*Arctic, Antarctic, and Alpine Research, Vol. 42, No. 2, 2010, pp. 152–163*

# Influence of Soil Chemical Variables and Altitude on the Distribution of High-alpine Plants: the Case of the Andes of Central Chile

*Vinka Anic**
*Luis Felipe Hinojosa**
*Javiera Díaz-Forester†*
*Elena Bustamante‡*
*Luz María de la Fuente‡*
*Jean Francois Casale‡*
*Jean Paul de la Harpe‡*
*Gloria Montenegro† and*
*Rosanna Ginocchio‡§*

*Facultad de Ciencias–Instituto de Ecología y Biodiversidad (IEB), Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile
†Facultad de Agronomía e Ingeniería Forestal, Pontificia Universidad Católica de Chile, Av. Vicuña Mackenna 4860, Macul, Santiago, Chile
‡Centro de Investigación Minera y Metalúrgica, Av. Parque Antonio Rabat 6500, Vitacura, Santiago, Chile
§Corresponding author: rginocc@cimm.cl

DOI: 10.1657/1938-4246-42.2.152

## Abstract

Temperature is one of the major abiotic factors influencing distribution and productivity of alpine plant species. Although some edaphic parameters (e.g. soil acidity) have also been suggested as determinants in the spatial distribution of alpine vegetation, there is little background on the importance of soil chemical properties in altitudinal gradients, particularly in the high Andes. The present study determined whether soil chemical properties affect spatial distribution and abundance of alpine plants in an altitudinal gradient in the Andes of central Chile, emphasizing metal content. A direct gradient analysis took place at Yerba Loca Natural Sanctuary (YLNS), based on a geobotanical sampling conducted in 73 sites distributed from 1970 to 3330 m a.s.l. According to a Canonical Correspondence Analysis, the main soil chemical factors that explain the pattern of compositional variation of high Andean vegetation are, besides altitude, total soil copper (Cu) content, percentage of soil organic matter, and available phosphorus and nitrogen. An analysis of shoot Cu content conducted in 19 plant species found in sites with highest soil Cu contents (>250 mg $kg^{-1}$) showed high levels of Cu in their shoots (>100 mg $kg^{-1}$). These results demonstrate species or ecotypes with optimal distribution in soils with high Cu contents, such as *Armeria maritima*, *Trisetum lasiolepis*, and *Montiopsis potentilloides*, which may have tolerance to this metal.

## Introduction

In high-mountain environments, temperature has been proposed as one of the major abiotic factors that influence the distribution and productivity of plant species (Sakai and Larcher, 1987). Such environments are notable for the presence of short growing seasons and low temperatures of air and soil (Mooney and Billings, 1965; Peterson and Billings, 1982; Sakai and Larcher, 1987), which determine morphological and physiological adaptations of alpine plant species (Bliss 1971; Billings, 1974). In addition to temperature, other abiotic factors such as the availability of soil nutrients, organic matter content, granulometry, radiation, winds, snow-cover gradient, and stability of the substrate have also been suggested as factors that considerably influence the spatial distribution of plant species in high-mountain ecosystems (Bliss, 1985; Squeo et al., 1993, 1996, 2006; Chambers, 1997; Körner, 2003).

Regarding chemical factors of soils, soil acidity (calcareous versus siliceous soils) has been one of the main factors to explain soil-plant relationships in alpine environments of Europe and North America, as well as in the Arctic (e.g. Lunde, 1962; Knapik et al., 1973; Jarvis, 1974; Gensac, 1990; Gough et al., 2000; Schmidtlein and Ewald, 2003; Darmody et al., 2004). However, the pattern of spatial variation of alpine vegetation and floristic composition is also associated with either varying contents of both iron (Fe) and sulfate (Wiser et al., 1996), available nitrogen (Bowman et al., 1993; Baddeley et al., 1994; Seastedt and Vaccaro, 2001; Körner, 2003), or available phosphorous (Arnesen et al., 2007), as the geochemical variation of bedrock is more complex than expressed by the carbonate/silica proportion (Arnesen et al., 2007).

In the case of high-alpine (high Andean) South American systems, studies have been conducted primarily to determine the regional flora, the importance of endemisms, and their historical and biogeographical relations (e.g. Young and Reynel, 1997; Ricardi et al., 1997; Squeo et al., 1998; Teillier 1998; Weigend, 2002, Young et al., 2002). Studies of the existing biotic relations, such as the nurse effect of some cushion plants (e.g. Arroyo et al., 2003; Cavieres et al., 2007, 2008), and the importance of pollinators in reproduction (e.g. Arroyo et al., 1985; Arroyo and Uslar, 1993, Pérez et al., 2006) have been also performed. However, little is known about abiotic factors controlling vegetation composition and distribution in high Andean systems. In general, there has been much less focus on chemical properties of soils that could restrict the distribution and composition of high Andean species than in alpine areas of the Northern Hemisphere (e.g. Squeo et al., 1993, 2006).

A geographical area of interest to study possible relationships between soil properties, in particular chemical factors, and the species composition and diversity is the Andes of north-central Chile. The area is included in the alpine flora of South America, the most-species-rich area of all high mountain regions in the world (Smith and Cleef, 1988; Luteyn and Churchill, 2000), and is well known for its complex mineralogical variation of substrates,

1523-0430/10 $7.00

as bedrock harbors igneous, sedimentary, and metasedimentary rocks, and metallogenic strips (Moreno and Gibbons, 2007). Specifically, in the high Andes of central Chile there is a metallogenic strip (31°30′ to 34°30′S) which has three of the largest systems of porphyry copper and molybdenum in the Andes and in the world (Camus, 2003). These systems are between 2000 and 4100 m a.s.l. and correspond to large deposits of minerals whose formation was triggered by tectonic events that took place 6.46 and 4.37 million years ago (Skewes and Stern, 1994; Deckart et al., 2003; Maksaev et al., 2004). The coexistence of these mineral deposits with high Andean vegetation since the Upper Miocene–Pliocene (e.g. Hinojosa, 1996; Hinojosa and Villagrán, 1997) suggests that the composition of the vegetation on the upper floors of the Andes of central Chile could be influenced by high levels of metal content in soils, mainly in terms of copper (Cu), molybdenum (Mo), iron (Fe), and sulfur (Camus, 2003).

Soils with high levels of metal content (metalliferous soils) may impose toxicity problems in plants (Reeves and Baker, 2000), acting as selecting agents for plant species or tolerant populations (ecotypes) that have mechanisms of adaptation or resistance to high levels of metal content (Baker, 1987; Ernst, 1990). Most metalliferous soils of natural origin are characterized by the presence of ecotypes and/or metal-tolerant plant species that are largely or entirely restricted to such soils (Antonovics et al., 1971; Reeves and Baker, 2000). For example, in metalliferous areas of natural origin and where there are superficial deposits of copper, like the province of Shaba and the Copper Belt in south-central Africa, there are several metal-tolerant plant species that dominate and are exclusively distributed in soils with high copper content (Drew and Reilly, 1972; Malaisse et al., 1978, 1979; Brooks et al., 1985).

In this context, the main objective of the present study was to determine whether the chemical properties of soils affect the spatial distribution of alpine plants in an altitudinal gradient in the Andes of central Chile, emphasizing metal contents. Further objectives were the identification of high Andean plants whose distribution is related to soils with elevated Cu contents, and assessment of Cu content in their aerial tissues (shoots).

## Materials and Methods

### *STUDY SITE*

The study was conducted in the high Andean area of Yerba Loca Natural Sanctuary (YLNS, 33°12′S; 70°16′W), located northeast of the city of Santiago in central Chile (Fig. 1). The reserve covers 39,129 ha, including the entire Yerba Loca estuary basin to the eastern slopes of the San Francisco estuary in the west, and high peaks of the El Plomo–La Parva mountains in the east. To the north, it borders La Paloma mountain and to the south includes part of the escarpment access to the winter ski complex of Farellones (Barceló, 1984). The upper part of the Yerba Loca estuary basin corresponds to the southern extension of the large copper deposit Rio Blanco–Los Bronces (Bassi, 1982) where a large copper deposit known as Paloma–Sulfatos (Bassi, 1982), which has never been exploited, exists (Fig. 1). The reserve covers an altitudinal range of 4040 m, between 1300 and 5340 m (Barceló, 1984).

The plant species in the reserve include mediterranean sclerophyllous shrubs (900–1500 m), mountain sclerophyllous forest dominated by *Kageneckia angustifolia* (1600–2000 m), and high Andean vegetation (2000–3600 m) (Arroyo et al., 2002). In the high Andean zone of central Chile, three vegetation belts have been described: (1) Subandean belt (2100–2500 m), dominated by shrub species and the presence of annual herbs; (2) lower Andean belt (2600–3400 m), mainly characterized by the abundance of cushion plant communities; and (3) upper Andean belt (3500–3700 m), which is dominated by perennial herbs (Cavieres et al., 2000).

The study site has a temperate semiarid microthermal high-alpine mediterranean climate (Santibáñez and Uribe, 1990). This climate has a thermal regime ranging between a maximum of 19.1 °C in January and a minimum in July of −2.4 °C, with the presence of frost throughout the year (Santibáñez and Uribe, 1990). In addition, the area is covered with snow from May to October (Rozzi et al., 1989).

### *VEGETATION AND SOIL SAMPLING*

A geobotanical sampling was conducted along an altitudinal gradient (1970 to 3330 m) in the high Andean environment at YLNS. The sampling was conducted during the spring–summer seasons of 2005–2006 and 2006–2007. A georeferenced grid of 800 × 800 m above the elevation of 2000 m was marked, where equidistant sampling sites were defined using aerial photographs, satellite images, and digital charts. The grid was modified according to the field site accessibility, resulting in a total of 73 sampling sites (Fig. 1). At each site, a composite sample of surface soil was taken and a vegetation sampling plot was established. The geographical location in UTM coordinates and the elevation of each site were established using GPS.

The vegetation sampling was conducted according to the Braun-Blanquet method (Kent and Coker, 1992). At every sampling site a plot of 25 $m^2$, subdivided into 100 quadrants (0.25 $m^2$ each), was established for determination of vascular plant richness and estimation of the percentage of plant species coverage. Within each plot of 25 $m^2$, a composite sample of surface soil was taken (0–20 cm depth). To obtain this sample, 3 subsamples of soil within a diagonal drawn on the plot were taken (one central sample and one at each end) using a stainless steel shovel and PVC tubes of standard volumes. The 3 subsamples were mixed in the field in a clean polyethylene bag and from this composite a soil sample of approximately 1.5 kg was taken and stored in a polyethylene bag sealed airtight. The soil samples were transported to the laboratory to be chemically characterized as described below.

### *CHEMICAL CHARACTERIZATION OF SOILS*

The analyzed variables for each soil sample were pH, available macronutrients [nitrogen (N), phosphorus (P), and potassium (K)], soil organic matter (SOM), and total concentrations of (Cu), zinc (Zn), and iron (Fe). Additionally, soil texture through the percentage of particulate matter >2 mm and <2 μm was determined. The soil samples were dried in an air oven at 30 °C, sieved to pass 2 mm, and stored in polyethylene containers (U.S. EPA, 1995); the total percentage of the sample corresponding to the soil whose particle size is greater than 2 mm was registered (retained by the sieve), and the fraction less than 2 μm was determined by granulometry using the method of Bouyoucos (USDA, 2004). The pH was measured in an aqueous solution (soil:water, 1:1) through potentiometric determination (USDA, 2004) and the available contents of N, P, and K according to the methods described by Sadzawka et al. (2006). Soil organic matter content was analyzed by the Walkley Black method according to USDA protocols (USDA, 1996).The total concentrations of Cu, Zn, and Fe were determined by atomic absorption spectropho-

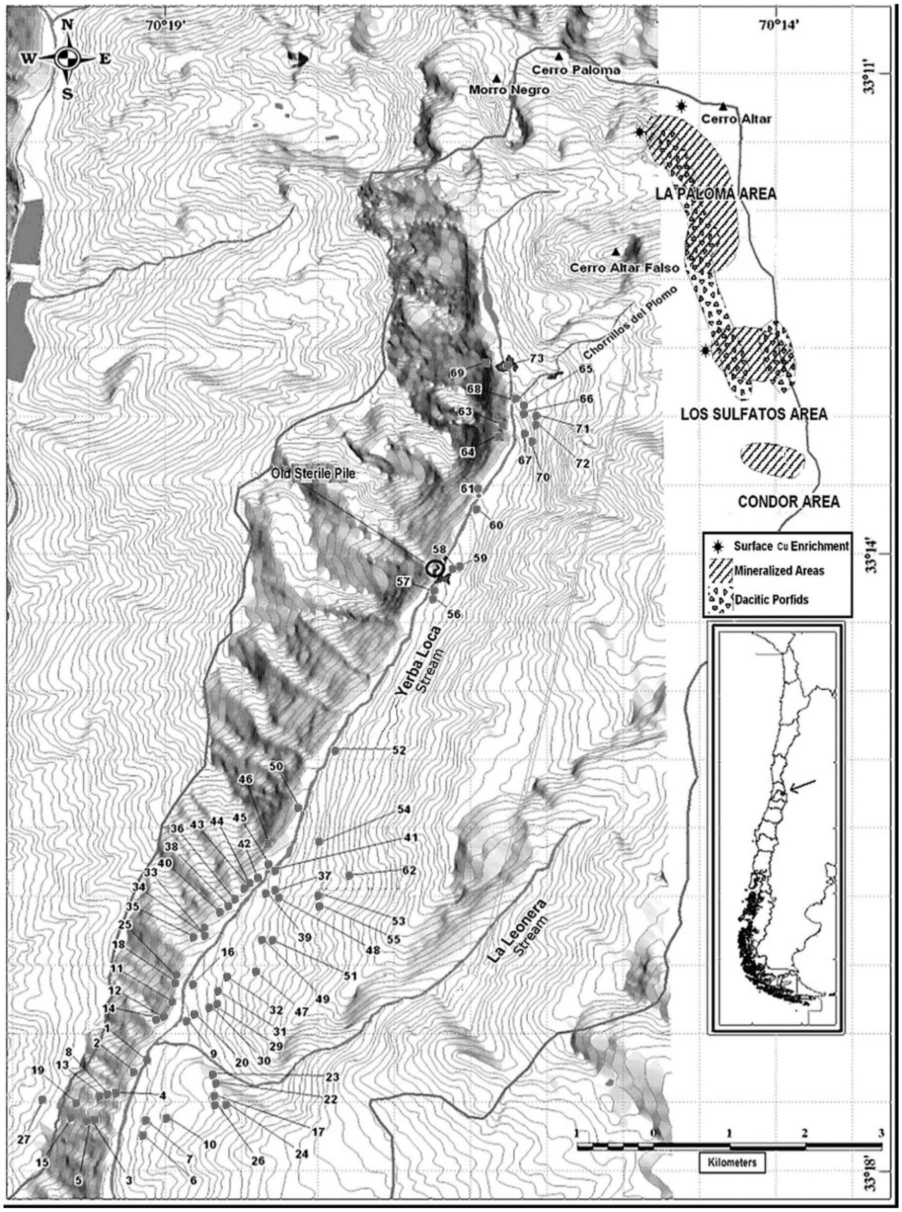

**FIGURE 1. Location of the Yerba Loca Natural Sanctuary (YLNS), the study site, in central Chile and relative location of high-altitude mineral deposits. Sites for soils and vegetation sampling (*N* = 73) are shown with gray circles.**

tometry (Perkin Elmer Analyst 300 equipment) after digestion and acid extraction ($HNO_3/HF/H_2O_2$) in a microwave oven (Milestone 1200), using the method 3051 of U.S. EPA (1995); duplicate samples, blank and certified reference material were considered (B-Loam, cat # CRM-LO-B purchased from High-Purity Standard, Charleston, South Carolina) in order to meet the criteria for quality assurance/quality control or QA/QC.

### *PLANT TISSUE SAMPLING AND COPPER CONTENT DETERMINATION*

From the information generated by the geobotanical sampling described above, an aerial plant-tissue sampling (shoots) was performed during February and March 2008. Six sites with soils presenting high levels of copper (>370 mg $kg^{-1}$) were selected. Furthermore, an additional sampling site was incorporated, which showed a dominance of one of the species with an optimal distribution in soils with high Cu content. For this site, a composite sample of surface soil was obtained following the methodology described above, and the total content of Cu, Zn, and Fe were determined. In each site of tissue sampling a plot of 25 $m^2$ was established where between 2 and 6 of the present plant species were collected. All collected species from each sampling site were placed in sealed airtight polyethylene bags and then processed in the laboratory as composite sampling. Roots and inflorescences were removed and discarded. The shoots were washed with deionized water and dried in an oven at 44 °C for 72 hours. They were then pulverized in a grinder with a stainless steel blade and placed in polyethylene containers (42 USDA report, 1996, and U.S. EPA method 600/R-95/077, 1995). They were then subjected to digestion and acid extraction ($HNO_3/HF/H_2O$) in a microwave oven (Milestone 1200) (U.S. EPA, 1995). The contents of Cu were determined by atomic absorption spectrophotometry in Perkin Elmer Analyst 300 equipment considering duplicate samples, blank and certified reference material (SRM 1573rd from Tomato Leaves, National Institute of Standards and Technology), to meet the QA/QC criteria (U.S. EPA, 1995).

### *STATISTICAL ANALYSIS*

Relationships between soil chemical variables and altitude, and between available nutrients (N and P) and SOM, were

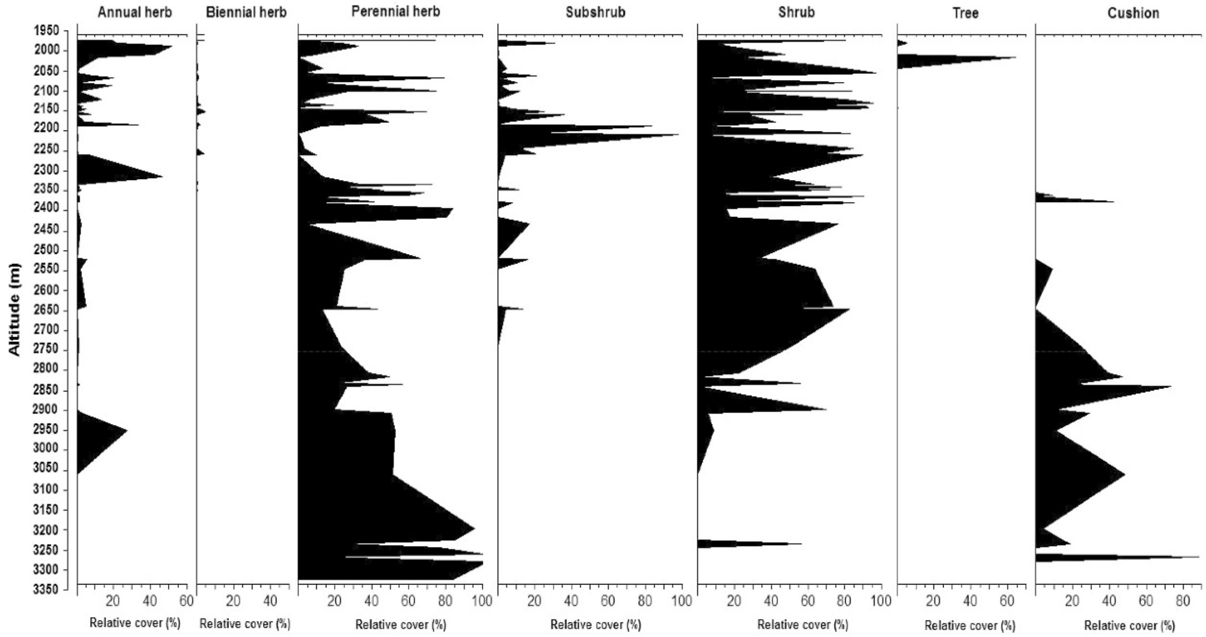

**FIGURE 2. Variation of relative cover (%) of plants by growth forms along an altitudinal gradient (*N* = 73 sampling sites for vegetation) at Yerba Loca Natural Sanctuary. Specimens identified to family or genus level were not considered.**

examined using nonparametric Spearman correlation analysis as there were variables that did not exhibit normal distribution, according to the Kolmogorov-Smirnov and Shapiro-Wilk tests (Zar, 1984). Additionally, a Kruskal-Wallis test was conducted in order to assess the statistical significance of differences among the average soil Cu concentrations in three altitudinal levels (1970–2260, 2310–2740, and 2800–3320 m), followed by nonparametric multiple comparisons among the groups according to the Dunn test (Zar, 1984).

A Canonical Correspondence Analysis (CCA) was conducted to determine whether selected soil chemical factors explain the compositional variation of vegetation present at the high Andean system at the YLNS. The CCA is a technique for direct gradient analysis where species composition is directly and immediately related to measured environmental variables (Palmer, 1993). This technique is based on the assumption of unimodal response of species to environmental gradients (ter Braak, 1986).

To obtain an ordination model (CCA) that includes only those soil chemical factors that contribute significantly to species composition, a forward selection of explanatory variables was made. The statistical significance of the contribution of soil chemical variables was assessed using a partial Monte Carlo permutation test with 1000 permutations. In this test, the candidate soil chemical variable was used as the only explanatory variable (ordination model with just one canonical axis), considering the other soil chemical variables already selected as coviariables (Lepš and Šmilauer, 2003). The statistical significance of the model (CCA), which included the pre-selected environmental variables, was evaluated using a permutation test of Monte Carlo based on the sum of all canonical eigenvalues (ter Braak and Šmilauer, 2002), and considering 1000 permutations. For those explanatory soil chemical variables that were correlated to altitude, partial CCA tests were conducted (Legendre and Legendre 1998), considering altitude as a covariable. These analyses allowed isolation of the effect of soil chemical variables on species abundance due to altitude.

The program CANOCO 4.5 was used to conduct the Canonical Correspondence Analysis (ter Braak and Šmilauer, 2002), and the program STATISTICA 8.0 (StatSoft, 2008) was used to perform the Kruskal-Wallis test and the Spearman nonparametric correlation analysis.

## Results

### *FLORA AND VEGETATION*

A total of 211 vascular plants, belonging to 53 families and 115 genera, and one bryophyte were identified in the 73 plant sampling sites located along the altitudinal gradient at YLNS. The most represented families were Asteraceae, Poaceae, and Iridaceae with 45, 36, and 10 species, respectively. Regarding life forms and according to an analysis of relative coverage of the life forms present at the sampling sites, perennial herbs and cushion species are the dominant life forms at high elevation sites (3100 to 3300 m), while shrub species are scarce and annual herbs are absent (Fig. 2). The sites located at lower elevations (1970 to 2300 m) are characterized by the dominance of shrub species and the presence of annual herbs.

### *SOIL CHEMICAL VARIABLES IN THE ALTITUDINAL GRADIENT*

Soils in the study area show a wide variation in the content of both available macronutrients (N, P, and K) and SOM (Table 1). For example, the values of K range between 28 and 810 mg $kg^{-1}$, while the values of SOM range between 0.5 and 12% (Table 1). The SOM and available soil N, P, and K show a significant and negative correlation to altitude (Fig. 3) and both available N and P show a significant and positive correlation to SOM ($r_s = 0.4$; $P < 0.05$, for both macronutrients). Above 2800 m, the majority of sampling sites present a decreased availability of N and P in soils compared to sites at lower altitude. Even though SOM is negatively correlated to altitude (Fig. 3), reduction in this

TABLE 1

**Mean and range values of soil chemical variables and soil particle size measured in 73 sampling sites at Yerba Loca Natural Sanctuary, high Andes of central Chile.**

| Environmental variable | Mean | Minimum | Maximum |
|---|---|---|---|
| Available nitrogen (mg kg$^{-1}$) | 16 | 0.5 | 76 |
| Available phosphorous (mg kg$^{-1}$) | 27 | 5 | 72 |
| Available potassium (mg kg$^{-1}$) | 245 | 28 | 810 |
| Total copper (mg kg$^{-1}$) | 198 | 31 | 1265 |
| Total iron (mg kg$^{-1}$) | $4.6 \times 10^4$ | $2.6 \times 10^4$ | $8.2 \times 10^4$ |
| Total zinc (mg kg$^{-1}$) | 168 | 71 | 357 |
| Soil pH | 5.7 | 4.1 | 7.5 |
| Soil texture – PM > 2 mm (%) | 36 | 11 | 71 |
| Soil texture – PM < 2 μm (%) | 13 | 6 | 25 |
| Soil organic matter (%) | 4 | 0.5 | 12 |

parameter is not as marked as in the case of soil nutrients (SOM $r_s = -0.35$ versus N and P $r_s = -0.67$ both macronutrients); when altitudinal variation in SOM is compared in terms of three altitudinal levels at the YLNS (Fig. 4), no significant differences are found ($P > 0.05$, Kruskal-Wallis test), with mean values ranging from 4.63% at 1970–2260 m to 3.20% at 2800–3320, due to increasing spatial variation in this parameter with altitude (Fig. 4).

Regarding soil texture, sites that are between 1970 and 2200 m have a higher percentage of fine particulate matter (<2 μm) compared to higher altitude sites (Fig. 3). The percentage of fine particulate matter presents a significant and negative correlation to altitude, while the percentage of coarse particulate material (>2 mm) is positively and significantly correlated to it (Fig. 3). The soil pH values range from 4.1 (acid) to 7.5 (slightly alkaline) and is not correlated to altitude (Fig. 3). Regarding the metal content of soils, the variability of the total concentration of Cu is relevant, which fluctuates between 31 and 1265 mg kg$^{-1}$ (Table 1). The total concentration of Zn also shows variation, with values ranging between 71 and 357 mg kg$^{-1}$. The soil chemical variables, total Zn concentration, and total Cu concentration present a positive and significant correlation to altitude, while the total concentration of Fe in the soil was not significantly correlated to this variable (Fig. 3).

To further analyze the altitudinal variation in soil Cu content, three groups of soil samples from three altitudinal levels of SNYL were compared (Fig. 4). A significant increase in total soil Cu content was observed with altitude ($P < 0.05$, Kruskal-Wallis test) and an increasing spatial variation in this parameter with altitude was found (Fig. 4). The lowest average concentration of total Cu (94.3 mg kg$^{-1}$) was located at the lowest altitudinal level (1700–2260 m), while the maximum average concentration (433.2 mg kg$^{-1}$) was in the upper one, finding here the highest concentrations of copper in the soil (1265 mg kg$^{-1}$); the former mean concentration is considered high since it exceeds the normal concentration of Cu described for soils worldwide ranging between 2 and 250 mg kg$^{-1}$ (Adriano, 2001).

## *SOIL CHEMICAL FACTORS RELATED TO THE VARIATION IN VEGETATION COMPOSITION IN A HIGH ANDEAN ALTITUDINAL GRADIENT*

From the 10 soil chemical factors considered in the present study (Fig. 3), 4 were selected for significantly contributing to the CCA ordination model ($P \leq 0.05$; partial Monte Carlo permutation test; Table 2). The selected variables (included in the CCA) were the total soil Cu concentration, concentrations of available P and N in the soil, and the percentage of SOM (Fig. 5). The soil chemical variables that were not included in the CCA ($P > 0.05$; partial Monte Carlo permutation test), and thus do not help explaining the variation in the composition of vegetation, are the total concentration of Zn and Fe in the soil, particulate material >2 mm and <2 μm, pH, and available K in soil.

The relationship between the variation in floristic composition and the four environmental variables included in the CCA was statistically significant (*F-ratio* = 1.579, $P = 0.001$). The CCA ordination diagram (Fig. 5) shows the distribution of the 73 sampling sites, according to the weighted average of species

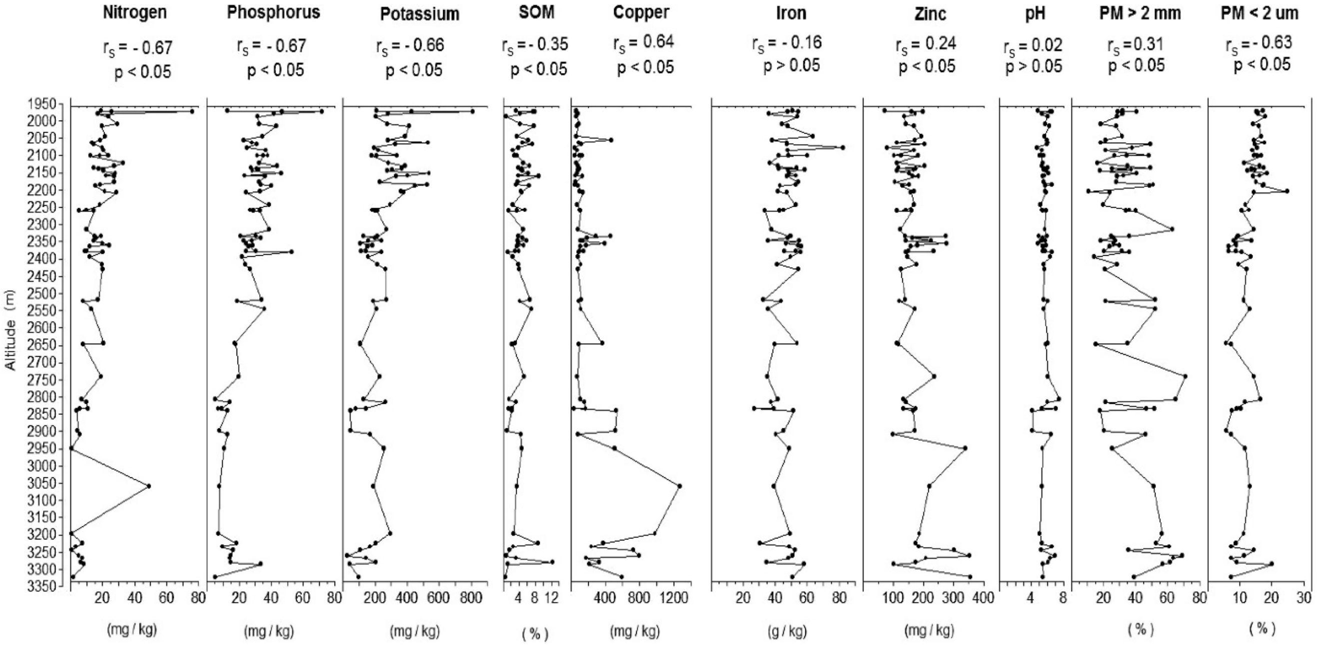

**FIGURE 3. Variation of soil chemical variables and soil size particle along an altitudinal gradient (*N* = 73 sampling sites for soils) at Yerba Loca Natural Sanctuary. Spearman correlation coefficient ($r_s$) and significance level between edaphic variables and altitude are given.**

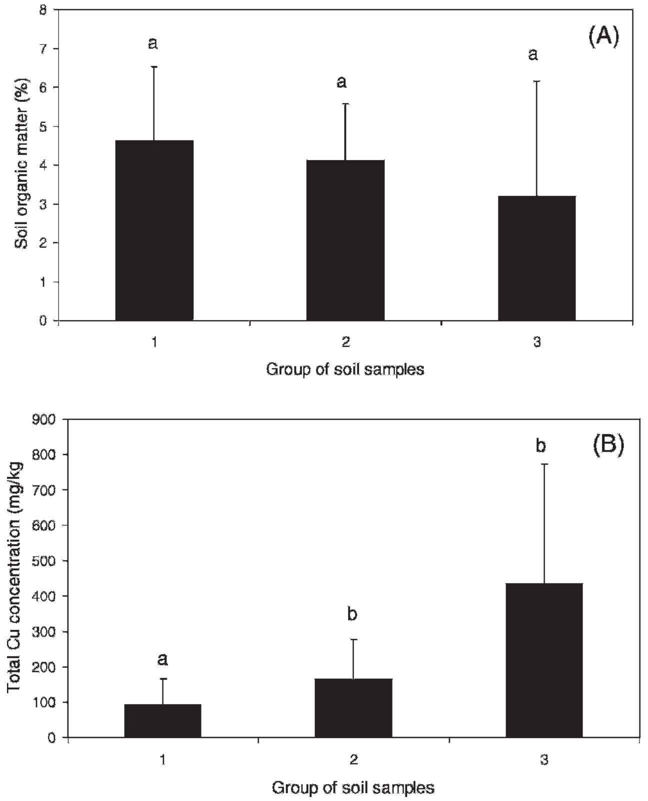

**FIGURE 4. (A) Soil organic matter (SOM) and (B) total soil copper concentrations for three altitudinal ranges at high Andean areas at Yerba Loca Natural Sanctuary. Group 1 ($N = 34$) corresponds to soils collected al lower altitude (1970 to 2260 m); group 2 ($N = 21$) corresponds to medium altitude (2310 to 2740 m); group 3 ($N = 18$) corresponds to higher altitude (2800 to 3320 m). Mean and standard deviation values are given. Different letters indicate significant differences ($P < 0.05$) according to a Kruskal-Wallis test and multiple comparisons among mean values.**

present in each of the sites, in direct relation to environmental variables determined for each site. The 59.6% of the total variation of species-environment relationship is explained by the first two axes of the ordination (Fig. 5), and the total inertia that is constrained corresponds to 8.5%. The total soil Cu concentration (canonical $r = 0.75$), the available P in soil (canonical $r = -0.70$), and the available N in soil (canonical $r = -0.63$) are the variables most correlated to the first canonical ordination axis while the SOM (canonical $r = 0.77$) is the variable most correlated to the second canonical ordination axis (Table 2), all of them explaining the distribution of sites in this area. The distribution of most of the plant sampling sites in the CCA ordination diagram (Fig. 5) indicates that there is mostly a gradual and progressive variation in species composition in the high Andean vegetation of the study site. However, there are sites that show a discontinuity in the pattern of compositional variation of vegetation, such as site 64, 65, 66, 68, and 69, which have the highest content of Cu in the soil.

All soil chemical variables included in the CCA (Fig. 5) are correlated to altitude (Fig. 3). Therefore, a partial CCA was conducted, considering altitude as a covariable, in order to determine the contribution to the model of every soil chemical factor that cannot be explained by altitude (Table 3). Results indicated that total soil Cu content explains 1.8% of total variation in plant species abundance while either available P or available N in soil explains 2.2% of the total variance. It was estimated that altitude significantly explains 2.6% of total variation in plant species abundance (*F-ratio* = 1.942, $P = 0.01$) when all selected chemical factors were used as covariables in the model. When altitude is considered as a covariable in the CCA ordination model that includes the four significant soil chemical factors, constrained inertia is only reduced in 6.4% and significance of the model remains (*F-ratio* = 1.498, $P = 0.02$). This result suggests that the effect of selected soil chemical factors (total Cu, available P and N, and SOM) on plant species composition would be independent of altitude.

### *HIGH ANDEAN PLANTS MAINLY DISTRIBUTED ON SOILS WITH HIGH COPPER CONTENTS*

Plant species present at the 73 sampling sites and based on the four selected soil chemical variables (Fig. 5) are displayed in the ordination diagram in Figure 6. In this diagram, the orthogonal projection of the plant species (triangles) on an environmental vector indicates approximately the relative value on a weighted average for each species regarding the vector (ter Braak, 1986). According to the above, the plant species *Armeria maritima* has the highest weighted average regarding the total soil Cu content, suggesting that its optimal distribution or greater coverage (%) is found in sites with the largest Cu content of soil. The vascular species *Caiophora coronata*, *Trisetum lasiolepis*, and *Montiopsis potentilloides* come secondly. These species, except *Trisetum lasiolepis*, were found only at sites where soils had high levels of Cu.

Regarding the variables available N and P, the plant species that are found mainly at sites where soils have the highest contents of these macronutrients are *Marrubium vulgare*, *Eccremocarpus scaber*, *Colletia hystrix*, *Phacelia cumingii*, and *Nicotiana acuminata* (Fig. 6). Furthermore, these plants have low weighted averages regarding the soil Cu content, indicating that they have a higher dominance in habitats where soils have lower concentrations of Cu.

Figure 7 shows the contents of Cu (average concentration) in the shoots of 19 high-alpine plant species that were found in soils with high Cu content (Table 4). Aerial tissues of these plants showed average concentrations of Cu exceeding the normal value of the metal described for plant tissues, which ranges between 5 and 20 mg $kg^{-1}$ (Fernandes and Henriques, 1991; Adriano, 2001). Plant species with the largest weighted averages of total soil Cu (Fig. 6), *Armeria maritima*, *Trisetum lasiolepis*, and *Montiopsis potentilloides*, have Cu concentrations in their aerial tissues that exceed 100 mg $kg^{-1}$ (Fig. 7), considered a high value (Brooks et al., 1985; Reeves and Baker, 2000). However, *Caiophora coronata* does not have a concentration of Cu in the aerial tissue considered high, despite having been collected at the site with 1265 mg of Cu per kilogram of soil. In addition to the high Andean plants already mentioned, there are other plant species with high contents of Cu in their shoots, such as *Calandrinia caespitosa*, *Azorella madrepora*, *Cerastium arvense*, and *Draba gilliesii* (Fig. 7). The content of Cu in their aerial tissues shows the presence of high levels of this element in soils.

## Discussion

The present study demonstrates that there are important soil chemical gradients in high Andean soils which seem to have an influence on vegetation and floristic composition, irrespective of altitude. Especially interesting are the gradients on available nitrogen and phosphorous, soil organic matter, and total copper content in soils. Specifically, the Canonical Correspondence

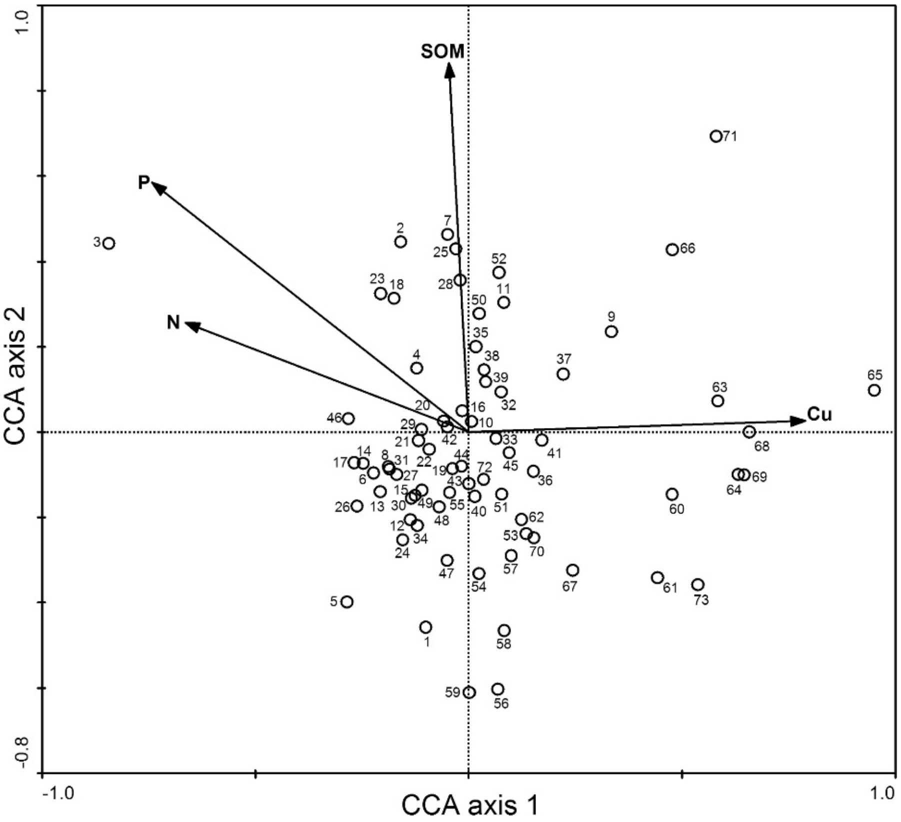

**FIGURE 5. Canonical ordination diagram illustrating the distribution of sampling sites for vegetation (circles; $N = 73$) and soil chemical variables (arrows, $N = 4$). The first two axes explain 59.6% of total variance of the species-environment relationship. Percentage of total inertia that is constrained is 8.5. Numbers of sampling sites follow the altitudinal gradient.**

Analysis showed that these four chemical properties of the soil explain 59.6% of total variance of species-environment relationship at the YLNS (Fig. 5), independently of the altitudinal range covered in the study site (1970 to 3330 m). It is also interesting to note that soil acidity (calcareous versus siliceous soils), one of the main factors to explain soil-plant relationships in alpine environments of Europe and North America, as well as in the Arctic (e.g. Lunde, 1962; Knapik et al., 1973; Jarvis, 1974; Gensac, 1990; Gough et al., 2000; Schmidtlein and Ewald, 2003; Darmody et al., 2004; Arnesen et al., 2007), seems not to be a relevant soil factor explaining alpine soil/plant relationships in high Andean areas of central Chile, at least at the study site.

It is well known that variations in the availability of the macronutrients N and P in soils are associated with changes in the composition of plant communities (Güsewell, 2004; Wijesinghe et al., 2005), as plant species have different nutrient requirements that determine their distribution (Tilman, 1982, 1984, 1987; Wenk and Dawson, 2007). Specifically, it has been proved that spatial variation about availability of P and N in the soil explains the floristic variation in high-mountain environments (Kirkpatrick and Bridle, 1998; Cavieres et al., 2000; Arnesen et al., 2007) as well as variations in species-specific abundance and diversity of alpine plant communities (Arnesen et al., 2007). Regarding the nitrogen content of the soil, Cavieres et al. (2000) suggested that this variable is related to the delimitation of the altitudinal vegetation belts in the Andes of central Chile, confirming the influence of N content of the soil on the spatial distribution of high Andean plants. On the other hand, Arnesen et al. (2007) suggested that bedrock-derived P in the soil influences the vegetation and floristic composition in alpine ridges from Troms, north Norway, through direct gradient analysis. Fertilization experiments have also been conducted in high mountain environments and have made possible to establish that the availability of N and P affects the specific abundance and diversity of plant communities (Theodose and Bowman, 1997; Heer and Körner, 2002).

**TABLE 2**

**Correlation coefficients among the first two axes of a Canonical Correspondence Analysis and four selected soil chemical variables. Significance *P*-value and *F*-ratio of a partial Monte Carlo permutation test (forward selection) are given.**

| Environmental variable | Correlation coefficients Axis 1 | Axis 2 | *F*-ratio (*P*-value) |
|---|---|---|---|
| Available phosphorus | −0.70 | 0.52 | 1.83 (0.001) |
| Total Cu | 0.75 | 0.02 | 1.51 (0.024) |
| Available nitrogen | −0.63 | 0.23 | 1.52 (0.017) |
| Soil organic matter | −0.04 | 0.77 | 1.40 (0.027) |

In general, deficiency or low availability of N and P in soils of high altitude in mountainous areas can be a limiting factor for alpine vegetation (Grubb, 1977; Aiba and Kitayama, 1999; Arnesen et al., 2007). The high Andean area of the YLNS is not an exception to this phenomenon, as the availability of N and P significantly decreases with altitude (Fig. 3). In the study site, available N and P show a significant and positive correlation to SOM, thus stressing the importance of dead litter as a source of these nutrients in high Andean systems. Soil organic matter does not show a marked altitudinal reduction in the study site, but decreased decomposition/mineralization rates under alpine climate may explain reduced availability of N and P in high Andean soils. Even though the other available source of P in alpine systems may be the weathering of apatite-rich igneous and metamorphic rocks (Holtan et al., 1988), the extent of and relevance of this phenomenon remains unclear (Arnesen et al., 2007), as weathering of rocks also depends on climate (Schaetzl and Anderson, 2005). Regarding SOM, its role on soil structure and moisture retention capability is well known (Schaetzl and Anderson, 2005); these effects may account for its relevance for determining plant species

TABLE 3

**Variance of the plant species data explained by the soil chemical variables total copper concentration, available N and P, percentage of soil organic matter (SOM) in a Canonical Ordination Model where altitude is considered as a covariable of the soil chemical factors. Percentage of total variance of plants species data only explained by altitude is also given (second column).**

| Soil variables | Percentage of total variance* explained by soil variable | Percentage of total variance* explained by altitude | Percentage of total variance* explained by soil variable and altitude | Percentage of total variance* that is not explained by environmental variables |
|---|---|---|---|---|
| Total Cu | 1.8 | 2.5 | 0.7 | 95.0 |
| Available P | 2.2 | 2.8 | 0.3 | 94.7 |
| Available N | 2.2 | 3.0 | 0.2 | 94.6 |
| Soil organic matter | 1.9 | 3.1 | 0.1 | 94.9 |

* Total inertia = 25.22.

distribution and abundance in high Andean systems, besides its role as a source of soil nutrients to plants.

Influence of total metal contents on vegetation and floristic composition in high-mountain environments has been less investigated (e.g. Petersen and Philipp, 1986). Results of the present study indicate that the total Cu content is one of the soil chemical properties with the greatest influence on the compositional variation of the high Andean vegetation, at least at the YLNS. This property is related to a discontinuity in the pattern of variation in plant species composition, which is mostly continuous throughout the altitudinal gradient in the study site, as has been demonstrated in other altitudinal gradients in mountainous areas (Whittaker, 1956; Auerbach and Shmida, 1993). The discontinuity in the vegetation pattern is generated by those sites whose soils have the highest total soil Cu concentrations within the study site, exceeding 250 mg kg$^{-1}$. Abrupt changes or discontinuities in the pattern of variation of plant species have been identified in metalliferous areas of natural origin in which the floristic composition of sites with normal concentrations of Cu contrast with the composition of the sites that have excessive Cu, dominated by metal-tolerant plants (Drew and Reilly, 1972; Malaisse et al., 1979; Babalonas et al., 1997).

Copper is an essential micronutrient for plants (Salisbury and Ross, 1992). However, stress from excess of Cu in the soil is a powerful inhibitor of vegetative growth and can cause mortality in those populations of plant species which have no resistance mechanisms (Baker, 1987; Fernandes and Henriques, 1991), limiting their distribution to metalliferous soils, such as those found at higher elevations in the study site (Fig. 3). Then, it is expected that populations of plant species with the largest weighted averages regarding total soil Cu content, such as *Armeria maritima*, have developed mechanisms of resistance to the presence of high levels of copper in soils, for example avoidance or tolerance (Baker, 1987; Orcutt and Nilsen, 2000).

The high content of Cu in the shoots of the plant species that have optimal distribution in soils with high contents of total Cu, such as *Armeria maritima*, *Trisetum lasiolepis*, and *Montiopsis potentilloides*, suggest that those species and/or ecotypes may have tolerance to Cu, accumulating this metal in their tissues (Ginocchio, 1997; Baker et al., 2000). It is worth mentioning that none of these species can be considered as a Cu hyperaccumulator since the concentrations in their shoots are well below the criteria of copper hyperaccumulation (>1000 mg kg$^{-1}$; Reeves and Baker, 2000). Those plant species that are distributed in soils with high Cu contents and have low contents of this element in their shoots, such as *Caiophora coronata*, could prevent the translocation of Cu from the root to the shoot and form species or exclusive tolerant ecotypes (Baker et al., 2000; Orcutt and Nilsen, 2000), or represent

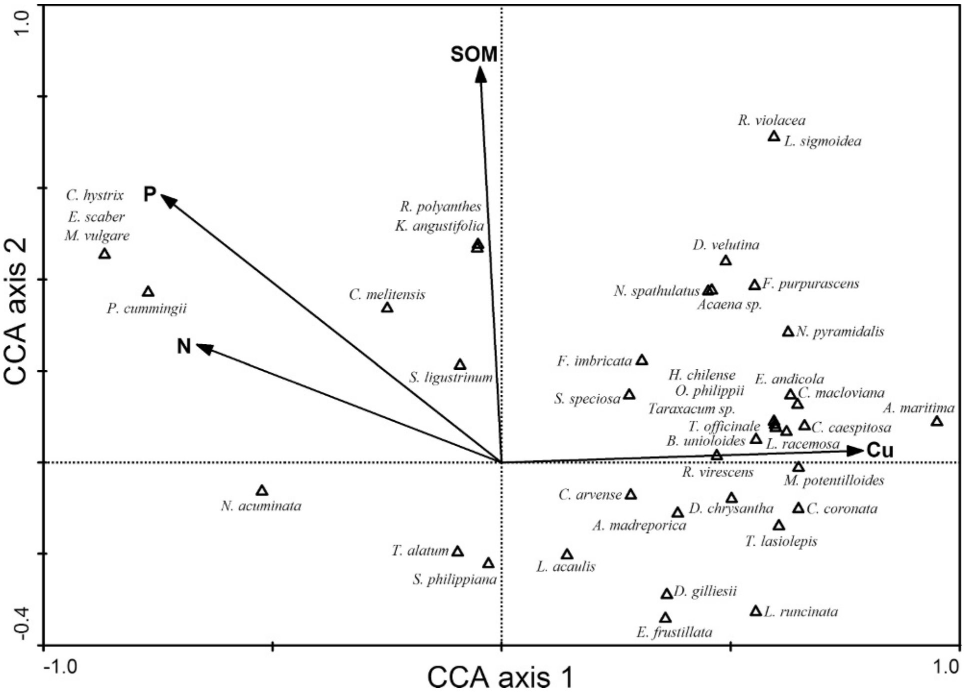

**FIGURE 6. Canonical ordination diagram illustrating the distribution of high Andean vascular plant species (triangles; $N = 48$) and soil chemical variables (arrows, $N = 4$). Distribution of 41 plant species (triangles) is shown according to their weighted average values for soil chemical factors. Only the species well related to the ordination axes are included (6% of minimal adjust).**

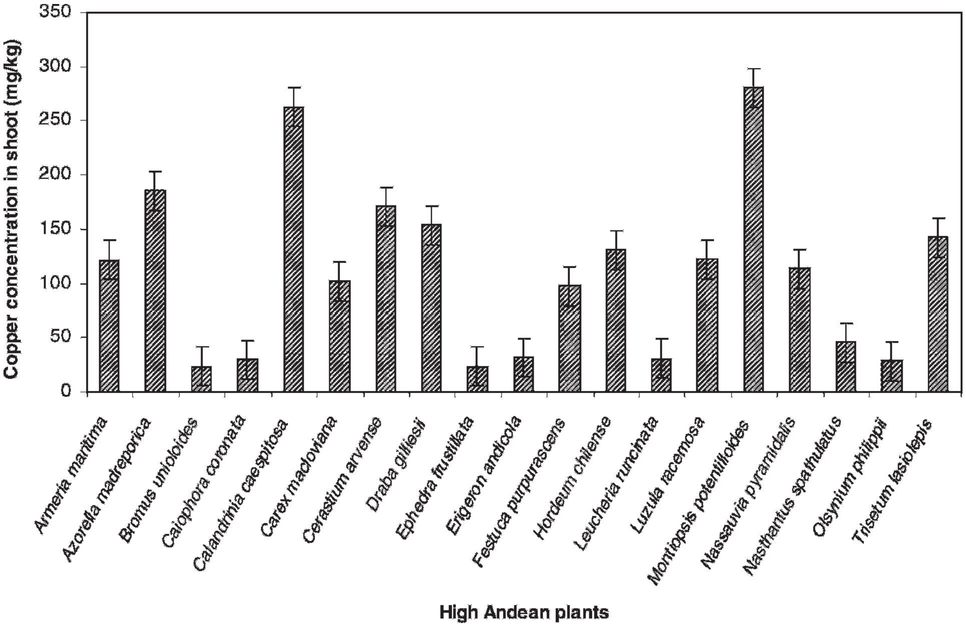

**FIGURE 7.** **Mean copper concentration in shoots of 19 vascular plant species growing on soils with elevated copper concentrations at Yerba Loca Natural Sanctuary. Concentrations are expressed in mg kg$^{-1}$ (dry weight). Typical error is given.**

evader species that grow in microsites where the metal is not bioavailable. There is evidence that one of the plant species with the highest weighted Cu average content of the soil, *Armeria maritima*, has tolerance to the presence of high concentrations of zinc and lead in soils, and it is also described as a local metallophyte (Antonovics et al., 1971; Simon, 1978), which means it has been found only in metalliferous soils (Baker, 1987). This species has been used as an indicator of the existence of high levels of Cu in soils (Antonovics et al., 1971; Orcutt and Nilsen, 2000). Furthermore, the subspecies *Armeria maritima* ssp. *halleri* is also described as metalliferous and is distributed in places where soils have high concentrations of copper and lead (Dahmani-Muller et al., 2000; Reeves and Baker, 2000). According to the above and based on the distribution of populations of *Armeria maritima* in the study site, this species could be indicative of soils with high contents of Cu in alpine areas of the Andes.

The effects of excess metal in plants, and consequently the development of tolerance, depends on the metal bioavailability in soils (Eijsackers, 1987), which is determined by the influence of certain physicochemical soil characteristics such as pH and organic matter content (Adriano, 2001). High concentrations of total copper in the soil within the study site would be available to alpine plants distributed in these sites since most have incorporated high levels of Cu in the aerial tissues (greater than 100 mg kg$^{-1}$), something considered toxic for most plants (Fernandes and Henriques, 1991; Orcutt and Nilsen, 2000; Adriano, 2001). However, the ability of copper tolerance of these high-alpine plants must be verified through standard dose-response laboratory testing.

**TABLE 4**

**Total soil copper concentration of seven sampling sites selected for collection of aerial plant tissues at high-alpine areas of the Yerba Loca Natural Sanctuary. Number of sampling sites follows codes of canonical ordination diagrams of CCAs.**

| Sampling plots of vegetal tissue (shoots) | Soil copper concentration (mg kg$^{-1}$) |
|---|---|
| 60 | 530 |
| 61 | 517 |
| 63 | 508 |
| 64 | 1265 |
| 65 | 979 |
| 66 | 372 |
| Additional plot | 652 |

Plant species richness and floristic variation are very high at YLNS, with a total described number of vascular plant species of 500 (Arroyo et al., 2002), even tough the site corresponds to a rather small and narrow glacial valley in the high Andes of central Chile. Indeed, Arroyo et al. (2002) estimated that the YLNS has 28% more plant species than expected from the surface area, thus being an extraordinary site in terms of plant diversity. The marked environmental variability present at the site, particularly in terms of soil chemical factors such as available N and P, SOM, and total Cu content, is important to explain the very high plant diversity of the site, as confirmed in the present study. However, only part of the great floristic variation found on the site is explained by the four soil chemical factors, besides altitude. Therefore, other environmental factors, such as topography, exposition, snow accumulation patterns, soil humidity, and microclimates (Kitayama, 1992; Aiba and Kitayama, 1999; Cavieres and Arroyo, 1999), among others—besides biotic interactions such as competition and facilitation—may explain this phenomenon. Indeed, most of these factors have been closely associated to the compositional variation of plant communities in high mountain ecosystems (e.g. Körner, 1995; Wiser et al., 1996; Ferreyra et al., 1998; Cavieres et al., 2000; Boyce et al., 2005). Although they were not considered in the present study, they could also explain the floristic variation associated with the altitudinal gradient in the study site.

## Conclusions

Despite the influence of the altitudinal gradient on the pattern of compositional variation of the high Andean vegetation, gradients of the variables P and N availability, soil organic matter, and total concentration of Cu account for part of the floristic variation, at least at the YLNS, showing that the chemical properties of the soil have an impact on the spatial distribution of alpine plants in the Andes of central Chile. It is worth mentioning that, within the study site, there is a great variation in the content of available macronutrients (P, N), soil organic matter, and total Cu in soils. The existence and permanence of heterogeneous spatial patterns of those soil resources could create long-term opportunities for niche differentiation and coexistence of plant species (Tilman, 1982; Fitter et al., 2000; Sommer and Worm, 2002), which could have important consequences on the pattern of spatial variation and on plant species richness of high Andean vegetation (Wilson, 2000).

In particular, soils with high contents of total Cu seem to alter the distribution of high Andean plant species, at least on the study site, as it is inferred from a discontinuity in the pattern of compositional variation of the vegetation at YLNS associated with anomalous Cu concentration in soils. Only plant species that have developed tolerance to Cu would develop in these soils. However, it must be determined experimentally if there are high Andean plants that have tolerance to Cu.

## Acknowledgments

The study was funded by FONDECYT 1050138 grant to R. Ginocchio. We would like to thank the support of Dr. Patricio H. Rodríguez (Centro de Investigación Minera y Metalúrgica, CIMM), the rangers at Yerba Loca Natural Sanctuary (YLNS), particularly Mr. Julio Bruna, the Director of the Centro Cordillera, Municipalidad de Lo Barnechea; Mr. Pablo Villoch; and Doctors Patricio Moreno and Lohengrin Cavieres for their comments on the manuscript.

## References Cited

Adriano, D. C., 2001: *Trace Elements in Terrestrial Environments. Biogeochemistry, Bioavailability and Risks of Metals.* Second edition. New York: Springer, 867 pp.

Aiba, S., and Kitayama, K., 1999: Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology*, 140: 139–157.

Antonovics, J., Bradshaw, A. D., and Turner, R. G., 1971: Heavy metal tolerance in plants. *Advances in Ecological Research*, 7: 1–85.

Arnesen, G., Beck, P. S. A., and Engelskjon, T., 2007: Soil acidity, content of carbonates, and available phosphorous are the soil factors best correlated with alpine vegetation: evidence from Troms, north Norway. *Arctic, Antarctic, and Alpine Research*, 39: 189–199.

Arroyo, M. T. K., and Uslar, P., 1993: Breeding systems in a temperate mediterranean-type climate montane sclerophyllous forest in central Chile. *Botanical Journal of the Linnean Society*, 111: 83–102.

Arroyo, M. T. K., Armesto, J. J., and Primack, R. B., 1985: Community studies in pollination ecology in the high temperate Andes of central Chile. II. Effect of temperature on visitation rates and pollination possibilities. *Plant Systematics and Evolution*, 149: 187–203.

Arroyo, M. T. K., Marticorena, C., Matthei, O., Muñoz, M., and Pliscoff, P., 2002: Analysis of the contribution and efficiency of the Santuario de la Naturaleza Yerba Loca, 33°S, in protecting the regional vascular plant flora (Metropolitan and Fifth regions of Chile). *Revista Chilena de Historia Natural*, 75: 767–792.

Arroyo, M. T. K., Cavieres, L. A., Peñaloza, A., and Arroyo-Kalin, M. A., 2003: Positive association between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology*, 169: 121–129.

Auerbach, M., and Shmida, A. V. I., 1993: Vegetation change along an altitudinal gradient on Mt Hermon, Israel—No evidence for discrete communities. *Journal of Ecology*, 81: 25–33.

Babalonas, D., Mamolos, A. P., and Konstantinou, M., 1997: Spatial variation in a grassland on soil rich in heavy metals. *Journal of Vegetation Science*, 8: 601–604.

Baddeley, J. A., Woodin, S. J., and Alexander, I. J., 1994: Effects of increased nitrogen and phosphorous availability on the photosynthesis and nutrient relations of 3 arctic dwarf shrubs from Svalbard. *Functional Ecology*, 8: 676–685.

Baker, A. J. M., 1987: Metal tolerance. *The New Phytologist*, 106: 93–111.

Baker, A. J. M., McGrath, S. P., Reeves, R. D., and Smith, J. A. C., 2000: Metal hyperaccumulator plants: a review of the ecology and physiology of a biological resource for phytoremediation of metal-polluted soils. *In* Terry, N., and Bañuelos, G. S. (eds.), *Phytoremediation of Contaminated Soil and Water*. Boca Raton, Florida: Lewis Publishers, 85–107.

Barceló, J., 1984: *Geología del Santuario de la Naturaleza Yerba Loca, Región Metropolitana*. Santiago, Chile: CONAF, 38 pp.

Bassi, H. G. L., 1982: Geología y potencialidad minera del distrito cuprífero Bronces–Yerba Loca, pcia. de Santiago, Chile. *Actas Quinto Congreso Latinoamericano de Geología*, 3: 111–145.

Billings, W. D., 1974: Adaptations and origins of alpine plants. *Arctic and Alpine Research*, 6: 129–142.

Bliss, L. C., 1971: Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics*, 2: 405–438.

Bliss, L. C., 1985: Alpine. *In* Billings, W. D., and Mooney, H. A. (eds.), *Physiological Ecology of North American Plant Terrestrial Communities*. New York: Chapman and Hall, 41–65.

Bowman, W. D., Theodose, T. A., Schardt, J. C., and Conant, R. T., 1993: Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology*, 74: 2085–2097.

Boyce, R. L., Clark, R., and Dawson, C., 2005: Factors determining alpine species distribution on Goliath Peak, Front Range, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research*, 37: 88–96.

Brooks, R. R., Malaisse, F., and Empain, A., 1985: *The Heavy Metal–Tolerant Flora of South-Central Africa: a Multidisciplinary Approach*. Rotterdam: A. A. Balkema, 352 pp.

Camus, F., 2003: *Geología de los Sistemas Porfíricos en los Andes de Chile*. Santiago, Chile: Servicio Nacional de Geología y Minería, 267 pp.

Cavieres, L. A., and Arroyo, M. T. K., 1999: Tasa de enfriamiento adiabático del aire en el Valle del Río Molina, Provincia de Santiago, Chile central (33°). *Revista Geográfica de Chile Terra Australis*, 44: 79–86.

Cavieres, L. A., Peñaloza, A., and Arroyo, M. T. K., 2000: Altitudinal vegetation belts in the high-Andes of central Chile (33°S). *Revista Chilena de Historia Natural*, 73: 331–344.

Cavieres, L. A., Badano, E. I., Sierra-Almeida, A., and Molina-Montenegro, M., 2007: Microclimatic modifications of cushion plants and their consequences for seedlings survival of native and non-native plants in the high-Andes of central Chile. *Arctic, Antarctic, and Alpine Research*, 39: 229–236.

Cavieres, L. A., Quiroz, C. L., and Molina-Montenegro, M. A., 2008: Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high-Andes of central Chile: are there differences between nurses? *Functional Ecology*, 22: 148–156.

Chambers, J. C., 1997: Restoring alpine ecosystems in the western United States: environmental constraints, disturbance characteristics, and restoration success. *In* Urbanska, K. M., Webb, N. R., and Edwards, P. J. (eds.), *Restoration Ecology and Sustainable Development*. Cambridge: Cambridge University Press, 161–187.

Dahmani-Muller, H., Van Oort, F., Gélie, B., and Balabane, M., 2000: Strategies of heavy metal uptake by three plant species growing near a metal smelter. *Environmental Pollution*, 109: 231–238.

Darmody, R. G., Thorn, C. E., Schlyter, P., and Dixon, J. C., 2004: Relationship of vegetation distribution to soil properties in Kärkevagge, Swedish Lapland. *Arctic, Antarctic, and Alpine Research*, 36: 21–32.

Deckart, K., Clark, A. H., Aguilar, C., Vargas, R., Serrano, L., and Ortega, H., 2003: Geochronology of the Río Blanco porphyry Cu-Mo deposit, principal Cordillera, central Chile (33°08′S). *10° Congreso Geológico Chileno, Concepción*. CD-ROM, 1 p.

Drew, A., and Reilly, C., 1972: Observations on copper tolerance in the vegetation of a Zambian copper clearing . *The Journal of Ecology*, 60: 439–444.

Eijsackers, H., 1987: The impact of heavy metals on terrestrial ecosystems: biological adaptation through behavioral and physiological avoidance. *In* Ravera, O. (ed.), *Ecological Assessment of Environmental Degradation, Pollution and Recovery*. Amsterdam: Elsevier Scientific Publishers, 245–259.

Ernst, W. H., 1990: Mine vegetation in Europe. *In* Shaw, A. J. (ed.), *Heavy Metal Tolerance in Plants: Evolutionary Aspects*. Boca Raton, Florida: CRC Press, 21–37.

Fernandes, J. C., and Henriques, F. S., 1991: Biochemical, physiological, and structural effects of excess copper in plants. *Botanical Review*, 57: 246–273.

Ferreyra, M., Cingolani, A., Ezcurra, C., and Bran, D., 1998: High-Andean vegetation and environmental gradients in northwestern Patagonia, Argentina. *Journal of Vegetation Science*, 9: 307–316.

Fitter, A., Hodge, A., and Robinson, D., 2000: Plant response to patchy soils. *In* Hutchings, M. J., John, E. A., and Stewart, A. J. A. (eds.), *The Ecological Consequences of Environmental Heterogeneity*. Oxford: Blackwell Science, 71–90.

Gensac, P., 1990: Plant and soil groups in the alpine grasslands of the Vanoise Massif, French Alps. *Arctic and Alpine Research*, 22: 195–201.

Ginocchio, R., 1997: Aplicabilidad de los modelos de distribución espacio-temporales de la vegetación en ecosistemas terrestres sujetos a procesos de contaminación. PhD thesis. Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, 209 pp.

Gough, L., Shaver, G. R., Carol, J., Royer, D. L., and Laundre, J. A., 2000: Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. *Journal of Ecology*, 88: 54–66.

Grubb, P. J., 1977: Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Review of Ecology and Systematics*, 8: 83–107.

Güsewell, S., 2004: N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, 164: 243–266.

Heer, C., and Körner, C., 2002: High elevation pioneer plants are sensitive to mineral nutrient addition. *Basic and Applied Ecology*, 3: 39–47.

Hinojosa, L. F., 1996: Estudio paleobotánico de dos tafofloras en la precordillera de Chile central (La Dehesa) e inferencias sobre la vegetación y el clima Terciario de Austrosudamérica. Master thesis. Facultad de Ciencias, Universidad de Chile, 156 pp.

Hinojosa, L. F., and Villagrán, C., 1997: Historia de los bosques del sur de Sudamérica, I: antecedentes paleobotánicos, geológicos y climáticos del Terciario del cono sur de América. *Revista Chilena de Historia Natural*, 70: 225–239.

Holtan, H., Kamp-Nielsen, L., and Stuanes, A. O., 1988: Phosphorous in soil, water, and sediment—An overview. *Hydrobiologia*, 170: 19–34.

Jarvis, S. C., 1974: Soil factors affecting the distribution of plant communities on the cliffs of Craig Breidden, Montgomeryshire. *The Journal of Ecology*, 62: 721–733.

Kent, M., and Coker, P., 1992: *Vegetation Description and Analysis: a Practical Approach*. Chichester: John Wiley and Sons, 363 pp.

Kirkpatrick, J. B., and Bridle, K. L., 1998: Environmental relationships of floristic variation in the alpine vegetation of southeast Australia. *Journal of Vegetation Science*, 9: 251–260.

Kitayama, K., 1992: An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio*, 102: 149–171.

Knapik, L., Scotter, G., and Pettapiece, W., 1973: Alpine soil and plant community relationships of the Sunshine area, Banff National Park. *Arctic and Alpine Research*, 5: A161–A170.

Körner, C., 1995: Alpine plant diversity: a global survey and functional interpretations. *In* Chapin, F. S., and Körner, C. (eds.), *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*. New York: Springer-Verlag, 45–62.

Körner, C., 2003: *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems.* Second edition. Berlin: Springer, 344 pp.

Legendre, P., and Legendre, L., 1998: *Numerical Ecology.* Second English edition. Developments in Environmental Modelling, 20. Amsterdam: Elsevier, 853 pp.

Lepš, J., and Šmilauer, P., 2003: *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge: Cambridge University Press, 269 pp.

Lunde, T., 1962: An investigation into the pH-amplitude of some mountain plants in the county of Troms. *Acta Borealia Ser. A*, 20: 103 pp.

Luteyn, J. L., and Churchill, S. P., 2000: Vegetation of the tropical Andes. *In* Lentz, D. L. (ed.), *An Imperfect Balance: Landscape Transformations in the Precolumbian Americas*. New York: Columbia University Press, 281–310.

Maksaev, V., Munizaga, F., McWilliams, M., Fanning, M., Mathur, R., Ruíz, J., and Zentilli, M., 2004: New chronology for El Teniente, Chilean Andes, from U/Pb, $^{40}$Ar/$^{39}$Ar, Re/Os and fission-track dating: implications for the evolution of a supergiant porphyry Cu-Mo deposit. *In* Sillitoe, R. H., Perelló, J., and Vidal, C. E. (eds.), *Andean Metallogeny: New Discoveries, Concepts Update*. Society of Economic Geologists, Special Publication, 11: 15–54.

Malaisse, F., Gregoire, J., Brooks, R., Morrison, R., and Reeves, R., 1978: *Aeolanthus biformifolius* De Wild.: a hyperaccumulator of copper from Zaïre. *Science, New Series*, 199: 887–888.

Malaisse, F., Gregoire, J., Morrison, R. S., Brooks, R. R., and Reeves, R. D., 1979: Copper and cobalt in vegetation of Fungurume, Shaba Province, Zaïre. *Oikos*, 33: 472–478.

Mooney, H. A., and Billings, W. D., 1965: Effects of altitude on carbohydrate content of mountain plants. *Ecology*, 46: 750–751.

Moreno, T., and Gibbons, W., 2007: *The Geology of Chile*. London: The Geological Society, 414 pp.

Orcutt, D. M., and Nilsen, E. T., 2000: *The Physiology of Plants under Stress: Soil and Biotic Factors*. New York: John Wiley and Sons, Inc., 683 pp.

Palmer, M. W., 1993: Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology*, 74: 2215–2230.

Pérez, F., Arroyo, M. T. K., Medel, R., and Hershkovitz, M. A., 2006: Ancestral reconstruction of flower morphology and pollination systems in *Schizanthus* (Solanaceae). *American Journal of Botany*, 93: 1029–1038.

Petersen, P. M., and Philipp, M., 1986: Growth and reproduction of *Viscaria alpina* on Greenland soils with high and low copper concentrations. *Arctic and Alpine Research*, 18: 73–82.

Peterson, K. M., and Billings, W. D., 1982: Growth of alpine plants under controlled drought. *Arctic and Alpine Research*, 14: 189–194.

Reeves, R., and Baker, A., 2000: Metal-accumulating plants. *In* Raskin, I., and Ensley, B. D. (eds.), *Phytoremediation of Toxic Metals: Using Plants to Clean Up the Environment*. New York: John Wiley and Sons, Inc., 193–229.

Ricardi, S. M. H., Gaviria, J., and Estrada, J., 1997: La flora del superpáramo venezolano y sus relaciones fitogeográficas a lo largo de los Andes. *Plántula*, 1: 171–187.

Rozzi, R., Molina, J. D., and Miranda, P., 1989: Microclima y períodos de floración en laderas de exposición ecuatorial y polar en los Andes de Chile central. *Revista Chilena de Historia Natural*, 62: 75–84.

Sadzawka, A., Carrasco, M. A., Grez, R., Mora, M. L., Flores, H., and Reaman, A., 2006: *Métodos de análisis de suelos recomendados para los suelos de Chile*. Santiago de Chile: Serie Actas INIA,34: 164 pp.

Sakai, A., and Larcher, W., 1987: *Frost Survival of Plants: Responses and Adaptation to Freezing Stress*. Berlin: Springer-Verlag, 321 pp.

Salisbury, F. B., and Ross, C. W., 1992: *Plant Physiology.* Fourth edition. Belmont, California: Wadsworth Publishing Company, 682 pp.

Santibáñez, F., and Uribe, J. M., 1990: *Atlas Agroclimático de Chile: Regiones V y Metropolitana*. Santiago de Chile: Facultad de Ciencias Agrarias y Forestales, Universidad de Chile, 66 pp.

Schaetzl, R. J., and Anderson, S., 2005: *Soils: Genesis and Geomorphology*. Cambridge: Cambridge University Press, 817 pp.

Schmidtlein, S., and Ewald, J., 2003: Landscape patterns of indicator plants for soil acidity in the Bavarian Alps. *Journal of Biogeography*, 30: 1493–1503.

Seastedt, T. R., and Vaccaro, L., 2001: Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research*, 33: 100–106.

Simon, E., 1978: Heavy metals in soils, vegetation development and heavy metal tolerance in plant populations from metalliferous areas. *New Phytologist*, 81: 175–188.

Skewes, M. A., and Stern, C. R., 1994: Tectonic trigger for the formation of late Miocene Cu-rich breccia pipes in the Andes of central Chile. *Geology*, 22: 551–554.

Smith, J. M. B., and Cleef, A. M., 1988: Composition and origins of the world's tropic-alpine floras. *Journal of Biogeography*, 15: 631–645.

Sommer, U., and Worm, B., 2002: *Competition and Coexistence.* Ecological Studies, 161. Berlin: Springer, 221 pp.

Squeo, F., Veit, H., Arancio, G., Gutiérrez, J. R., Arroyo, M. T. K., and Olivares, N., 1993: Spatial heterogeneity of high mountains vegetation in the Andean desert zone of Chile. *Mountain Research and Development*, 13: 1–10.

Squeo, F. A., Rada, F., García, C., Ponce, M., Rojas, A., and Azócar, A., 1996: Cold resistance mechanisms in high desert Andean plants. *Oecologia*, 105: 552–555.

Squeo, F. A., Cavieres, L. A., Arancio, G., Novoa, J. E., Matthei, O., Marticorena, C., Rodríguez, R., Arroyo, M. T. K., and Muñoz, M., 1998: Biodiversidad de la flora vascular en la Región de Antofagasta, Chile. *Revista Chilena de Historia Natural*, 71: 571–591.

Squeo, F. A., Warner, G. G., Aravena, R., and Espinoza, D., 2006: Bofedales: high altitude peatlands of the central Andes. *Revista Chilena de Historia Natural*, 79: 245–255.

StatSoft, Inc., 2008: Statistica. Data analysis software system (http://www.statsoft.com).

Teillier, S., 1998: Flora y vegetación alto-andina del área de Collahuasi, salar de Coposa, Andes del norte de Chile. *Revista Chilena de Historia Natural*, 71: 313–329.

ter Braak, C. J. F., 1986: Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67: 1167–1179.

ter Braak, C. J. F., and Šmilauer, P., 2002: *Canoco Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Ithaca, New York: Microcomputer Power, 500 pp.

Theodose, T. A., and Bowman, W. D., 1997: Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology*, 78: 1861–1872.

Tilman, D., 1982: *Resource Competition and Community Structure*. Princeton: Princeton University Press, 296 pp.

Tilman, D., 1984: Plant dominance along an experimental nutrient gradient. *Ecology*, 65: 1445–1453.

Tilman, D., 1987: Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, 57: 190–214.

USDA, 1996: *Soil Survey Laboratory Methods Manual*. Washington, D.C.: U.S. Department of Agriculture, Soil Survey Investigations Report 42, Version 3.0.

USDA, 2004: *Soil Survey Laboratory Methods Manual*. Washington, D.C.: U.S. Department of Agriculture, National Soil Survey Center, Natural Resources Conservation Service, Soil Survey Investigations Report 42, version 4.0.

U.S. EPA, 1995: Test methods for evaluating solid waste: physical/chemical methods—Physical/chemical methods, Method SW-846. Third edition. Springfield, Virginia: Department of Commerce, National technical Information Service.

Weigend, M., 2002: Observations on the biogeography of the Amotape-Huancabamba zone in northern Peru. *Botanical Review*, 68: 38–54.

Wenk, E., and Dawson, T., 2007: Interspecific differences in seed germination, establishment, and early growth in relation to preferred soil type in an alpine community. *Arctic, Antarctic, and Alpine Research*, 39: 165–176.

Whittaker, R. H., 1956: Vegetation of the Great Smoky Mountains. *Ecological Monographs*, 26: 2–80.

Wijesinghe, D. K., John, E. A., and Hutchings, M. J., 2005: Does pattern of soil resource heterogeneity determine plant community structure? An experimental investigation. *Journal of Ecology*, 93: 99–112.

Wilson, S. D., 2000: Heterogeneity, diversity and scale in plant communities. *In* Hutchings, M. J., John, E. A., and Stewart, A. J. A. (eds.), *The Ecological Consequences of Environmental Heterogeneity*. Oxford: Blackwell Science, 53–69.

Wiser, S. K., Peet, R., and White, P. S., 1996: High-elevation rock outcrop vegetation of the southern Appalachian Mountains. *Journal of Vegetation Science*, 7: 703–722.

Young, K. R., and Reynel, C., 1997: Huancabamba region, Peru and Ecuador. *In* Davies, S. D., Heywood, V. H., Herrera-MacBride, O., Villalobos, J., and Hamilton, A. C. (eds.), *Centers of Plant Diversity: a Guide and Strategy for Their Conservation. Volume 3. The Americas*. Cambridge: IUCN Publications Unit, 465–469.

Young, D. R., Ulloa, C. U., Leteyn, J. L., and Knapp, S., 2002: Plant evolution and endemism in Andean South America: an introduction. *Botanical Review*, 68: 4–21.

Zar, J. H., 1984: *Biostatistical Analysis.* Second edition. Englewood Cliffs, New Jersey: Prentice-Hall, 718 pp.

*MS accepted January 2010*