

FLORA AND VEGETATION OF NORTHERN CHILEAN ANDES

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ABSTRACT

In northern Chilean Andes two rainfall patterns are found: a summer rain region (17°-24°S) and a winter rain region (25°-32°S). The transition between both rain regions (24°-25°S) correspond also with the driest area ('arid diagonal').

The Andes Mountains started to emerge in the Upper Tertiary. The existence of high mountains in the Miocene/Pliocene, together with the likely birth of the cold Humboldt-current at about this time, led to an aridization of northern Chilean Andes. The Quaternary with its generally dry conditions is characterized by the occurrence of relative moist phases during the glacials. The models, concerning the northwards or southwards shift of climatic belts (e.g., the westerlies) during glacial periods, are discussed.

The flora of northern Chilean Andes include 865 plant species, 21% of these species are endemic to Chile. In the winter rain region exist twice higher endemism than the summer rain region. Species richness decreases by 80% and cover by 50% over the very severe rainfall gradient from 18°S to 24°S. Perennial herbs are most abundant in areas of highest rainfall, annual herbs gain greatest prominence in areas of intermediate aridity, while woody species are more frequent under extreme dry/warm and extreme dry/cold conditions.

Four vegetation belts can be distinguished along northern Chilean Andes: a) **Pre-alpine belt** (also called Desertic or Pre-Puna belt) located at lower elevations, b) **Subalpine belt** (or Puna belt), c) **Low Alpine belt** (the cushion belt), and d) **High Alpine belt**.

At 18°S flowering occurs year round with two marked peaks, before and after the rainy season. For the winter rain site at 33°S, flowering extends from September through early May, with a peak in mid-summer (January). The flowering periods of individual species are 4 times longer at 18°S compared with 33°S. The anemophily increases towards drier areas. The biotic pollination is primarily carry out by diptera and himenoptera in both summer and winter rain regions.

Temperature plays a role in determining life forms and, in consequence, the physiognomic similitude among vegetation belts. Tall species are less cold tolerant than ground-level species in both summer and winter rain regions. Tall species have supercooling capacity; in contrast, all ground-level species have freezing tolerance as the main mechanism of resistance to cold temperatures. Also in both regions, shrubs showed lower stomatic conductance to water vapor, lower photosynthetic rates and lower water potential than perennial herbs.

Consequences of global climate change on the flora and vegetation of northern Chilean Andes are discussed.

RESUMEN

En los Andes del norte de Chile se encuentran dos patrones de precipitación: una región con lluvias de verano (17°-24°S) y otra región con lluvia de invierno (25°-32°S). La zona de transición entre las lluvias de verano e invierno (24°-25°S), coincide con la parte más árida ('diagonal árida').

La Cordillera de los Andes comenzó a levantarse en el Cenozoico Superior. La existencia de altas montañas en el Mioceno/Plioceno, junto con el probable nacimiento de la Corriente de Humboldt en este tiempo, determinó el comienzo de la aridización de los Andes del norte de Chile. El Cuaternario fue en general seco pero con fases relativamente húmedas durante las glaciaciones. Se discuten los modelos de desplazamiento hacia el Norte o hacia el Sur de los cinturones climáticos (p.e., los 'westerlies') durante los períodos glaciales.

La flora de los Andes del norte de Chile posee 865 especies, 21% de estas especies son endémicas a Chile. En la región de lluvia de invierno existe el doble de especies endémicas que en la región de lluvia de verano. La riqueza de especies disminuye un 80% y la cobertura un 50% en el severo gradiente de precipitación entre los 18°S y 24°S. Las hierbas perennes son más abundantes en áreas con mayor precipitación, las hierbas, anuales aumentan en importancia en áreas de aridez intermedia, mientras que las especies leñosas son más frecuentes bajo condiciones árido/cálidas y árido/frías.

Cuatro pisos de vegetación se pueden distinguir en los Andes del norte de Chile: a) el piso **Pre-andino** (o piso Desértico o Pre-Puna) localizado a bajas elevaciones, b) el piso **Subandino** (Puna), c) el piso **Andino Inferior** (el piso de los cojines), y d) el piso **Andino Superior**.

La floración a los 18°S ocurre a lo largo de todo el año con dos máximos marcados, antes y después de la estación de lluvia. Para el sitio con lluvia de invierno a los 33°S, la floración se extiende entre Septiembre hasta principios de Mayo, con un máximo a mitad del verano (Enero). Los períodos de floración de especies individuales son 4 veces más largos a los 18°S comparado con los 33°S. La anemofilia incrementa hacia las áreas más áridas. La polinización biótica es principalmente realizada por dípteros e himenópteros bajo los dos patrones de precipitación.

La temperatura tiene un papel importante en determinar las formas de vida, y en consecuencia la similitud fisonómica a lo largo de los pisos de vegetación. Bajo los dos patrones de precipitación, las especies altas son menos tolerantes a las bajas temperaturas comparados con las especies que crecen a nivel del suelo. Las especies altas poseen la capacidad de sobre-enfriar; en contraste, todas las especies que crecen al nivel del suelo poseen tolerancia al congelamiento como principal mecanismo de resistencia a bajas temperaturas. También en ambas regiones los arbustos muestran menor conductancia estomática al vapor de agua, menor tasas de fotosíntesis y menores potenciales hídricos comparados con las hierbas perennes.

Se discuten las consecuencias del cambio climático global sobre la flora y vegetación de los Andes del norte e Chile.

Palabras claves: Andes del norte de Chile, clima, paleoclima, riqueza de especies, endemismo, forma de vida, tolerancia al frío, intercambio de gases, cambio global.

INTRODUCTION

The northern Chilean Andes Mountains rise abruptly from a narrow lowland area bordering the Pacific Ocean to elevations over 6,000 m. The highland present a steep climatic gradient providing a good scenario to inquire about evolution of the flora and their adaptations to different environmental constrains.

In this chapter the high-altitude, mountainous environment of northern Chile will be discussed, in terms of their climate, paleohistory, species richness, vegetation, reproduction and ecophysiological adaptations.

I. Climate in the northern Chilean Andes.

Extremely arid climates in western South America extend from 15° S in southern Perú to around 30°S in Chile. In lowlands of these regions, annual rainfall average is usually lower than 100 mm (Fig. 1). At low elevation, between 17°S and 25°S, annual precipitation is between 0-10 mm. In this absolute desert, vegetation is present, only around few river valleys and in areas exposed to coastal fog.

The Chilean-Peruvian Desert is a 'rain shadow' and a 'cold air' desert (Rauh, 1983). The present climate is determined by three major factors: a) the annual behavior of the Intertropical Convergence situated over equatorial latitudes (Gómez & Little, 1981) which brings moisture from the northeast ('easterlies'), b) a Polar front bringing precipitation from the west ('westerlies'), and c) the Humboldt Current - Niño/Niña events (Zinsmeister 1978; Aceituno *et al.*, 1993). As a consequence of the interplay of these parameters, northern Chilean Andes can be divided in two regions: a) a **winter rain region**, south of 24-25°S (rains occur during winter, as snow over 3,000 m, and summers are warm and dry), b) a **summer rain region**, north of 24°S (rains occur during summer, and winters are cold and dry). There is a small overlap between these two rainfall patterns in the driest area in between, the 'Arid Diagonal'.

Air-temperature is reduced by 6.5°C/1,000 m in the northeast Chilean Andes (Fig. 2). For instance, mean annual temperature at Murmuntane (3,280 m) is 9.7°C, while at Parinacota (4,395 m) is 2.5°C.

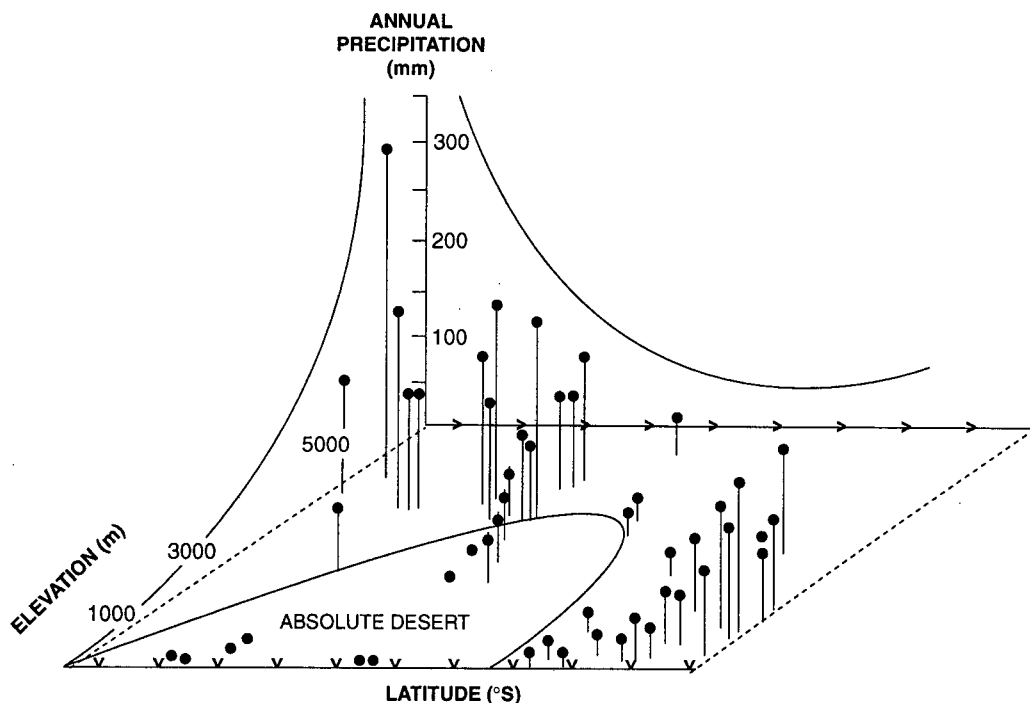


Fig. 1. Mean annual precipitation related to elevation and latitude in northern Chile (from Arroyo *et al.*, 1988)

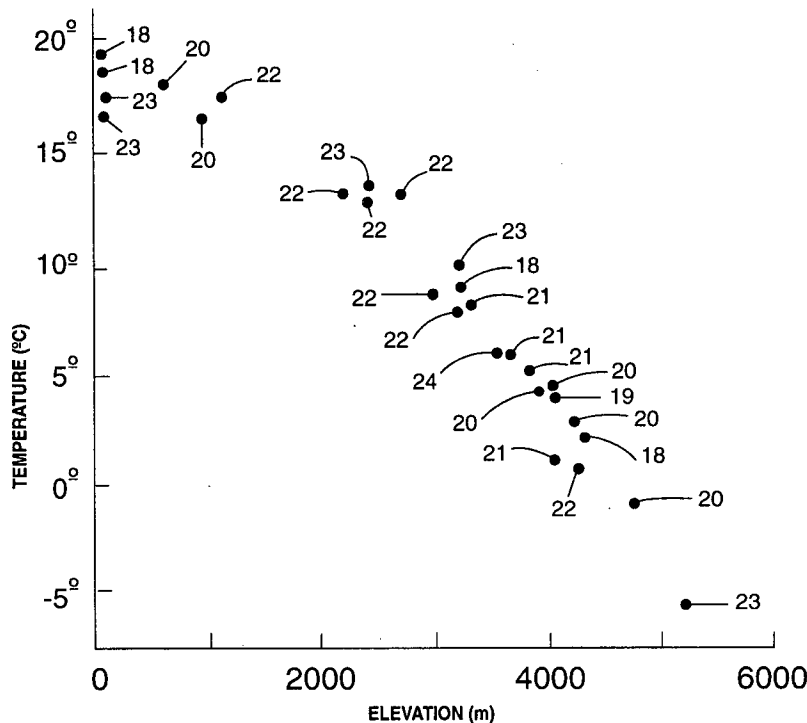


Fig. 2. Mean temperature plotted against elevation for areas between latitude 18° and 24°S in northern Chilean Andes (from Arroyo *et al.*, 1988).

II. Andes Mountain Paleohistory

Emergence of the Andes. The strong uplift of the Chilean Andes started in the Upper Tertiary, accompanied by volcanic activity since the Miocene some 23 my B.P. (Mortimer, 1975, 1980; Zeil, 1979). The existence of high mountains in the Miocene / Pliocene, together with the likely-birth of the cold Humboldt-current at about this time, led to an aridization of northern Chilean Andes (Herm 1969; Paskoff, 1979; Mortimer 1980; Naranjo & Paskoff 1985; Alpers & Brimhall 1988; Arroyo *et al.*, 1988). Favored by the high elevation, glaciations of the Altiplano probably occurred as early as Pliocene (Clapperton, 1979). The Quaternary with its generally dry conditions is characterized by the occurrence of relative moist phases. The number and the age of such periods is not well known. However, a simple model with the alternation of humid glacials and dry interglacials can no longer hold true. As can be seen for the Upper Pleistocene, strong climatic fluctuations, especially variations of the moisture regime, occurred during one single glacial period, which reflected by glacial variations and changes of the Altiplano lake-levels. In light of these facts, the established models of the past decades, concerning the northwards or southwards shift of climatic belts (e.g., the westerlies) during glacial periods, have to be discussed in much more detail.

Pleistocene-Holocene climates. From the Altiplano in Perú and Bolivia three to five pleistocene periods with increased moisture are documented by glacier advances. The Mid- to Upper Pleistocene periods of glacier advances seem to correspond with higher levels of Lake Titicaca (Dobrovolsky 1962; Servant 1977; Ballivian *et al.*, 1978; Hastenrath & Kutzbach, 1985; Lauer & Rafiqpoor, 1986; Seltzer, 1993). During the Last Glacial Maximum (around 20,000 yr B.P.) the maximum temperature depression reached about 6-7°C. In spite of this, the prevailing dry conditions led to the formation of only small glaciers and low lake levels on the Altiplano. More humid conditions are documented > 28,000 yr B.P. (Minchin Period) as well as during lateglacial times (Tauca Period, 3-4°C colder). They have been interpreted as an intensification or slight southward shift of the tropical easterly winds (Kessler, 1984, 1991). A moist late glacial period with high lake levels is also documented in the Argentine and, Chilean Andes until 30°S (Veit & Stengl 1991; Grosjean *et al.*, 1991; Veit, 1993a, b; Garleff *et al.*, 1993; Messerli, *et al.*, 1993). The more humid conditions in Chile south of 27°S at this time have their origins from intensified westerlies (Veit, 1993a). A stronger influence of the westerlies in the south and of the easterly winds in the north led to a narrowing of the 'Arid Diagonal'. However, the dry core of the 'Arid Diagonal' persisted in its present position around 24°S.

The increased moisture on the Altiplano led to intensified runoff, which is documented by the down-cutting of the rivers. This holds true, for example, in the Río Lluta Valley, east of Arica at Poconchile, where 14C-dates of ancient valley floors show the beginning of this process around 16,000 yr B. P. (Veit, 1993b). Similarly one might interpret various 'humid' indicators in the Atacama desert as effects of runoff from the Altiplano and not of increased precipitation in the Atacama itself. Thus, the 'Arid Diagonal' apparently has a long Pleistocene to Tertiary history and is not a very recent feature (e.g. Ochsenius, 1982).

Compared to lateglacial times, the climate became drier at the transition to the Holocene, but was relatively moist until 7,500 yr B.P. This is indicated by the levels of Lake Titicaca, that remained rather high (Wirrmann & de Oliveira, 1987), and by the activity of alluvial fans and by soil formation above 2,500 masl in the Norte Chico (Veit, 1991, 1993b) and at 23°S (Messerli *et al.*, 1993). From 7,500 yr B.P. on, the climatic conditions in the Andes became significantly drier. With the exception of a probably very short moisture oscillation in the Mid-Holocene, these dry conditions prevailed until 3,700 B.P., indicated by a fall of Lake Titicaca of about 50 m below the present level, the lack of activity of alluvial fans and by soil erosion processes in the Norte Chico. From 3,700 yr B.P. on, the climate became slightly moisture and cooler in the Norte Chico and approached to the present arid to semiarid conditions. At the Altiplano a similar trend of climatic evolution is indicated by the rise of Lake Titicaca, though palynological findings at 23°S (Messerli *et al.*, 1993) indicate drier conditions from 2,200 yr B.P. on.

III. Species Richness

Endemic patterns: The total number of species in northern Chilean Andes (not including the desert preAndean shrubland) is 865 representing 16.9% of the Chilean flora (Table 1). 21% of these species are endemic to Chile. Now, in the same relative area (7° latitude), the winter rain region (25-32°S) has twice more endemism to Chile (27% versus 14%) and twice more endemism to the respective rain region (19% versus 10%) than the summer rain region (17-24°S). These differences could be a consequence of the continuity of the Altiplano flora to the north inside the same rain pattern, and migration. Despite these differences, the high endemism in northern Chilean Andes (ca.14%) shows that recent evolution *in situ* occurred.

Latitudinal patterns: Species richness drops off by 80% from 18°S (heaviest summer rain in northern Chilean Andes) to 24°S (lightest summer rain) (Table 2); whereas, number of species increases to the south with an increase in winter rains. Arroyo *et al.* (1988) showed that, under similar thermal conditions, species richness was positively correlated with precipitation. Under both precipitation regimes, as aridity increases, trends for fewer species per genus and fewer genera per family are seen (Table 2). Thus fewer species or fewer genera have been able to survive in the most arid regions, and/or less local speciation exists. These latitudinal changes in species richness also reflect reduced north-south species migration there on account of the absolute desert extending above 3,000 m at 24°S (Arroyo *et al.*, 1982; Villagrán, 1983).

Altitudinal patterns: Flora of the two rain regions show different responses to elevation. In the summer rain region, the maximum number of species occurs at mid elevation (Fig. 3); while on the winter rain region species richness decreases with increase in elevation. Additionally, at the same elevation, the number of species decreases towards the 'Arid Diagonal' where the east-west precipitation gradient is most pronounced and a absolute desert exists.

TABLE 1.

ENDEMISM PATTERNS IN NORTHERN CHILEAN ANDES (NO INCLUDING THE DESERT PRE-ANDEAN SHRUBLAND). DATA ARE FROM THE 'FLORA DE CHILE DATA BASE' BASED IN 112,000 RECORDS OF HERBARIUM COLLECTIONS AND THE LITERATURE.

Latitudinal Range	Rain Patterns	Total Species numbers	Chile		Endemic Species to the rain region	
17°00' to 24°59'S	Summer	523	71	13.6%	51	9.8%
25°00' to 31°59'S	Winter	449	121	26.9%	84	18.7%
17°00' to 31°59'S	both	865	182	21.0%	119	13.8%

TABLE 2.

COMPARISON OF THE NUMBER OF SPECIES PRESENT (SPECIES RICHNESS) AT DIFFERENT LATITUDES IN THE NORTHERN CHILEAN ANDES. DATA FROM ARROYO *ET AL.* (1988)

	Summer rain				Winter rain	
	18°S	19°S	21°S	24°S	26°S	28°S
Number of species	391	219	164	77	144	270
Number of genera	195	138	110	55	90	162
Species/genus	2.0	1.6	1.5	1.4	1.6	1.7
Number of families	64	53	37	30	42	58
Genera/family	3.0	2.6	3.0	1.8	2.1	2.8

III. Vegetation

Cover: There is also a clear reduction in total plant cover with aridity (Fig. 4). In the wettest areas in the northern Andes, total cover does not exceed 50%. However, at 24°S, less than 20% of the total surface is covered. Arroyo *et al.*, (1988) found that plant cover was positive correlated with species richness, showing that increases in aridity also affect plant biomass.

Life forms: Dividing the altitudinal gradient in three elevation levels (2,000-3,000 m, 3,000-4,000 m and 4,000-5,000 m), Arroyo *et al.*, (1988) showed that life form composition changes along the aridity gradient (Table 3). Comparing the wet and arid extremes of the summer rain region, perennial herbs are underrepresented at the arid extreme in the three elevations. Contrary to expectations, annual herbs did not increase with greater aridity. Annuals were significant less represented in the driest (2,000-3,000 m) of the three elevations. Woody species, in contrast, tend to be more highly represented as aridity increases; the trend is clear in the driest elevation and where aridity is overlaid with cold stress (4,000-5,000 m).

In the elevation gradient, a lower fraction of annual species are present at the highest elevation along all the latitudinal gradient, suggesting less tolerance to low temperatures. The higher proportion of annuals at midelevation in 21-24°S suggests that the annual habit is adapted in arid climates up to a certain moisture limit.

TABLE 3.
LIFE FORMS ON NORTHERN CHILEAN ANDES. DATA FROM ARROYO ET AL. (1988).

	18-19°S	21-24°S	26-28°S
2,000 - 3,000 m			
Shrubs & trees	(28) 40.6%	(7) 70.0%+	(62) 42.5%
Perennial herbs	(24) 34.8%	(2) 20.0%+	(41) 28.1%
Annual herbs	(17) 24.6%	(1) 10.1%+	(43) 29.4%
	(69 spp.)	(10 spp.)	(146 spp.)
3,000 - 4,000 m			
Shrubs & trees	(70) 32.4%	(32) 36.0%	(54) 35.8%
Perennial herbs	(107) 49.5%ac	(32) 36.0%bd	(61) 40.4%cd
Annual herbs	(39) 18.1 %	(25) 28.1%	(36) 23.8%
	(216 sp)	(89 spp.)	(151 spp.)
4,000 - 5,000 m			
Shrubs & trees	(25) 17.4%ac	(32) 37.6%bd	(25) 26.0%cd
Perennial herbs	(107) 74.3%a	(43) 50.6%b	(48) 50.0%b
Annual herbs	(12) 8.3%a	(10) 11.8%a	(23) 24.0%b
	(144 spp.)	(85 spp.)	(96 spp.)

Same letters show no significant differences with G-test, + =G-test not applicable.

Vegetation belt: Despite the existence of a disruption in the latitudinal distributions of the Andean taxa around determining floristic differences between the summer and winter rain regions (Arroyo *et al.*, 1981; Villagrán *et al.*, 1983), four vegetation belts can be distinguished on a physiognomic basis along northern Chilean Andes (Fig. 5): a) **Pre-alpine** belt (also called Desertic or Pre-puna belt) located at lower elevations, is a low shrubland with few tree species present in wet areas, b) **Subalpine** belt (or Puna belt): dominated by shrubs, c) **Low Alpine** belt: dominated by sub-shrubs and grasses, also cushion species are present, and d) **High Alpine** belt (Subnival or Alpine desert belt): the highest vegetation belt, permafrost is usually close to the soil surface, only a few species forming small rosettes and grasses are present (Ruthsatz, 1977; Villagrán *et al.*, 1981, 1983; Squeo *et al.*, 1994).

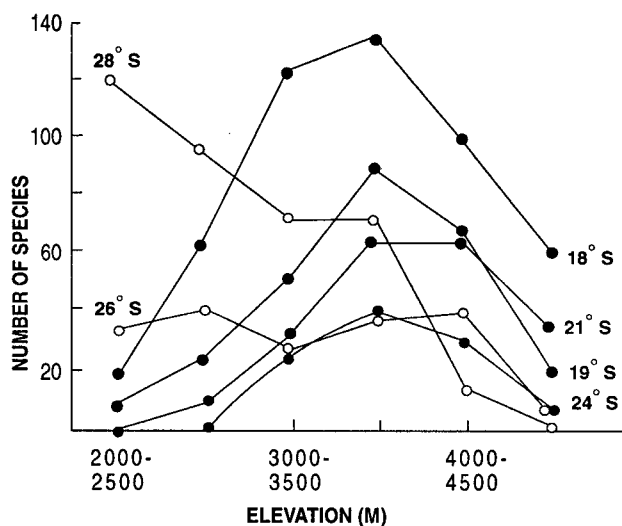


Fig. 3. Variation in number of species (species richness) with elevation at different latitudes in northern Chilean Andes. Summer rain region (solid circles), winter rain region (open circles) (from Arroyo et al., 1988).

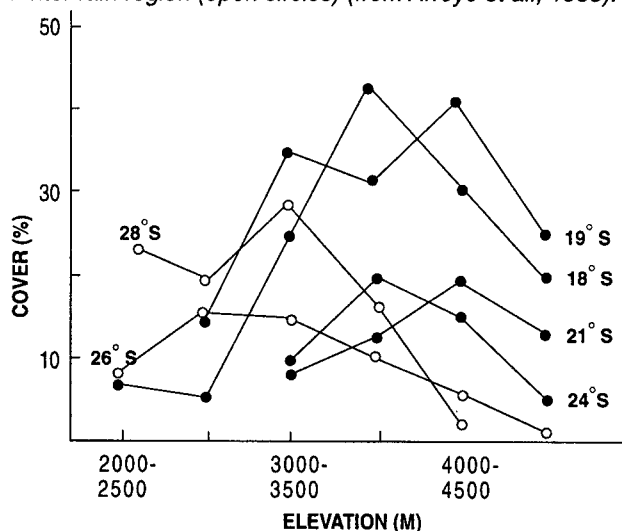


Fig. 4. Variation in plant cover (% of ground vegetated) with elevation at different latitudes in northern Chilean Andes. Summer rain region (solid circles), winter rain region (open circles) (from Arroyo et al., 1988).

IV. Phenology

Phenological data of summer (18°S) and winter (33°S) rain sites are compared using data from sampling stations in the Sub-alpine vegetation belt (Fig. 6). At 18°S flowering occurs year round with two marked peaks, one in October-November before the rainy season, and a second in March-April after the end of the rainy season. Above 4,000 m, there is some decrease in flowering during the colder months (Belmonte & Moscoso, 1985). The flowering periods of individual species are 3.8 months in average.

For the winter rain site at 33°S, flowering extends from September, immediately at snow-melt, through early May, with a peak in mid-summer (January). In addition to the seasonal differences, the flowering periods of individual species are shorter on the winter rain site (one month on average). At 30°S and in the last three vegetation belts (between 3,000 and 4,500 masl) flowering extends only from November to May (Squeo, et al., 1994), suggesting that differences because of increasing in aridity may also occurs.

V. Pollination

Total importance of anemophily in the flora increases towards drier areas (26% of the flora at 22°S) in comparison with wet areas (21.7% at 18°S, and 19.3% at 30°S) (Arroyo et al., 1983). Arroyo et al. (1987) showed that biotic pollination is primarily carry out by diptera and himenoptera in both 18°S and 33°S (Fig. 7). However, dipterans are the most frequent visitors at 18°S (ca. 50% of the total flora), while plant visit by hymenopterans and dipterans are very similar in the winter rain site. Plant visit by butterflies are lower than 10% at 18°S and close to 20% at 33°S. Hummingbird (higher at 18°S) and coleoptera (higher at 33°S) are the visitors less represented. These differences in pollinators between summer and winter regions could be related with different biota sources and differences in energetic requirements of the pollinators.

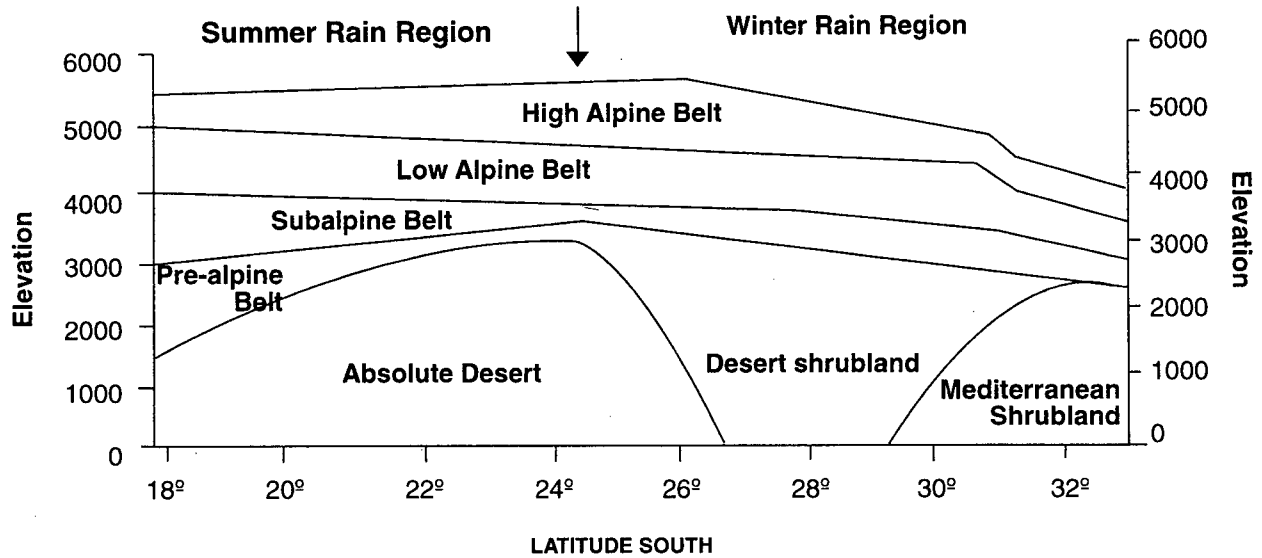


Fig. 5. Vegetation belt on the western side of the northern Chilean Andes (from Squeo et al., 1994).

VI. Ecophysiological patterns

No ecophysiological data are available from the summer rain region in northern Chilean Andes, but information available from the Páramo vegetation in Venezuelan Andes (8°N) could be used as representative of the summer rain region.

Temperature: Temperature plays a role in determining life forms and, in consequence, the physiognomic similitude among vegetation belts. Data from Venezuelan Páramo (8°N, a wet summer rain region close to the Puna) and north-central Chile (30°S) show that tolerance to low temperatures increases with elevation at the same rate as decreases in mean annual temperature (Goldstein et al. 1985; Squeo et al. 1996). That is, plant species growing at higher elevations are more tolerant to low temperatures.

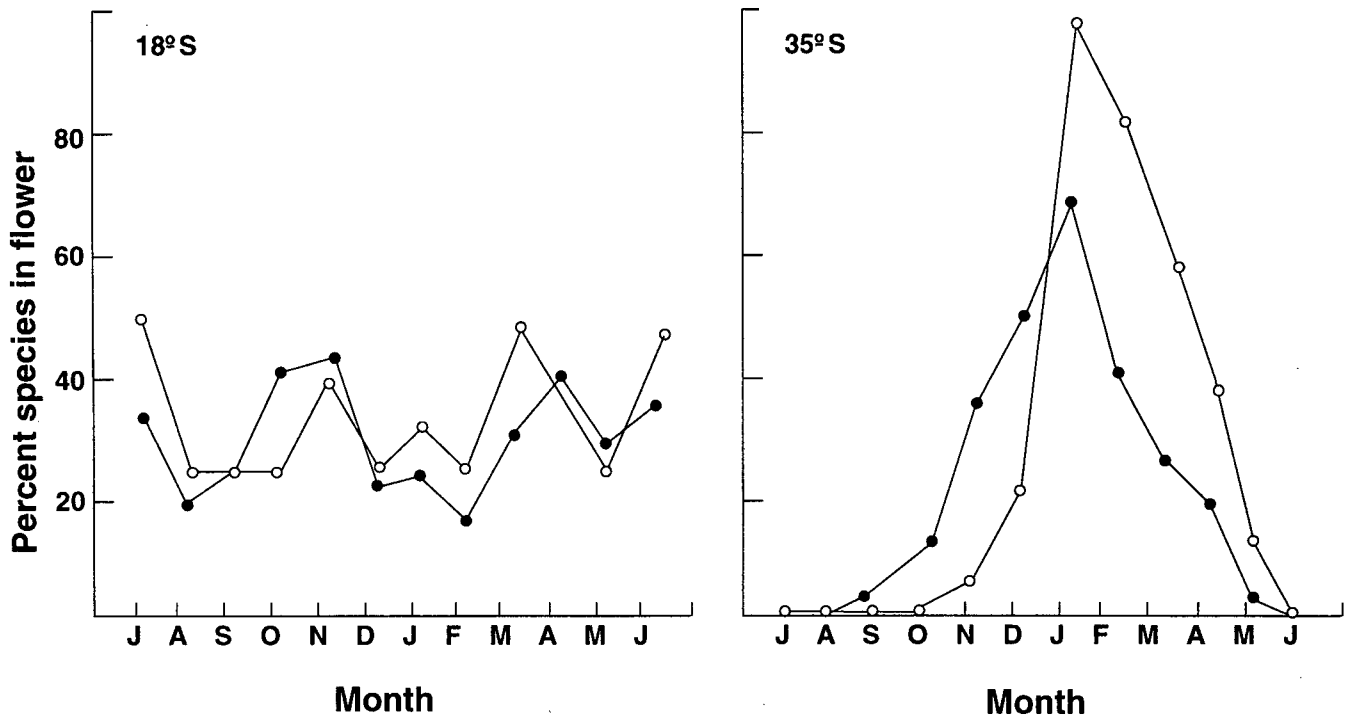


Fig. 6. Percent of species of all families present in flower (solid circles) as compared with percent of Compositae (open circles) in flower at 18°S (3,400 m, 36 spp.) and 33°S (2,500 m, 42 spp.) (from Arroyo et al., 1990)

Temperature and plant height: At the same elevation (4,200 m), plant height and lethal temperature was positively correlated in the Páramo (Squeo *et al.*, 1991). A similar pattern was also found at 30°S, where injury temperature was 2.5°C lower in small plants (< cm height) than in tall plants (Squeo *et al.*, 1996).

Cold resistance mechanisms: Two main cold resistance mechanisms are present in plants inhabiting high mountains: a) freezing avoidance (e.g., supercooling capacity, insulations) and b) freezing tolerance (Rada *et al.*, 1985a, Körner and Larcher, 1988; Scheibe and Beck, 1990; Squeo *et al.*, 1991, 1996). Freezing tolerance provides a best protection to the plants against cold injury, but freezing avoidance, that can endure plants for a few hours, does not decrease their photosynthetic capacity.

Tall species, at both 8°N and 30°S, have supercooling capacity preventing ice formation in their tissues (e.g., *Polylepis sericea*, *Espeletia* spp., *Adesmia hystrix*, *Tetraglochin alatum*); in constrast, all ground-level species have freezing tolerance as main mechanism resistance to cold temperatures (e.g., *Azorella* spp., *Adesmia* spp., *Viola* spp.) (Goldstein *et al.*, 1985; Rada *et al.*, 1985a, 1985b, 1987; Azócar *et al.*, 1988; Squeo, *et al.*, 1991, 1996). This pattern probably exists because during the growing season the lowest, night-temperatures occur at ground-level.

Gas exchange: Similar to found for the Páramo plant species at 8°N (Goldstein and Meinzer, 1983; Rada, *et al.*, in press), shrubs at 30°S showed lower stomatic conductance to water vapor, lower photosyntetic rates and lower water potential than perennial herbs (Table 4). All of the studied species showed a reduction in stomatal conductance to water vapor, closing stomata at midday suggesting that this is a common mechanism to overcome the strong water stress. Plant species at 30°S showed lower water potential than at 8°N.

TABLE 4.
MEAN OF GAS EXCHANGE PARAMETERS FOR SHRUBS AND PERENNIAL HERBS FROM
30°S (3,350 M A.S.L.) (RADA ET AL IN PRESS, SQUEO AND AZÓCAR, UNPUBL DATA.)

n= number of species, g= leaf conductance to watervapor ($\text{mmol m}^{-2} \text{ s}^{-1}$), A= CO_2 assimilation rate ($\mu \text{mol m}^{-2} \text{ s}^{-1}$), Y= Water potential (MPa), Mean $\pm$ SD. In parenthesis are showed maximum values of g and A, and minimum values of Y.

	n	g	A	Y
Shrubs	3	128 $\pm$ 54 (199 $\pm$ 91)	1.4 $\pm$ 0.5 (2.9 $\pm$ 1.2)	-4.3 $\pm$ 0.7 (-5.1 $\pm$ 0.9)
Perennial herbs	4	223 $\pm$ 11 (325 $\pm$ 66)	3.5 $\pm$ 1.0 (5.0 $\pm$ 1.8)	-2.8 $\pm$ 0.5 (-3.6 $\pm$ 0.6)

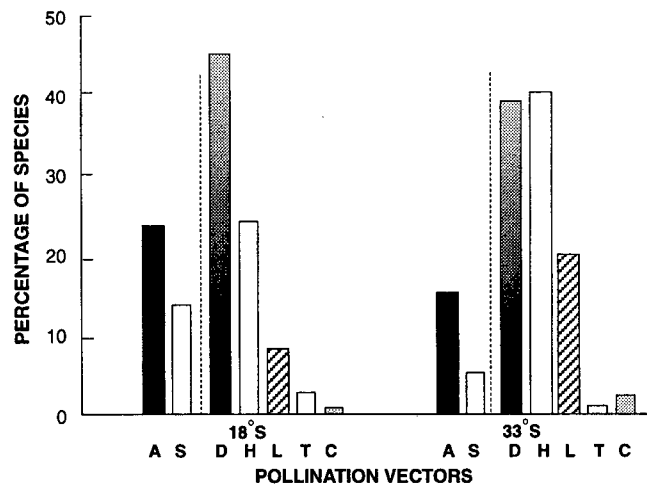


Fig. 7. Pollination mechanisms at 18°S (2,000 - 5,000 m, 128 spp.) and at 33°S (2,200 - 3,900 m, 127 spp.). A= wind pollinated, S= without visits; visited by diptera (D), by hymenoptera (H), by lepidoptera (L), by hummerbird (T) and coleoptera (C) (modified from Arroyo *et al.*, 1987).

VII. Perspectives.

Global Climate Change: According to present global circulation models (GCMs), temperature and precipitation in the earth are changing (Schlesinger & Mitchell, 1987; Stouffer *et al.*, 1989). Arroyo *et al.* (1993) predicted that between 30° and 18°S, the mean annual temperature will be 2.3°C higher in 2030 than in 1958. In the same period the atmospheric CO₂ concentration will be doubled. This increment in mean annual temperature is equivalent to a decrease of 354 m in elevation. What do these temperature changes mean for vegetation? Alpine vegetation would be forced to move 350 m upward in 72 years!. The life spans of many woody species and high-elevation cushion plants extend longer than 72 years.

GCMs also predict a reduction in precipitation at mid-latitudes on the west side of South America in contrast to the global precipitation trend (that would increase between 7 and 11 %) (Schlesinger & Mitchell, 1987). The amount of precipitation and latitudinal limit between summer and winter rain regions will change same than in the past, as discussed in the paleoclimate section. The summer rain region will increase in precipitation and its south limit will extend further than 24°S; in contrast, precipitation in the winter rain region will decrease. Alpine vegetation would have to move several degree of latitude south within 72 years!

The 'simplest' option for any species to cope with rapid global warming, either short-or long-lived, should be that of tracking its preferred temperature and precipitation through migration. Arroyo *et al.* (1993) suggest that the most important factors for a successful migration in a rapidly changing temperature and precipitation environment are dispersal capacity, presence of pollinators in migration sites, and recruitment.

Spatial heterogeneity: Existence of spatial heterogeneity in the Andes Mountains could help to reduce long distance migration's problems. Squeo *et al.* (1993) showed that under the same macroclimatic conditions, different thermal environment are present at 30°S. Thermal refuges (e.g., rocky sites, equatorial facing slopes) are used by tall shrubs while, in areas with snow accumulation in winter, woody cushion species are more abundant. In the Altiplano at 18°S, *Polylepis* forest are also located in rocky sites of equatorial facing slopes, similar to *Polylepis sericea* in the Venezuelan Páramo (Rada *et al.*, 1985a). These thermal differences between polar and equatorial facing slopes also determines differences in phenological and reproductive processes in sub-shrubs from central Chilean Andes at 33°S (Rozzi *et al.*, 1989).

The previous studies on plant species inhabiting northern Chilean Andes have heavily rely on a basic descriptive analysis. New studies and long term monitoring are still essential to know how these changes will affect the high alpine plant communities. Information about most of ecological and ecophysiological mechanisms and processes operating in these communities is still insufficient.

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