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# Vegetational history of the Late glacial–Holocene transition in the grasslands of eastern Argentina

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## Abstract

Palynological records from eight sites located in the eastern plains of Argentina, from the humid Pampa in the east to the xerophytic woodland–dry Pampa ecotone in the west, allow a regional reconstruction of the vegetation of Late glacial–Holocene transition. Fossil pollen records were interpreted in terms of palaeoenvironmental information using the modern pollen–vegetation–climate relationship as an analogue. Although an exact analogue does not exist today, Late glacial vegetation consisted mostly of psammophytic steppe in large areas of the central and south-western Pampa grassland which, in the south west, is associated with a shrub steppe, suggesting subhumid–dry to semi-arid climatic conditions. The replacement of dry steppe by humid grassland and the rapid evolution of pond environments during the early Holocene (starting during the Late glacial–Holocene transition) suggests a shift towards subhumid to humid climate conditions. The Late glacial–Holocene transition is indicated in the pollen records by repeated abrupt changes in the proportions and concentrations of some taxa, such as Brassicaceae, Asteraceae and *Carduus*-type. In the modern vegetation they represent species of common occurrence in human-induced disturbance habitats, suggesting an environment that was subject to frequent natural disturbance such as rapid and repeated flooding episodes that inundated the depressions along the valley floodplains, caused by unusual rainfall events. Some species of *Carduus* may have been native and not introduced by the Europeans, suggesting that Late glacial vegetation of the Pampa grasslands may account for the abundance of ruderal species. Of special interest is the presence of Myrtaceae in some pollen assemblages between 11,000 and 9000 yr B.P. At present, Myrtaceae are not part of the natural vegetation in the Pampa grassland. Their presence in the fossil pollen records may be interpreted as local deposition instead of extra-regional origin. Myrtaceae formed part of the psammophytic steppe, and after Late glacial–Holocene transition they disappeared from the regional flora, perhaps due to the climatic change that occurred at the beginning of the Holocene. It is the most significant cause of extending the area of some Pampa grassland taxa, but it may have reduced the area for others. Of the Late glacial vegetation, at least Myrtaceae were probably not able to adapt to the new habitats and hence disappeared from the regional flora at the Pleistocene–Holocene transition. Although other plants may have disappeared as well, these cannot be identified because pollen from these plants cannot be differentiated morphologically. During the Late glacial–Holocene transition, communities with no modern counterparts probably formed and disappeared. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Argentina; palynology; Pampa grasslands; late glacial–Holocene; vegetation history

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## 1. Introduction

The Pampa grasslands are the most extensive area covered by grasses in Argentina. The entire region has been the scene of the development of a vast livestock industry and of a rapid increase in arable agriculture, especially during this century (Soriano, 1991). The distribution of grasslands was modified by human activities, and the grasslands were invaded by ruderal taxa and other non-native grasses. Human activities have also modified the land surface as a result of the extension of agriculture in marginal areas, although some relicts of pristine vegetation are preserved (León, 1991). In addition to that, flood, drought and fire induced floristic changes in the Pampa grasslands (e.g. Insausti and Soriano, 1987; Chaneton, et al., 1988; Chaneton and Facelli, 1991). During the Late Quaternary the vegetation underwent several changes related to palaeoclimatic variations and sea level changes (e.g. Prieto, 1989, 1996; Quattrocchio et al., 1995). Taking into account that the Pampa grasslands are one of the largest humid temperate grassland regions in the world, and given the sensitivity of grassland to climatic change and episodic weather events (Parton et al., 1994), it is important to know the environmental response of this area to Late glacial–Holocene transition climatic change as a possible indicator of the future sensitivity of the Pampa grasslands to human-induced global climate change. The Late glacial–Holocene transition in South America was a time of marked climate variability, characterised by repeated climate oscillations that included the maximum warmth (Holocene Hypsithermal conditions) (Clapperton, 1993) and the controversial Younger Dryas period (see Markgraf, 1991, 1993; Heusser, 1993). At about this time, the earliest palaeoindians appeared in the Pampa grassland (Flegenheimer and Zárate, 1993) and numerous families of autochthonous and holoarctic vertebrates became extinct (Cione and Tonni, 1995). In this article, several dated pollen records from the Pampa grasslands were analysed for the Late glacial–Holocene transition and interpreted in terms of palaeoenvironmental information using the modern pollen–vegetation–climate relationship as an analogue. The purpose of these analyses was:

(1) to consider how the climatic variability during the Late glacial–Holocene transition may have affected the Pampa grasslands; and (2) to elucidate possible vegetation responses to future climate change.

## 2. Geographical features of Pampa grasslands

### 2.1. Stratigraphy and age

The late Pleistocene and Holocene periods are represented in the Pampa grasslands by the ‘Lujanense’ and ‘Platense’ stratigraphic units (Fidalgo et al., 1975 and references cited therein). The names ‘Lujanense’ and ‘Platense’ have been used for several types of sediment (Fidalgo, 1992). The ‘Lujanense’ consists of fluvial or lacustrine–fluvial facies (Fidalgo et al., 1973; Tonni and Fidalgo, 1978; Dangavs and Blasi, 1995) and aeolian facies (sandy loess to loessial sands) (Zárate and Blasi, 1991) with extinct fossil megafauna (Cione and Tonni, 1995). The ‘Platense’ corresponds in continental areas to a fluvio-lacustrine and paludal facies in morphological depressions and eolian facies (e.g. Dangavs and Blasi, 1995; Zárate et al., 1995) with vertebrate remains of extant fauna only and of some species only recently extinct, such as *Dusicyon avus* (Cione and Tonni, 1995).

According to Fidalgo et al. (1973) and Fidalgo (1992), the ‘Lujanense’ is equivalent to the Guerrero Member of the Luján Formation, the ‘Platense fluvial’ is equivalent to the Rio Salado Member of the Luján Formation and the eolian facies of both units correspond to the ‘La Postrera’ Formation.

Deposition of the ‘Lujanense’ began prior to ca. 29,000 yr B.P. and ceased some time between 10,000 and 11,000 yr B.P., and that of the ‘Platense’ ranges between ca. 11,000 and 3000 yr B.P. (Carbonari et al., 1992; Bonadonna et al., 1995; Prieto et al., 1998). A relatively well-developed soil is formed on top of the ‘Lujanense’ (Suelo Puesto Callejón Viejo; Fidalgo et al., 1973). The uppermost part of the A Horizon of this soil has been dated at  $9000 \pm 70$  yr B.P. at La Horqueta II, Río Quequén Grande (Zárate et al., 1995).

Table 1  
Pampa grassland vegetation units

	Frenguelli (1940)	Cabrera (1968)	León (1991)	Bailey (1989)
Humid Pampa	Central Zone	Oriental District	rolling pampa; inland pampa (flat Pampa); major part of the flooding pampa	subtropical prairies (humid steppe and wooded steppes); humid temperate domain
Dry Pampa	Peripheral Zone	Occidental District Southern District	inland pampa (west pampa) southern pampa and western part of the flooding pampa	steppes and shrub of moderate continental climate; dry domain
Xerophytic woodland	Monte puntano–pampeano	Caldén District	Espinal	dry steppes, open woodland and shrub of continental climate

All radiocarbon dates given in this paper are in  $^{14}\text{C}$  yr B.P. on bulk sediment samples.

## 2.2. Climate and vegetation

Pampa grasslands include humid temperate prairies (humid Pampa) and dry steppes of moderate continental climate (dry Pampa). Climate in this region is classified as southern temperate. Temperatures are lowest in July–August and highest in January–February. The Pampa grasslands are influenced by the South Atlantic quasi-stationary high pressure, with prevailing light tropical humid north-eastern winds. Intermittent polar front irruption from the south modifies this pattern. Due to the prevailing circulation, most of the humidity comes from the N and the NE. Therefore, when the westerly flow reaches latitudes to the north of their mean position, lower than normal rains can be expected over the Pampa grasslands and conversely, when it is south of its mean position, prefrontal and frontal rains are more abundant (Castañeda and Barros, 1997). As a result, the annual total rainfall increases towards the east from ca. 400 mm in the SW to 1000 mm in the NE. In addition, precipitation also becomes seasonal with two well-defined rainy seasons, spring and fall (Burgos, 1968). The ratio of annual rainfall to potential evapotranspiration ranges from 1 to 1.3 in the humid Pampa, 0.8 to 1 in the dry Pampa, and 0.5 to 0.8 in the xerophytic woodland–grassland ecotone, revealing an increase in aridity from east to west across the Pampa grasslands. The transition from the maritime

winter rains in the NE to the subtropical continental summer rains in the W (Prohaska, 1976) is reflected in the change in natural vegetation between the humid and the dry Pampas.

Frenguelli (1940), Cabrera (1968) and León (1991) have described the major regional Pampa grassland plant formations (Table 1, Fig. 1). The humid Pampa is characterised in the north-eastern part by a well-integrated drainage provided by a distinct network of fluvial valleys, whereas the eastern part is characterised by a poor drainage due to the negligible slope of the plain in this area. These topographical characteristics result in extensive and lengthy flooding during periods of abundant precipitation. Vegetation is dominated by grass species (*Bothriochloa laguroides*, *Stipa neesiana*, *Piptochaetium montevidense*, *Aristida murina* and *Stipa papposa*). Shrubs and suffrutices (several genera of Asteraceae) are poorly represented, although in some places they are dominant. Pond, swamp and floodplain communities are frequent, with wet-ground and aquatic plants such as *Schoenoplectus californicus*, *Typha domingensis* and *T. latifolia*, *Zizaniopsis bonariensis* and *Spartina* spp. Common broad-leaved herbs include species of the genera *Alternanthera*, *Vicia* and *Eryngium*. Halophytic communities with Chenopodiaceae (*Salicornia*, *Cressa*, *Atriplex*), and Poaceae (*Spartina* and *Distichlis*) are important in this part of the pampas. Some of the more common introduced weeds in these grasslands are *Carduus acanthoides*, *Cirsium vulgare*, *Cynara cardunculus*, *Carthamus lanatus* and several species of *Centaurea*. The humid Pampa is characterised by

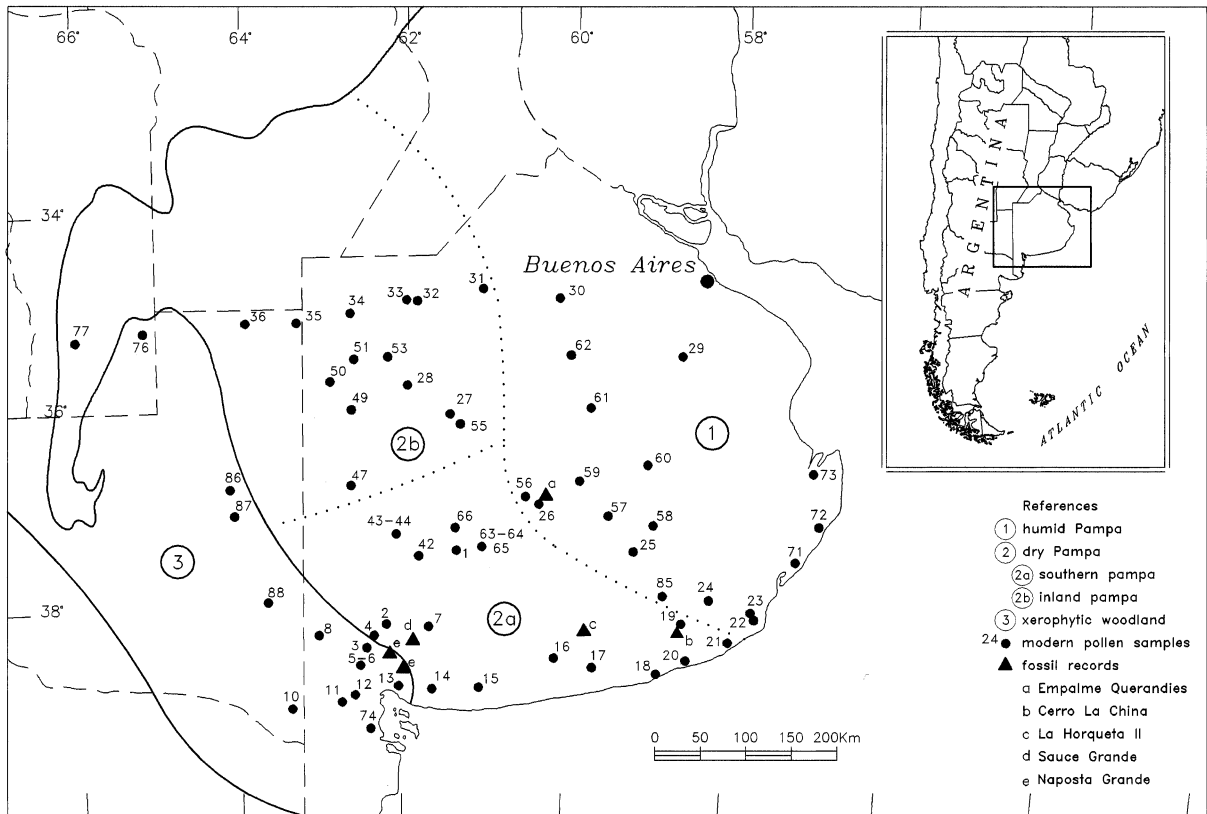


Fig. 1. Location of pollen fossil sites and surface pollen sites in relation to vegetation and physical features in Pampa grasslands.

a mean precipitation of 900 mm/yr and average temperatures of 22°C in January (summer) and 9°C in July (winter) and annual water excess between 50 and 200 mm.

The dry Pampa includes two units, the inland pampa and the southern pampa (Fig. 1). The former is located to the NW of the Pampa grassland and also in a continuous narrow belt which penetrates into the region of xerophytic woodland (León and Anderson, 1983). It lacks a fluvial network and is characterised by fixed sand dunes. The dominant grasses are *Sorghastrum pellitum*, *Elyonurus muticus* and various species of *Stipa*. The most important edaphic communities are those developed on dunes (psammophytic steppe) with predominance of *Panicum urvilleanum*, *Poa ligularis* and *Hyalis argentea*. Species of *Baccharis* and other shrubby members of the Asteraceae are frequent. Halophytic communities appear in flat,

low-lying areas and along the margins of ponds. The southern pampa constitutes the southernmost unit. It includes the only two low-altitude mountain systems of the Pampa grassland, the Tandilia and Ventania ranges, as well as their piedmonts and the coastal plain. The fluvial network is well defined. *Stipa* and *Piptochaetium* are the dominant steppe grasses. The dominant species in the range areas are the grass *Paspalum quadrifarium* and several species of *Eryngium*. *Colletia paradoxa* and *Dodonaea viscosa* represent the shrubby edaphic community. In the Tandilia range this community is accompanied by *Eupatorium buniifolium* and *Baccharis tandiliensis* and in the Ventania range by *Discaria longispina* associated with various endemic grasses.

Introduced weeds in the dry Pampa, such as *Centaurea solstitialis*, *Cynodon hirsutus*, *Kochia scoparia*, *Diplotaxis tenuifolia*, *Carduus nutans* and

*Salsola kali*, often dominate in several communities.

The dry Pampa is delimited by the isohyets of 700–800 mm in the east and 500–600 mm in the west. One characteristic property of this region is that it belongs during some years to the humid eastern part, and during others to the dry western part (Krepper et al., 1987). In the southern pampa the average temperature is between 21°C (summer) and 7°C (winter), with incipient water deficit. The climate in the inland pampa is drier than in the rest of the dry Pampa. Temperatures are higher than in the southern Pampa in summer (23°C) as well as in winter (8°C), causing an increase in water deficit.

The boundary of the Pampa grasslands is determined by its contact with xerophytic woodland vegetation, the 'Espinal', which is characterised by the dominant trees *Prosopis flexuosa* and *P. caldenia*. In the west and southwest, the xerophytic shrubs form a broad ecotone with the dry Pampa. *Prosopidastrum globosum*, *Condalia microphylla* and *Discaria longispina* make up the thorn shrub communities, together with few *Prosopis caldenia* and *P. flexuosa*. These taxa coexist with a psammophytic steppe with thorn shrub communities and herbaceous and shrub halophytic steppe taxa near the Atlantic coast. Part of this woodland has been destroyed by clearing at the beginning of the 20th century. Annual precipitation is <500 mm with water deficit >300 mm. The annual temperature is between 20 and 7°C.

Based on the climatic classification proposed by Burgos and Vidal (1951), the humid Pampa can be classified as humid–subhumid (C<sub>2</sub>) with incipient water excess, the dry Pampa as subhumid–dry (C<sub>1</sub>) with incipient water deficit, and the xerophytic woodland–grassland ecotone as semi-arid (D).

### 3. Palynology laboratory methods

Pollen samples from the Empalme Querandías, Cerro La China and La Horqueta II profiles and modern surfaces were treated following standard pre-treatment methods (Gray, 1965; Faegri and Iversen, 1989). Samples from Napostá Grande and Sauce Grande were processed by Grill (1993)

and Borromei (1995), respectively in the Universidad Nacional del Sur (Bahía Blanca), following the technique used by Heusser and Stock (1984).

Xerophytic woodland pollen includes *Schinus*, *Ephedra*, *Prosopidastrum globosum*, *Prosopis*, *Acacia*, *Celtis*, Zygophyllaceae, Rhamnaceae, Cactaceae and Oleaceae. Wet-ground and aquatic pollen includes Cyperaceae, *Typha*, *Myriophyllum*, *Potamogeton*, Alismataceae, Juncaginaceae and Iridaceae. *Carduus*-type includes the species and subspecies of *Carduus* and a *Silybum marianum*.

Myrtaceae pollen from La Horqueta II profile were identified as *Eugenia uruguayensis*-type (Plate I) by comparison with the reference pollen collection at the Palaeoecology and Palynology Laboratory at the Universidad Nacional de Mar del Plata and published keys (Acevedo and Anzótegui, 1998).

Pollen clumps (or aggregates) have been defined according to Davis and Buchmann (1994) as cohesive masses of two or more pollen grains of the same type. A few clumps were found which consist of two or three pollen types. Each pollen clump was taken as a unit and the percentage was calculated as follows:

$$(\text{pollen clumps})\% = \sum \text{clump } i / \text{total } i \times 100$$

clump *i* = number of clumps of taxon *i*

total *i* =  $\sum$  grains of taxon *i* + clumps *i*.

Each type of fossil pollen was photographed under LM at  $\times 1000$  (Plates I and II).

### 4. Modern pollen data

A suite of 65 modern pollen rain samples was used in the interpretation of fossil sequences of the Pampa grassland (Fig. 1). Summary statistics for modern pollen values of the representative taxa, Poaceae, Chenopodiineae, wet-ground and aquatic plants, Brassicaceae, Asteroideae, *Carduus*-type, Cichorioideae and xerophytic woodland plants, found in the samples were assigned to one of the following broad units: humid Pampa, dry Pampa (southern and inland pampa) and xerophytic woodland–grassland ecotone (Fig. 2,

## PLATE I

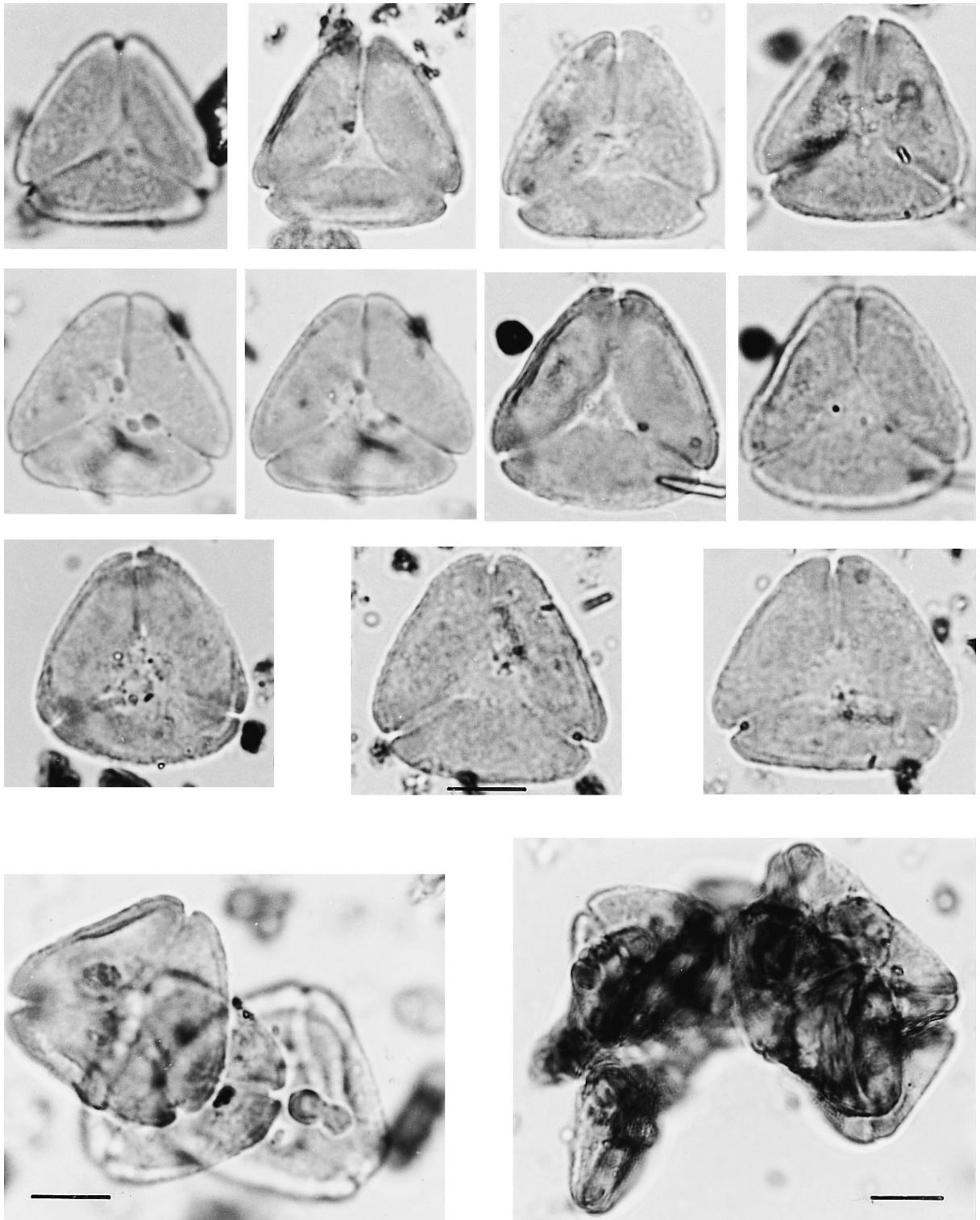


PLATE I. Light micrographs of fossil Myrtaceae pollen identified at La Horqueta II (Figs. 1 and 5). The bar-line represents 10  $\mu\text{m}$ .

PLATE II

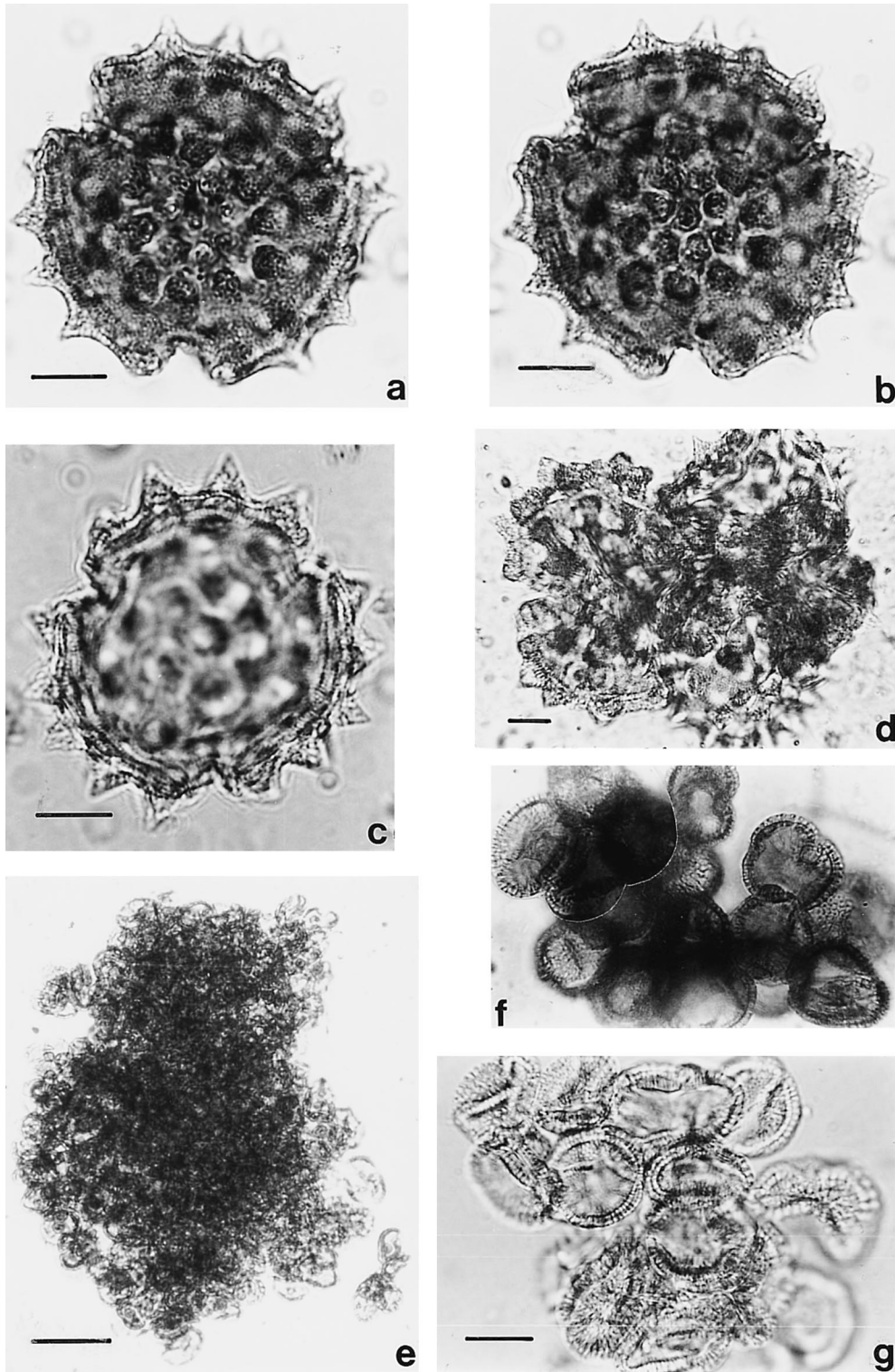


PLATE II. Light micrographs of fossil pollen. a–c, *Carduus*-type; d, clump of *Carduus*-type; f, g, details of clump of Brassicaceae; e, clump of Brassicaceae. The bar-line represents 10  $\mu\text{m}$  in all micrographs except e, where it represents 50  $\mu\text{m}$ .

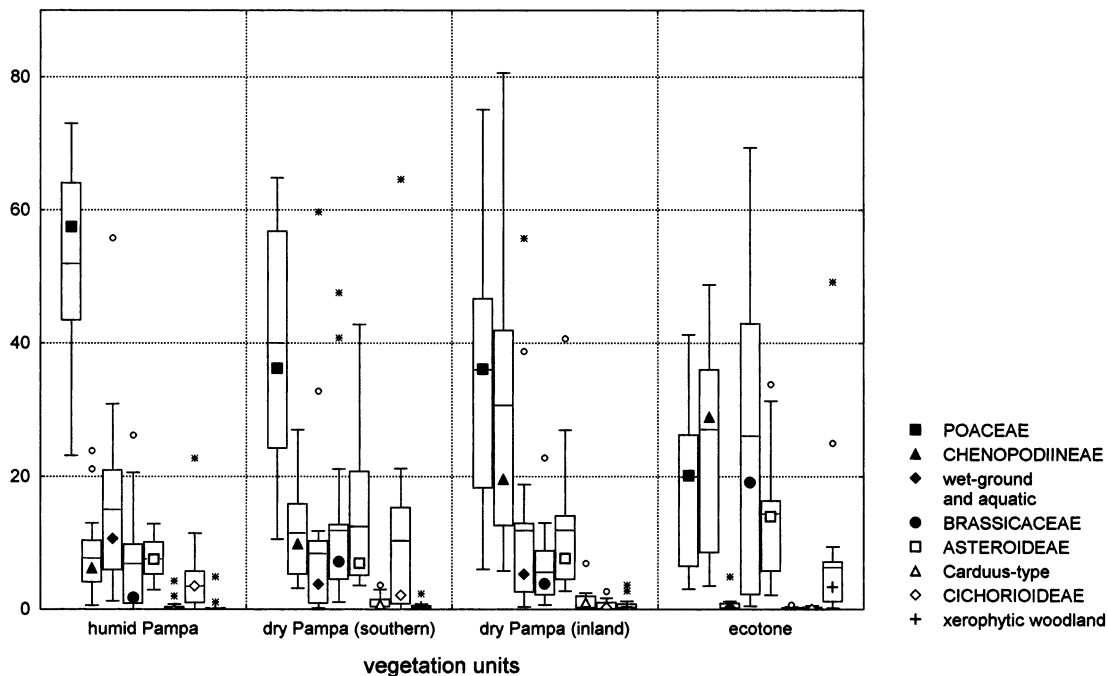


Fig. 2. Boxplot (SYSTAT Inc., 1992) of modern pollen percentages for selected taxa of humid Pampa, dry Pampa and xerophytic woodland–grassland ecotone (Fig. 1). The box encloses the middle half of the data between the first and third quartiles. The symbols are at the value of the median. The bisecting line is at the value of the mean. The vertical line extending from top to bottom of the box indicates the range of typical data values. Outliers are displayed as “\*” for outside values and “o” for far outside values.

Table 1). Regional pollen spectra reflect in general the vegetation and climate gradient.

(1) Humid Pampa: pollen spectra of this unit are characterised by high percentages of Poaceae (mean 50%), wet-ground aquatic plants (mean 15%), and Chenopodiineae, Asteroideae, Brassicaceae and Cichorioideae <8%. *Carduus*-type and xerophytic woodland appear as traces.

(2) Dry Pampa is represented by two different units:

(a) southern pampa, characterised by high percentages of Poaceae (mean 40%) and by values <13% of Asteroideae, Cichorioideae, Brassicaceae, Chenopodiineae and wet-ground and aquatic plants. *Carduus* and xerophytic woodland taxa appear as traces;

(b) inland pampa: Poaceae (mean 36%), Chenopodiineae (mean 29%) and Asteroideae (mean 12%). Wet-ground and aquatic <10%, Brassicaceae 7% and *Carduus*-type <3%.

Cichorioideae and xerophytic woodland appear as traces.

(3) Xerophytic woodland–grassland ecotone is characterised by high percentages of Chenopodiineae (mean 28%), Brassicaceae (mean 26%), Poaceae (mean 20%), Asteroideae (mean 15%) and xerophytic woodland plants (mean 9%). Wet-ground and aquatic, *Carduus*-type and Cichorioideae appear as traces. From an ecological point of view this unit can be considered as a broad ecotone between the dry Pampa and xerophytic woodland, with a semi-arid and cooler climate.

Prieto (1992, 1996) provides additional data showing the distribution of the taxa from a related Pampa grassland surface pollen study.

All species included in *Carduus*-type are introduced weeds and some genera of Brassicaceae, Asteroideae, Chenopodiaceae and Cichorioideae represented in the modern vegetation arable weeds



and ruderal species. All of them are common in human-induced disturbance habitats in many parts of the Pampa grasslands. Due to the inability to identify these taxa to the species level, it is impossible to separate natural from introduced species. Brassicaceae and Asteraceae are found in high percentages and concentrations in several fossil pollen samples included in this study and, just like the *Carduus*-type, they appear prior to the European settlement (16th century) and the advance of agriculture. For this reason, these taxa have been included in the modern pollen data set, to be compared with fossil pollen in order to provide some insight into the character of the vegetation on the Pampa grassland in the Late glacial–Holocene transition.

The mean values of Brassicaceae vary from 6% in the humid Pampa to 9% in the dry Pampa and rise to 26% in the xerophytic woodland–grassland ecotone, suggesting the importance of semi-arid conditions as a factor in the increase of this type of pollen. In contrast, the relatively high percentages indicated as outliers (Fig. 2) are related to disturbed sites or dunes. When *Cakile maritima* is dominant in the plant communities of dunes of the Mar Chiquita lagoon, it is represented by 45% of Brassicaceae in the modern pollen samples (Stutz, 1996). Brassicaceae tend to be over-represented locally because of their self-pollination (autogamy).

The mean values (expressed in percentages) of Chenopodiineae and Asteroideae pollen are inversely related to precipitation from humid Pampa to xerophytic woodland–grassland ecotone (Fig. 2). Chenopodiineae are dominant in low-lying areas in the inland pampa and halophytic communities where soils are salty, such as in both the humid Pampa and the xerophytic woodland–grassland ecotone. By contrast, both the mean and the median of Poaceae are directly related to the increase in precipitation (Fig. 2).

## 5. Fossil pollen records

For comparative palaeovegetation analysis, eight pollen sequences are available: (1) Sauce Grande and Napostá Grande (Profiles 1 and 2)

located in the xerophytic woodland–southern pampa ecotone; (2) La Horqueta II and Cerro La China situated in the dry Pampa; and (3) Empalme Querandías (Profiles 1, 2 and 3) located in the western edge of the humid Pampa (Fig. 1). Pollen data of the Empalme Querandías sequences are from Prieto (1989) and those of Cerro La China from Prieto and Paez (1989). The Napostá Grande sequences are from percentage tables (Grill, 1993). Data from Sauce Grande (Borromei, 1995) were digitised from figures. The previously unpublished pollen records from Empalme Querandías and La Horqueta II are shown in detail (Figs. 5, 6, 8–10); for the other, previously published diagrams, only the major taxa are reproduced in synthesis diagrams (Figs. 3, 4, 7). Data from the upper part of ‘Lujanense’ (Late glacial) and the lower part of ‘Platense’ (early Holocene) were taken into account and are presented in the form of frequency diagrams and total concentration in grains/gram. With the exception of the Cerro La China profile that comes from a loess sequence in the Tandilia range, the rest are alluvial records along the fluvial valleys with similar stratigraphic sequences. It should be made clear that in a paper published recently, Tonni et al. (1999) have mistakenly claimed that the sedimentary section assigned by Borromei (1995) to the Late Pleistocene (‘Lujanense’) and included in this paper is in fact late Ensenadan (“younger than 0.6 Ma but older than about 0.5 Ma”, p. 270). The above mentioned authors have mistaken this profile located on Terrace II of Río Sauce Grande for the section located 300 m downstream in Terrace I, of Ensenadan age (Quattrocchio and Borromei, 1998).

### 5.1. Sauce Grande (38° 29' S; 61° 47' W; 100 m)

The ‘Lujanense’ unit is characterised by 22% Chenopodiineae, 17% Brassicaceae, 16% Poaceae, 6.5% Asteraceae and low percentages of wet-ground and aquatic plants (Fig. 3). The Brassicaceae pollen percentage shows three peaks with 65%, 43% and 41%. Pollen from woodland xerophytic plants <15%. Myrtaceae pollen ranges from 2 to 28%. Pollen clumps of Brassicaceae, Asteraceae and Chenopodiineae were observed

## Sauce Grande

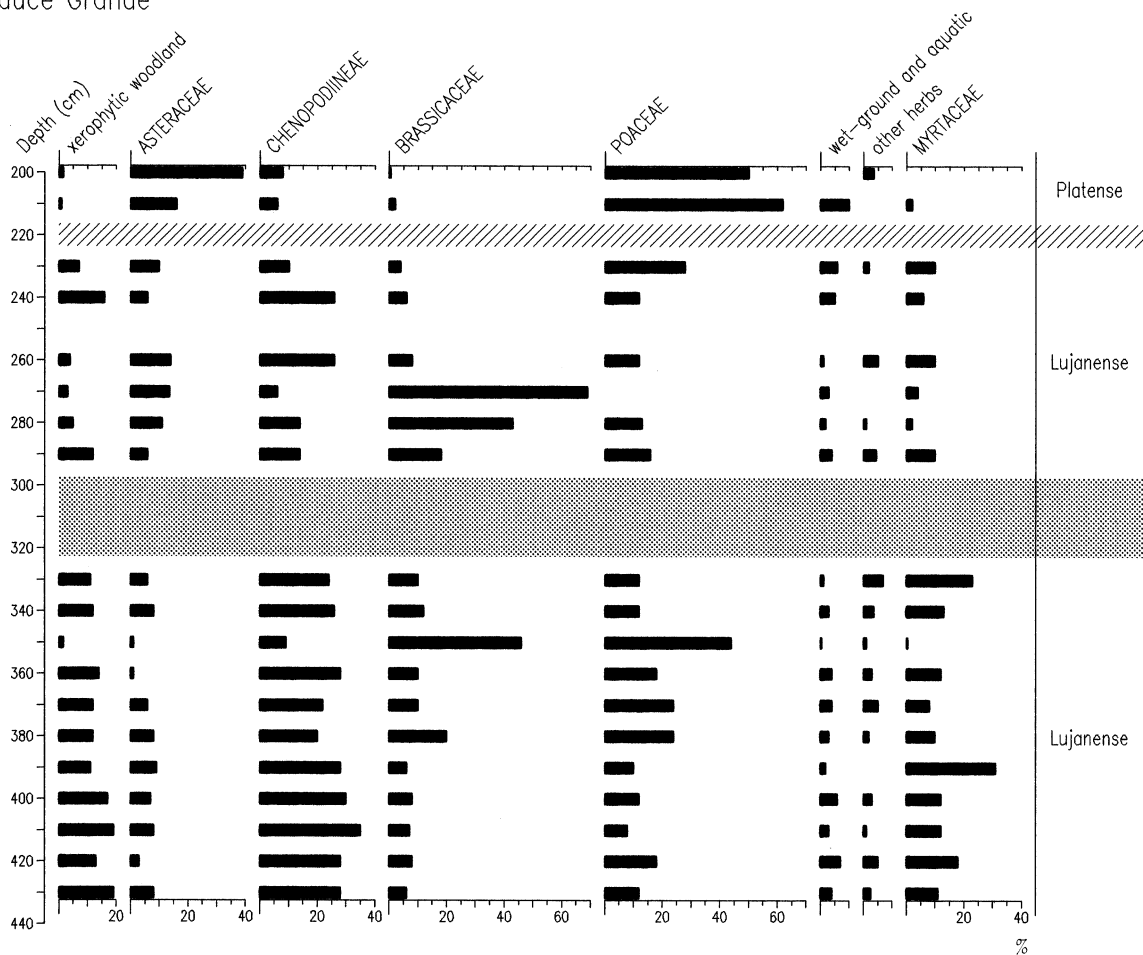


Fig. 3. Fossil pollen diagram at Sauce Grande (Fig. 1) including stratigraphic units. Total pollen sum includes all pollen taxa. Modified from Borronei (1995). Dotted zone = sterile. Dashed zone = gap.

(Grill, personal communication, 1996). These pollen spectra are similar to the inland pampa and the xerophytic woodland–grassland ecotone.

The base of the ‘Platense’ interval is characterised by high percentages of Poaceae (60%), 25% Asteraceae and 10% wet-ground and aquatic taxa. Pollen from woodland xerophytic plants is <1%. These pollen assemblages resemble the modern humid Pampa.

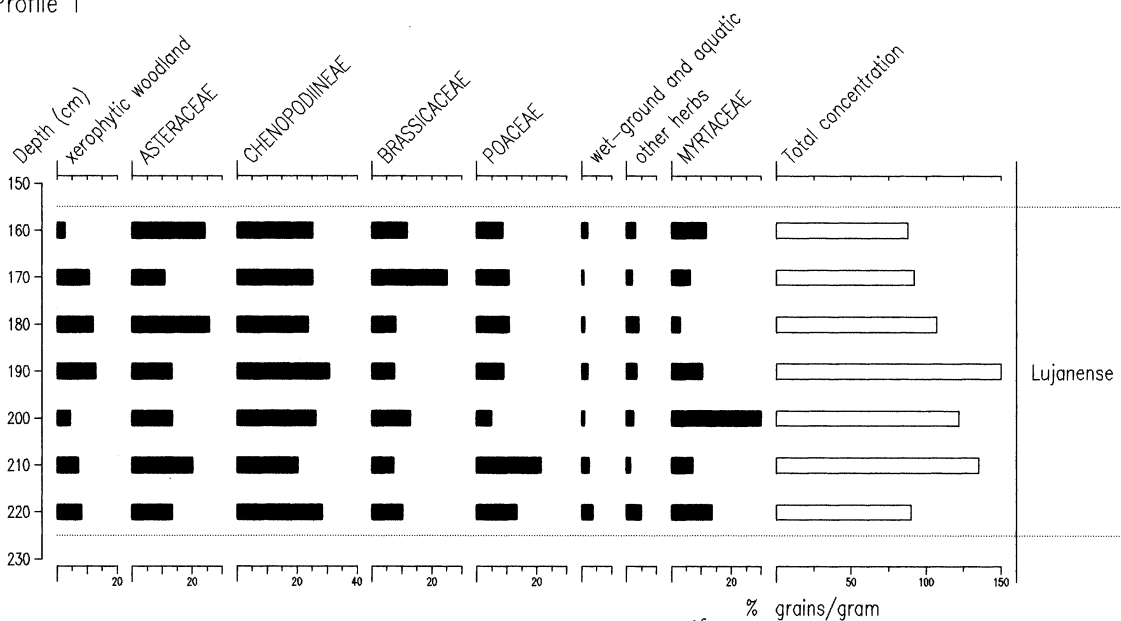
### 5.2. Napostá Grande

Profile 1 (38° 21’ S; 62° 20’ W; 180 m) (Fig. 4). Pollen assemblages from the ‘Lujanense’ unit are

dominated by 26% Chenopodiineae, 17% Asteraceae, 12% Brassicaceae, 11% Poaceae. Pollen from woodland xerophytic plants is <10%. Pollen from wet-ground and aquatic plants is <5%. Myrtaceae pollen ranges from 3 to 30%. Pollen concentration ranges from 80 to 150 grains/g.

Profile 2 (38° 32’ S; 62° 03’ W; 87 m) (Fig. 4). Pollen assemblages from the ‘Lujanense’ unit are dominated by 43% Brassicaceae, 25% Chenopodiineae, 10% Asteraceae, 4% Poaceae. Pollen from woodland xerophytic plants is <3%. Pollen from wet-ground and aquatic plants is <10%. Myrtaceae pollen ranges from 0 to 8%.

Naposta Grande  
Profile 1



Profile 2

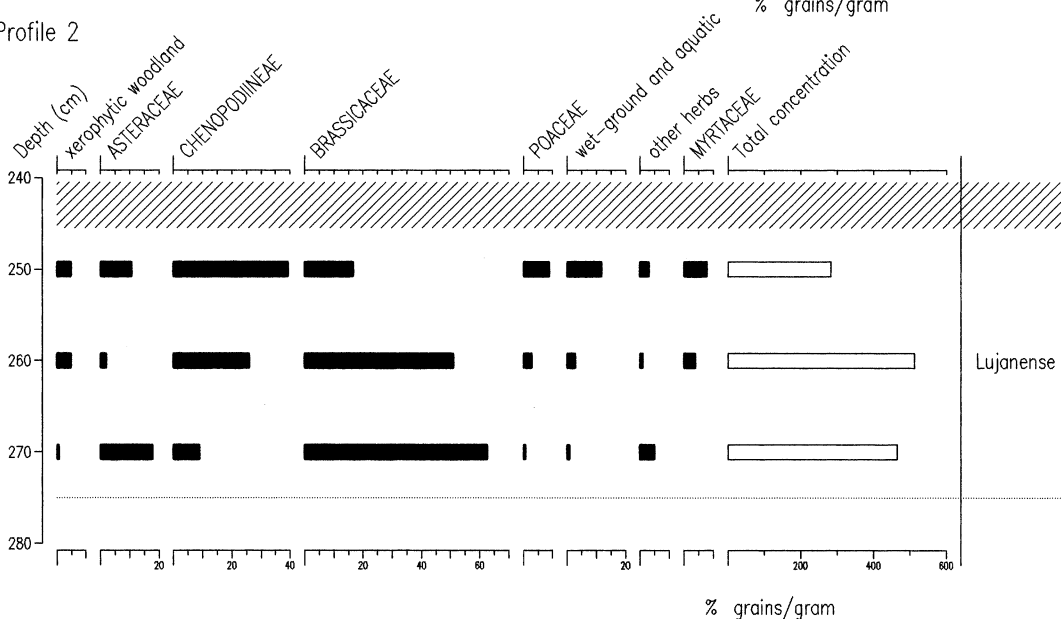


Fig. 4. Fossil pollen diagrams at Napostá Grande, Profiles 1 and 2 (Fig. 1) including stratigraphic units and total pollen concentration (grains/gram). Total pollen sum includes all pollen taxa. Modified from Grill (1993). Dashed zone in Profile 2 = gap.

Pollen concentration ranges from 280 to 500 grains/g.

These pollen assemblages resemble the modern inland pampa with less Poaceae and more shrubs.

In both profiles, pollen clumps of Brassicaceae, Asteraceae and Chenopodiineae were observed (Grill, personal communication, 1996). Pollen samples from the lower 'Platense' unit are sterile.



## La Horqueta II

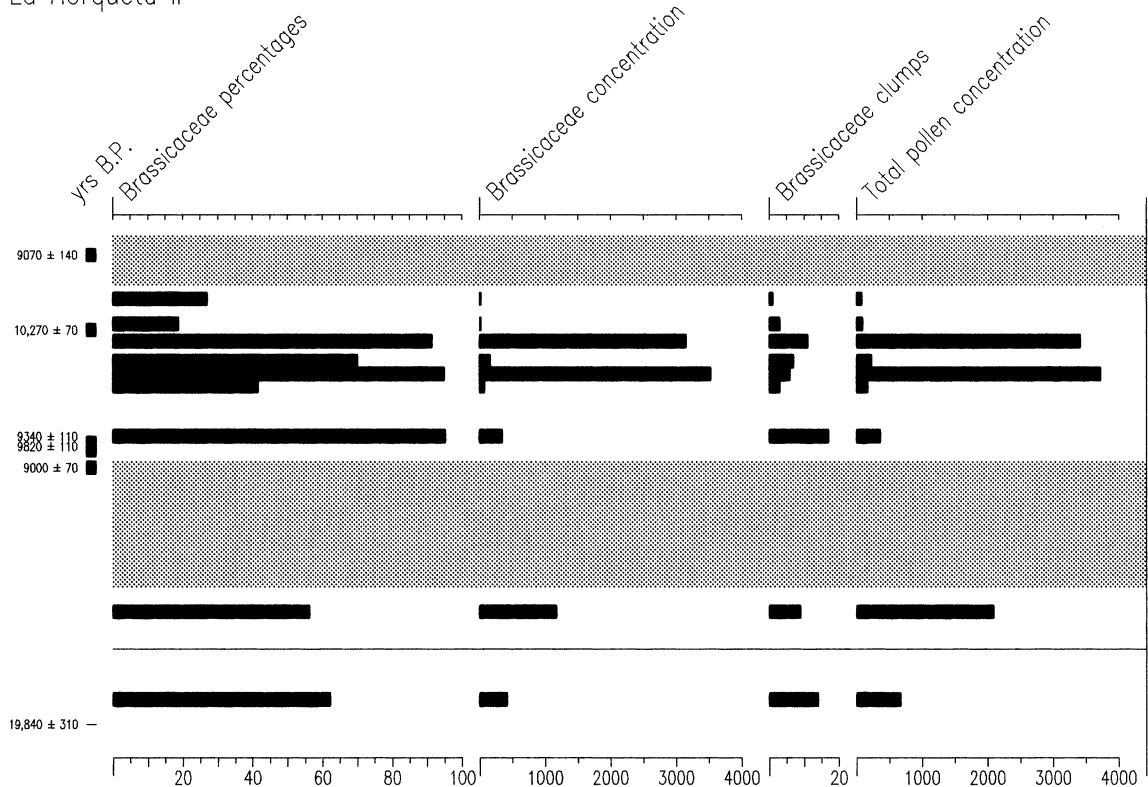


Fig. 6. Fossil pollen diagram at La Horqueta II for Brassicaceae in percentage and concentration.

### 5.3. La Horqueta II (38° 18' S; 58° 49' W; 40 m)

In the 'Lujanense' interval, only one sample from fluvial facies and one of the eolian facies contain pollen (Figs. 5 and 6). The former is dominated by 56% Brassicaceae (16% are clumps) and 32% Asteroideae. Myrtaceae and the other pollen types appear as traces. Pollen concentration is 2100 grains/g. The latter is dominated by 62% Brassicaceae (14% are clumps), 20% Asteroideae (11% are clumps), 11% *Carduus*-type (8% are clumps, Plate II) and 6% Cichorioideae (6% are clumps) and pollen concentration is 670 grains/g. This sample is younger than 19,840 ± 310 yr B.P. and was obtained from a nearby sediment section that is interdigitated with the fluvial facies (Zárate et al., 1995). The pollen assemblage does not have a modern analogue.

The samples corresponding to the 'Platense' interval span between 10,270 ± 70 and 9070 ± 140 yr B.P. The pollen assemblages are dominated by 62% Brassicaceae (between 1 and 17% are clumps, Plate II), 13% Poaceae and 11% Asteroideae, accompanied by *Carduus*-type (Plate II), *Ambrosia/Xanthium*, Cichorioideae and Chenopodiineae. Pollen from pond plants include Cyperaceae, *Myriophyllum*, *Typha* and colonies of the freshwater algae *Pediastrum*. Pollen from dune vegetation include *Calycera*, *Daucus* and *Phacelia*. Myrtaceae (*Eugenia uruguayensis*-type, Plate I) pollen ranges from 0 to 27% (8% are clumps). Total pollen concentrations range between 80 and 3700 grains/g. This pollen assemblage does not have a modern analogue. Excluding the Brassicaceae pollen, the assemblage resembles pond vegetation in interdune areas.

#### 5.4. Cerro La China Profile 2 (37° 57' S; 58° 37' W; 150 m)

The pollen profile between 10,610 and ca. 9000 yr B.P. is dominated by a high proportion (up to 60%) of wet-ground and aquatic pollen (Cyperaceae only), 30% Poaceae and 12% Asteroideae (Fig. 7). Cichorioideae, Chenopodiineae and Brassicaceae pollen together are <10%. Myrtaceae pollen range from 1 to 20%. Total concentrations range from 6240 to 12,300 grains/g. These pollen assemblages are similar to those of the humid Pampa.

#### 5.5. Empalme Querandíes (37° 00' S; 60° 07' W; 180 m)

Three laterally connected alluvial sections along the Tapalqué Creek were selected. These sections represent the coexistence of different sedimentary environments, reflecting a notable sedimentologic facial variability across the former floodplain during the late Quaternary. Profiles 1 and 2 represent the most extensive pollen sequence for the 'Platense' and 'Lujanense', respectively. An integrated pollen diagram was published by Prieto (1996).

Profile 1 (Fig. 8). The 'Lujanense' pollen assemblage is dominated by 42% Poaceae, 23% Chenopodiineae, 11% Asteroideae. Brassicaceae

pollen is <1%, wet-ground and aquatic pollen <5%. Calycera, Rubiaceae (*Rubia* and *Relbunium* type), Malvaceae, Verbenaceae (*Glandularia* type) pollen are each <5%. Xerophytic woodland pollen is <1%. Total pollen concentration ranges from 10,500 to 2800 grains/g. The 'Platense' is characterised by 35% wet-ground and aquatic pollen (mainly Cyperaceae), 33% Poaceae, 11% Chenopodiineae, 8% Asteroideae and 5% Apiaceae and Rannunculaceae. Total pollen concentration ranges from 21,000 to 144,000 grains/g.

Profile 2 (Fig. 9). The 'Lujanense' unit is characterised by 53% Poaceae, 17% Chenopodiineae, 10% Asteroideae, Brassicaceae <2% with the exception of two samples with 73% (16% are clumps) and 19%. *Calycera*, Rubiaceae, Malvaceae and Papilionatae pollen are each <5%. Plant communities of the interdunes (*Alternanthera*, *Triglochin striata* and wet-ground and aquatic) <5%. Xerophytic woodland <1%. Total pollen concentration is variable, ranging from 67 to 16,157 grains/g with a peak of 56,000 grains/g. Pollen clumps of the *Carduus*-type and Asteroideae were observed. Myrtaceae pollen is represented by only a few grains. The base of the 'Platense' unit is represented by one sample dated 9490–10,750 yr B.P. It is characterised by 84% Asteroideae, 9% Chichorioideae and 5% Brassicaceae. Poaceae, Chenopodiineae and wet-ground and aquatic taxa

#### Cerro La China Profile 2

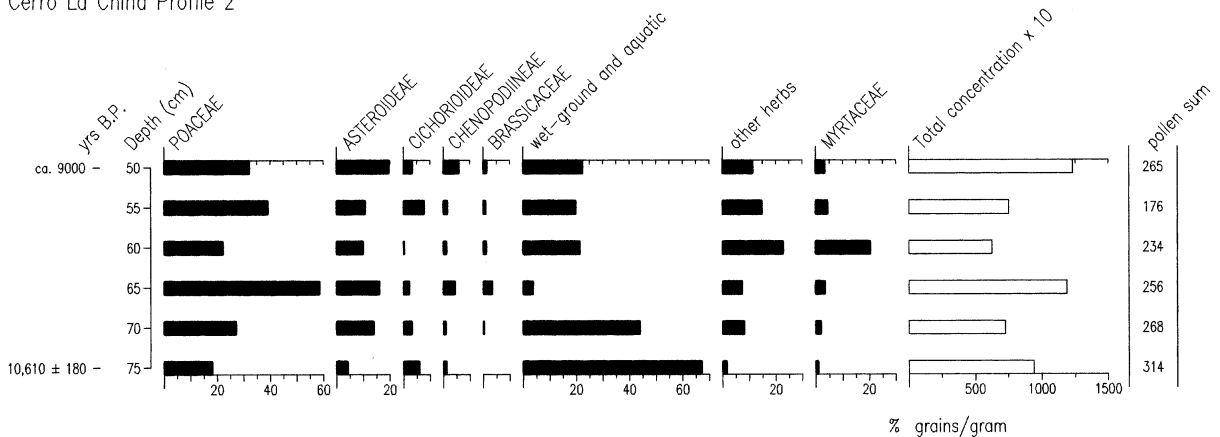


Fig. 7. Fossil pollen diagram at Cerro La China, Profile 2 (Fig. 1) including radiocarbon-dated horizon (yr B.P.) and total pollen concentration (grains/gram). Long-distance excluded for the pollen sum. Redrawn from Prieto and Paez (1989). Estimated age ca. 9000 yr B.P. from Zárate and Blasi (1991).

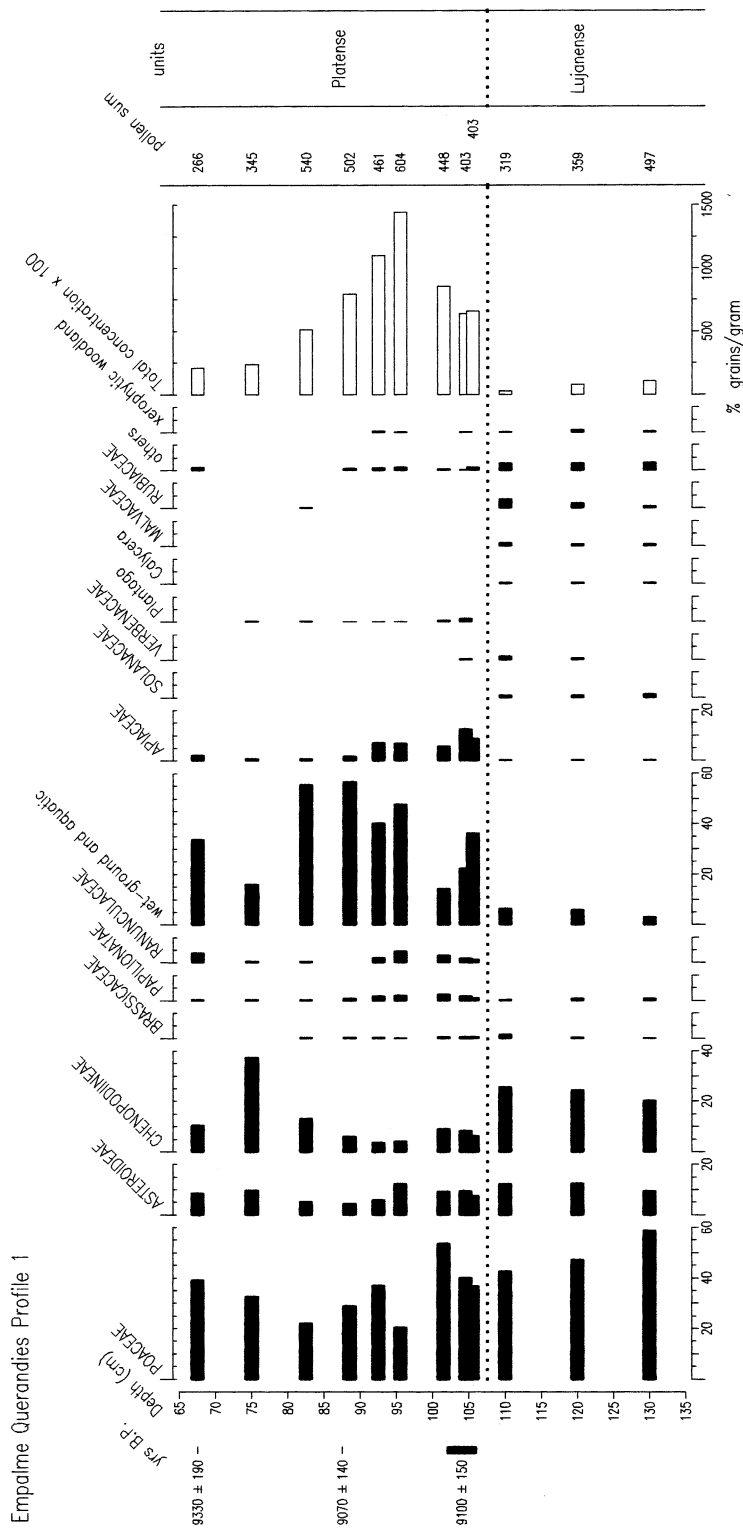


Fig. 8. Fossil pollen diagram at Empalme Querandies, Profile 1 (Fig. 1) including radiocarbon-dated horizons (yr B.P.), total pollen concentration (grams/gram) and stratigraphic units. Total pollen sum includes all pollen taxa.

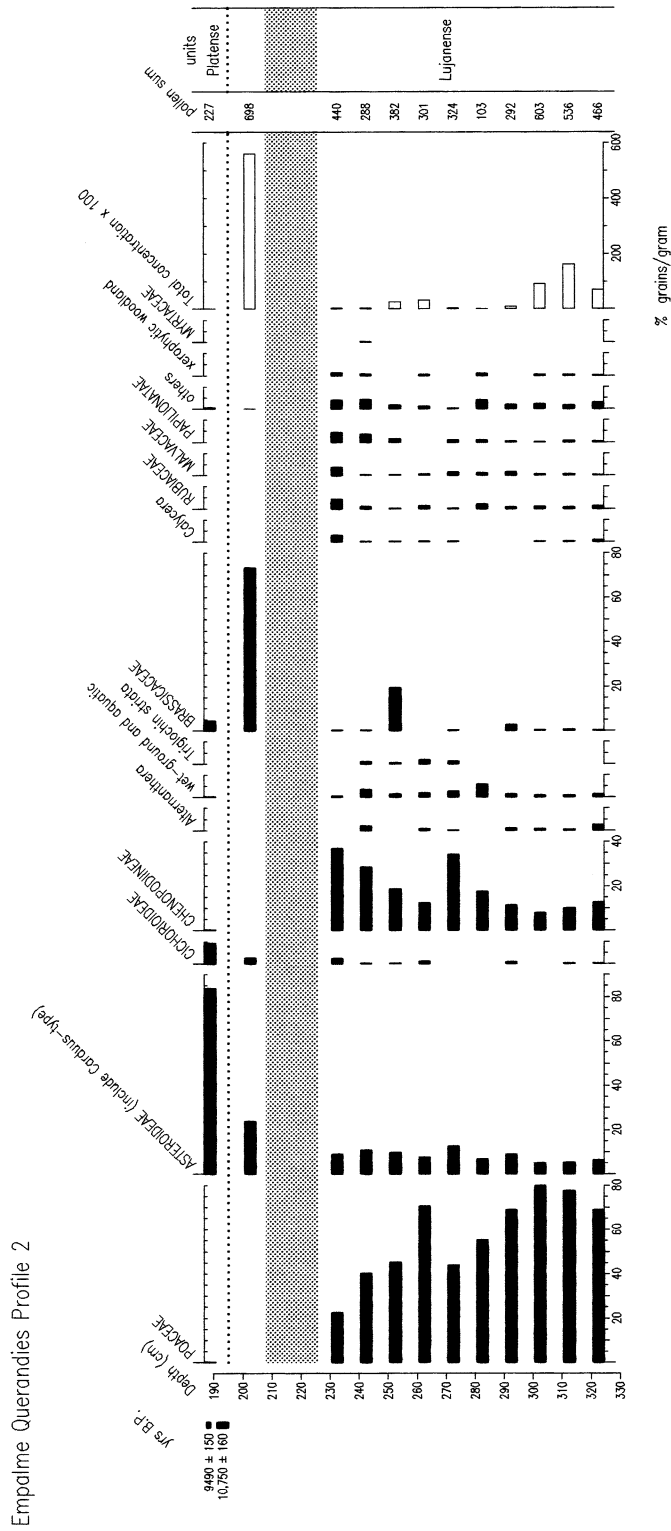


Fig. 9. Fossil pollen diagram at Empalme Querandies, Profile 2 (Fig. 1) including radiocarbon-dated horizons (yr B.P.), total pollen concentration (grains/gram) and stratigraphic units. Total pollen sum includes all pollen taxa. Dotted zone = sterile.



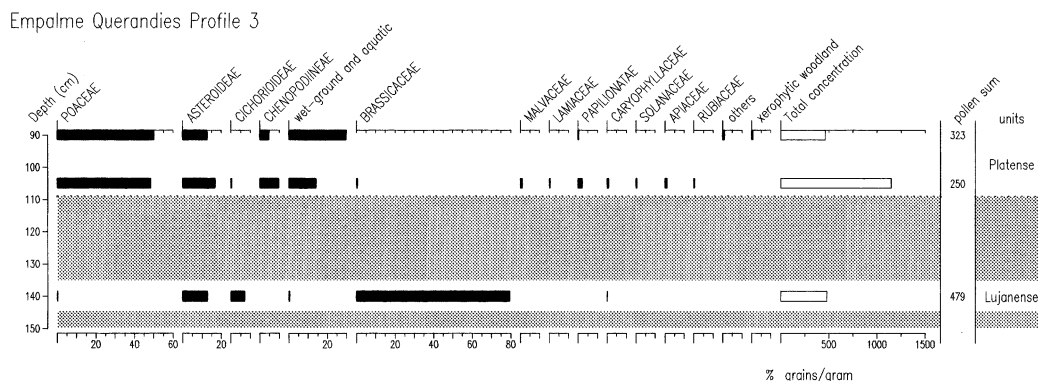


Fig. 10. Fossil pollen diagram at Empalme Querandies, Profile 3 (Fig. 1) including total pollen concentration (grains/gram) and stratigraphic units. Total pollen sum includes all pollen taxa. Dotted zone = sterile.

occur in traces. Total pollen concentration is 137 grains/g.

Profile 3 (Fig. 10). The 'Lujanense' unit is represented by only one sample. It is dominated by 80% Brassicaceae, 6% Asteroideae and 5% Cichorioideae. Poaceae, wet-ground and aquatic and Caryophyllaceae occur in traces. Total pollen concentration is 480 grains/g. Pollen clumps of Brassicaceae were observed. This sample is situated at the same stratigraphic level as the one sampled at 205.5 cm in Profile 2. The base of the 'Platense' unit is characterised by 49% Poaceae, 22% wet-ground and aquatic, 15% Asteroideae and 7% Chenopodiineae. The other types appear as traces. Total pollen concentration ranges from 460 to 1150 grains/g.

The 'Lujanense' pollen assemblages resemble the modern inland pampa assemblages. The closest modern analogue to the 'Platense' pollen assemblage is the humid Pampa, in particular the eastern part where extensive and lengthy floodings occur.

## 6. Palaeovegetation analysis and palaeoenvironmental inferences

Late glacial pollen assemblages at Sauce Grande and Napostá Grande share pollen characteristics with the inland pampa and the xerophytic woodland-grassland ecotone units, suggesting that these steppe environments may have been a mixture of herbs and shrub species, where shrub communities

covered more extensive areas than they do today. Quattrocchio et al. (1995) have interpreted these pollen assemblages as halophytic and psammophytic steppe with shrubby elements. However, the pollen assemblages do not correspond to those of the modern halophytic steppe, represented in the modern assemblages by a predominance of Chenopodiineae (50–80%) (Grill and Guerstein, 1995). To the contrary, Chenopodiineae in the fossil records suggest the development of halophytic communities in low-lying areas near the edges of intermittent ponds, where soils are salty. Late glacial pollen assemblages at Empalme Querandies are related to the modern spectra from the inland pampa, but with comparatively more Poaceae. Pollen concentration is low in all the profiles, suggesting a reduced vegetation cover.

Brassicaceae pollen is present in variable percentages in all the pollen fossil records in the 'Lujanense', with higher percentages in the SW and SE sequences than in the central ones. A similar tendency is seen for Chenopodiineae and Asteraceae, while Poaceae values increase towards the centre of the present Pampa grassland. The present spectra show similar tendencies, suggesting a progressive increase in arid conditions from the centre to the SW. When Brassicaceae pollen appears as peaks, forming clumps, they suggest a local deposition related to some form of local disturbance and/or communities dominated by Brassicaceae. They are often associated with occur-

rence of other ruderal plants such as *Carduus*-type, Cichorioideae and Asteroideae.

Although these pollen records do not have an exact analogue today, they show that large areas of the central and south-western Pampa grassland during the Late glacial were covered with a psammophytic steppe, which in the southwest is associated with a shrubby steppe with thorn-shrub plant communities, suggesting subhumid–dry to semi-arid climatic conditions. This interpretation is compatible with the palaeoecological inferences from the late Pleistocene mammalian faunas (Prado et al., 1997). The presence of vegetated sandy areas could be an indication of dune stabilisation and could be interpreted as an indicator of greater former aridity during the full glacial. This stabilisation is in agreement with the soil development at the end of the ‘Lujanense’ interval, related to a period of floodplain stability (Zárate et al., 1998).

The conditions of the Late glacial–Holocene transition are indicated in the pollen records by abrupt changes of proportions of several taxa. Some pollen changes are typically quantitative (the same taxa, but changes in abundance), while others show qualitative changes (the taxa change, some disappear and are replaced by others).

The pollen record from Sauce Grande indicates that a humid grassland replaced the psammophytic–shrubby steppe at the beginning of the Holocene, while the xerophytic woodland plants decreased notably. At Empalme Querandías and Cerro La China a humid grassland started to develop during the Late glacial–Holocene transition. In Empalme Querandías the transition is related to a pond and floodplain vegetation, and in Cerro La China to environments with locally more effective moisture. A sudden replacement of Brassicaceae by Asteroideae in Empalme Querandías (Profile 2, Fig. 8) suggests a local disturbance in the interfluvial environment, simultaneous with the development of ponds in the fluvial area (Profiles 1 and 3, Figs. 7 and 9). These habitat variations are induced by different topographic positions. The beginning of the evolution of ponds in the NE of Pampa grasslands has been dated as 11,160–11,060 yr B.P. Nowadays, the humid Pampa is subject to periodic occurrence of

floods of varying size and magnitude. In rainy years, several connected or isolated shallow ponds form rapidly. Due to the low relief, the reduced slope and the lack of an integrated drainage system, these temporary ponds merge with permanent ones, creating extensive inundated areas

The pollen assemblages of La Horqueta II suggest the development of small shallow ponds in interdune areas during the Late glacial–Holocene transition. This is in agreement with the diatom, ostracod and sedimentologic analyses which indicate 1 to 3 m deep shallow freshwater ponds (Zárate et al., 1998). The variable percentages of Brassicaceae pollen clumps and the abrupt changes in percentage and concentration values (Fig. 6) suggest a local pollen deposition, and a habitat exposed to severe and rapid disturbances, respectively. A physical disturbance such as the rapid and repeated flooding episodes that inundated the depressions along the valley floodplain (Zárate et al., 1998), caused by unusual rainfall events, could strongly affect the plants, favouring grasses and inhibiting dicotyledonous taxa (Insausti and Soriano, 1987). At present the floodings are a consistent driving force of the humid Pampa (Chaneton et al., 1988), and extreme infrequent floods may act as a disturbance at the community level (Chaneton and Facelli, 1991).

Both the pollen and sedimentary analyses support the argument of a rapid evolution of these pond environments in most of the Pampa grassland at the beginning of the Holocene, suggesting a shift towards subhumid to humid climate conditions. Some studies of mammal remains disagree with this interpretation, while others support it. Tonni (1990) and Tonni and Cione (1994), for example, conclude that the early Holocene was a dryer and cooler time than today, while Prado et al. (1997) argue that between 12,000 and 8500 yr B.P. the conditions were transitional from temperate and semi-arid to more humid.

Brassicaceae are represented in the Pampa grassland by about 50 species, of which 60% are introduced weeds and the other 40% are native species (Cabrera, 1968). Among the latter, many are weeds or are common in disturbed sites. Native as well as introduced taxa occur in dunes or sandy soils (e.g. *Diplotaxis muralis*, *Cakile maritima* and

*Lepidium bonariense*) or halomorphic soils. They can often be dominant in several communities and are remarkably encouraged by frequent disturbance (Facelli et al., 1988). Are Brassicaceae over-represented in some fossil pollen samples due to a differential preservation? The best indicators that pollen assemblages have been altered by differential pollen preservation are: (1) high frequencies of deteriorated grains; (2) low total pollen concentration; and (3) abundance of indeterminate grains (Hall, 1981). In the fossil pollen records, the only sample with deteriorated grains is found at Empalme Querandías (Profile 2, 232.5 cm depth). It contains 77% of grains with evidence of microbial decay and 7% of indeterminate grains. However, in this sample Brassicaceae pollen does not exceed 1%. To the contrary, when Brassicaceae percentage and concentration values are high, there is no evidence of differential preservation. Conversely, during the early and middle Holocene, Brassicaceae values are less than 5% in all the Pampa grassland records and increase notably during the late Holocene (Prieto, 1996). Because this taxon depends on repeated disturbance for its establishment, Brassicaceae populations could likely decline quickly if the climate stabilises, whereas they have the potential to become extremely important as early colonisers as climate changes (Bazzaz, 1998). Based on these findings, it is possible to interpret the over-representation of Brassicaceae as a rapid local deposition in a natural disturbed environment where ruderals prevail, instead of a record of differential pollen preservation.

Of special interest in the fossil pollen assemblages is the presence of Myrtaceae. They are a persistent component in the Sauce Grande and Napostá Grande pollen assemblages before ca. 10,000 yr B.P. and in the Cerro La China and La Horqueta II pollen assemblages between 11,000 and 9000 yr B.P. At present, Myrtaceae are not part of the natural vegetation in the Pampa grasslands and only one native species (*Psidium luridum*) was found once in the Tandilia range (38° S) (Cabrera, 1968). Taking into account that: (1) they occur in clumps in the La Horqueta II pollen record (Plate I); (2) they are found in relatively high percentages in all the fossil pollen records;

and (3) only small amounts of pollen are dispersed within short distances of tree/shrub populations due to their bee-pollination dominated system (Nic Lughadha and Proença, 1996), their presence may be interpreted as local deposition and may indicate local occurrence of taxa instead of extra-regional origin as suggested by Prieto and Paez (1989), Grill (1993) and Borromei (1995). In the fossil pollen records Myrtaceae are associated with psammophytic steppes, with interdune plant communities and with humid grassland in hill areas. It can thus be inferred that Myrtaceae probably formed part of these communities during the Late glacial–Holocene transition, growing as erect or creeping xerophyllous shrubs able to tolerate both deflation and accumulation of sand as they do now on the crests or flanks of fixed or vegetated dunes (Rambo, 1956). The fixation of the sand, soil development and the invasion of non-psammophytic species due to the climatic change that occurred during the Late glacial–Holocene transition probably caused the destruction of the psammophytic communities. Soil development may have resulted in a change in pH and the invasive species may have affected the community through competitive interactions with the psammophytic plants. As a consequence of the development of new habitats, Myrtaceae and other plants were probably not able to acclimatise and were eliminated.

## 7. Conclusions

Pollen analysis indicates vegetational response to environmental change. Some taxa such as Brassicaceae, Asteraceae and *Carduus*-type that represent, in the modern vegetation, arable weeds and ruderal species of common occurrence in human-induced disturbance habitats in many parts of the Pampa grassland, are found in high percentages and concentrations in several pollen samples during the Late glacial–Holocene transition. They had already evolved in habitats subject to natural disturbance, suggesting that Late glacial vegetation of Pampa grasslands may account for the abundance of ruderal species, and there exists the possibility that some species of *Carduus* may have

been native and not just introduced by the Europeans. Climatic change at the beginning of the Holocene is the most significant cause of extending the area of some Pampa grassland taxa, but it may have reduced the area for others. Of the Late glacial vegetation, at least Myrtaceae were probably not able to adapt to the new habitats and hence disappeared from the regional flora at the Pleistocene–Holocene transition. Although other plants may have disappeared as well, these cannot be identified because pollen from these plants cannot be differentiated morphologically. During the Late glacial–Holocene transition, communities with no modern counterparts probably formed and disappeared.

The replacement of dry steppes by different humid grassland environments and the rapid evolution of pond environments beginning at the Late glacial–Holocene transition suggests a shift towards subhumid to humid climate conditions. The palaeoclimatic inferences indicate that the major change is in precipitation, probably in terms of seasonality, suggesting a westward displacement of the isohyets. During the present century, a displacement of the isohyets westward by ca. 200 km in the Pampa grassland occurred. This positive trend in precipitation has been explained as a consequence of the poleward displacement of the Atlantic Subtropical high pressure by 6° in latitude, due to the decrease in mean meridional temperature gradient and in particular to the warming of the high latitudes (Castañeda, 1995; Barros et al., 1996). A similar situation at the beginning of the Holocene can thus be suggested.

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