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Vegetation and pollen dispersal in the subtropical–temperate climatic transition of Chile and Argentina

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Abstract

The interpretation of the late Quaternary pollen records in terms of palaeoclimate requires an accurate study on the relationship between modern pollen rain, the composition of the source vegetation and climatic factors. We present the results of present pollen rain and its relation to modern vegetation and climate on a trans-Andean transect through the steppe formations that occur between Zapala, Argentina (38°53′S, 70°02′W) and Lonquimay, Chile (38°26′S, 71°15′W). This area constitutes a climatic transition between the westerlies of mid-latitudes and the subtropical eastern circulation. It also represents the easternmost limit of the temperate rain forest and sclerophyllous subtropical forest in Chile and of the westernmost limit of the Monte Desert and Patagonian Steppe formations in Argentina. Systematic sampling of vegetation and superficial soil samples were taken every 100 m along an altitudinal gradient at both slopes of the Andes and isolated samples were taken at the summits of the Cordillera de las Raíces and at the foothills of Lonquimay volcano. Multivariate analysis (cluster analysis and principal components analysis) were applied for 32 pollen samples. Five pollen units were recognized: (1) subdesert shrublands; (2) *Mulinun*-dwarf-shrubland steppe; (3) mid-grass steppe; (4) High Andean and Volcanic scoria steppes; and (5) *Acaena*-shrubland and rhamnaceous thickets. These units were correlated with the vegetation communities, precipitation and temperature. The most important discontinuity in the composition of the pollen rain corresponds to that between the subdesert shrubland and the *Mulinum* steppe, on the eastern end of the transect and the spectra corresponding to the High Andean formations, of the western slopes. This sharp transition in modern vegetation and recent pollen rain lies upon the 71°W longitude, and is possibly determined by the strong differences in distribution and amount of precipitation and temperature.

Keywords: modern pollen; vegetation; climate; trans-Andean transect; South America

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1. Introduction

The palaeoclimatic record found at mid- and high latitudes in the Southern Hemisphere is a valuable source of data to understand the dynamics of global climatic changes in the late Quaternary. Among the proxy-data that may be used as palaeoclimatic indicators, pollen has proven to be one of the most useful, due to its sensibility to climatic change.

This paper presents the results of present pollen deposition and its relation to modern vegetation and climate, with the aim to provide modern analogues to calibrate fossil records. This study focuses on a trans-Andean transect (Fig. 1) along the steppe formations that occur between Zapala, Argentina (38°53′S, 70°02′W) and Lonquimay, Chile (38°26′S, 71°15′W). We selected this study area because of the sensibility of this region to changes in global atmospheric circulation patterns, as it constitutes a transition between the two major climate systems that affect the southern cone of South America: the westerlies of mid-latitudes, and the subtropical eastern circulation (Prohaska, 1976).

The distinct transition between both climate systems is also expressed by the vegetation: in Chile, the temperate rain forest formation gives way to the sclerophyllous subtropical forest; and in Argentina, this area forms the transition between

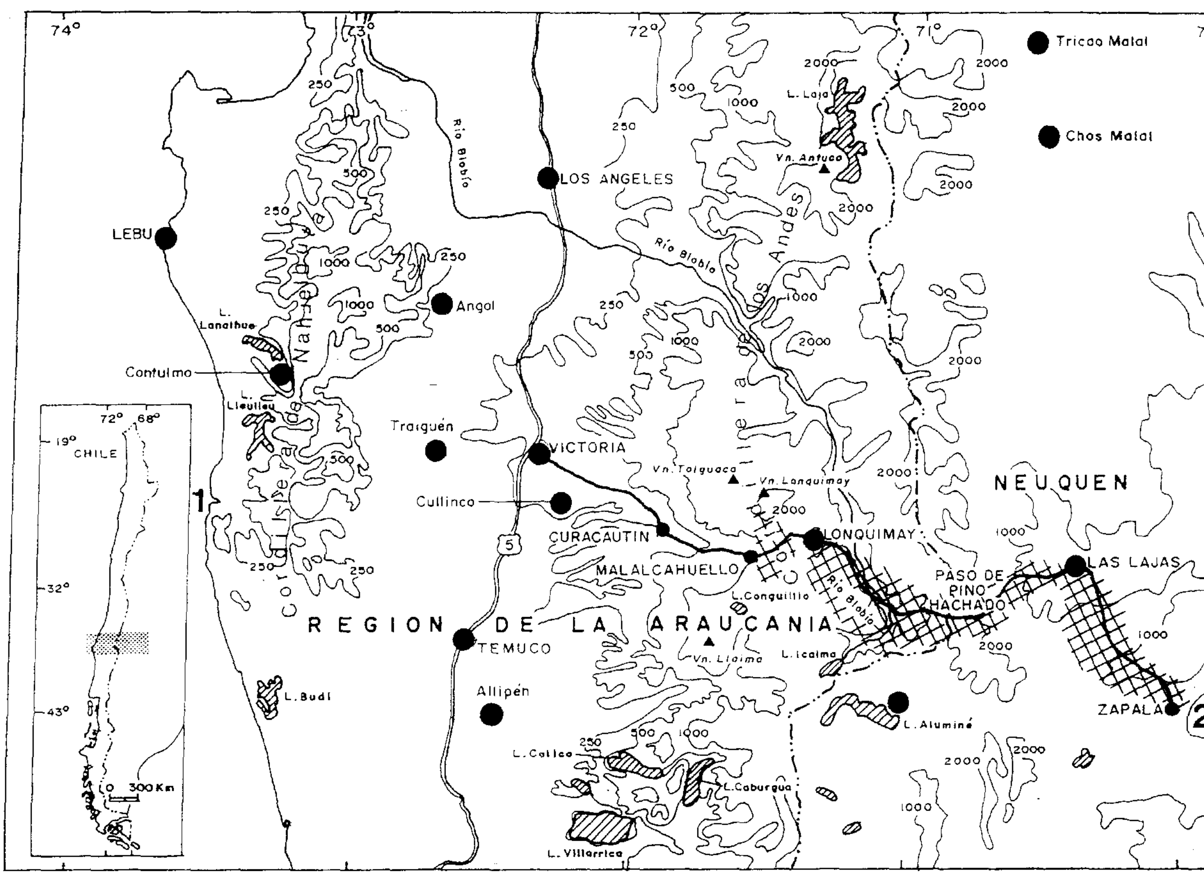

Fig. 1. Study area and transect. Altitudinal levels are shown, and meteorological stations cited in the text are marked with circles. Number 1 refers to two stations at Isla Mocha, 35 km westward of Arauco coast. Number 2 refers to Cipolletti and Cutral-Có stations, 76 and 185 km eastward Zapala, respectively. Stippled zones indicate areas of sampling stations for vegetation and modern pollen rain.

the Monte Desert and Patagonian Steppe formations. Floristically, the area corresponds to the confluence of four major phytogeographical provinces: Patagonian, Monte, Upper Andean and Subantarctic (Cabrera and Willink, 1973; Soriano et al., 1983). Most of the Argentinian sector included in the transect corresponds to the Occidental District (Soriano et al., 1983) and Subandean District (Movia et al., 1982) of the Patagonian Province. Only the eastern border of the transect, between Zapala and Las Lajas, corresponds to the transition towards the Monte Province (Soriano, 1956; Morello, 1958; Ragonese and Piccinini, 1969; Movia et al., 1982). The Chilean–Argentinian border sector and both slopes of the Andes correspond mainly to the Upper Andean Province and include isolated fragments of Subantarctic vegetation, mostly represented by *Araucaria araucana* coppices and *Nothofagus antarctica* thickets.

2. Climate

The major discontinuity in the annual cycle of precipitation in Chile is found at 38°S (Van Husen, 1967). North of 38°S extends the so-called mediterranean zone, with subtropical winter rains; south of this latitude, rains occur year-round in a temperate climate zone. Likewise, in Argentina, the basins of the Colorado and Negro rivers mark the limits of winter rains that originate from the west, and the subtropical summer rains that originate from the east (Prohaska, 1976).

Table 1 shows the temperature and precipitation data available for the study area. In Chile, the importance of topography is evident from the higher levels of precipitation registered at the foothills and the main Cordillera of the Andes. Lower levels of precipitation are registered at Angol and Traiguén stations, which lie downwind from the Cordillera de la Costa (Nahuelbuta, Fig. 1). In comparison, precipitation records in stations with marine influence are somewhat higher. According to Van Husen (1967), this orographic effect is more obvious in the winter rains. It is noteworthy that Lonquimay lies in the upper Bío Bío River Valley, downwind from the high volcanic barrier formed by Tolguaca, Lonquimay and Llaima peaks and the Cordillera de las Raíces (Fig. 1).

The rain shadow effect of the Andes is shown by the considerable decrease in mean annual precipitation registered by Argentinian stations (Table 1). Additionally, a sharp change in precipitation regimes is shown between the Andean region and the Patagonian Plateau, where stations east of the 71°W longitude, register less than 350 mm annually. West of the 71°W longitude, isohyets show an abrupt rise in precipitation, with values up to 1500 mm near the Chilean–Argentinian border (Prohaska, 1976).

Mean annual temperatures (Table 1) are relatively homogeneous along the sea coast and the Longitudinal Valley, with values from 12 to 13°C. These values decrease to 8.6°C at 900 m asl in the Andes, at the Lonquimay station, where mean minimal temperatures between April and October lie between 0.5 and −2.6°C. At this station, snow remains on the ground until November. On the Patagonian Plateau, mean annual temperatures are higher than at Lonquimay (between 11 and 14°C). Annual thermal amplitudes show a sharp east–west contrast, with low values at the sea coast (5–8°C), moderate values along the Longitudinal Valley and the Andean foothills (9–12°C) and high values in both Andean slopes (26–30°C). According to Prohaska (1976), the Argentinian region between 33 and 44°S would be characterized by a maximum difference between extreme annual temperatures, which may exceed 50°C.

3. Material and methods

Systematically the vegetation was sampled at 33 stations from Zapala in Argentina to Lonquimay in Chile. Sampling was done every 100 m along an altitudinal gradient in both Andean slopes. Additionally, isolated samples were taken west of Lonquimay, at the summits of the Cordillera de las Raíces and at the foothills of Lonquimay volcano (Fig. 1).

For each station, a quadrat, with two or three replicates, corresponding to minimal areas (2–8 m^2), was sampled. On each plot, the length and width of each individual plant (except annuals) was

Table 1
Temperature and precipitation at selected stations in the study area (Hajek and Di Castri, 1975; Di Castri and Hajek, 1976; Garleff, 1977; Schäbitz, 1989; Servicio Meteorológico Nacional, 1969, 1985, 1986)

Stations	Latitude S	Longitude W	Altitude (m asl)	Mean annual pp (mm)	Mean annual *T* (°C)	Annual thermal amplitude (°C)
Coast						
I. Mocha W	38°21′	73°58′	20	1372.9	12.6	5.4
I. Mocha E	38°22′	73°54′	30	1260.2	12.7	6.4
Lebu	37°37′	73°40′	20	1302.2	13.0	7.4
Contulmo	38°02′	73°12′	38	1896.1	12.6	8.2
Longitudinal Valley						
Los Angeles	37°28′	72°21′	130	1310.5	13.7	12.4
Angol	37°40′	72°39′	67	933.2	12.8	11.1
Traiguén	38°15′	72°40′	170	1241.2	12.0	6.6
Temuco	38°45′	72°35′	114	1324.8	12.0	9.2
Allipén	39°01′	72°30′	–	2164.6	–	–
Andean Foothills						
Victoria	38°13′	72°21′	360	1329.3	12.4	11.9
Cullinco	38°22′	72°15′	377	1557.9	10.6	10.1
Western Andes						
Lonquimay	30°26′	71°15′	900	1944.6	8.6	13.2
Eastern Andes						
Aluminé	38°22′	71°05′	1150	969.0	8.3	–
Patagonian Plateau						
Las Lajas	38°32′	70°23′	713	210.0	11.8	29.3
Tricao Malal	37°03′	70°20′	1300	331.0	11.8	–
Chos Malal	37°23′	70°17′	848	267.0	13.5	31.7
Cutral-Có	38°57′	69°13′	612	177.0	13.1	29.9
Cipolletti	38°57′	67°59′	265	217.0	13.8	26.1

measured. From these values, the area covered by each taxon was calculated, and it was expressed as a percentage of the total area of the plot (Fig. 2). For annual herbs, the presence of individual plants was registered every 10 cm along 5–10 m transects, with two or three replicates. The frequency of herbs in each transects were expressed as percentage (Fig. 3). Description of the vegetation followed Mueller-Dombois and Ellenberg (1974). Hence, physiognomic units were recognized according to combinations of the dominant life-forms as suggested by the above authors.

To analyse the modern pollen rain at each station, superficial soil samples were taken in each vegetation plot. 32 samples were processed according to standard palynological techniques including HCL, KOH and HF treatment, followed by acetolysis (Kummel and Raup, 1965). Pollen percentages of all taxa were calculated over pollen sums that varied from 300 to 1160 grains per sample, according to conventional and minimal area methods (Bianchi and D'Antoni, 1986). Microscopic analysis revealed 89 pollen taxa. Taxa that reached $\geq 3\%$ are plotted in Fig. 4. Pollen units (pollen assemblages) were defined using cluster analysis (CA), cosine measure, average-linkage methods between groups (UPGMA) and principal components analysis (PCA). In these multivariate analysis were considered all taxa with percentages $\geq 5\%$ in more one sample (Fig. 5). *Rumex*, with high per-

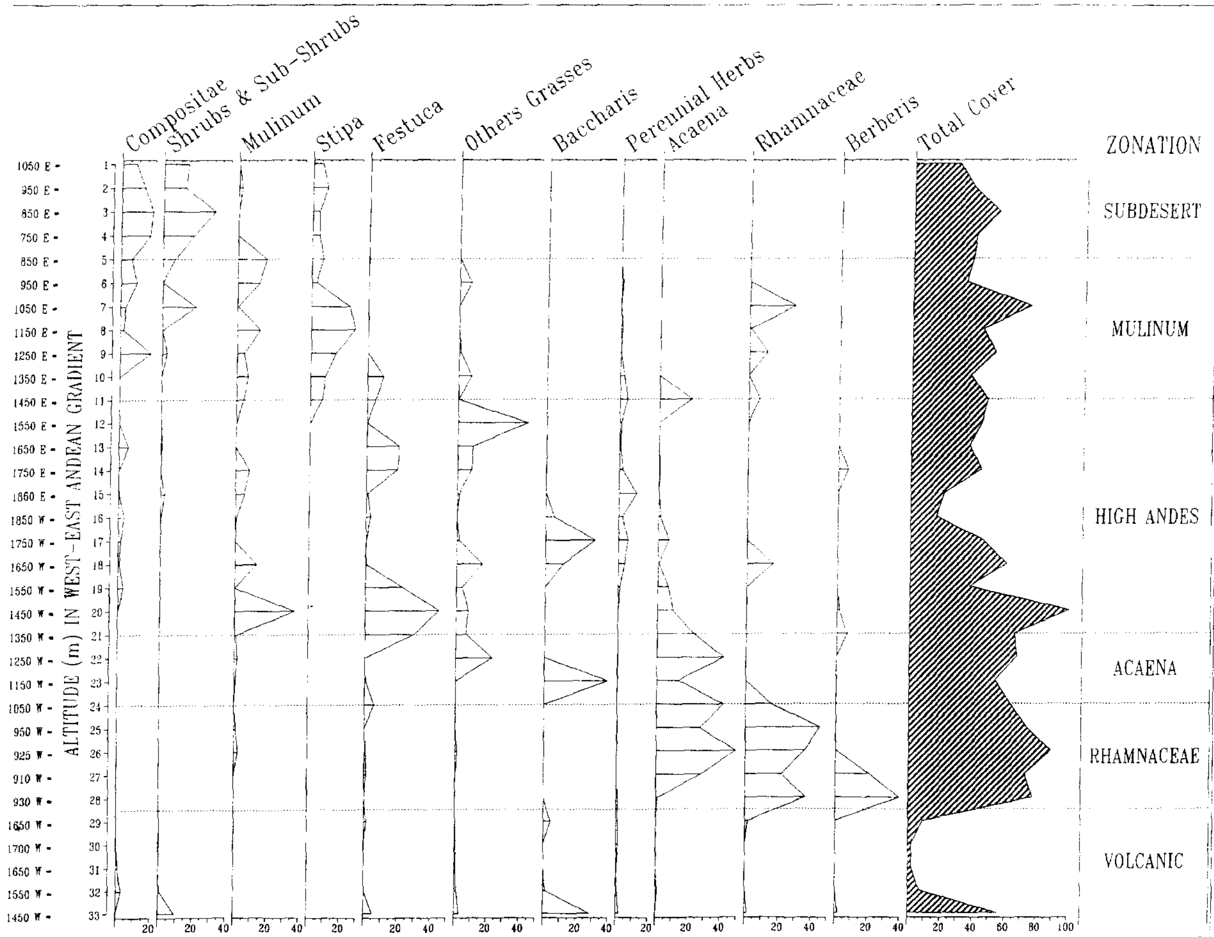

Fig. 2. Percentage cover of dominant perennial taxa and variation of total vegetation cover (hatched) in different steppe formations along a east–west Argentinian–Chilean Andean transect, 38–39°S (*E* = eastern samples; *W* = western samples).

centages in both Andean slopes, was excluded because it reflects anthropogenic disturbance.

4. Vegetation

Figs. 2 and 3 show the altitudinal distribution of the percentages of cover and frequency determined for dominant life-forms and taxa. Considering changes in vegetation physiognomy, and the variation in the abundance and composition of taxa, the following six floristic-vegetational units were established for the area (Figs. 2 and 3).

4.1. *Subdesert shrublands*

This formation corresponds to a transition between the Monte Desert and the Patagonian Steppe, that develops between Zapala and Las Lajas, from 750 to 1050 m elevation. Vegetation is relatively sparse, with cover values ranging from 30 to 40%, exceeded only at intermediate levels, where there is an overlap between the two main formations. Dominant life-forms are xeromorphic shrubs and sub-shrubs with small, resinous leaves. Among the dominant shrubby species are: *Colliguaja integerrima* (up to 20%), *Schinus* aff. *marchandii* (up to 16%) and *Hyalis argentea* (up to

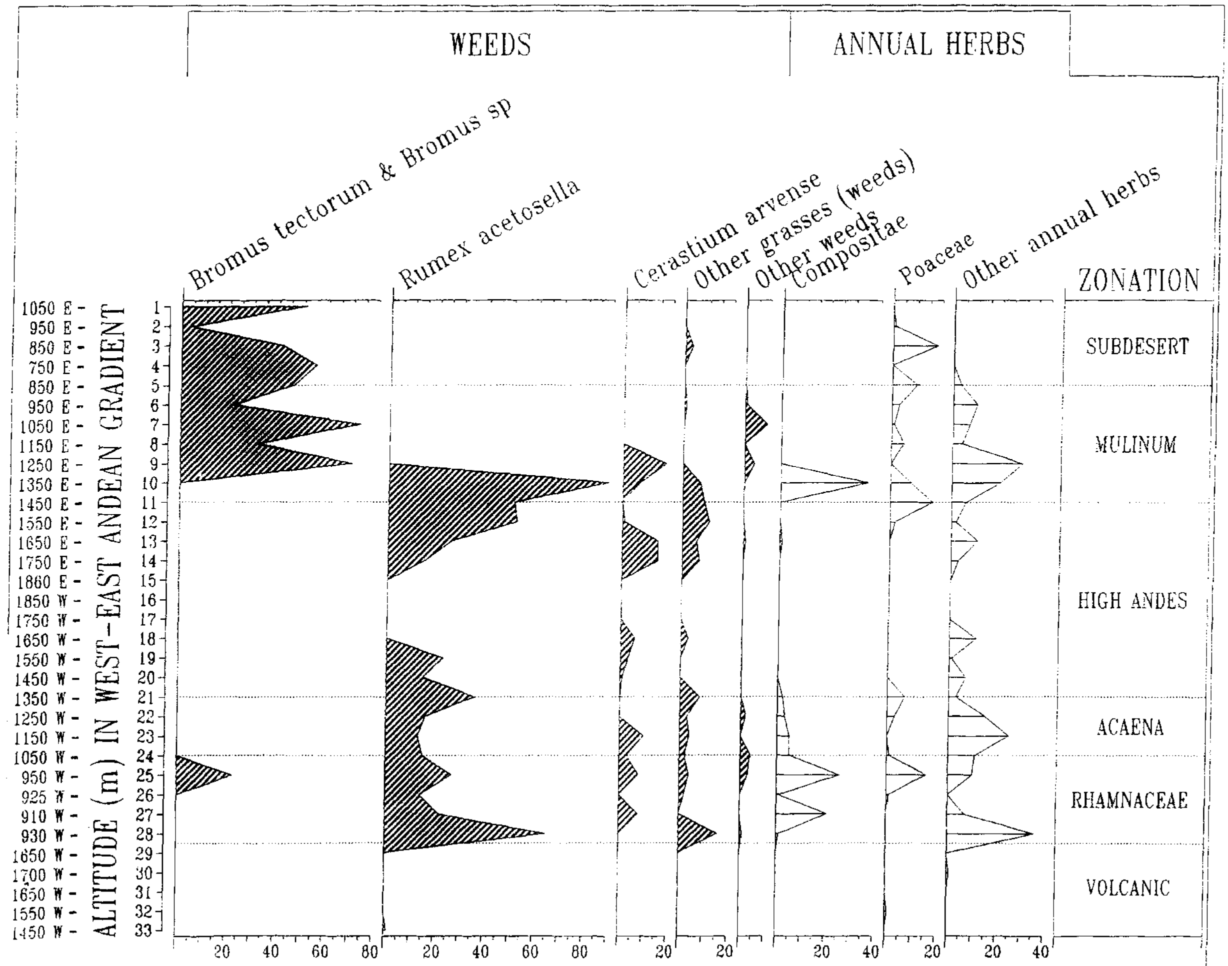

Fig. 3. Variation of the frequency, expressed as percentage, of annual herbs and weeds (hatched) in different steppe formations along a east–west Argentinian–Chilean Andean transect, 38–39°S (*E*=eastern samples; *W*=western samples).

14.5%). The indicator specie for the Monte Desert, *Larrea nitida*, only grows at low elevation (750 m asl) and shows low cover values (2.2%). In contrast, *Mulinum spinosum*, the dominant cushion shrub in the Patagonian Steppe, has a high cover (17%) at the highest level. Among sub-shrubs, Compositae taxa like *Senecio filaginoides* (up to 6%), *Haplopappus pectinatus* (up to 11%) and *Senecio subulatus* var. *erectus* (up to 5%), stand out. As a group, perennial Poaceae do not exceed a 9% cover and are represented mostly by *Stipa speciosa* and *S. neaei*. However, ephemeral annual herbs are represented by several weed species, whose frequency values often reach 20%. Among these, dwarf Poaceae like *Bromus tectorum*, *Hordeum murinum* and species of *Poa* and *Bromus* are dominant.

4.2. *Mulinum-dwarf-shrubland steppe*

Between 850 and 1450 m asl, between Las Lajas and near Pino Hachado, a physiognomically mixed vegetation dominated by perennial Poaceae, dwarf shrubs and therophytes is present. Their cover values are relatively homogeneous, and together they may reach up to 74% cover, corresponding to the maximum values found on the Argentinian side of the transect. Dominant grasses are *Stipa* *speciosa* (up to 27%) and species of *Poa* (up to 8%). Among shrubs, *Colletia hystrix* stands out because of its high cover values (up to 27%). Locally high cover values are also shown by *Fabiana imbricata* (up to 20%) and *Chuquiraga straminea* (up to 12%). Among cushion shrubs, *Mulinum spinosum* stands out for its high cover, which may reach up to 14%. Among sub-shrubs, the Compositae present in the formation described above grow sporadically, and, as a characteristic species *Senecio neaei* (up to 4.4%) makes its appearance. Among perennial herbs *Euphorbia portulacoides* and *Calceolaria* aff. *germanii* stand out for their frequency. At the highest altitudinal level, *Solenomelus segetii, Tropaeolum incisum, Astragalus curvicaulis, A. vesiculosus, Galium araucanum, Perezia pilifera, Leucheria achillaefolia* and *Sisyrinchium* aff. *arenarium* are found. In the carpet of annual ephemeral herbs, a new series of taxa appears, like *Heliotropium paronychioides, Triptilion achilleae, Boopis pozoaeformis* and *Camissonia dentata*. Among weeds, *Erodium cicutarium, Rumex acetosella* and *Cerastium arvensis* may be found. The weedy pygmy grasses found in the formation described above continue to be present.

4.3. *Complex Upper Andean formations*

4.3.1. *Mid-grass steppe of the eastern slopes*

Between 1450 and 1800 m asl, the physiognomy turns steppe-like, with a net dominance of perennial grasses, which reach cover values of up to 43%. There is a relative rise in the cover of perennial herbs of up to 25% and a marked reduction in the cover of shrubs, sub-shrubs and annual herbs. Dominant grasses are species of *Poa* (up to 30%), *Festuca scabriuscula* (up to 20%) and *Chusquea* (up to 13%). Other graminoid forms of lesser importance are: *Bromus setifolius, Poa* aff. *bonariensis, Luzula hieronymi* and *Carex sorianoi*. Perennial herbs are represented mainly by rossete-forming hemicryptophytes like *Acaena splendens, A. pinnatifida, Phacelia secunda* and *Valeriana fonckii*, all of which form cushions. In the ground between shrubs, the herbs *Polygala salasiana, Galium araucanum* and *Vicia bijuga* are frequent. Among annual herbs, the only abundant forms are weeds like *Rumex acetosella* and *Cerastium arvensis*. At 1450 m asl the first discontinuous patches of *Araucaria araucana* trees penetrate the grassy steppe.

4.3.2. *Ñire-cold-deciduous thickets and sedge peat swamps*

From the Pino Hachado Customs Post near the Chilean–Argentinian border (at 1550 m asl), the steppe formation gradually looses homogeneity until it turns into a vegetational mosaic, where sedge peat swamps of Cyperaceae and Juncaceae develop on level surfaces, deep ravines and along water courses. Dense *Nothofagus antarctica* (ñire) thickets, and dwarf shrubs develop in the cold, southerly exposed slopes. Small coppices of *Araucaria araucana* develop on rocky substrates, and patches of grasses cover the more exposed slopes.

4.3.3. *Subnival mat-patches*

Above 1800 m asl on the eastern Andean slopes, and above 1600 m asl on the western slopes, an open subnival formation, dominated by chamaephytes and cushion hemicryptophyes, develops. Shrubs and therophytes are practically absent. The minimal cover values (16–21%) registered for the transect are found in the Chilean–Argentinian border at 1850 m asl. These values rise sharply westward, reaching 60% at 1650 m asl. Among cushion chamaephytes, *Mulinum echinus* (up to 5%), *Baccharis magellanica* (up to 30%) and *Discaria nana* (up to 16%) stand out for their cover values. Low sub-shrubs and grasses are frequent, but they show low cover values. Among the former, several species of *Senecio* stand out. And among the latter, *Festuca scabriuscula, Poa tristigmatica, Rytidosperma virescens, Trisetum* and *Luzula chilensis* are the most important species. In spite of low cover values, the floristic richness of the herbaceous cover is the highest determined along the transect. Cushion plants like *Oreopolus glacialis, Adesmia glomerula, Acaena pinnatifida, A. andina, Pozoa volcanica, Euphorbia portulacoides, Polygala salasiana, Arenaria serpens* and *Quinchamalium gracile* are present. Several species of Compositae, like *Nassauvia lagascae, N. revoluta, Erigeron cinereus* and *Hypochaeris tenuifolia* are among the rossette-forming hemicryptophytes. Other taxa like

Viola cotyledon, *Draba gilliesii*, *Armeria maritima*, *Anemone multifida* and *Loasa pinnatifida* also show this habit. Among geophytes, *Chloraea alpina*, *Rhodophiala andicola* and species of *Sisyrinchium* are frequent.

4.3.4. *Dwarf-shrubland steppes of the western slopes*

On the Chilean slope, between 1600 and 1350 m asl, the physiognomy of the vegetation is again steppe-like, with a marked decrease of the varied perennial herb cushion cover characteristic of the subnival formations. The dominant grass species are *Festuca thermarum* (22–44%) and *Chusquea sp.* (4–8%). Dwarf shrubs are represented mainly by *Mulinum spinosum* (up to 37%), and *Haplopappus prunelloides* (up to 3%). On the lower reaches of the slope, a progressive rise in the cover values of *Acaena splendens* (3–22%) is noteworthy. Among weeds, *Cerastium arvense*, *Rumex acetosella* and *Taraxacum officinale* are frequent. Thus, vegetation cover of these slopes reaches the maximum values determined for the whole transect (99%).

4.4. *Acaena-mixed dwarf-shrubland herbaceous formations*

Between 1350 m asl and the Liucura Border Station at 1050 m asl, a low, even, prairie dominated by *Acaena splendens* cushions develops. These cushions reach cover values of up to 42%, and sparse patches of cushion chamaephytes like *Baccharis magellanica* (up to 39%), and *Discaria trinervis* (up to 15%) are also found. As a group, grasses show low cover values; although *Bromus setifolius* var. *setifolius* may acquire more abundance locally (up to 23%). *Agrostis uliginosa* and *Trisetum* spp. are also frequent. Pygmy annual herbs like *Microsteris gracilis*, *Triptilion achilleae*, *Collomia biflora*, *Madia sativa* and weeds like *Cerastium arvense*, *Rumex acetosella* and *Taraxacum officinale* are very frequent, but show low cover values. The monotony of the landscape, and the abundance of weeds suggests intense grazing pressures.

4.5. *Microphyllous Rhamnaceae thickets*

Between Liucura and Lonquimay, along the upper Bío Bío Valley, at altitudes between 900 and 1000 m asl, a dense, spiny, aphyllous shrub Matorral develops. Total vegetation cover is high, from 73 to 89%, and is basically formed by *Colletia hystrix*, which reaches cover values of up to 36%. However, shrubs like *Berberis buxifolia* and *Discaria chacaye*, together with *Colletia*, may reach values of up to 80%. *Acaena splendens* is the main subcanopy cushion plant. Human-induced disturbances are expressed by the abundance of annual weeds like *Bromus tectorum*, *Verbascum*, *Cerastium arvense*, *Rumex acetosella*, *Trifolium*, *Hypochaeris*, *Geranium*, *Bromus hordeaceus*, *Poa annua*, *Arrhenatherum elatius* and *Holcus lanatus*.

4.6. *Volcanic scoria steppes*

On the Volcanic scoria substrates found on the southern slopes of Lonquimay volcano (1450–1650 m asl) and on the summits of the Cordillera de las Raíces (1650–1700 m asl), open formations of shrubby and grassy steppes, related floristically and physionomically to the Andean formations described above, may be found. Herbaceous and grassy steppes with low cover values (2–9%) are found on the upper levels. Dominant species are: *Poa tristigmatica*, *Festuca thermarum*, *Pozoa volcanica*, *Hypochaeris tenuifolia*, *Nassauvia lagascae*, *Euphorbia portulacoides* and *Senecio poeppigii*. At lower elevation, shrubs like *Baccharis zoellnerii*, *Adesmia emarginata*, *Viola cotyledon*, and *Acaena alpina* reach cover values up to 56%. *Araucaria* and *Nothofagus* forests occur around these formations.

5. Pollen

The analysis of the percentages of the pollen rain (Fig. 4) and the results of the CA and PCA, allowed us to recognize two main groups and five pollen units along the transect (Fig. 5).

Both multivariate analyses divided the samples into two main groups, A and B (Fig. 5). The first

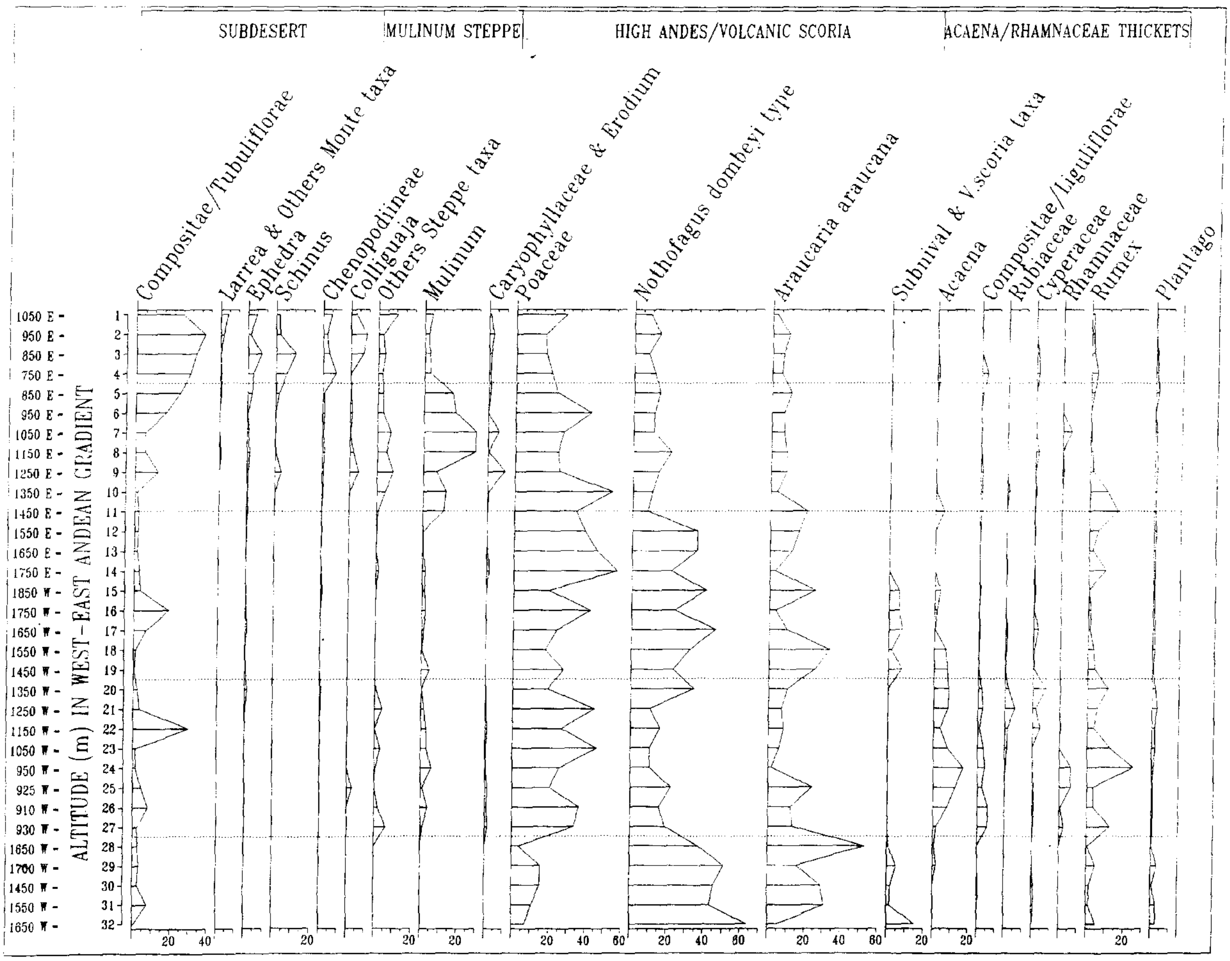

Fig. 4. Pollen percentage diagram along a east–west transect in different steppe formations in the Argentinian–Chilean Andes, 38–39°S. Taxa reaching ≥3% are shown (*E* = eastern samples; *W* = western samples).

four principal components account for 75.23% of the total variance.

Group A can be divided into A1, which corresponds to subdesert shrublands samples, and A2, wich includes the *Mulinum*-steppe samples. Subgroup A1 includes the pollen spectra from 750 to 1000 m altitudinal levels. This subgroup is represented in the first component (32.87% of the variance), the dominant taxa are: *Ephedra, Schinus,* Compositae/Tubuliflorae, Chenopodiineae and *Colliguaja* with high loadings. Only the spectra corresponding to the altitudinal levels near to Zapala present taxa typical of the Monte Desert formation, such as *Larrea, Chuquiraga* and *Prosopis* with values of 4% (Fig. 4). Subgroup A2 represents the *Mulinum*-dwarf-shrubland steppe unit. It includes the pollen spectra from 850 to 1450 m asl along the eastern slopes. This is mainly represented in the third component (12.54% of the variance) with *Mulinum* and Poaceae, and in the fourth component (8.88% of the variance) with *Mulinum, Colliguaja* and Rhamnaceae with high loadings. Fig. 4 shows that in addition to the taxa with high PCA loadings in both subgroups, Caryophyllaceae and *Erodium* and other steppe taxa like *Verbena, Nassauvia, Fabiana, Adesmia* and *Lycium* also occur.

Group B shows three subgroups: B1 and B2, which represent Upper Andean spectra, and the B3 subgroup, which represents *Acaena* shrublands

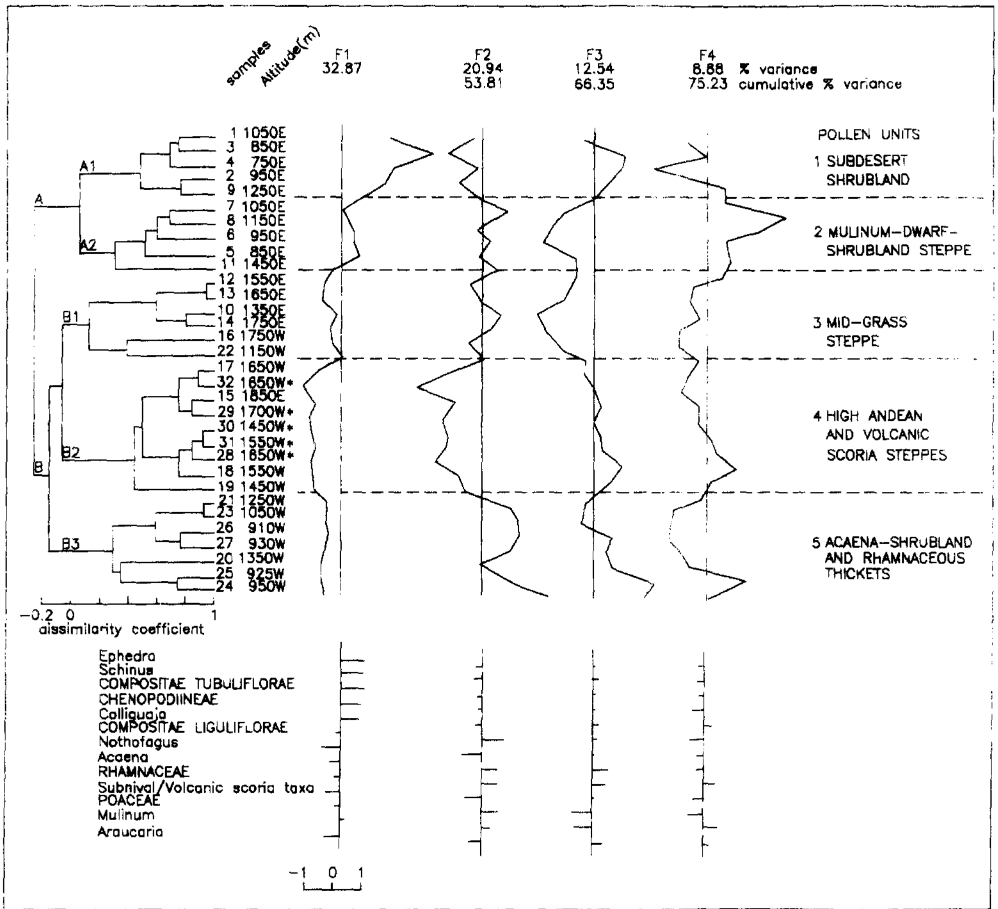

Fig. 5. Dendrogram, principal components analysis, and pollen units of 32 pollen samples along a east–west transect in the Argentinian–Chilean Andes, 38–39°S. The loadings of the pollen taxa on each of the principal components are given (E = eastern samples; W = western samples; * = pollen spectra from Volcanic scoria steppes at Volcán Lonquimay and Cordillera Raíces).

and Rhamnaceae thickets of the western slope. Subgroup B1 includes the spectra from Upper Andean mid-grass steppe from 1350 to 1750 m asl, on the eastern slope, and spectra of 1150 and 1750 m asl on the western slope. This subgroup is represented in the third component (12.54% of the variance) dominated by Poaceae, with the highest values determined along the transect (40–60%, Fig. 4). Subgroup B2 includes the High Andean pollen spectra, above 1800 m asl on the eastern slopes, above 1450 m asl on the western slope, and the samples from Volcanic scoria steppes. This is mainly represented in the first and second component (32.87 and 20.94% of the variance, respectively), with *Araucaria*, *Nothofagus* and Subnival/Volcanic scoria taxa (*Pozoa*, *Oreopolus*, *Polygala*, *Viola–Azara*, *Embothrium*, *Lomatia*, *Alstroemeria*, among others) with high loadings. High Andean herbaceous taxa are underrepresented in the pollen rain spectra (up to 7%, Fig. 4). In the pollen spectra from vegetation on Volcanic scoria, arboreal taxa of local significance are dominant, except for the highest altitudinal levels taken from Volcán Lonquimay, where *Nassauvia* represents 10% (Fig. 4). The samples of subgroup B3 include the spectra of the lower altitudinal slopes of the western Andes and Bío Bío Valley from 900 to 1350 m asl. This subgroup is represented in the last three components with Compositae/Liguliflorae, *Acaena*, Rhamnaceae and Poaceae with high loadings. Above 1000 m asl these taxa are associated with Rubiaceae, Cyperaceae, *Mulinum*, *Plantago* and Compositae/Tubuliflorae (Fig. 4).

6. Discussion

The strong east–west vegetational changes reflect a marked gradient of precipitation and temperature. This gradient is reflected in the sequence of vegetation formations along the transect. The most important discontinuity in the composition of the pollen rain corresponds to that between the subdesert shrubland and the *Mulinum* steppe on the eastern end of the transect (below 1450 m), and the spectra corresponding to the High Andean formations on the western slopes. The limit between both groups represents phytogeographically the limit between the Patagonian and Upper Andean provinces (Cabrera and Willink, 1973). This limit lies at 71°W longitude and coincide with the main climatic discontinuity in the study area: (a) the zone east of 71°W, with low and all-year-round precipitation and mean annual temperatures from 11 to 14°C; and (b) the zone with mean annual temperatures from 8 to 9°C and a strong seasonal and geographical precipitation gradient, with mean annual values that rise drastically to the west of 71°W (from 350 to ca. 1500 mm on the Andean summits and ca. 2000 mm on the western end of the transect; Prohaska, 1976). Similar results have been obtained by Paez et al. (1994a) in an analysis of the pollen dispersal along a trans-Andean transect at 42–44°S. In that study, the main discontinuity shown by the pollen spectra also is between the Monte Desert and Patagonian Steppe formations to the east, and the High Andean and temperate rain forests formations to the west.

The results of the multivariate analysis of the pollen rain evidence that the five recognized pollen units are strongly correlated with the vegetation communities along the transect. Below we discuss the degree to which the pollen units are related to the different vegetation formations and climatic conditions.

6.1. Pollen spectra of the subdesert shrubland (pollen unit 1)

The pollen spectra on the eastern portion of the transect, between Zapala and Las Lajas (750–1050 m asl), are dominated by shrubby and sub-shrubby taxa like *Ephedra*, *Schinus*, Compositae/Tubuliflorae, Chenopodiineae and *Colliguaja*, and show low values for Poaceae. They relate to a mean annual precipitation above 200 mm, and a mean annual temperature of around 11.8°C. Similar pollen spectra, reflecting similar climatic conditions, have been described for the Central District of the Patagonian Steppe, between 42 and 44°S (Paez, 1991; Paez et al., 1994a). Even though Soriano et al. (1983) have established the distribution of the Central District south of 40°S, our results show that the northeastern limit of this community lies further north in the study area, above 800 m.

The pollen samples near Zapala, on the eastern end of the transect, show low values for some typical Monte taxa like *Larrea*, *Chuquiraga* and *Prosopis*. Similar pollen spectra have been interpreted as showing the transition between the Monte Desert and the Patagonian Steppe formations (Stutz, 1992; Paez et al., 1994b). On the study area the western limit of the Monte Desert lies about 30 km east of Zapala, and extends from an altitude of 800 m to the Atlantic Ocean. This formation is associated to a mean annual precipitation ≤200 mm and mean annual temperatures above 13°C.

6.2. Pollen spectra of the Mulinum-dwarf-shrubland steppe (pollen unit 2)

The pollen samples that characterized this unit were taken west of Las Lajas, from 850 to 1450 m asl on the eastern slope of the Andes. They are dominated by *Mulinum* and Poaceae. They are similar to those that have been published from 38 to 44°S (Paez, 1991; Stutz, 1992; Schäbitz, 1994) and interpreted as corresponding to the vegetation of the Occidental District of the Patagonian Province. They are associated to a mean annual precipitation ≥400 mm and a mean annual temperature of 8°C. According to Soriano et al. (1983), the vegetation of the Occidental District is dominated by several species of *Stipa* and by the invasion of *Mulinum spinosum* in overgrazed sectors. However, palynological data (Paez, 1991, 1993) show that the grass/*Mulinum* association is older than 5000 yr B.P.

6.3. Pollen spectra of the Upper Andean formations and Volcanic scoria steppes (pollen units 3–4)

The uppermost belt of both Andean slopes, above 1300 m asl, show pollen spectra dominated by Poaceae (pollen unit 3). They correspond to the change from the *Mulinum* shrubby steppe to the grassy steppe and represents the mid-grass steppe units. The replacement of *Stipa* species by *Festuca* species represents the western limit of the Patagonian Steppe formation (Soriano, 1956); but according to Movia et al. (1982) this grassy steppe corresponds to the Subandean District. This replacement is documented by the vegetation analysis, but not by the recent pollen rain, because it is not possible to distinguish between taxa within the Poaceae. Even though, it is possible to set apart both pollen units by the dominance shown by the Poaceae, and the decrease of *Mulinum* in the Upper Andean formations. Climatic data show a marked increase in precipitation (1000–2000 mm) on the higher Andes (Prohaska, 1976).

The pollen samples collected in the Subnival formations on the summits, as well as those from the Volcanic scoria steppes west of the village of Lonquimay (pollen unit 4), are characterized by high percentages of *Nothofagus* and *Araucaria* pollen. Even though both taxa occur discontinuously in ecologically suitable sites in the Upper Andean formations, their overpresentation in the pollen rain obscures the representation of the highly diverse herbaceous Andean flora. Two facts may account for this: (1) the increasing influence of the westerlies, that does increase pollen supply from the forests that lie west of the transect; and (2) the low cover values shown by subnival vegetation that allow for a relatively important effect of pollen supplied by long-distance transport compared to locally produced pollen. Both facts have been accounted for in the Coastal Range (Carrillo, 1990) and in the Altiplano (Graf, 1986).

6.4. Pollen spectra of the Acaena-shrubland and rhamnaceous thickets (pollen unit 5)

The pollen spectra of the lower western Andean belt, from 900 to 1350 m asl, are characterized by *Rumex* (probably *R. acetosella*), Rhamnaceae, Compositae/Liguliflorae (probably species of *Hypochaeris* and *Taraxacum*), *Acaena* and Poaceae. The dominance of the spiny chamaephyte *Acaena splendens* and of weeds in the present-day vegetation suggests anthropic disturbance and overgrazing in the sector. The record from Lonquimay station shows mean annual precipitation values around 1945 mm, and mean annual temperatures around 8.6°C. The vegetation corresponds to the transitional formation towards the temperate *Nothofagus* and Coniferous rain forests that lie to the west.

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