

Zeitschrift: Candollea : journal international de botanique systématique = international journal of systematic botany

Herausgeber: Conservatoire et Jardin botaniques de la Ville de Genève

Band: 53 (1998)

Heft: 2

Artikel: A chorological analysis of the mountains from Central Argentina : is all we call Sierra Chaco really Chaco? ; Contribution to the study of the flora and vegetation of the Chaco : XII

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DOI: <https://doi.org/10.5169/seals-879495>

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A chorological analysis of the mountains from Central Argentina.
Is all what we call Sierra Chaco really Chaco?
Contribution to the study of the flora and vegetation
of the Chaco. XII.

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ABSTRACT

CABIDO, M., G. FUNES, E. PUCHETA, F. VENDRAMINI & S. DIAZ (1998). A chorological analysis of the mountains from Central Argentina. Is all what we call Sierra Chaco really Chaco? Contribution to the study of the flora and vegetation of the Chaco. XII. *Candollea* 53: 321-331. In English, English and Spanish abstracts.

The aim of the study is to provide a chorological interpretation of the mountains in Central Argentina in order to establish its actual phytogeographic position and to discuss the status of the Sierra Chaco District within Argentina. A subdivision of the regional flora (more than 600 species) into 6 chorotypes (phytogeographic groups or categories) and the classification and ordination of 20 sites along an altitudinal gradient (1000 to 2600 m) on the basis of chorotypes frequencies are presented. The classification analysis shows that the sites are grouped according to their chorotype frequencies into two main clusters comprising sites above and below 1850 m respectively. It is discussed whether sites above that boundary belong to the Chaco Phytogeographic Province or should be included in a different unit.

RESUMEN

CABIDO, M., G. FUNES, E. PUCHETA, F. VENDRAMINI & S. DIAZ (1998). Análisis corológico de las montañas del centro de Argentina. Es todo lo que llamamos Chaco Serrano realmente chaqueño? Contribución al estudio de la flora y vegetación del Chaco. XII. *Candollea* 53: 321-331. En inglés, resúmenes en inglés y en español.

El objetivo de este trabajo es realizar un análisis corológico de las montañas del centro de Argentina con el propósito de establecer su posición fitogeográfica y discutir el alcance del Distrito Chaqueño Serrano en Argentina. La flora regional (más de 600 especies) es subdividida en 6 corotipos (categorías fitogeográficas) y, en base a la frecuencia de corotipos, se clasifican y se ordenan 20 sitios ubicados a lo largo de un gradiente altitudinal entre 1000 y 2600 m de altitud. El análisis de clasificación muestra que los sitios se agrupan, de acuerdo a sus frecuencias de corotipos, en dos grupos principales que incluyen sectores por arriba y por debajo de 1850 m, respectivamente. Se discute si los sitios por arriba de ese límite altitudinal pertenecen a la Provincia Fitogeográfica Chaqueña o si deberían ser incluidos en una unidad fitogeográfica diferente.

KEY-WORDS: Phytogeography – Chorotypes – Chaco Phytogeographic Province – Sierra Chaco District.

Introduction

In a recent contribution to the study of the flora and vegetation of the Chaco Phytogeographical Province of South America, PRADO (1993a) highlighted the need for a phytogeographical redefinition of the Gran Chaco. This extended territory occupies nearly 1.000.000 km² and includes plant communities with taxa of markedly different lineages (PRADO, 1993b). The most accepted concept of the Chaco Phytogeographical Province before Prado's contributions was that of CABRERA (1976), who simply equated the Chaco Province with the Chaco Geographical Region (PRADO, 1993a, b). Cabrera subdivided the Chaco into four main Districts within Argentina: Eastern, Western, Sierra (Mountain) and Savanna Chaco.

After his exhaustive revision, PRADO (1993a, b) presented a new map of what he called the Chaco *sensu stricto*, and concluded that some plant communities previously included in the Chaco Phytogeographical Province should no longer be regarded as chaquenian and some others should be considered as transitional. Although the changes introduced by Prado in his redefinition of the Chaco mostly involved the Eastern District, he pointed out that some Sierra Chaco communities (*Polylepis australis* woodlands occurring in the mountains from central and north-western Argentina) should also be excluded from the Chaco *sensu stricto*.

Floristic knowledge of the Sierra Chaco was limited by the time CABRERA (1951) first published his phytogeographic map of Argentina. Therefore, and regardless of changes in floristic composition through altitudinal gradients, most of the mountains located within the Chaco Geographical Region in central and northwestern Argentina were wholly included in the Sierra Chaco. The Sierra Chaco was further subdivided by different authors (SAYAGO, 1969; LUTI & al., 1979; VERVOORST, 1982) into vegetation belts (mountain woodland, shrubland and grassland) but its chaquenian status was not discussed. As phytosociological data became available in the last two decades, evidence emerged supporting the idea that plant communities above ca. 1800 m should no longer be regarded as chaquenian. Moreover, FUNES & CABIDO (1995) stressed the importance of Andean taxa in floristic lists from outcrop communities above 1900 m in the mountains from central Argentina. Similar findings have also been reported for reptiles (di TADA, SALUSO & MARTORI, 1984) and birds (NORES, IZURIETA & MIATELLO, 1983).

The aim of this paper is to provide a chorological interpretation of the vegetation of the Córdoba mountains in central Argentina, in order to establish its actual phytogeographical position. A subdivision of the regional flora into six chorotypes (phytogeographic groups or categories) and the classification and ordination of 20 sites along an altitudinal gradient on the basis of chorotypes frequencies are presented. It is predicted that the chorotypes frequencies will vary along the gradient and that the vegetation of the upper sites is not actually chaquenian.

Materials and Methods

Study area

The mountains of Córdoba Province occupy a vast area of more than 50.000 km² lying west to the Argentine "pampas" (between 29°30'-33°30'S and 63°40'-65°20'W) (Figs. 1 and 4). Its altitude ranges from 800 to 2600 m with Mt. Champaqui (2790 m) being the highest peak. Most of the area is metamorphic but granitic batholiths ("horsts") delimited by regional N-S oriented faults also occur. Steep slopes alternate with plateaus dissected by deep ravines with rivers. The formation of this mountain began in Pre-cambrian time (granite was intruded during the early Paleozoic), and it was re-activated through tectonic movements during the Tertiary (Andean orogeny) and even the Quaternary period.

Mean annual temperature is 14°C at lower altitudes (Ascochinga Station) and 8°C at 2100 m (La Ventana Station), where frosts are likely to occur during the whole year. Temperatures are perhaps lower at 2600 m but no data are available. Annual precipitation is 750-970 mm and most

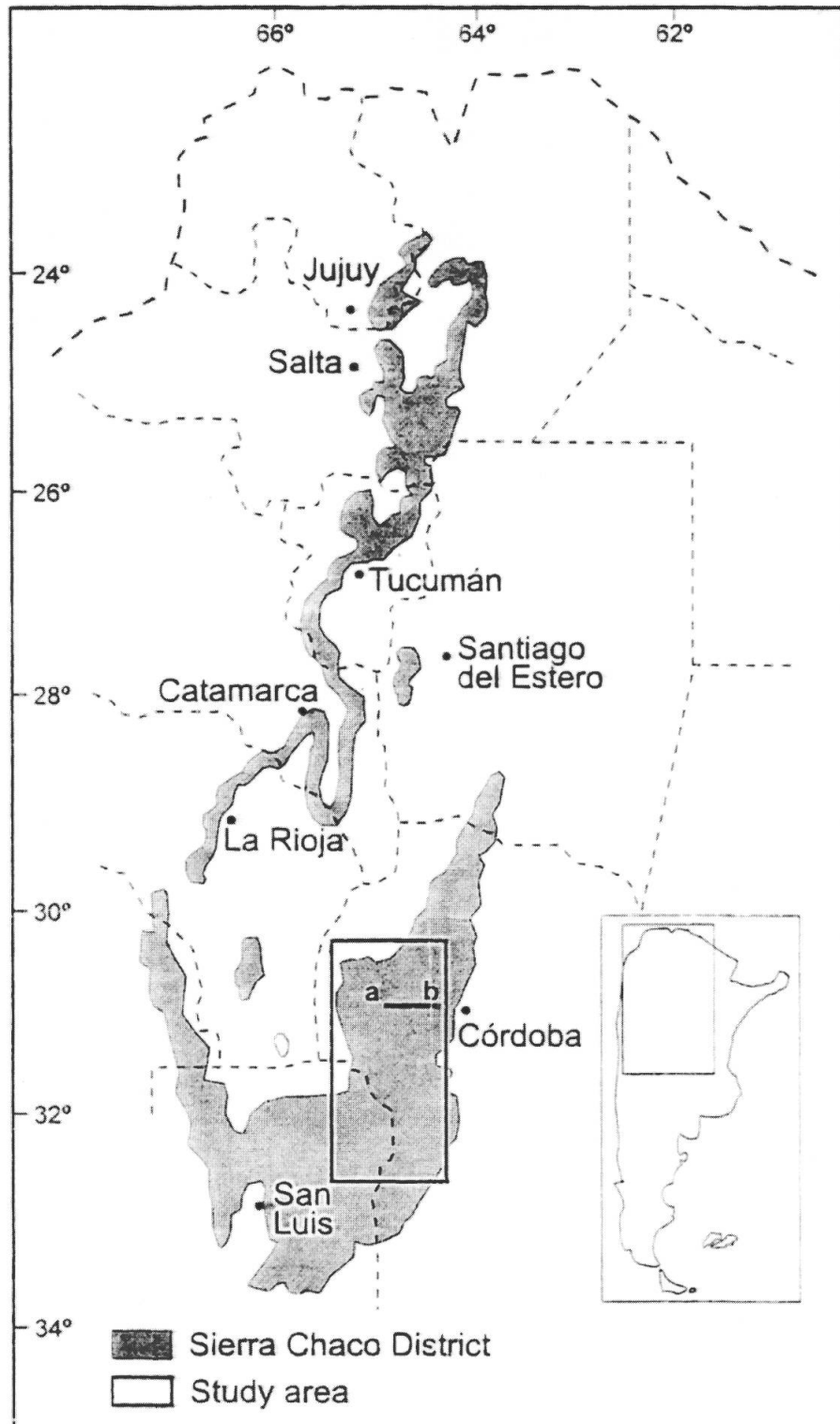


Fig. 1. – Map showing the location of the study area in Argentina. **a-b** indicates the location of the profile in Fig. 4. Boundaries of the Sierra Chaco District according to RAGONESE & CASTIGLIONI (1970).

of it falls during late spring and summer (November to March) (FUNES & CABIDO, 1995). At higher altitudes the formation of ice needles in the soil has been reported by CABIDO, BREIMER & VEGA (1987). There is general agreement about the occurrence of periglacial climatic events during the Pleistocene, though the whole area was ice-free during major glaciations (CAPITANELLI, 1979).

The vegetation of Córdoba Province was described by KURTZ (1904) and LUTI & al. (1979). More detailed descriptions of mountain plant communities were provided by CABIDO (1985), CABIDO & ACOSTA (1985, 1986), CABIDO & al. (1991) and FUNES & CABIDO (1995). The main vegetation belts are, from lower to higher altitudes, mountain woodland (700 to 1200 m), mountain shrubland (1000 to 1500 m) and mountain grassland (1000 to 2600 m). Though not considered as a vegetation belt, *Polylepis australis* woodland occur at higher altitudes than the mountain woodland upper boundary. While grasslands at lower altitude are dominated by Subtropical grass genera, above 1900 m Andean taxa predominate and the physiognomy of the vegetation strongly resembles that of the high Andean meadows (KURTZ, 1904). According to CABRERA (1976) the whole area belongs to the Sierra Chaco District within the Chaco Phytogeographical Province.

Data analysis

The chorological analysis was based on the occurrence of vascular plant species in 20 sites along an altitudinal gradient from 1000 m to 2600 m. The data base of species distribution was based on previous phytosociological studies by CABIDO (1985), CABIDO & ACOSTA (1986), CABIDO, ACOSTA & DIAZ (1989 and 1990), CABIDO & al. (1991) and FUNES & CABIDO (1995). The species were grouped into phytogeographical categories (chorotypes) and the frequencies of the different chorotypes calculated for each site. The chorotypes were derived from KURTZ (1904), de La SOTA (1973) and LUTI & al. (1979). They include 6 categories:

- 1) Andean or upper montane chorotype. Species included in this category are most frequent at higher elevations in the mountains of north-western Argentina and some of them also in Andean habitats of neighbouring countries (Perú and Bolivia). Examples of this chorotype are: *Azorella biloba* Wedd., *Alchemilla pinnata* R. & P., *Gentiana prostrata* Haenke, and *Polylepis australis* Bitt.
- 2) Lower montane chorotype. Includes species distributed at low altitudes (lower than 1500 m) in extra-Andean Mountains of central and north-western Argentina and Bolivia. Although some of the species are also likely to occur in the lowlands surrounding the mountains, the decline in number is pronounced as altitude decreases. Examples are: *Lithraea ternifolia* (Gill.) Barkley, *Aristida achalensis* Mez., *Stipa tenuissima* Trin., and *Festuca hieronymi* Hack.
- 3) Southern-brasilian chorotype. It includes species widely distributed through the lowlands of central and north-eastern Argentina, and the adjacent territories of Paraguay, Brasil and Uruguay. They may also reach the mountains but sharply decline in number above 1500 m. Examples of this chorotype are: *Axonopus fissifolius* (Raddi) Kuhlman, *Eryngium horridum* Malme, *Baccharis coridifolia* DC., and *Vernonia incana* Less.
- 4) Western Chaquenian chorotype. It includes species distributed mainly through the dry Chaco lowland territories of central and north-western Argentina. Some of these taxa are also present in the Monte Phytogeographical Province. Examples of this chorotype are: *Cottea pappophoroides* Kunth, *Pappophorum caespitosum* Fries, and *Capsicum chacoense* A. T. Hunz.
- 5) Patagonian chorotype. Species characterized by ranges extending over the whole Patagonian Phytogeographical Province, both in Andean and extra-Andean habitats. Examples of this chorotype are: *Geranium magellanicum* Hook., *G. patagonicum* Hook., *Sisyrinchium chilense* Hook., and *Sisyrinchium valdivianum* Phil.

- 6) Cosmopolitan and Subcosmopolitan chorotype. It includes species with very broad ranges (all the Americas, Europe, Asia, etc.). Introduced species are also included in this category. Examples of this chorotype are: *Cirsium vulgare* (Savi) Tenore, *Rumex acetosella* L., *Cerastium arvense* L., and *Conyza bonariensis* (L.) Cronquist.

The geographic ranges of the species involved in this study were determined according to the localities at which the species have been recorded (extent of occurrence according to GASTON, 1991). The information about the distribution ranges of plant species was derived from regional floras and from many other publications containing maps or other distribution data. Specimens from the herbarium of the Córdoba National University were used as an extra source of information. Species were assigned to chorotypes established a priori. Since reliable distribution maps are not available for most of the species, it is not yet possible to create groups of species with similar distributions in a completely objective way (that is through numerical analysis of distribution maps). NIMIS (1984) and NIMIS & al. (1995) have discussed this topic. It is worth noting that one of the main reasons why NIMIS & al. (1995) were able to divide the Putorana flora into objectively derived chorotypes was the existence of a reliable flora as a basis for quantitative phytogeographic analysis.

In order to obtain clusters of sites with similar phytogeographical features, the matrix of chorotypes frequencies \times sites along the altitudinal gradient was subjected to numerical classification using average linkage clustering (JONGMAN, TER BRAAK & VAN TONGEREN 1995). The matrix was also ordinated through detrended correspondence analysis (DCA; HILL & GAUCH, 1980), and DCA I and II scores for the 20 sites were correlated to chorotypes frequencies using the Spearman Correlation Coefficient (FOWLER & COHEN, 1992).

Results

The chorotype frequencies for each study site along the altitudinal gradient in Central Argentina are presented in Table 1. The Andean chorotype increases with altitude, with sites above 2000 m displaying a maximum relative importance of this chorotype (frequencies higher than 35%), and with sites below 1900 m showing intermediate to low frequencies as altitude decreases. In contrast, the Southern Brazilian chorotype is most important at lower altitudes with frequencies up to 64 %. The remaining chorotypes do not show a clear-cut affinity to a particular altitudinal level, although the Lower Montane chorotype shows higher frequencies at intermediate to lower elevations (1400 to 1200 m).

The results of the DCA performed on the 20 altitudinal sites and 6 chorotypes matrix are shown in Fig. 2. The ordination of sites along the DCA axis I reflects a regular left to right increase in altitude from about 1000 m to 2600 m. DCA axis I is significantly correlated with altitude ($r = .94$; $n = 20$; $p < .001$), Andean chorotype frequencies ($r = .94$; $n = 20$; $p < .001$), and Southern Brazilian chorotype frequencies ($r = -.87$; $n = 20$; $p < .001$). DCA axis II is probably associated to local changes in composition (substrate, rockiness) and is significantly correlated to the Lower Montane chorotype ($r = -.71$; $n = 20$; $p < .001$).

A more precise picture of the chorological structure of the study area is given by the chorogram obtained by classification of the sites \times chorotype frequencies matrix (Fig. 3). Two main clusters are formed: 1) sites located over 1900 m; 2) sites at lower elevations. The latter can be further subdivided into two main subgroups, each one including sites at similar altitudes.

Cluster 1: comprises sites in the 1900-2600 m elevation interval. More widespread plant communities are low and tall grasslands, shrublands and low woodlands, dominated respectively by *Deyeuxia hieronymi* (Hack.) Türpe, *Poa stuckertii* (Hack.) Parodi, *Alchemilla pinnata* R. & P., *Muhlenbergia peruviana* (Beauv.) Steud., *Festuca circinata* Gris., *Berberis hieronymi* Schneider, *Polylepis australis* Bitt., and other species, gene-

	A	LM	SB	WCh	P	C
1	3	21	65	—	—	11
2	2	25	60	—	4	9
3	3	18	59	—	4	15
4	1	20	64	—	3	11
5	12	16	59	2	4	8
6	9	24	58	—	—	9
7	8	20	60	2	2	8
8	20	13	50	2	4	11
9	18	21	50	1	1	8
10	12	20	56	2	2	8
11	19	10	45	1	5	18
12	17	20	50	1	—	10
13	16	9	55	1	1	17
14	17	8	50	1	7	15
15	20	13	47	1	3	15
16	44	6	24	—	6	19
17	35	14	31	—	4	14
18	40	23	28	—	1	7
19	35	8	30	1	5	20
20	36	20	25	—	4	15

Table 1. — Percentages of chorotypes in floristic lists of 20 sites along an altitudinal gradient in the mountains of Córdoba, Central Argentina. The digits were rounded, therefore the sum of the percentages is not always reaching 100. References for chorotypes: **A** = Andean; **LM** = Lower montane; **SB** = Southern-brasilian; **WCh** = Western chaquenian; **P** = Patagonian; **C** = Cosmopolitan and subcosmopolitan. **1** to **8** are sites between 1000 and 1450 m altitud; **9** to **15** between 1500 and 1850 m; **16** to **20** between 1900 and 2600 m.

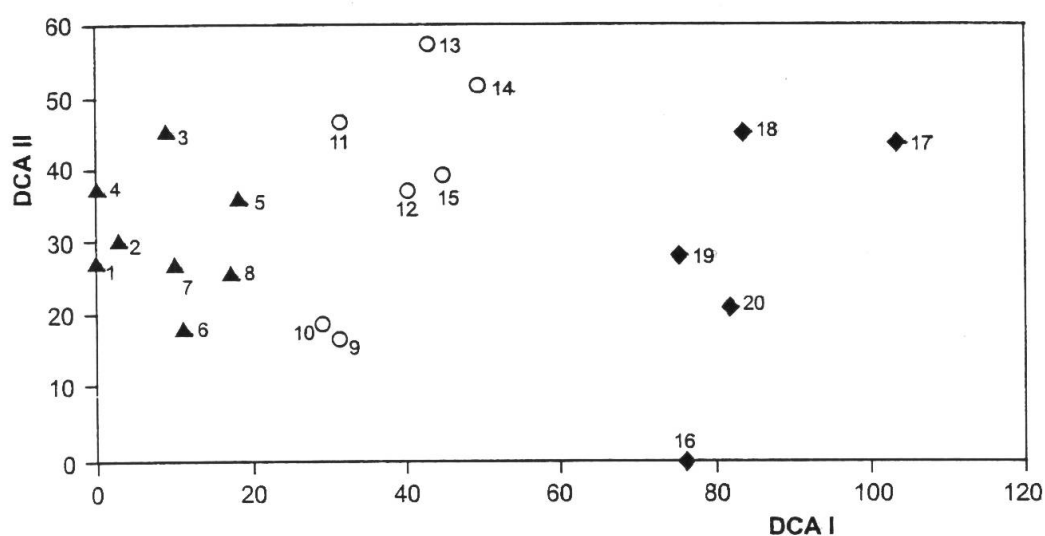


Fig. 2. — Detrended correspondence analysis based on the matrix of 6 chorotypes \times 20 sites along the altitudinal gradient in the mountains of Córdoba, Central Argentina. For references of the sites see Table 1. Triangles = sites between 1000 and 1450 m; circles = sites between 1500 and 1850 m; rhombs = sites between 1900 and 2600 m. Groups of sites defined by cluster analysis (Fig. 3).

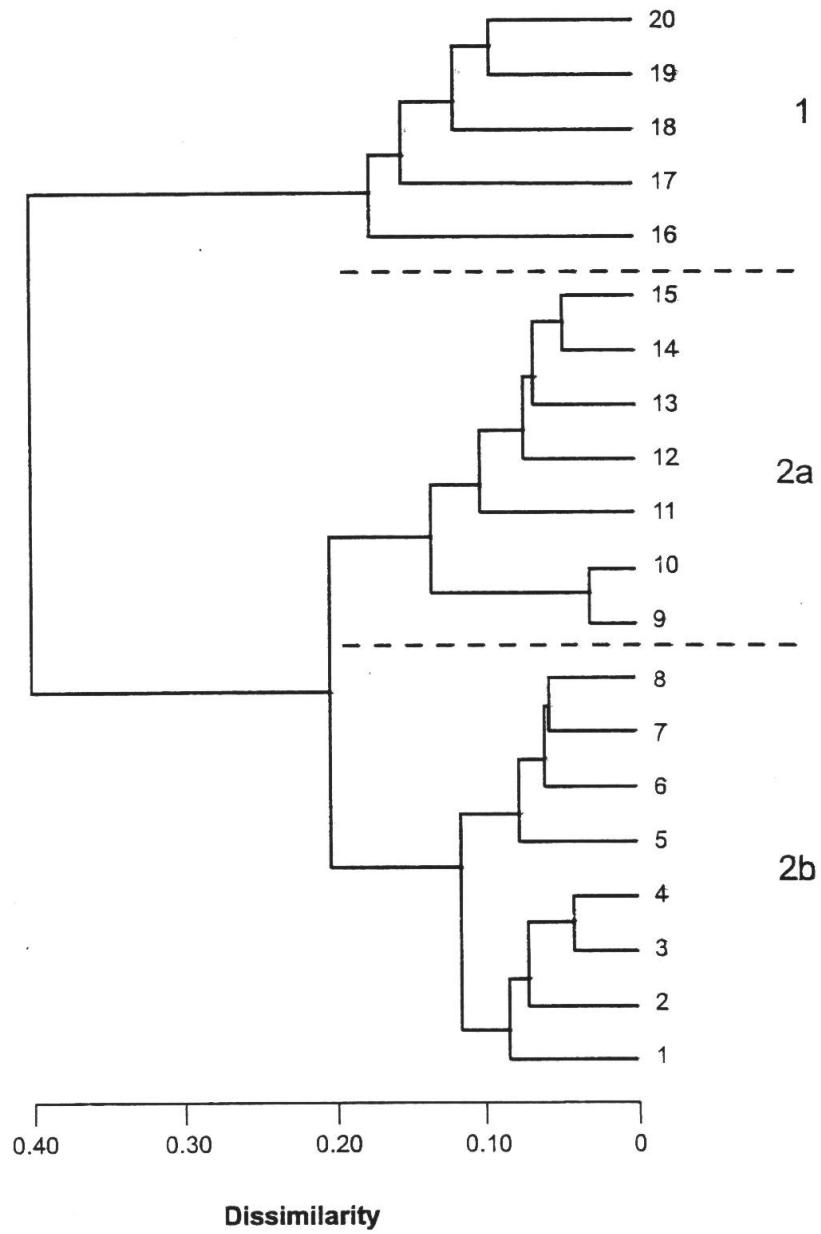


Fig. 3. – Chorogram showing the clusters of sites obtained by numerical clasification of the 6 chorotypes \times 20 sites matrix. References for sites as in Table 1. For description of clusters 1, 2a and 2b see the text.

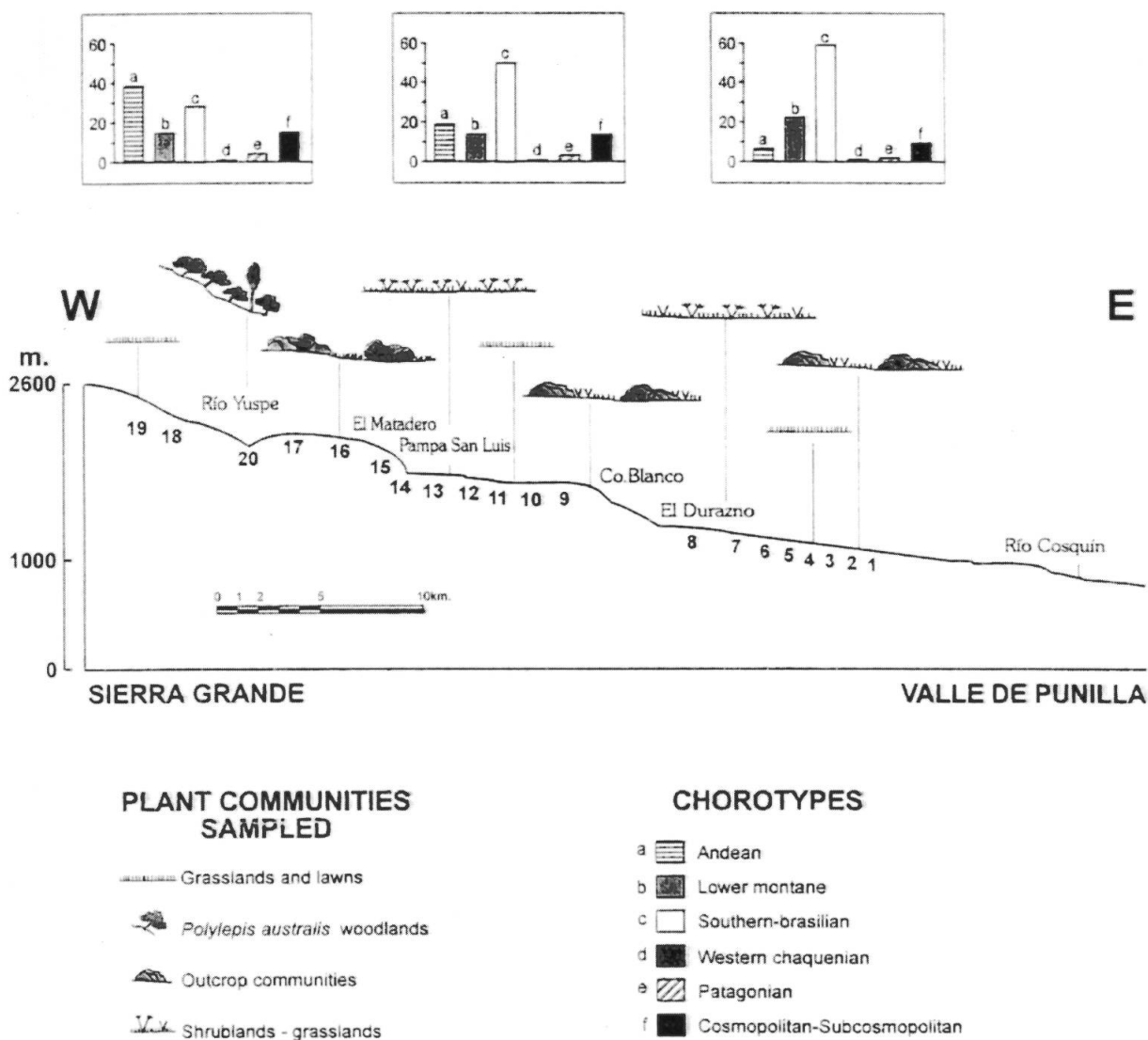


Fig. 4. – Diagram showing the chorotype composition of the sites included in the three clusters of Fig. 3 (top). The bars are averages of the frequencies of chorotypes of the sites included in each cluster. The distribution of the sampling sites along the altitudinal gradient and the types of communities sampled are also displayed.

rally widely distributed at high altitudes in the mountains from north-western Argentina and neighbouring countries. The Andean chorotype predominates in all the sites. Six local (restricted to these mountains) and eighteen regional (restricted to the highest vegetation belts in central Argentina) endemisms reveal the biogeographic relevance of this territory.

Cluster 2: Includes the sites in the 1000-1850 m elevation interval. Physiognomically, parts of this territory above 1500 m (subcluster 2a in Fig. 3) are dominated mostly by C3 grasslands (mainly species of *Stipa*, *Piptochaetium*, and *Festuca hieronymi* Hack.; CABIDO & al., 1997). At lower altitudes (subcluster 2b in Fig. 3) C4 grass genera such as *Aristida*, *Paspalum*, *Schizachyrium* and *Setaria*, predominate. The most frequent chorotype in this cluster is the Southern-brasilian. Subclusters 2a and 2b differ

mainly in that the former shows frequency values of the Andean chorotype ranging from 12 to 20%, while frequencies in the latter are always under 11%. No local endemisms occur in the sites included in this cluster.

Discussion

The vegetation of the mountains from central Argentina vary in chorotypic composition along altitudinal gradients. From the chorological analysis of 673 species, clear cut boundaries emerge between sites above and below approximately 1850 m. Both the ordination and classification techniques performed show that sites are grouped according to their chorotype frequencies into two main clusters reflecting the major phytogeographical discontinuity mentioned above.

The general pattern in chorotype frequencies is observed even if different community types are compared along the altitudinal gradient. The sites above 1850 m, whether grasslands, lawns, shrublands, outcrop communities or *Polylepis australis* woodlands, have the Andean chorotype as the most frequent with percentages over 35%. At lower altitudes the most frequent chorotype is the Southern-brasilian, with varying frequencies of the remaining categories (Fig. 4).

A point central to our study is the high frequency of Andean floristic elements at the highest sites. Not only common species are found between the Andes and this extra-Andean range, but also entire plant assemblages (e.g., the communities dominated by *Alchemilla pinnata* R. & P., *Eleocharis albibracteata* Nees and *Muhlenbergia peruviana* (Beauv.) Steud. described by RUTHSATZ, 1977 in the high-Andean semideserts of north-western Argentina). The physiognomic similarity between the vegetation of the upper Córdoba mountains and Andean communities was highlighted by Kurtz as early as in 1904 (KURTZ, 1904). Unfortunately, floristic and phytosociological data from other extra-Andean mountain ranges are still lacking. Hence, hypothesis about dispersal or vicariance events are difficult to relate to the occurrence of Andean elements in central Argentina.

Sites at higher altitude (above 1900 m) are distinct not only due to their richness in Andean species, but also due to the occurrence of highly restricted endemisms (named here “local endemisms”). Besides the degree of endemism is low when compared with other mountains of the world (see MAJOR, 1990 and references there in), it is locally relevant since sites below 1850 m lack this type of highly restricted endemisms. Endemisms that occur below 1850 m have more widespread distribution and are shared with other mountains of central and northwestern Argentina (called here “regional endemisms”). The presence of endemic species of so small range at higher altitudes in these mountains has also been reported for different vertebrate taxa (di TADA & al., 1984; NORES & al., 1983). On that basis, RINGUELET (1961) included the area within the Subandean Faunistic District, excluding it from the surrounding chaquenian territories. The occurrence of both, animal and plant endemic species, is of high biogeographical significance and supports the idea that the upper Córdoba mountains might have been isolated for some time. Whether this isolation is the result of Pleistocene or current climatic conditions is out of the scope of this study.

In conclusion, we propose that Sierra Chaco plant communities above 1850 m altitude should no longer be regarded as chaquenian. This statement applies not only to *Polylepis australis* woodlands, as already pointed out by PRADO (1993b), but also to other different types of communities occurring in the mountains of Córdoba above 1850 m in which the Andean is the most important chorotype. The question now is to which phytogeographical unit should these territories be related to. We believe that further phytosociological and phytogeographical information of the whole extra-Andean mountains in central Argentina is needed. Only when these data are available we will be able to support the hypothesis about the existence of Andean enclaves in extra-Andean habitats.

ACKNOWLEDGEMENTS

This study was sponsored by the CONICET (PID 3-105900/88), the CONICOR (Res. N° 3054/94, 3457/95), the Universidad Nacional de Córdoba (Res. 263/95, 2045/97) and The British Council-Fundación Antorchas (BNS 992/21). We thank our research team and D. Abal Solís for drawing the figures.

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