

Altitudinal vegetation belts in the high-Andes of central Chile (33°S)

Pisos altitudinales de vegetación en los Andes de Chile central (33°S)

LOHENGRIN A. CAVIERES¹, ALEJANDRO PEÑALOZA² & MARY KALIN ARROYO²

¹ Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile, e-mail: lcaviere@udec.cl

² Departamento de Biología, Facultad de Ciencias, Universidad de Chile

ABSTRACT

The limits of alpine vegetation belts have been established mainly based on physiognomic criteria. However, a more objective approach for fixing limits of vegetation belts are methods based on species composition and relative abundance of each species. While these methods are more time consuming, they are more detailed and permit the detection of physical factors affecting the limits of vegetation belts. In this paper we: 1) describe the altitudinal changes of vegetation above timberline, 2) compare vegetation belts defined with physiognomy and two floristic methods (a qualitative one based on altitudinal changes in species composition, and a quantitative one based on changes in dominant species); and 3) detect some environmental factors responsible for the altitudinal distribution of alpine vegetation between 2100 and 3700 masl in the Andes of Santiago, central Chile (33°S). There was a complete agreement between the different methods in delimiting the subalpine belt. However, in the lower alpine belt (the cushion's belt) floristic methods subdivided it in 2-3 sub-belts. In the floristic methods, elevations 3500-3700 that formed the higher alpine belt segregated in separate ways because they have no species in common. Physiognomic descriptions lose relevant information about species distribution, especially at higher elevations. Mean annual temperature and nitrogen content of soil are the main environmental factors affecting the altitudinal limits of vegetation belts in the central Chilean Andes.

Key words: altitudinal vegetation belts, alpine vegetation, Andes, central Chile, cluster analysis.

RESUMEN

La delimitación de los pisos altitudinales de vegetación andina se ha basado principalmente en criterios fisionómicos. Sin embargo, un criterio más objetivo para la delimitación es usar métodos basados en la composición y abundancia relativa de las especies presentes. Mientras estos métodos requieren de un mayor esfuerzo de muestreo, son más detallados y permiten detectar factores físicos involucrados en la delimitación altitudinal de la vegetación. Los objetivos de este artículo son: 1) describir los cambios altitudinales de la de vegetación por sobre el límite arbóreo, 2) comparar la delimitación de los pisos de vegetación usando fisionomía y métodos florísticos (uno cualitativo basado en cambios en la composición de especies, y otro cuantitativo basado en cambios en la abundancia relativa de las especies); y 3) detectar algunos factores medioambientales responsables de los patrones de distribución altitudinal de la vegetación entre los 2.100 y 3.700 msnm en los Andes de Santiago, Chile central (33°S). Se encontró una completa concordancia entre los diferentes métodos en delimitar el piso subandino. Sin embargo, en el piso andino inferior (el piso de los cojines) los métodos florísticos lo subdividieron en 2-3 sub-pisos. Las altitudes 3.500-3.700 m que forman el piso andino superior segregaron en forma separada en los métodos florísticos ya que no tienen especies en común. En consecuencia, la descripción fisionómica pierde información relevante sobre la distribución de las especies, especialmente a mayores altitudes. La temperatura media anual y el contenido de nitrógeno del suelo fueron los principales factores medioambientales involucrados en la delimitación altitudinal de la vegetación de los Andes de Chile central.

Palabras clave: pisos altitudinales de vegetación, vegetación andina, Andes, Chile central, análisis de agrupamiento.

INTRODUCTION

In high mountains, climate change abruptly with elevation, especially above timberline (Ferreira et al. 1998). Temperature, depth of permafrost and growing season decrease with elevation,

whereas solar radiation and wind speed increase with elevation, affecting the composition and relative importance of plant species inhabiting these zones (Bliss 1971, Billings 1974). In addition to macroclimate, other environmental variables such as slope aspect, slope inclination and substrate

may affect plant distribution in high mountain systems (Squeo et al. 1993).

On an altitudinal gradient, vegetation changes are often gradual, though at certain elevations those variations are sufficiently conspicuous to allow the recognition of discrete units usually called *altitudinal vegetation belts* (Moravec 1989, Kitayama 1992). The definition and delimitation of vegetation belts has been mainly based on physiognomic criteria, where the relative abundance of different life-forms at different elevations has been the most used (Squeo et al. 1993).

Vegetation limits based on physiognomic methods is relatively easy to obtain in the field, and often is considered meaningful for habitat description (Goldsmith & Harrison 1983). However their results are highly subjective because they depend on the investigator criterion (op. cit.). For example, several authors have described altitudinal changes in alpine vegetation at different latitudes in the Chilean Andes (e.g., Villagrán et al. 1980, 1981, 1983, Quintanilla 1980, 1996, Arroyo et al. 1988, Squeo 1991, Squeo et al. 1993, 1994), defining three to four altitudinal vegetation belts depending on latitude and the physiognomic criteria used (Squeo et al. 1994). In the Andes of central Chile (33°S) Quintanilla (1980, 1996) based on altitudinal transects done in the Río San Francisco basin, defined only two altitudinal belts: an Andean belt located between 2300 and 3000 masl characterized by a shrubby steppe dominated by spiny species, and a nivoglacial belt from 3000 up to 3600 m with many rosette and cushion plants. Arroyo et al. (1981), for this same area, defined three altitudinal belts: 1) a Sub-andean scrub belt between 2200-2600 m elevation, characterized by the dominance of prostrate shrubs, 2) a lower Andean belt between 2700-3100 m, characterized by the dominance of cushion plants, and 3) an upper Andean belt between 3200-3800 m, characterized by a sharp decrease in vegetation cover, with dominance of gramineous (tussock grasses) and small rosette plants. Teillier et al. (1994), in the El Morado National Park, also located in the Andes of Santiago, defined the following limits for vegetation belts: Sub-Andean belt 2000-2500 m, lower Andean belt 2600-3000 m and higher Andean belt: 3000-3500 m.

A more objective approach for delimitation of vegetation belts are methods based on species composition and relative abundance of each species (Goldsmith & Harrison 1983). While these methods are more time consuming, because they rely on measurements or samples of vegetation, they are more detailed in the description and delimitation of vegetation. The delimitation can

be done only based on changes in the species composition, only based on changes in the dominant species, or both (Goldsmith & Harrison 1983). The main difference between these methods is the sampling effort involved and the accuracy of the realized delimitation (op.cit). However, the most relevant feature of these methods is that they permit (with the aid of correlative methods) the detection of physical factors involved in the delimitation of vegetation belts (Goldsmith & Harrison 1983). For example, many studies in different alpine zones have established that temperature and some characteristic of the substrate are the main determinants of the vegetation belt limits (Chabot & Billings 1972, Squeo et al. 1993, Velázquez 1994, Fernández-Palacios & de Nicolas 1995, Ferreyra et al. 1998). As far as we are aware, only Squeo et al. (1993) have determined physical factors that affect the limits of alpine vegetation in the Chilean Andes.

The objectives of this paper are: 1) to describe the altitudinal changes of vegetation above timberline, 2) to compare vegetation belts defined with 1 physiognomic and 2 floristic methods, and 3) to detect some environmental factors that may be responsible for the altitudinal distribution of vegetation belts in the Andes of central Chile.

MATERIAL AND METHODS

Study area

This study was carried out between Farellones and Valle Nevado (33°20'S 70°16' W), 50 and 80 Km east of Santiago, respectively (Fig. 1).

The Andes of central Chile is characterized as a young mountain range. The geology of the study zone is composed by two large lithological facies: "Farellones Formation" and "La Parva-Cerro Colorado Formation" (sensu Thiele 1980). Farellones Formation (2100 to 3000 masl) is a stratified lithologic sequence, assigned to a Miocene age (18-20 m.y BP), made up by lavas, tuffs and breccias of andesitic, rhyolitic and basaltic composition alternating with sedimentary rocks (Thiele 1980). The sedimentary rocks are mainly of lacustrine origin corresponding to conglomerates, sandstones and finely stratified shales (Vergara et al. 1988, Thiele 1980). La Parva - Cerro Colorado Formation is a set of volcanic and subvolcanic rocks mainly made up by rhyolitic porphyry, often found in structures such as domes and necks, associated with stratified rocks compound of lava flows, tuffs and breccias of andesitic and rhyolitic composition. Thiele (1980) assigned a Pliocene age to this formation, however some

recent data, suggests a Miocene age, and therefore including this formation within the Farellones Formation (Beccard et al. 1986).

According to the structural composition of soil, because of the complex geology and geomorphology, there is a gradient from loam-type soils at lower elevation to clay-type soils at higher elevations. Organic matter content is < 3% and, as

occur in alpine soils (Retzer 1973), decreases with elevation.

Central Chile is characterized by a Mediterranean-type climate (di Castri & Hajek 1976), with high interannual variability in rainfalls (Aceituno 1990). Precipitation mainly occur in the form of snow during winter, although at higher elevations there occur summer storms with either

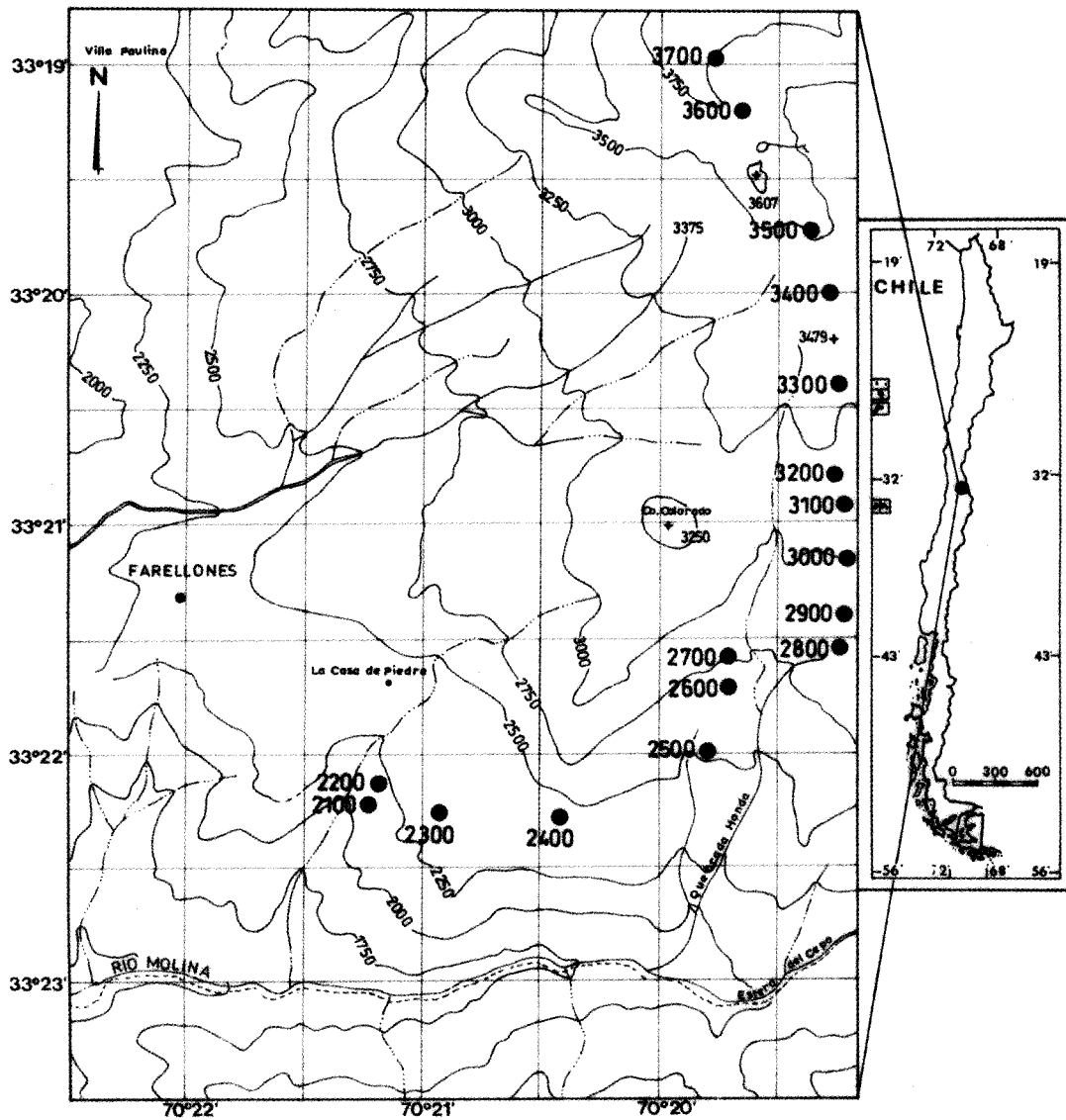


Fig. 1. Map of the study zone showing the elevations where vegetation was sampled. Mapa de la zona de estudio donde se indican las altitudes de muestreo de la vegetación.

flash hail or snow fall (Santibañez & Uribe 1990). Snow cover remains for 3 to 5 months depending on elevation and solar exposure (Rozzi et al. 1989). Mean annual temperature at 2600 masl is close to 6.5°C decreasing to 3°C at 3150 m (Cavieres & Arroyo, 1999). Annual lapse rate is 6.1°C/km, but showing seasonal variation, 4.0°C/km in winter and 7.0°C/km in summer (op. cit.).

Vegetation sampling

Immediately above the *Kageneckia angustifolia* D. Don (Rosaceae) treeline, that is found at 2000 m (León 1991), vegetation was sampled every 100 m between 2100 and 3700 m. Eighteen -50 m long transect, perpendicular to slope, were established and plants sampled with the point-intercept methods. We estimated species richness, absolute and relative cover of vegetation for the following life forms: Annuals, Perennial herbs, Cushions and Shrubs, according to Marticorena (in press). From 2100 to 2900 m, transects were sampled on south-facing slopes, while between 3000-3700 m transects were placed on southeast-facing slopes due to topographic difficulties. Inclination of slopes, and percent of rocks were also registered at each transect.

At each elevation, a soil sample (0.2 m depth) were taken with a metallic bore, stored in sealed plastic bags and sent it to a chemical laboratory (Agrolab Ltda.) where content of available nitrogen and phosphorous, pH, electric conductivity and texture (percent of clay) were determined. Content of available nitrogen and phosphorous were determined with the methods of Bremen and Olsen, respectively (Pearcy et al. 1989, Agrolab Ltda., comm. pers.), while electric conductivity and texture were determined with atomic absorption in ammonia acetate (pH = 7) and Bouyoco's densimeter method, respectively (op.cit.).

Vegetation belts

The relative abundance of the different life-forms at each elevation was used (sensu Squeo et al. 1993) to determine the limits vegetation belts (physiognomic approach).

In the floristic approach we used both a qualitative and a quantitative method (cf., Krebs 1989). For the qualitative analysis, we built a matrix with presence and absence of species at each elevation. We calculated the similarity index proposed by Baroni-Urbani & Buser (1976) for each pair of elevations. We chose this index because it can be easily tested for statistical significance. Afterwards

with the similarity index we built a dendrogram using an UPGMA-type algorithm. To determine clusters that are statistically significant we used the method described by McCoy et al. (1986). First we calculated the significance of similarities using the table provided in Baroni-Urbani & Buser (1976). Then we transformed the similarity matrix into a matrix of statistical significance in which we replaced the actual values by "+", "-", and "0" signs, according to whether the value of the index is significantly higher than expected at random, significantly lower, or not significantly different, respectively. Afterwards, at every fork we tested the significance of the segregation between groups with an analysis of independence that compared the distribution of pluses and minuses between the elevations that are clustered at any particular fork. In those forks that showed significant differences in the independence test, the homogeneity of each group was tested throughout the parameter DW (see McCoy et al. 1986 for details). We considered a group of altitudes as a significant cluster if the independence showed significant differences and DW was positive.

In the quantitative analysis we carried out an analysis of similarity using both species composition and relative cover of each species at each altitude. The Pearson's correlation index was used as a distance index for the analysis of similarity (Krebs 1989). Correlation coefficients are completely insensitive to proportional differences between communities (op.cit.). With the correlation matrix we built a dendrogram using an UPGMA-type algorithm with SYSTAT 6.0, which re-scales data, calculating and plotting $1-r$, where r is the correlation coefficient. The statistical significance of the resulting clustering was established calculating the distance $1-r_c$, where r_c is the critical value of the correlation index at 95% of confidence.

Gradient analysis

As a general approach to relating the floristic and structural variation of the vegetation with environmental variation a principal component analysis (PCA), as included in the SYSTAT 6.0 package, was applied using plant cover as the primary variable. In order to detect environmental factors involved in the altitudinal delimitation of vegetation, the first two unrotated factors extracted with the PCA were multiple-regressed against the following environmental variables: mean annual temperature, slope inclination, nitrogen content of soil, phosphorous content of soil, pH, electric conductivity of soil, percentage of clay in soil and percentage of rocks in transects (Table 1).

TABLE 1

Environmental parameters between 2100-3700 m elevation in the Andes of Santiago, central Chile (33°S). * Estimated from data in Cavieres & Arroyo (1999)

Parámetros ambientales entre los 2.100 y 3.100 m de altitud en los Andes de Santiago, Chile central (33°S). * Estimada de los datos de Cavieres & Arroyo (1999)

Altitude (masl)	Mean annual temperature (°C)*	Slope (%)	Nitrogen inclination (ppm)	hosphorous in soil (ppm)	Soil pH in soil	Electric conductivity (mmho/c)	Clay (%)	Rocks (%)
2100	9.7	10	22.5	22.5	5.9	0.04	15.5	5.6
2200	9.0	10	21.8	35.8	5.8	0.04	17.5	1.8
2300	8.4	15	21.0	49.0	5.7	0.04	19.5	2.7
2400	7.8	10	18.5	38.3	5.9	0.04	24.0	12.7
2500	7.2	10	16.0	27.5	6.2	0.04	28.5	4.0
2600	6.6	20	14.5	16.5	6.0	0.03	33.0	15.3
2700	6.1	30	13.0	5.5	5.9	0.03	37.5	19.6
2800	5.4	50	13.3	4.5	6.1	0.03	29.0	1.8
2900	4.8	30	13.5	3.5	6.3	0.03	20.5	8.0
3000	4.2	40	13.8	8.3	6.3	0.03	22.0	19.8
3100	3.6	40	14.0	13.0	6.2	0.03	23.5	21.7
3200	3.0	40	14.5	7.3	6.5	0.03	32.8	4.0
3300	2.4	30	15.0	1.5	6.8	0.03	42.0	5.2
3400	1.8	30	14.8	2.0	6.7	0.02	44.5	22.2
3500	1.2	20	14.5	2.5	6.7	0.03	47.0	0.0
3600	0.6	20	13.3	4.0	6.4	0.02	50.0	10.8
3700	-0.1	50	12.0	5.5	6.2	0.02	53.0	16.0

RESULTS

Vegetation

The altitudinal transect included 103 vascular plant species belonging to 68 genera and 35 families. The most represented families were Asteraceae (22 species), Papilionaceae (10 species), Gramineae (8 species) and Umbelliferae (7 species).

As an overall trend, species richness significantly decreased with elevation ($r = 0.82$, $n = 17$, $P < 0.05$) (Fig. 2a). However, species richness initially increased from 33 at 2100 m to 39 species at 2400 m. A decrease to 27 species was observed at 2500 m, followed with a rise to 45 species at 2700 m. From this altitude upwards, species richness decreased monotonically up to 3700 m where only one species (*Bromus setifolius*) was found (Fig. 2a). This indicates a loss of ca. 5 species for each 100 m increase in elevation.

Vegetation cover also significantly decreased with elevation ($r = 0.95$, $n = 17$, $P < 0.05$) (Fig. 2b). Between 2100 and 2900 m vegetation cover averaged around 50% with a maximum value of

66% at 2400, decreasing abruptly toward higher elevations (Fig. 2b).

Dominance of plant life-forms varied with elevation (Fig. 3). Shrubs were the dominant life-form from 2100 to 2500 m, decreasing in importance at higher elevations, although a secondary peak was observed at 2700 m (Fig. 3). A clear replacement of shrubs by cushion plants was observed at 2500 masl. Cushion plants reached maximum cover at 2500-2900 m, with a second peak at 3100-3400 m (Fig. 3). Perennial herbs showed high cover throughout all the altitudinal transect, being the dominant life-form between 2500-3300 m, and the only life form found from 3500 up to 3700 m. Annual herbs, the life form with the narrowest elevation range, were found between only 2100 and 2500 m, with low relative abundance (Fig. 3).

Vegetation belts

According to the distribution of life forms, physiognomic limits for the three Andean vegetation belts could be defined as follow: the

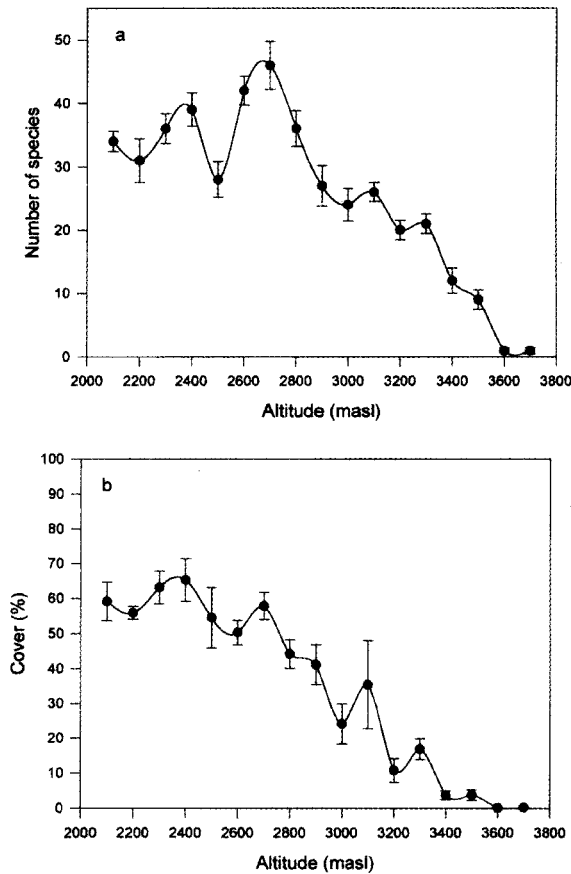


Fig. 2. Altitudinal variation of species richness (a) and vegetation cover (b) from 2100 to 3700 m elevation in south-facing slopes in the Andes of Santiago (33°S). Error bar represent ± 2 SE.

Variación altitudinal de la riqueza de especies (a) y cobertura vegetal (b) entre los 2.100 a 3.700 m de altitud en laderas de exposición sur en los Andes de Santiago (33°S). Barras error representan ± 2 EE.

subandean belt: 2100 - 2500 m, characterized by the dominance of shrubs and the presence of annuals (Fig. 3). The lower Andean belt: 2600 - 3400 m, characterized mainly by the abundance of cushion plants. The higher Andean belt: 3500 - 3700 m with dominance of perennial herbs (Fig. 3).

Figure 4a shows the dendrogram resulting from applying the UPGMA on the Baroni-Urbani & Buser similarity index matrix. According to the McCoy et al. (1986) method there were 4 significant clusters, with 3600 and 3700 elevations segregating individually. Cluster 1 encompassed 2100 - 2500 m, being characterized by the presence of the shrubs *Chuquiraga oppositifolia*, *Ephedra chilensis*, *Acaena andina* y *A. splendens*; the annual species *Collomia biflora*, *Leucheria congesta* and *Chaetanthera spp.*; and the perennial herbs *Euphorbia collina*, *Montiopsis umbellata* and *M.*

andicola. Cluster 2 included 2600 - 2800 m characterized by the presence of the cushion-plants *Laretia acaulis* and *Anarthrophyllum gayanum*, and the perennial herbs *Nassauvia aculeata*, *Plantago barbata*, *Hypochaeris tenuifolia*, *Calopappus acerosus*, *Montiopsis cistiflora* and *Tristagma spp.* Cluster 3 included elevations 2900 - 3100 m characterized by the presence of the cushion-plant *Azorella monantha* and the perennial herbs *Nassauvia pyramidalis* and *Senecio francisci*. Cluster 4 comprised elevations 3200 - 3500 m, characterized by the presence of the cushion *Azorella madreporica* and the perennial herbs *Nastanthus caespitosus*, *Oxalis compacta* and *Viola philippii*. The highest two altitudinal stations (3600 and 3700 m), with the presence of single species (*Barneoudia major* and *Bromus setifolius*, respectively) segregated early in the cluster analysis.

According to the cluster analysis using Pearson Correlation there were 7 significant groups (Fig. 4b). The cluster 1, included elevations 2100 - 2500 m, was characterized by the dominance of shrubs such as *Berberis empetrifolia*, *Chuquiraga oppositifolia*, *Acaena alpina* and *A. splendens*, also the presence and relative importance of annuals such as *Microsteris gracilis* and *Chaetanthera euphrasioides* (Table 2). Cluster 2, comprised elevations 2600 - 2800 m, characterized by the dominance of *Laretia acaulis*, and perennial herbs such as *Senecio pentaphyllus*, *Hordeum comosum*, *Poa holciformis* and *Hypochaeris tenuifolia* (Table 2). Cluster 3 included 2900 - 3100 m, being characterized by the dominance of the cushion

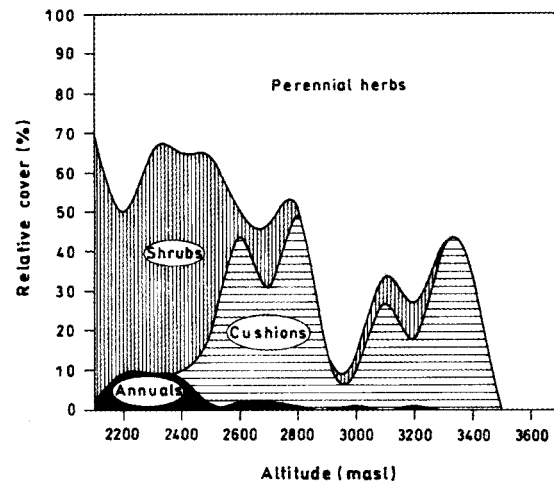


Fig. 3. Altitudinal variation of different life-forms cover from 2100 to 3700 m elevation in the Andes of Santiago (33°S).

Variación altitudinal de diferentes formas de vida entre los 2.100 - 3.700 msnm en los Andes de Santiago (33°S).

TABLE 2 (cont.)

Family	Species	Life form	Altitude (masl)																	
			2100	2200	2300	2400	2500	2600	2700	2800	2900	3000	3100	3200	3300	3400	3500	3600	3700	
	<i>Lathyrus subandinus</i>	PH	1,9																	
	<i>Vicia sp.</i>	PH	1,2																	
Plantaginaceae	<i>Plantago barbata</i>	PH						0,4	3,0											
	<i>Plantago uniglumis</i>	CSH		0,9																
Polemonaceae	<i>Collomia biflora</i>	ANN	0,2	0,5	0,7															
	<i>Microsteris gracilis</i>	ANN	1,5	5,7	3,3			0,1	1,0	0,4	0,3	0,2								
Polygalaceae	<i>Polygala gnidioides</i>	PH							0,2	0,2										
Polygonaceae	<i>Polygonum aviculare</i>	PH		0,6	0,2	0,5	1,8	0,7	0,9											
Portulacaceae	<i>Calandrinia caespitosa</i>	CSH																		2,4
	<i>Montiopsis andicola</i>	PH		0,2	0,2															
	<i>Montiopsis cisiflora</i>	PH						1,0	0,1			0,9								
	<i>Montiopsis penttilloides</i>	PH						0,2												
	<i>Montiopsis sericea</i>	PH						0,8	0,1	0,3	1,0	2,6								45,4
	<i>Montiopsis umbellata</i>	PH		1,5	0,8															
Ranunculaceae	<i>Barneoudia chilensis</i>	PH				0,8														
	<i>Barneoudia major</i>	PH																		
	<i>Discaria nana</i>	PH																		1,0
Rhamnaceae	<i>Discaria nana</i>	CSH																		
Rosaceae	<i>Acaena alpina</i>	SHR	18,2	14,0	3,7	2,2														
	<i>Acaena pinnatifida</i>	PH	3,3	9,5	6,4	2,3	4,4	1,9	6,4	3,7										
	<i>Acaena splendens</i>	SHR	17,4	0,7	0,6	2,4														
	<i>Galium eriocarpum</i>	PH																		
Rubiaceae	<i>Galium eriocarpum</i>	PH		0,3	0,7	0,7	0,6	0,3	0,1	0,1										
Santalaceae	<i>Quinchamalium chilense</i>	PH																		
	<i>Quinchamalium parviflorum</i>	ANN																		
	<i>Calceolaria biflora</i>	PH																		0,6
Scrophulariaceae	<i>Calceolaria purpurea</i>	PH																		
	<i>Calceolaria purpurea</i>	PH																		
	<i>Melosperma andicola</i>	PH																		
	<i>Azorella madreporica</i>	CSH																		
Umbelliferae	<i>Azorella monantha</i>	CSH																		
	<i>Bowlesia tropaeifolia</i>	PH																		
	<i>Laretia acaulis</i>	PH																		
	<i>Pozoa coriacea</i>	CSH		0,1	0,5	1,7	18,5	42,6	29,4	27,3										
	<i>Sanicula graveolens</i>	PH																		
	<i>Sanicula graveolens</i>	PH		1,0	1,8	0,3	0,8	1,6	6,5	0,1										
Violaceae	<i>Viola atropurpurea</i>	PH																		
	<i>Viola philippii</i>	PH																		
									0,6	0,7	2,2	1,9	1,2	1,5	2,6	27,7				

Azorella monantha, and the perennial herbs *Nassauvia pyramidalis*, *Phleum alpinum*, *Senecio francisci*, *Cerastium arvense* and, *Montiopsis sericea* (Table 2). Cluster 4 comprised elevations 3200 - 3400 m, dominated by the cushion *Azorella madreporica* and the perennial herbs *Hordeum comosum*., *Poza coriacea*, *Nastanthus spathulatus* and *Phacelia secunda* (Table 2). Elevations 3500 - 3700 m segregated individually. 3500 m is characterized by the abundance of the perennial herbs *Viola atropurpurea*, *Hordeum comosum*, *Oxalis squamata*, and *Montiopsis sericea* (Table 2). 3600 m has the single presence of the geophyte *Barneoudia major*, while 3700 m has the single presence of the gramineous *Bromus setifolius* (Fig. 4b).

Gradient analysis

The ordination of each elevation with the 2 principal factors extracted with PCA is shown in Fig. 5. The 2 principal factors accounted for 39.6% of the total variance. Factor 1 accounted for 21.9% while factor 2 accounted for 17.7%. According to a multiple regression analysis factor 1 was significantly correlated with mean annual temperature (Table 3), while factor 2 was significantly correlated with nitrogen content of soil (Table 3).

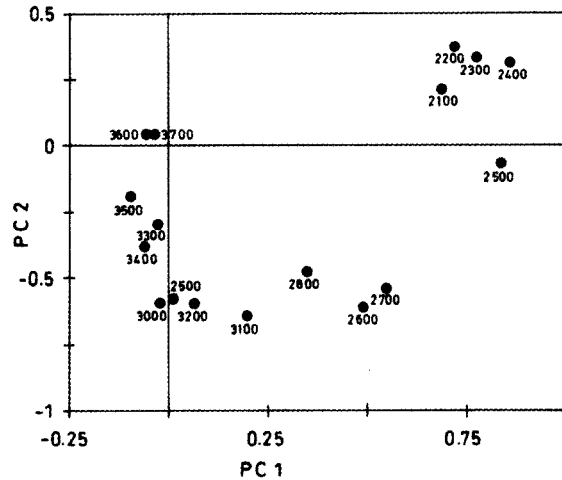


Fig. 5. Ordination of elevations along the two principal components extracted with a PCA for the relative cover of each species from 2100 to 3700 m elevation in the Andes of Santiago (33°S).

Ordenación de las altitudes con los dos componentes principales obtenidos con un PCA para la cobertura relativa de cada especie desde los 2.100 a 3.700 m en los Andes de Santiago (33°S).

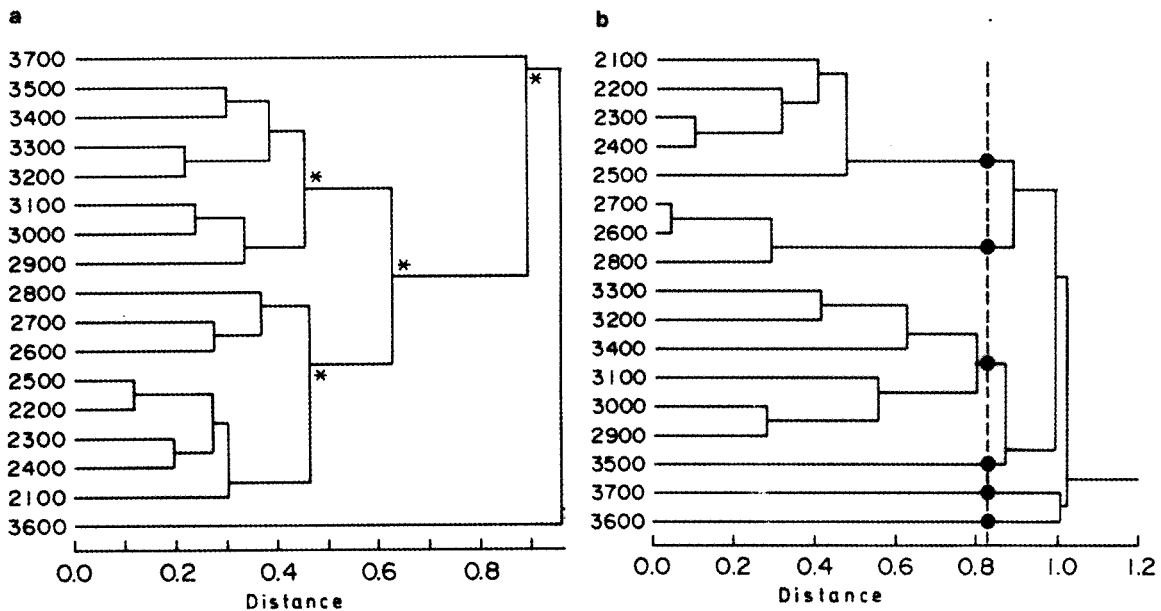


Fig. 4. Dendrograms resulting with: a) the Baroni-Urbani & Buser (1976), index of similarity, where (*) indicates significant clusters ($P < 0.05$) according to the method of McCoy et al. (1986), and b) the Pearson correlation coefficient, where black circles indicate significant cluster ($P < 0.05$).

Dendrogramas obtenidos con: a) el índice de similitud de Baroni-Urbani & Buser (1976), donde (*) indica agrupamientos significativos ($P < 0,05$) de acuerdo a McCoy et al. (1986), y b) el índice de correlación de Pearson, donde los círculos negros indican agrupamientos significativos ($P < 0,05$).

TABLE 3

Multiple-regression summary for principal factors extracted with PCA for the relative cover of each species from 2100 to 3700 m elevation in the Andes of Santiago (33°S). * Indicate significant regression ($P < 0.05$)

Resumen de la regresión lineal múltiple para factores extraídos con un PCA de la cobertura relativa de cada especie desde los 2.100 a los 3.700 m de altitud en los Andes de Santiago (33°S). * Indica regresión significativa ($P < 0,05$)

a) FACTOR 1 (Adjusted $R^2 = 0.946$, $n = 17$, $F_{(8,8)} = 35.764$, $P < 0.0001$)

Variable	Slope	Partial correlation	R-square	t(9)	P-level
Temperature	0.7394	0.6581	0.9620	2.4721	0.0354 *
Slope inclination	-0.0404	-0.1180	0.7646	-0.3360	0.7446
Nitrogen	-0.3401	-0.6567	0.8216	-2.4631	0.0660
Phosphorous	0.1646	0.2581	0.9284	0.7556	0.4692
pH	-0.3743	-0.4719	0.9444	-1.5140	0.1643
Electric conductivity	0.4420	0.5547	0.9381	1.8857	0.0920
Clay (%)	0.4654	0.7818	0.8026	3.5460	0.0630
Rocks (%)	-0.0552	-0.2544	0.3814	-0.7439	0.4759

b) FACTOR 2 (Adjusted $R^2 = 0.781$, $n = 17$, $F_{(8,8)} = 8.135$, $P < 0.01$)

Variable	Slope	Partial correlation	R-square	t(9)	P-level
Temperature	-0.4155	-0.2378	0.9620	-0.6924	0.5061
Slope inclination	-0.1715	-0.2439	0.7646	-0.7112	0.4950
Nitrogen	0.8676	0.7422	0.8216	3.1326	0.0121 *
Phosphorous	0.5769	0.4229	0.9284	1.3201	0.2194
pH	-0.2007	-0.1416	0.9444	-0.4046	0.6952
Electric conductivity	-0.4375	-0.3125	0.9381	-0.9303	0.3765
Clay (%)	0.3264	0.4014	0.8026	1.2397	0.2464
Rocks (%)	-0.1149	-0.2635	0.3814	-0.7725	0.4596

DISCUSSION

The number of species found in this study (103 spp.) is in agreement with figures reported for other alpine vegetations with similar climates. Chabot & Billings (1972) reported 72 species for the alpine vegetation of Bishop Creek, Sierra Nevada, California. Ferreyra et al. (1998), in the Patagonian Andes of Argentina reported 137 species analyzing the alpine vegetation of 3 different mountains, while Squeo (1991) reported 99 species for the alpine vegetation of Cerro Diente in the Chilean Patagonia. These numbers compare, for example, with the 332 species found in the alpine vegetation of 2 volcanoes in Mexico (Velázquez 1994), or the 294 vascular plant species found for the alpine vegetation in the southern Appalachian mountains (Wiser et al. 1996). The xeric conditions that characterize the Andes of central Chile and Argentina (Villagrán et al. 1983) explain, in part, the lower species richness and vegetation cover (that never exceeded 50%) in comparison with other mountains of the world (Villagrán et al. 1981, Arroyo et al. 1988).

Shrubs and annuals were restricted to lower elevations (Fig. 3), suggesting that those life-forms are more vulnerable to the colder climatic conditions of higher elevations. The height of plant, or how close to the soil the plant grows, is a very important factor for survival in cold habitats (Körner & Larcher 1988). In cold windy climates, small plants maintain higher temperatures than the surrounding air (Cabrera et al. 1998, Cavieres et al. 1998), enabling them to maintain a metabolic activity irrespective of a low ambient temperature. This may explain the restriction of shrubs to relatively low elevations while cushions and rosette perennial herbs, which grow close to the ground, are dominants at higher elevations. Additionally, Squeo et al. (1991, 1996) reported that the decrease in plant heights with elevation is closely related with the capacity to tolerate low temperatures. While tall shrubs avoided freezing temperatures, mainly through super-cooling, small plant tended to tolerate such condition. Recently, Rada et al. (1999) suggested that limitation in growth rate due to low temperature and water availability could also be involved

in the altitudinal zonation of life-forms. The decrease in shrub cover with elevation would also be related with the fact that long-lasting snow at higher elevations reduces the growing season and permafrost impedes root growth, both factors affecting secondary growth (Squeo et al. 1996).

The restriction of annuals to lower elevations has been reported for other alpine zones (Billings & Mooney 1968, Bliss 1971, Villagrán et al. 1981). Annuals require completing their life cycle within a single growing season. Favorable period for growth decrease with elevation (Kudo 1991, Stanton et al. 1994), thus annuals could not complete their life cycle at higher elevations. Furthermore, at higher elevations germination and establishment of seedling of annual plants could be inhibited strongly due to repeated freeze-thaw events in soil (Callaghan & Emmanuëlsson 1985).

The absolute dominance of perennial herbs at higher elevations suggests that a very limited range of life forms is viable on sites with short snow-free period and freezing temperatures. The low stature, the capacity to tolerate freezing temperatures, and the possession of underground perennial organs (such as rhizomes and bulbs) that help in maintaining the plant alive under the snow, allow them to take advantage of the short snow-free period (Billings & Mooney 1968).

According to the physiognomic criterion, limits for the subandean belt were 2100 - 2500 m. In the floristic approach, both qualitative and quantitative cluster analysis joined elevations from 2100 to 2500 m (Figs. 5 and 6). These clusters were characterized by the presence and dominance of prostrate shrubs and annual species, which corresponded to the definition of the subandean belt, thus there were a complete agreement between both approaches. According to physiognomy, the lower Andean belt (the cushion's belt) extended from 2600 to 3400 m. In the qualitative floristic method, 3 clusters (including elevation 3500 m) were recognized (Fig. 5), while in the quantitative method only 2 clusters were found (Fig. 6). These differences could be related with the fact that in the qualitative floristic method each cluster was characterized by the presence of cushions (*Laretia acaulis* 2600-2800 m; *Azorella monantha* 2900-3100 m; *A. madreporica*: 3200-3500 m), however the dominance of other species (e.g., *Phacelia secunda*, *Senecio* spp.) between 2900-3400 m excluded elevation 3500 m in the quantitative methods irrespective of the replacement of *Azorella monantha* by *A. madreporica*. Thus, the lower Andean belt can be divided in 2-3 sub-belts depending on the floristic method used. A similar result was reported by Squeo et al. (1993), who also divided this belt in 2 sub-belt

depending on the dominant cushion species. This suggests that delimitation of alpine vegetation based only on a physiognomic criterion lose relevant information about the distribution of cushion species.

According to physiognomy limits for the higher Andean belt, characterized by the dominance of perennials herbs, were 3500-3700 m. In the quantitative analysis all these elevations segregate in separate ways because they have no species in common, however in all cases the dominant species was a perennial herb. Thus, there is a complete correspondence between both types of delimitation. However, in the qualitative analysis, the presence (although with a very low cover) of *Azorella madreporica* at 3500 m joined this elevation with the cluster characterized by the presence of cushion plants, irrespective of the dominance of perennial herbs.

It has been reported that diversity and productivity on mountains decrease with elevation (MacArthur 1972), although there are mountains were extreme aridity at lower elevations override this general trend (Villagrán et al. 1983, Arroyo et al. 1988). The major role of altitude and associated low temperatures on vegetation in mountains has been largely recognized (e.g., Ward & Dimitri 1966, Troll 1973, Fernández-Palacios & Nicolás 1995, Ferreyra et al. 1998). The results of the present study seem to confirm this rule, because mean annual temperature showed a significant correlation with factor 1 in the PCA analysis. Although, there is a difference around 10°C in mean annual temperature between 2100-3600 m, according to the observed seasonal variation in lapse-rate (Cavieres & Arroyo 1999) the difference in temperature is higher (ca., 12 °C) during the growing season. Such a steep decrease in temperature could explain in part the abrupt decrease in species richness reported here (Fig. 2).

Many studies have shown that in addition to temperature, variables related to the substrate affect plant distribution in high mountain systems (Kitayama 1992, Squeo et al. 1993, Velázquez 1994, Wiser et al. 1996). In this study we found that the nitrogen content of soil, is the second most relevant factor that determined the altitudinal distribution of vegetation in the Andes of central Chile. Kitayama (1992) found that in addition to nitrogen, phosphorous and exchangeable magnesium and potassium were the properties of soil that determined the altitudinal distribution of vegetation in Mount Kinabalu, Borneo. Wiser et al. (1996) reported that pH, and exchangeable cations were determinants on distribution of vegetation in the southern Appalachian mountains. Squeo et al. (1993) found that in the

Andes of the desert zone of Chile, the altitudinal zonation of vegetation produced by thermic and radiation gradients is further modified by the chemical characteristic of soil mentioning pH, manganese, copper, zinc, iron, calcium, etc. but failing to establish what chemical element is the main determinant of vegetation changes. An additional property of soil that has been reported as relevant for explain the distribution of vegetation is soil moisture (Velázquez 1994, Wiser et al. 1996, Ferreyra et al. 1998), especially in mountains with mediterranean-type climates where xeric conditions develop during the growing season (Morefield 1992).

In summary, altitudinal delimitation of alpine vegetation based on physiognomic methods, while fast and easy to apply, it is highly subjective and loses relevant information about species distribution, especially at higher elevations. On the other hand, methods based on species composition and relative abundance of each species, while more time consuming, they are more detailed and permits the detection of physical factors involved in the altitudinal delimitation of alpine vegetation.

ACKNOWLEDGMENTS

To Chris Lusk and the reviewers for their comments and improvement of English. Research financed by FONDECYT N° 2950072 (LAC). Graduate studies of LAC supported in part by a grant from the Andrew W. Mellon Foundation, USA. Final redaction of manuscript supported by and Endowed Presidential Science Appointment (Cátedra Presidencial en Ciencias) to MTKA.

LITERATURE CITED

- ACEITUNO P (1990) Anomalías climáticas en la región sudamericana durante los extremos de la oscilación austral. *Revista Geofísica* 32: 65-78.
- ARROYO MTK, JJ ARMESTO & C VILLAGRAN (1981) Plant phenological patterns in the high andean cordillera of central Chile. *Journal of Ecology* 69: 205-223.
- ARROYO MTK, F SQUEO, JJ ARMESTO & C VILLAGRAN (1988) Effects of aridity on plant diversity in the northern Chilean Andes: results of a natural experiment. *Annals of the Missouri Botanical Garden* 75: 55-78.
- BARONI-URBANIC & MW BUSER (1976) Similarity of binary data. *Systematic Zoology* 25: 251-259.
- BECCARD I, M VERGARA & F MUNIZAGA (1986) Edades K/Ar de la formación Farellones, en el cordón del cerro La Parva. Cordillera de Los Andes de Santiago, Chile. *Revista Geológica de Chile* 28-29: 109-113.
- BILLINGS WD (1974) Adaptations and origins of alpine plants. *Arctic and Alpine Research* 6: 129-142.
- BILLINGS WD & HA MOONEY (1968) The ecology of arctic and alpine plants. *Biological Review* 43: 481-529.
- BLISS LC (1971) Arctic and alpine plant life cycle. *Annual Review of Ecology and Systematics* 2: 405-438.
- CABRERA HM, F RADA & LA CAVIERES (1998) Effects of environmental temperature on photosynthesis of two plant species along an altitudinal gradient in the tropical high Andes. *Oecologia* 114: 145-152.
- CAVIERES LA & MTK ARROYO (1999) Lapse-rate in the Río Molina valley, province of Santiago, central Chile (33°S). *Revista Geográfica Terra Australis* 44: 79-86.
- CAVIERES LA, A PEÑALOZA, C PAPIĆ & M TAMBUTTI (1998) Efecto nodriza del cojín *Laretia acaulis* (Cav.) Gill. et Hook. (Umbelliferae) en la zona alto-andina de Chile central. *Revista Chilena de Historia Natural* 71: 337-347.
- CALLAGHAN TV & U EMANUELSSON (1985) Population structure and processes of tundra plants and vegetation. In: White J (ed) *The Population Structure of Vegetation*: 399-349. Dordrecht, Junk.
- CHABOT B & WD BILLINGS (1972) Origins and ecology of the sierran alpine flora and vegetation. *Ecological Monographs* 42: 163-199.
- DI CASTRI F & E HAJEK (1976) *Bioclimatología de Chile*. Ediciones de la Pontificia Universidad Católica de Chile, Santiago. 170 pp.
- FERNANDEZ-PALACIOS JM & JP DE NICOLAS (1995) Altitudinal patterns of vegetation on Tenerife. *Journal of Vegetation Science* 6: 183-190.
- FERREYRA M, A CINGOLANI, C EZCURRA & D BRAN (1998) High-Andean vegetation and environmental gradients in northwestern Patagonia, Argentina. *Journal of Vegetation Science* 9: 307-316.
- GOLDSMITH FB & CM HARRISON (1983) Description and analysis of vegetation. In: Chapman SB (ed) *Methods in plant ecology*: 85-155. Blackwell Sci, Oxford.
- KITAYAMA K (1992) An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102: 149-171.
- KÖRNER CH. & W LARCHER (1988) Plant life in the cold climates. In: Long S & P Woodward (eds.) *Plants and Temperature*: 25-57. Cambridge University Press, Cambridge.
- KREBS CJ (1989) *Ecological Methodology*. Harper Collins Pub., British Columbia. 215 pp.
- KUDO G (1991) Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arctic and Alpine Research* 23: 436-443.
- LEON P (1991) Efecto del espaciamiento entre plantas de *Kageneckia angustifolia* D Don (Rosaceae). Tesis de Magister, Facultad de Ciencias, Universidad de Chile. 76 pp.
- MACARTHUR R (1972) *Geographical Ecology. Patterns in the Distribution of Species*. Harper & Row, New York. xii + 222 pp.
- MARTICORENA C (in press) *Catálogo de la Flora Vascular de Chile*. Ed. Universidad de Concepción.

- McCOY ED, S BELL & K WALTERS (1986) Identifying boundaries along environmental gradients. *Ecology* 67: 749-759.
- MORAVEC J (1989) Influences of the individualistic concept of vegetation on syntaxonomy. *Vegetatio* 81: 29-39.
- MOREFIELD JD (1992) Spatial and ecologic segregation of phytogeographic elements in the White Mountains of California and Nevada. *Journal of Biogeography* 19: 33-50.
- PEARCY RW, JR EHLERINGER, HA MOONEY & PW RUNDEL (1989) *Plant Physiological Methods*. Chapman & Hall, New York, 457 pp.
- QUINTANILLA V (1980) Observaciones fitogeográficas en la alta cordillera de Santiago. *Revista Geográfica Terra Australis* 24: 3-14.
- QUINTANILLA V (1996) Zonación altitudinal de la vegetación en una cuenca andina de Santiago de Chile. In: *Actas I Taller Internacional de Geoecología de Montaña y Desarrollo Sustentable de Los Andes del sur: 477-484*. Universidad de Chile, Facultad de Arquitectura y Urbanismo.
- RADA F, FA SQUEO, A AZOCAR, HM CABRERA (1999) Water and carbon relations in the genus *Adesmia* (Papilionaceae) at different altitudes in the high north-central Chilean Andes. *Revista Chilena de Historia Natural* 72: 201-211.
- RETZER JL (1973) Alpine soils. In: Ives JD & RD Barry (eds) *Arctic and Alpine Environments: 771-802*. Methuen, London.
- ROZZIR, JD MOLINA & P MIRANDA (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.
- SANTIBAÑEZ F & FURIBE. (1990). *Atlas Agroclimático de la V región y Región Metropolitana*. Facultad de Agronomía, Universidad de Chile. 103 pp.
- SQUEO F (1991) Estructura de comunidades vegetales andinas en relación con la polinización en la cordillera de los Baguales, Patagonia, Chile. Tesis Doctoral, Facultad de Ciencias, Universidad de Chile. xii + 263 pp.
- SQUEO F, F RADA, A AZOCAR & G GOLDSTEIN (1991) Freezing tolerance and avoidance in high tropical Andean plants: is it equally represented in species with different plant height? *Oecologia* 86: 378-382.
- SQUEO F, H VEIT, G ARANCIO, JR GUTIERREZ, MTK ARROYO & N OLIVARES (1993) Spatial heterogeneity of high mountain vegetation in the Andean desert zone of Chile. *Mountain Research and Development* 13: 1-10.
- SQUEO F, R OSORIO & G ARANCIO (1994) *Flora de los Andes de Coquimbo: Cordillera de Doña Ana*. Ediciones Universidad de La Serena, Chile. 168 pp.
- SQUEO F, FRADA, CE GARCIA, ME PONCE, AL ROJAS & A AZOCAR (1996) Cold resistance mechanism in high desert Andean plants. *Oecologia* 105: 552-555.
- STANTON ML, MREJMANEK & C GALEN (1994) Changes in vegetation and soil fertility along a predictable snowmelt gradient in the mosquito range, Colorado, USA. *Arctic and Alpine Research* 26: 364-374.
- TEILLIER S, AJ HOFMANN, F SAAVEDRA & L PAUCHARD (1994) *Flora del Parque Nacional El Morado (Región Metropolitana, Chile)*. *Gayana Botanica* 51: 13-47.
- THIELE R (1980) *Carta Geológica de Chile*. Hoja Santiago. Instituto de Investigaciones Geológicas, Santiago, carta 39.
- TROLL C (1973) High mountain belts between the polar caps and the equator: their definition and lower limit. *Arctic and Alpine Research* 5: 19-27.
- VELAZQUEZ A (1994) Multivariate analysis of the vegetation of the volcanoes Tláloc and Pelado, Mexico. *Journal of Vegetation Science* 5: 263-270.
- VERGARA M, R CHERRIER, FMUNIZAGA, S RIVANO, P SEPULVEDA, R THIELE & R DRAKE (1988) Miocene volcanism in the central Chile Andes. *Journal of South American Earth Sciences* 1: 199-209.
- VILLAGRAN C, J ARMESTO, MTK ARROYO & P USLAR (1980) Vegetación de los Andes de Arica 18°-19°S. Unesco, Program MAB, P. 6, Vol I: 71-89.
- VILLAGRAN C, J ARMESTO & MTK ARROYO (1981) Vegetation in a high Andean transect between Turi and Cerro León in northern Chile. *Vegetatio* 48: 3-16.
- VILLAGRAN C, MTK ARROYO & C MARTICORENA (1983) Efectos de la desertización en la distribución de la flora andina de Chile. *Revista Chilena de Historia Natural* 56: 137-157.
- WARD RT & MJ DIMITRI (1966) Alpine tundra on Mt. Cathedral in the southern Andes. *New Zealand Journal of Botany* 4: 42-56.
- WISER SK, R PEET & PS WHITE (1996) High-elevation rock outcrop vegetation of the southern Appalachian Mountains. *Journal of Vegetation Science* 7: 703-722.