season in the same seasonal pasture site as this study. As a consequence, the A:B ratio for this site is 1:37.5, remarkably lower than the obtained by Smith and Klinger from the Venezuelan páramo (1985) and Hofstede and Rossenaar (1995) from different sites of a

TABLE 3

Relative cover and mycorrhizal status of the dominant vegetation in the shrub-rosette (SR) site

Family	Plant species	Relative cover (%)	Mycorrhizal status <sup>b</sup>
Hypericaceae	<i>Hypericum laricifolium</i>	42.4	M
Asteraceae	<i>Espeletia shultzii</i>	18.6	M
	<i>Espeletia flocosa</i>	8.8	M
	<i>Gnaphalium moritzianum</i> (Klatt)	1.2	M
	<i>Aristeguieta</i>		
	<i>Bidens andicola</i> H.B.K.	0.3	M
	<i>Hinterhubera ericoides</i> Wedd	0.3	M
	<i>Blakiella bartisiaefolia</i>	—	M
	<i>Conyza lasseriana</i> Aristeguieta	—	NM
	<i>Lucilia radians</i> (Benth) Cuatrecasas	—	M
	<i>Hypochoeris setosus</i> (Nedd) Ruaby	—	M
Poaceae	<i>Stipa philippii</i> Steud	14.6	M
	<i>Poa petrosa</i>	1.2	M
	<i>Aciachne pulvinata</i>	0.3	M
Juncaceae	<i>Luzula racemosa</i> Desv.	4.0	M
Caryophyllaceae	<i>Arenaria</i> sp.	2.1	M
Polygonaceae	<i>Rumex acetosella</i> L.	0.3	NM
Crassulaceae	<i>Echeverria venezuelensis</i>	0.3	M
Campanulaceae	<i>Lobelia ternera</i> H.B.K.	—	M

<sup>a</sup> Relative cover = point intercept method (Fariñas, 1975).

<sup>b</sup> M, NM, indicate mycorrhizal and nonmycorrhizal root, respectively.

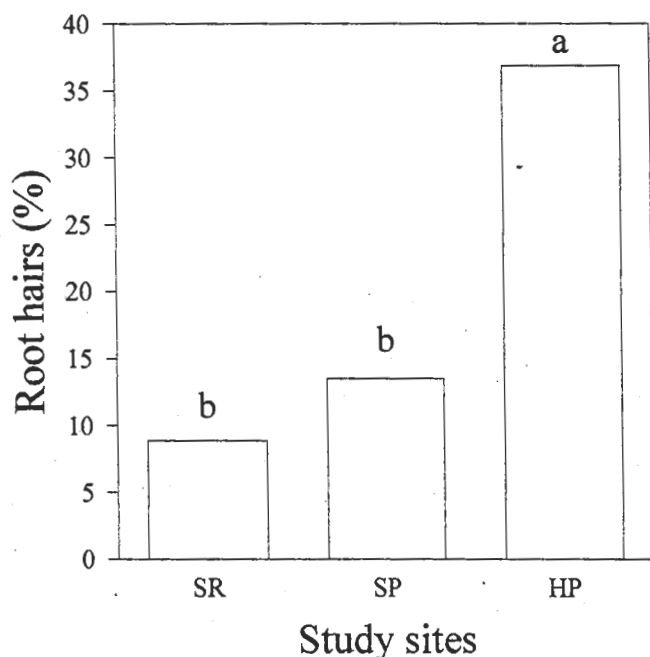


FIGURE 3. Average values of percentage root hairs ( $n = 30$ ) in shrub-rosette (SR), seasonal pasture (SP), and humid pasture (HP). Bars with different letters differ at 0.05 level.

TABLE 4

Relative cover and mycorrhizal status of the dominant vegetation in the seasonal pasture (SE site)

Family	Plant species	Relative cover <sup>a</sup> (%)	Mycorrhizal status <sup>b</sup>
Poaceae	<i>Muehlenbergia ligularis</i> (Hack) Hitch.	15.3	M
	<i>Calamagrostis mulleri</i> Luces	13.4	—
	<i>Agrostis triclodes</i> (H.B.K.) Roen & Schult	1.9	M
	<i>Vulpia australis</i> (L.) S.F. Gray	1.0	M
	<i>Acicahne pulvinata</i>	0.3	M
	<i>Trisetum irazuense</i> (Kuntze) Hitch.	—	M
Cyperaceae	<i>Eleocharis acicularis</i> Speg.	24.0	M
	<i>Carex albolutescens</i> Schwein	4.4	NM
Rosaceae	<i>Lachemillia</i> sp.	7.2	M
Asteraceae	<i>Lucilia venezuelensis</i>	1.2	M
	<i>Oritrophum paramense</i> (Arist. & Cuatrec.)	—	M
	<i>Hypericum brathys</i> SM.	—	M
	<i>Taraxacum officinale</i> Webber	—	M
Geraniaceae	<i>Geranium</i> sp.	1.5	M
Polygonaceae	<i>Rumex acetosella</i> L.	0.2	M
Iridaceae	<i>Sysyrinchium</i> sp.	—	M

<sup>a</sup> Relative cover = point intercept method (Fariñas, 1975).

<sup>b</sup> M, NM, indicate mycorrhizal and non-mycorrhizal root, respectively.

Colombian páramo. The low A:B ratio obtained for the seasonal pasture resembles those reported for the arctic tundra, characteristic of extreme environments. A drier climate in this study site (SP), differences in vegetation structure, and an extremely heavy grazing activity concentrated during the dry season, may account for this remarkable A:B ratio reduction.

Among the study sites, the shrub-rosette was the least fertile. These soils were formed on igneous and metamorphic rocks and have a coarse texture with a large percentage of sand, which is highly conducive to needle ice growth (Pérez, 1992). Available phosphorus is very low and soils are extremely acid. This may represent a limiting factor for plant growth in this area. The main form of nitrogen in well-drained soils is nitrate, with significant fluxes at the beginning of rainfall mainly due to an increase in the soil microbial activity.

The more poorly drained soils from the seasonal pasture accounts for a noticeable increase in organic matter, and hence, the cation exchange capacity. Some authors have also reported a strong positive correlation between both variables in Andean soils (Malagón, 1982; Pérez, 1992). In the humid pasture the water table was near the surface throughout the year. Under this condition, ammonium accumulates mainly due to a decrease in oxygen levels, which interrupts nitrification, and the increase of nitrogen fixation biological mechanisms (Ponnampertuma, 1972). Phosphate hydrolysis due to a pH increase in the poorly drained soils would increase available phosphorus in the humid pasture (Ponnampertuma, 1972).

Mycorrhizal colonization in the shrub-rosette site was the highest. This symbiosis may play an important role in the uptake of scarce nutrients in this area. Pérez (1992) obtained a significant accumulation of organic matter and nutrients in the surface soil layer below rosette canopies (*Coespeletia timotensis* and *Espeletia semiglobulata*) compared to adjacent bared soils. It is suggested that mycorrhizal roots are particularly important in an efficient nutrient cycling by rosettes near the shoot base, where element leaching from the standing (stem) litter generally occurs. As a consequence, the horizontal distribution of mycorrhizae in the shrub-rosette is not homogeneous but rather distributed into patches within the plant community.

Mycorrhizal colonization decreased in the seasonal and humid pastures, respectively, as soils became more poorly drained. Organic matter and available nutrients became more available in the pasture sites, compared with the shrub-rosette site. It is then suggested that mycorrhizal colonization decreased in the seasonal pasture site due to the increase of soil fertility. A low diffusion of oxygen in the humid pasture may explain the abrupt decrease of mycorrhizal colonization in this site, promoting a physiological inhibition in the symbiotic activity, as has been demonstrated by several authors (Khan, 1974; Keeley, 1980; Gianinazzi-Pearson and Diem, 1982; Janos, 1987; Van Duin et al., 1991).

The percentage of root hairs significantly increased in the humid pasture where nutrients became more available compared with the other study sites. Vegetation in the shrub-rosette, on the other hand, shows the typical magnolioid root system, roughly branched with scarce root hairs (Baylis, 1975). Montilla et al. (1992) also observed the same characteristic in another shrub-rosette vegetation in the Venezuelan páramo. In this study, mycorrhizal colonization and percentage of root hairs from all sites, depths, and sampling dates were negatively correlated. It may indicate that vegetation growing in the more poorly drained soils from the study area is less dependent on mycorrhizae than plants growing in the well-drained soil from the shrub-rosette site.

Mycorrhizal colonization was higher during the dry season compared to the wet season in all study sites. This difference does not necessarily represent an overall increase of nutrient uptake due to a more extensive mycorrhizal root colonization during the dry season. It has been well documented that a mutualistic phase, under field conditions, normally takes place during flowering or seedling establishment (McGonigle and Fitter, 1988). Mullen and Schmidt (1993) confirmed that arbuscules were present in *Ranunculus adoneus*—a perennial alpine herb—only for a few weeks during the growing season, when the plant tissue phosphorus accumulation reached a maximum. Further research is needed to assess the physiological effect of the symbiosis in particular species at different developmental stages under natural conditions.

Mycorrhizal colonization was highest in the top 0 to 5 cm, decreasing with soil depth which may indicate a noticeable ac-

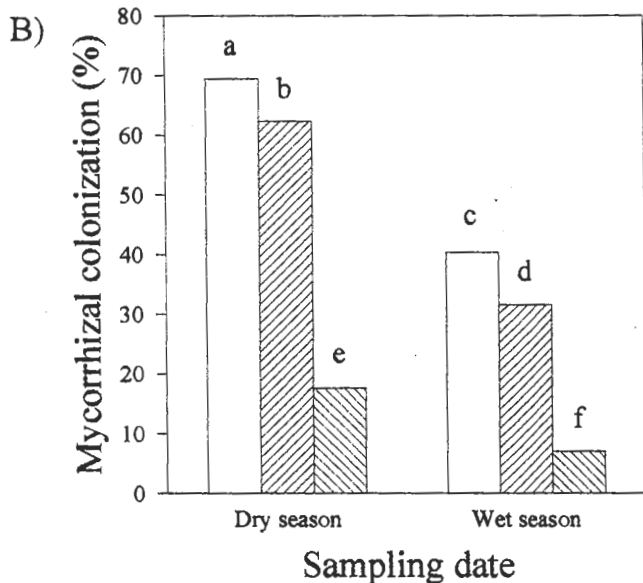
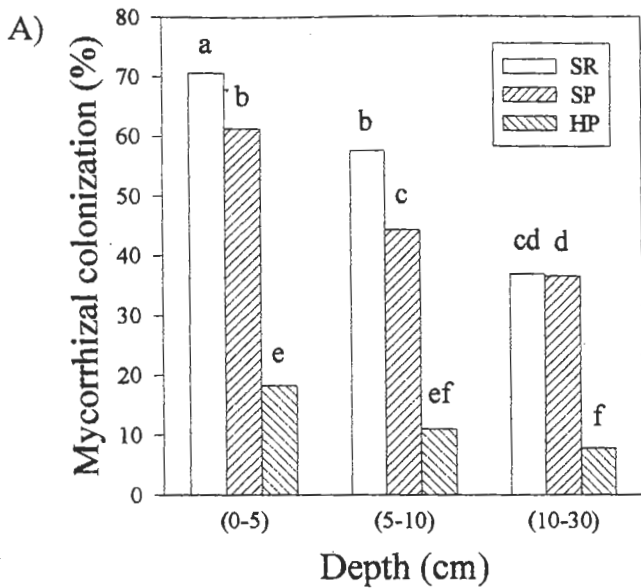


FIGURE 4. Average values of percentage mycorrhizal colonization in shrub-rossette (SR), seasonal pasture (SP), and humid pasture (HP) at three different depths (A) and two sampling dates (B). Bars with different letters differ at 0.05 level.

accumulation of nutrients in this soil layer. Abbott and Robson (1991) suggested that there is an exponential decrease of both mycorrhizal colonization and number of spores with soil depth. However, Montilla et al. (1992) did not observe significant differences in the vertical distribution of mycorrhizal colonization in a tillage soil from a similar area in a Venezuelan páramo. Tillage may change soil conditions, affecting the vertical distribution of AM inoculum and even decrease mycorrhizal colonization (Abbott and Robson, 1991). Furthermore, several reports indicate that undisturbed plots contained more spores in the topmost soil than ploughed plots (Kruckelmann, 1975, Smith, 1978, both cited by Abbott and Robson, 1991). Tillage may also affect the soil fauna which is an important vector of AM propagule distribution (Johnson and Pflieger, 1992).

Some roots with a thin mycorrhizal mycelium were observed. It resembled the corresponding mycelium of *Glomus tenue*, widely distributed in some Alpine areas (Haselwandter and

Read, 1980; Read and Haselwandter, 1981; Blashke, 1991). A considerable amount of a slightly stained, septate fungal mycelium was also observed. Further survey research is needed in order to properly identify this septate endophyte as well as the arbuscular mycorrhizal fungi of ecological importance in this barely unknown area. Some of them will presumably be endemic species adapted to the particular conditions of the Tropical high mountain.

The present study demonstrates that the topographic position determines changes in soil drainage which in turn affects soil conditions, vegetation, and incidence of mycorrhizal colonization. Well-drained soils were less fertile and mycorrhizal colonization higher than the more poorly drained soils, which were more fertile, with a lower mycorrhizal colonization, and more root hairs. Vertical distribution of roots and mycorrhizal colonization suggest that nutrients are mainly distributed in the surface soil layer. Further research is needed to understand better the basis of mycorrhizal functioning in the Tropical high mountain to effectively restore extensive degraded land as well as to propose sustainable alternatives to agriculture production for those who have inhabited this area for centuries.

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