



Modern vegetation–pollen–climate relationships for the Pampa grasslands of Argentina

Marcela Sandra Tonello^{1,2*} and Aldo Raúl Prieto^{1,2}

¹Laboratorio de Paleoecología y Palinología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina and ²CONICET, National Council of Scientific and Technological Research, Ciudad de Buenos Aires, Argentina

ABSTRACT

Aim To analyse the relationships between potential natural vegetation, pollen and climate in order to improve the interpretation of fossil pollen records and provide the background for future quantitative palaeoclimatic reconstructions.

Location Pampa grasslands of Argentina, between 33–41° S and 56–67° W.

Methods Modern pollen data were obtained from a pollen data base developed by the Grupo de Investigación de Paleoecología y Palinología, Universidad Nacional de Mar del Plata, Argentina (143 surface samples and 17 pollen types). Analysis of pollen and climate data involved multivariate statistics (cluster analysis and principal components analysis), scatter diagrams, Pearson's correlation and isopoll mapping.

Results Vegetation patterns at regional scales (grasslands and xerophytic woodlands) and local scales (edaphic communities) were identified by cluster analysis of pollen surface samples. The main climatic variables that appear to constrain the vegetation distribution and abundance of taxa are mean annual precipitation, annual effective precipitation and summer temperature. Individual pollen types such as Chenopodiaceae, Apiaceae, Cyperaceae, *Prosopis*, *Schinus*, *Condalia microphylla* and other xerophytic taxa are good indicators of moisture regime. Many pollen types are significantly correlated with summer temperature. The modern vegetation–pollen–climate relationships vary in a broadly predictable manner, supporting the contention that fossil pollen assemblages can be related to particular climatic characteristics.

Main conclusions An expanded suite of modern analogues facilitated new insights into vegetation–pollen–climate relationships at the regional scale in Pampa grasslands. Relationships between individual pollen types and climate are appraised at a regional scale and new modern analogues are presented. The results provide the basis for improved vegetation and climate reconstruction from fossil records of the study area.

Keywords

Argentina, climate, isopoll maps, modern analogue, multivariate analysis, palaeoecology, Pampa grasslands, pollen analysis, vegetation.

*Correspondence: Marcela Tonello, Laboratorio de Paleoecología y Palinología, Departamento de Biología, UNMdP, Funes 3250 (7600) Mar del Plata, Argentina.
E-mail: mtonello@mdp.edu.ar.

INTRODUCTION

Fossil pollen data have been widely used to reconstruct past environmental and climatic conditions. Recent advances in calibrating modern pollen data in terms of specific climate variables have made it possible to provide quantitative climatic reconstructions for many different ecosystems (e.g. Seppä &

Birks, 2001; Bigler *et al.*, 2002; Markgraf *et al.*, 2002; Davis *et al.*, 2003; Herzschuh *et al.*, 2004; Seppä *et al.*, 2004). The quantitative approaches are based on the collection of modern pollen surface samples and on comparison of the occurrence and abundance of modern pollen types or modern pollen assemblages with modern climate data in order to produce a pollen–climate calibration or training set (Seppä *et al.*, 2004).

In grassland ecosystems, however, few studies have analysed the quantitative relationships between modern pollen representation and climate variables. Grasses are potentially good indicators of past climates as, in general, they have short life cycles (relative to woody perennial trees and shrubs) and are likely to respond quickly to environmental changes including variation in $p\text{CO}_2$, temperature and moisture (Wooller & Beuning, 2002). However, one of the problems in using pollen data to reconstruct past environmental and climatic conditions in grass-dominated biomes is the low taxonomic resolution, resulting in a loss of ecophysiological information (Wooller & Beuning, 2002). However, Hoyt (2000) showed that tall-grass, short-grass, mixed-grass and desert grasslands could be differentiated when assemblages of pollen types are considered.

This study presents a comprehensive analysis of the quantitative relationships between modern pollen, vegetation and climate for the Argentine Pampa region and adjacent xerophytic woodlands using a modern pollen data base developed at the Universidad Nacional de Mar del Plata. Previous palaeoecological studies using qualitative approaches to determine modern pollen–vegetation–climate relationships were carried out at different spatial scales, separately for both the Pampa grasslands (Prieto, 1992, 1996; Stutz & Prieto, 2003; Fontana, 2005; Vilanova *et al.*, 2006) and the adjacent xerophytic woodland (Schäbitz, 1999; Paez *et al.*, 2001). Understanding the spatial and temporal shifts of the grassland–xerophytic woodland ecotone, located between 35 and 40° S, is important for reconstructing past climatic change during the late Quaternary.

Our study focuses on: (1) using cluster analysis and isopoll maps to analyse the correspondence between modern pollen and vegetation patterns, based on potential natural vegetation units, (2) using multivariate analysis to explore the relationships between climate variables and vegetation units, their distribution and taxon abundance, and (3) using correlation coefficients and scatter diagrams to investigate the quantitative relationships between modern pollen and climate.

STUDY AREA

Location and topography

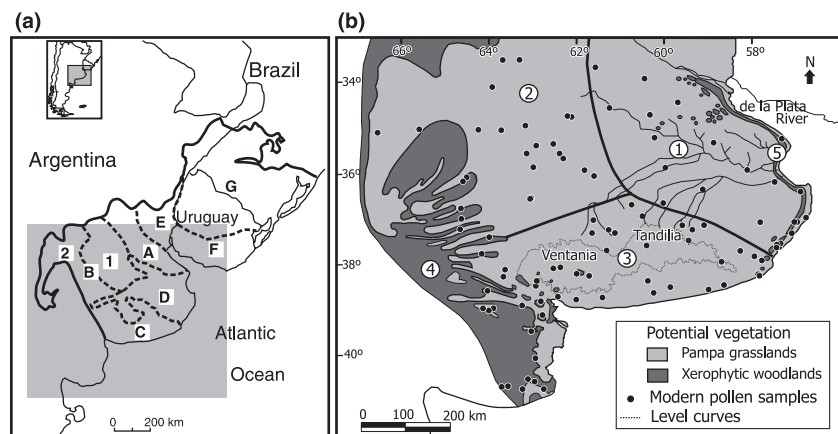
Temperate humid grasslands extend in the eastern part of South America from 28 to 38° S, covering the vast plains of central-eastern Argentina, Uruguay and southern Brazil (Fig. 1a). This region can be divided into the Pampa grasslands in Argentina and the Campos in Uruguay and southern Brazil (Soriano, 1991). The Pampa grasslands are limited by the Atlantic Ocean to the east and south-east, and surrounded by a xerophytic woodland that extends to the west and north and along de la Plata River and the Atlantic coast to 38° S (Fig. 1b). Grasslands have been the predominant vegetation in the Pampa region during the late Quaternary, as evidenced by pollen records (Prieto, 1996, 2000; Quattrocchio & Borromei, 1998) and fossil faunal studies (Tonni *et al.*, 1999).

The study area extends between 33 and 41° S and 56 and 67° W (Fig. 1b). The region is a continuous plain, covered by late Pleistocene–Holocene loess deposits of variable thickness (Zárate, 2003), interrupted by two low mountain systems in the south-central part, the Tandilia ranges (highest altitude 524 m a.s.l.) and the Ventania ranges (highest altitude 1247 m a.s.l.). To the west, plains alternate with plateau areas ranging between 100 and 200 m a.s.l. Despite this uniformity the landforms are of different origins and age, reflecting a complex geological history (Zárate & Rabassa, 2005).

Climate

The climate of the study area is temperate, with maritime influence decreasing to the west and south-west. From east to west, four climatic types can be distinguished along this gradient: humid, subhumid–humid, subhumid–dry and semi-arid (Fig. 2a). Mean annual temperature ranges between 16 and 13°C, with a maximum in summer (December–February) and a minimum in winter (June–August; Fig. 2b). Mean annual isotherms decrease from north to south in response to the moderating effect of the Atlantic Ocean (Prohaska, 1976). Mean annual precipitation decreases from c. 1000 mm in the

Figure 1 Location map of the study area. (a) Grasslands division: (A) rolling pampa, (B) inland pampa, (B.1) flat pampa, (B.2) western pampa, (C) southern pampa, (D) flooding pampa, (E) mesopotamic pampa, (F) southern campos, (G) northern campos (Soriano, 1991). (b) Location of modern pollen sites and potential vegetation units: (1) Eastern Pampa, (2) Inland Pampa, (3) Southern Pampa, (4) Caldenal, (5) Talar (modified from Tonello, 2006).



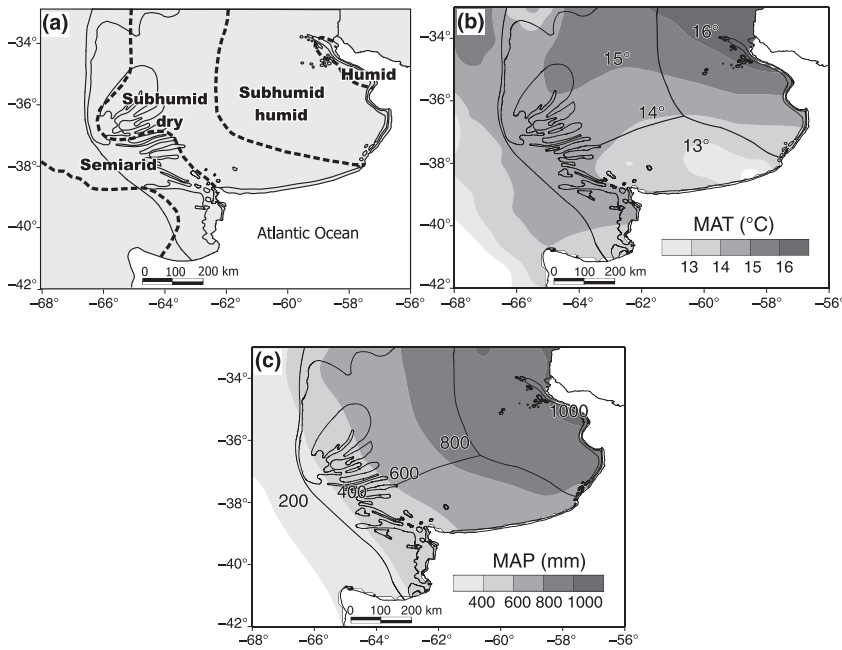


Figure 2 Maps of (a) climatic types (modified from Burgos & Vidal, 1951); (b) mean annual temperature (MAT); (c) mean annual precipitation (MAP).

north-east to c. 400 mm in the south-west, related to the position of the Atlantic semi-permanent high-pressure system (Fig. 2c). The region is transitional between summer subtropical continental and winter maritime-influenced rain, resulting in two rainy seasons: a maximum in autumn (March–May) and a lesser peak in spring (September–November; Prohaska, 1976).

Vegetation

The Pampa grasslands are divided into three potential vegetation units: Eastern Pampa, Inland Pampa and Southern Pampa, based on phytosociological characteristics, historical observations about land use, and climatic and geomorphological differences (Tonello, 2006) (Fig. 1b). The vegetation is dominated by Poaceae, in terms of both species number and abundance, and potential vegetation units can be identified from presence/abundance of different Poaceae genera. Other important components of the vegetation are Asteraceae, Cyperaceae, Solanaceae, Apiaceae and Chenopodiaceae (León, 1991).

The natural vegetation of the Pampa grasslands lacks trees despite overall climatic conditions and soil characteristics that are similar to other world regions where forests predominate. Possible causes of this absence are seedling inhibition and competition from grasses, fine texture and poor aeration of soils, and summer drought (Facelli & León, 1986). Today, planted woody species are frequent near to the settlements or in disturbed areas where the competitive effect of grasses is low.

Agricultural practices have changed the Pampa grasslands in some areas, causing the extinction of some native species and allowing the establishment of exotic species (León, 1991). However, natural or semi-natural grasslands are found in uncultivated or undisturbed areas.

The xerophytic woodland is divided into two potential vegetation units: Caldenal and Talar (Tonello, 2006) (Fig. 1b). Caldenal is an open xerophytic woodland dominated by the trees *Prosopis caldenia* Burkart, *Prosopis flexuosa* D.C., *Geoffraea decorticans* (Gillies ex Hook. & Arn.) Burkart, and *Schinus fasciculata* (Griseb.) I.M. Johnst., and accompanied by shrubs including *Condalia microphylla* Cav., *Lycium gilliesianum* Miers., *Prosopidastrum* sp. Burkart, *Ephedra triandra* Tul. emend. J.H. Hunz., and *Larrea divaricata* Cav. (Cano *et al.*, 1980). Along the ecotone between the Pampa grasslands and the xerophytic woodland (Caldenal) to the south-west, grasslands alternate with shrubby communities, with scattered trees and agricultural lands. It has been difficult to determine if this transitional zone reflects expansion of the woodland into the grasslands or whether it is a woodland relict.

The Talar is an impoverished form of xerophytic woodland characterized by *Celtis tala* Gillies ex Planch. and accompanied by *Jodina rhombifolia* H. et A., *Schinus longifolia* (Lindl.) Speg., and *Sambucus australis* Cham et Schlecht (Cabrera, 1976). The Talar was defined as an edaphic community within Pampa grasslands (Cabrera, 1976), suggesting that its geographical distribution is more related to geomorphological than to climatic conditions.

DATA AND METHODS

Pollen

Modern pollen data representing 143 sites were obtained from the pollen data base developed by the Grupo de Investigación de Paleoecología y Palinología, Universidad Nacional de Mar del Plata, Argentina. The data base included 102 published surface samples from Pampa grasslands (Prieto, 1992, 1996; Stutz & Prieto, 2003; Tonello & Prieto, 2003) and the

south-western xerophytic woodland–grassland ecotone (Schäbitz, 1999; Paez *et al.*, 2001), and 41 unpublished samples.

The surface samples came from soils (70%), flooded depressions (22%) and core-top samples of shallow lakes (8%), and were collected from minimally disturbed sites and uncultivated areas. Pollen processing followed standardized laboratory methods (Faegri & Iversen, 1989). The total pollen sum varied between 330 and 8000 grains. Clustered samples that come from sites within 100 m of each other, which represented the same plant community and had similar pollen assemblage values, were grouped and the mean for each pollen type was calculated. The reduced data matrix contained 103 surface pollen samples.

A total of 95 pollen types were represented in the original data base. Pollen nomenclature followed the nomenclature system of the Institute of Botany Darwinion, Argentina (<http://www.darwin.edu.ar>). For the analysis, exotic arboreal pollen taxa (Myrtaceae, Cupressaceae, Lauraceae, *Salix*, *Pinus*, *Betula*, *Casuarina*, *Araucaria*, *Alnus*, *Ulmus*, *Corylus*, *Juglans*, *Populus*, *Quercus* and *Pisonia*), extra-regional pollen (*Podocarpus* and *Nothofagus dombeyi*-type) and Brassicaceae were excluded from the pollen sum. *Podocarpus* and *Nothofagus dombeyi*-type are long-distance pollen from the Subantarctic forests in the Andean region between 36 and 54° S, c. 750 km west of the Pampa grasslands. Brassicaceae is represented by about 50 species, of which 60% are introduced taxa (Prieto, 2000). Several species from the genera *Brassica* and *Raphanus* were introduced by European settlement and have invaded and colonized grassland communities.

Cyperaceae pollen was included in the pollen sum as it is a potentially important component of the general flora, rather than being restricted to wetlands. Surface pollen samples with Cyperaceae values higher than 10% were found primarily in samples from flooded depressions (65%), shallow lakes (21.5%) and interdune depressions (13.5%). High percentages of this pollen type in late Quaternary pollen records from temperate grasslands of South America (e.g. Prieto, 2000; Behling, 2002; Iriarte, 2005) have been interpreted to indicate wetland or floodplain vegetation, associated with subhumid to humid climate conditions.

Some taxa were combined into higher taxonomic categories whenever pollen identification was not uniform (e.g. Asteraceae subf. Asteroideae included undifferentiated Asteraceae subf. Asteroideae, *Centaurea*, *Hyalis*, *Crisanthemum*-type and *Carduus*-type; and Apiaceae included undifferentiated Apiaceae, *Apium*-type, *Hydrocotyle* and *Eryngium*). Pollen types with low percentages (< 1%) and similar ecological requirements were combined to provide broad functional types, for example other xerophytic taxa (Caesalpinoideae, Rhamnaceae, Cactaceae, *Prosopidastrum*, *Lycium*, *Larrea*, *Acacia*, *Capparis*, *Monttea*, *Berberis* and *Buddleja*), aquatic-type (undifferentiated Solanaceae, *Solanum*, *Typha*, *Alternanthera*, *Ranunculus*, *Myriophyllum*, *Potamogeton*, *Triglochin* and Monocotyledonae), psammophytic-type (Caryophyllaceae, Rosaceae, Rutaceae, Onagraceae, *Daucus*, *Adesmia*, *Calycera*, *Blakstonia*/*Centarium*,

Polygala and *Ambrosia*), and other herbs (Papilionaceae, Urticaceae, Polygonaceae, Plumbaginaceae, Convulvaceae, Malvaceae, Geraniaceae, Campanulaceae, Valerianaceae, Papaveraceae, Loganiaceae, Portulacaceae, Boraginaceae, Rubiaceae, Lamiaceae, Scrophulariaceae, Euphorbiaceae, Orchidaceae, Verbenaceae, *Gomphrena*, *Spergularia*, *Corrigiola*, *Paronychia*, *Plantago*, *Gilia*-type, *Phyla* and *Oxalis*).

As a result, 17 pollen types were selected for the analysis (Fig. 3). Pollen percentages were calculated and pollen diagrams were drawn using the program TGVIEW 2.0.2 (Grimm, 2004). Surface pollen samples were grouped using cluster analysis applying a square-root transformation with Edward & Cavalli-Sforza's chord distance and Ward's method.

Isopoll maps allowed us to characterize spatial patterns of the pollen types analysed for comparison with the distribution of the potential natural vegetation. Pollen percentages were interpolated by applying the kriging method, which is an unbiased estimator and has the smallest square-error prediction (Siska *et al.*, 2001). Different contour intervals were used for each map.

Climate

Each of the 103 surface samples sites was attributed values for annual and seasonal temperature, precipitation and effective precipitation, extracted from the climate data base developed by Leemans & Cramer (1991). Effective precipitation was calculated as the ratio between precipitation and potential evapotranspiration. Potential evapotranspiration values were estimated according to Thornthwaite (1948).

Values from the Leemans and Cramer data base were checked against data from meteorological stations. Correlation coefficients between the two sets of climate data were 0.96 and 0.85 ($n = 17$, $P < 0.01$) for precipitation and temperature, respectively.

The climate data were standardized and centred, and each sample was assigned to a potential vegetation unit. Principal components analysis (PCA) was applied to achieve a reduction of the dimensionality of the climate matrix with a minimal loss of total variance.

Pollen–climate analysis

A square-root transformation was applied to the pollen percentages to stabilize the variance and emphasize the variability of pollen types with low percentages. Pearson's correlation coefficients were calculated between individual pairs of pollen and climatic variables and illustrated in scatter diagrams. The scatter diagrams allowed us to identify anomalous or outlier observations and to analyse the relationships between pollen and climatic variables. Three outliers of execution error type (Howe & Webb, 1983), with unusually high pollen values indicating overrepresentation by pollen types [*Prosopis* L. (35.5%), *Schinus* L. (46.4%) and *C. microphylla* (35.4%)], were eliminated and scatter diagrams were replotted.

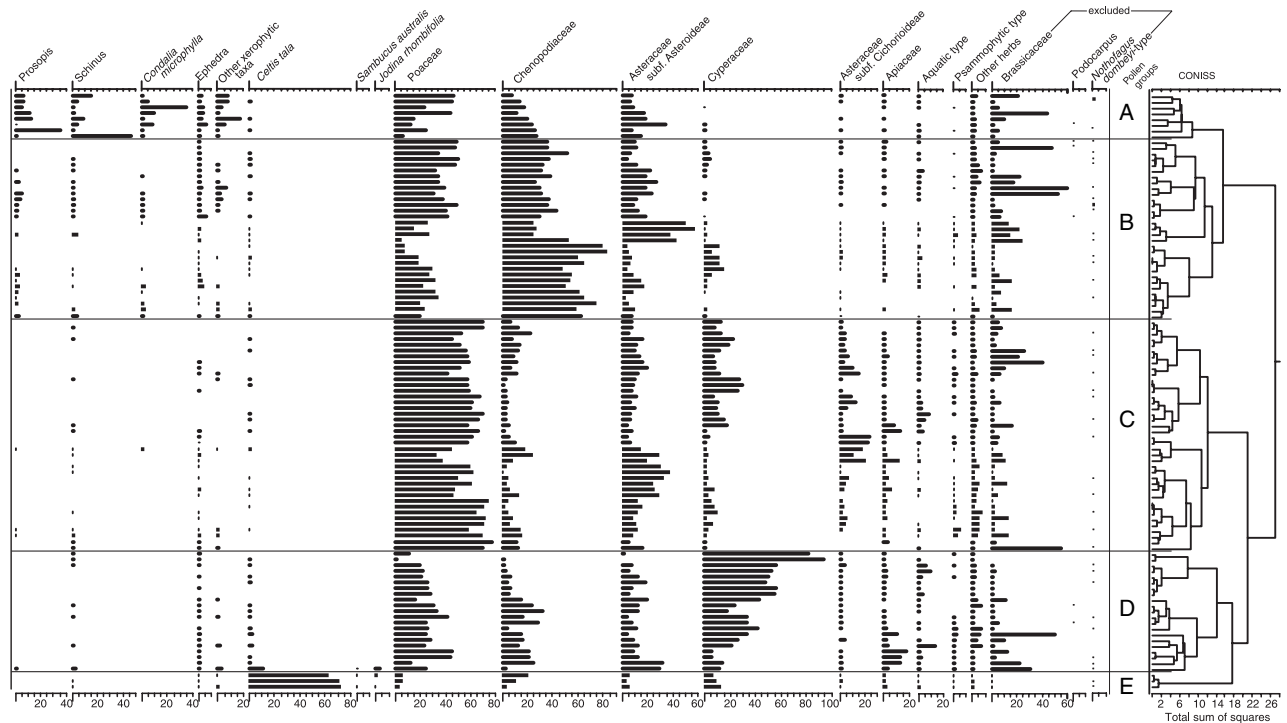


Figure 3 Pollen percentage values of selected pollen types (full data available on request) and cluster analysis of 103 surface pollen samples. Clusters were defined by qualitative analysis.

RESULTS AND DISCUSSION

Pollen–vegetation relationships

Cluster analysis

Pollen samples from the Pampa grasslands are distinguished from those from xerophytic woodland by cluster analysis (Fig. 3). Pampa grasslands pollen assemblages are divided into three groups (B–D) and xerophytic woodland into two groups (A and E). The groups are described in terms of main pollen type.

Group B is characterized by Chenopodiaceae, Poaceae and Asteraceae subf. Asteroideae, with values between 10% and 50%. This group includes samples that represent psammophytic grasslands on sandy dunes of Inland Pampa and plant communities of grassland–xerophytic woodland ecotone of Inland and Southern Pampa. Pollen samples characterized by the highest Chenopodiaceae values (up to 80%) represent halophytic communities from different vegetation units.

Group C represents the grasslands biome, characterized by high Poaceae pollen percentages (40–70%) in association with Chenopodiaceae, Asteraceae subf. Asteroideae, Asteraceae subf. Cichorioideae, Apiaceae and Cyperaceae, together occurring with values < 30%.

Group D includes samples from communities belonging to different grassland units that represent flooded depressions, shallow lakes and humid interdune depressions. These samples are characterized by Cyperaceae with values up to 90%,

accompanied by low values of Poaceae (< 30%), Chenopodiaceae (< 30%) and Asteraceae subf. Asteroideae (< 20%).

Group A comprises samples from the xerophytic woodland (Caldenal) and the grassland–xerophytic woodland ecotone, characterized by the presence of *Prosopis*, accompanied by *Schinus*, *C. microphylla*, *Ephedra* and other xerophytic taxa with values between 5% and 40%. Values of Poaceae, Chenopodiaceae and Asteraceae subf. Asteroideae (together totalling < 40%) represent the herbaceous and shrubby aspect of the Caldenal vegetation.

Group E represents the Talar vegetation, characterized by high values of the indicator taxon *C. tala* (> 50%) accompanied by *S. australis* and *J. rhombifolia*. Poaceae, Chenopodiaceae, Asteraceae subf. Asteroideae and Cyperaceae are present with low values representing the herbaceous component.

Isopoll maps

The isopoll maps reflect the vegetation patterns at regional scales, separating grasslands from xerophytic woodland (Fig. 4), and supporting the results obtained by cluster analysis.

Poaceae, Chenopodiaceae, Asteraceae subf. Asteroideae and Cyperaceae are the main pollen types of the grassland communities. Higher percentages of Poaceae characterize the central part of the grasslands with values > 50% (Fig. 4a). Chenopodiaceae values > 30% characterize edaphic communities such as salt marshes and alkaline flat areas, whereas values < 30% are widespread (Fig. 4b). Asteraceae subf.

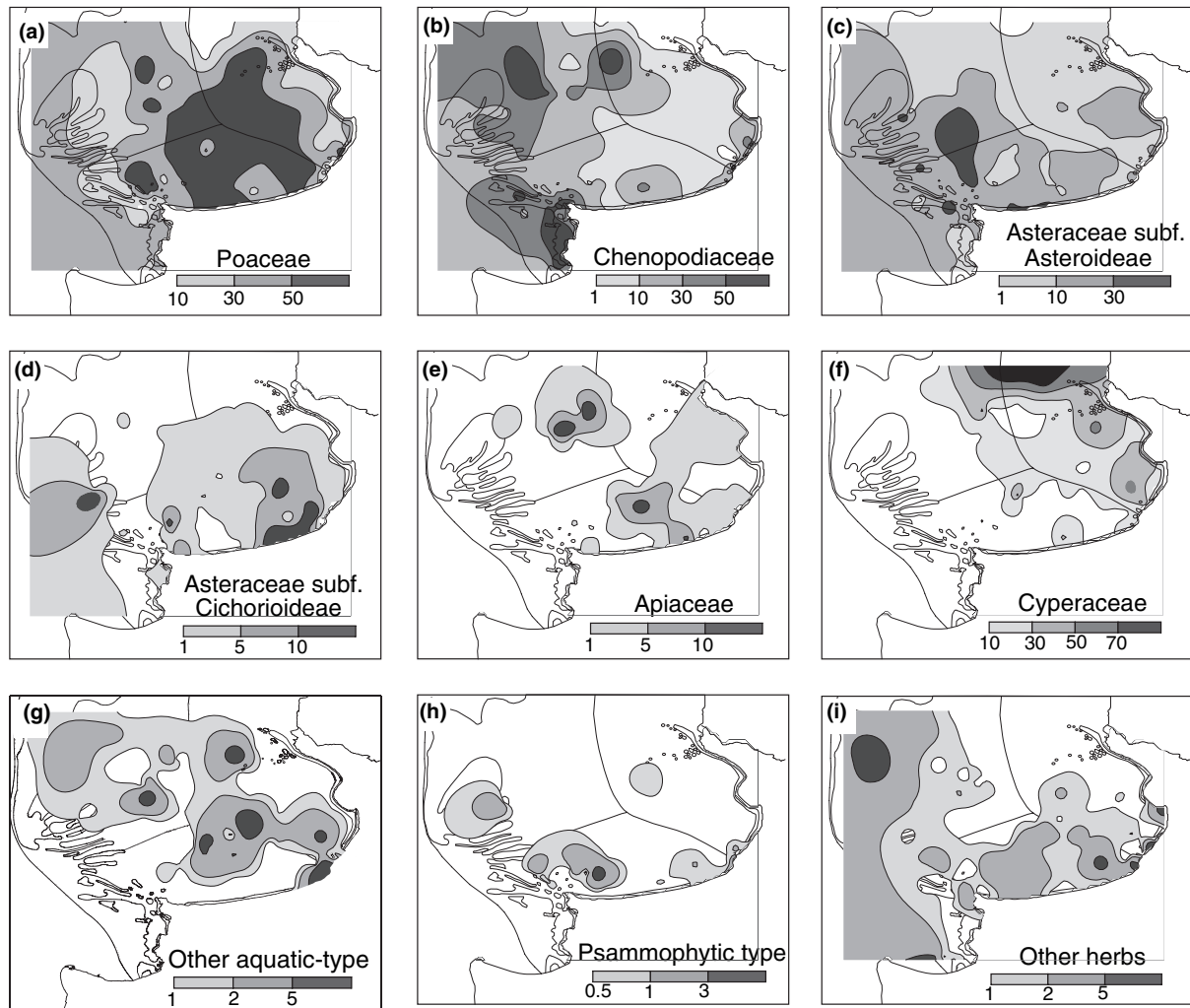


Figure 4 Isopoll maps showing interpolated pollen percentages of the surface samples. The intervals used for each map are indicated in the lower right corner. A variable colour gradient was used for each pollen type.

Asteraceae appearing with low percentages (1–10%) represent grassland herbs, while values > 10% represent mainly shrub genera from plant communities in the south-western grasslands (Fig. 4c). Cyperaceae values > 10% characterize aquatic and wet-ground communities of flooded depressions and shallow lakes mainly from the Eastern Pampa (Fig. 4f). Two samples from flooded depressions at the northern boundary of the grasslands had Cyperaceae pollen values of 50–70%. These isopoll curves should be interpreted with caution because they could be an artefact of the spatial interpolation methodology. Asteraceae subf. Cichorioideae and Apiaceae are present in grasslands with low abundance, and values > 10% represent local communities (Fig. 4d,e). Rare pollen types, e.g. aquatic-type, psammophytic-type and other herbs, represent herbaceous taxa from various grassland communities (Fig. 4g–i).

The isopoll maps for *Prosopis*, *Schinus*, *C. microphylla*, *Ephedra* and other xerophytic taxa correctly reflect Caldenal vegetation and the grassland–xerophytic woodland ecotone (Fig. 4j–n). These pollen types have a limited pollen dispersal range because most are insect-pollinated. The highest percent-

ages of *Prosopis* and *Schinus* (> 20%) indicate sites where undisturbed *Prosopis* woodland can be found.

The isopoll maps for *C. tala*, *S. australis* and *J. rhombifolia* represent the Talar vegetation (Fig. 4o–q). *Celtis tala* values between 30% and 50% and *S. australis* and *J. rhombifolia* values < 1% characterize the mixed Talar woodland, and *C. tala* values > 70% represent a monospecific woodland. Values between 1% and 10% for *C. tala* indicate discontinuous presence.

The main vegetation patterns were identified on the basis of the more abundant pollen types. The Pampa grasslands are characterized by high frequencies of Poaceae (group C). Chenopodiaceae, Asteraceae subf. Asteroideae, Apiaceae and Cyperaceae represent those taxa found to accompany Poaceae at a regional scale (group C), and define different edaphic communities locally (groups B and D). Group B represents grassland communities primarily from samples in Inland and Southern Pampa, while group D represents communities from the Eastern Pampa and the eastern part of the Inland and Southern Pampa.

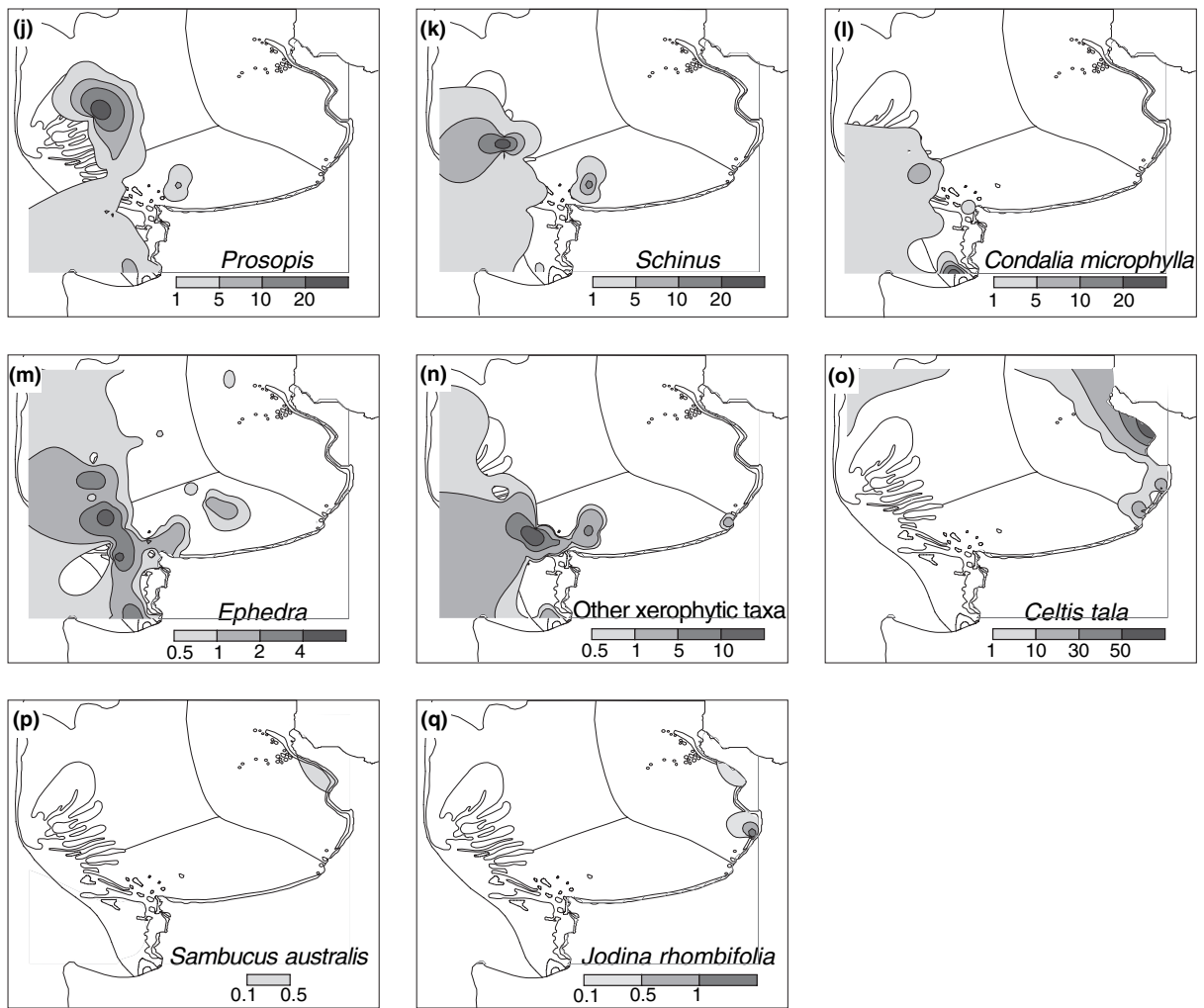


Figure 4 continued

Despite these differences, potential natural vegetation units in the Pampa grasslands were largely indistinguishable based on their pollen spectra or floristic attributes. These results confirm previous modern pollen analyses that have demonstrated the difficulty of separating Pampa grasslands into different vegetation units (Prieto, 1992, 1996; Tonello & Prieto, 2003). In contrast, the xerophytic woodland vegetation types (groups A and E) were readily distinguishable by the presence of arboreal and shrubby indicator pollen types such as *Prosopis*, *Schinus*, *C. microphylla*, *Ephedra*, other xerophytic taxa and *C. tala*.

Climate–vegetation relationships

The PCA results identify the main climatic variables that appear to constrain the potential vegetation units (Fig. 5). The first two axes of the PCA explain 89% of total variance in the climate matrix. The highest loadings on axis 1 correspond to mean annual precipitation (MAP), annual effective precipitation (AEP), autumn precipitation (AuP) and spring effective precipitation (SpEP). This axis is correlated with MAP

($r = 0.998$), AEP ($r = 0.971$), AuP ($r = 0.970$) and SpEP ($r = 0.951$). Mean annual precipitation, mean annual effective precipitation, autumn precipitation and spring effective precipitation are thus the principal climatic variables defining the vegetation units along the strong northeast–southwest gradient.

The highest loadings on the second axis correspond to summer temperature (SuT), spring temperature (SpT) and mean annual temperature (MAT). This axis has $r = 0.959$ with SpT and SuT, and $r = 0.924$ with MAT, showing the influence of the north-to-south temperature gradient on vegetation patterns. Temperature controls the distribution of grasslands indirectly by modulating water demand and water availability (Sala *et al.*, 2001).

The Eastern Pampa and Caldenal vegetation units are separated by the first axis, illustrating the control of the moisture gradient on the physiognomic characteristics in grasslands vs. xerophytic woodland. The Eastern Pampa belongs to the humid and subhumid–humid climatic type, while the Caldenal belongs to the semi-arid type (Fig. 2a). The Talar has the same climatic conditions as the Eastern Pampa.

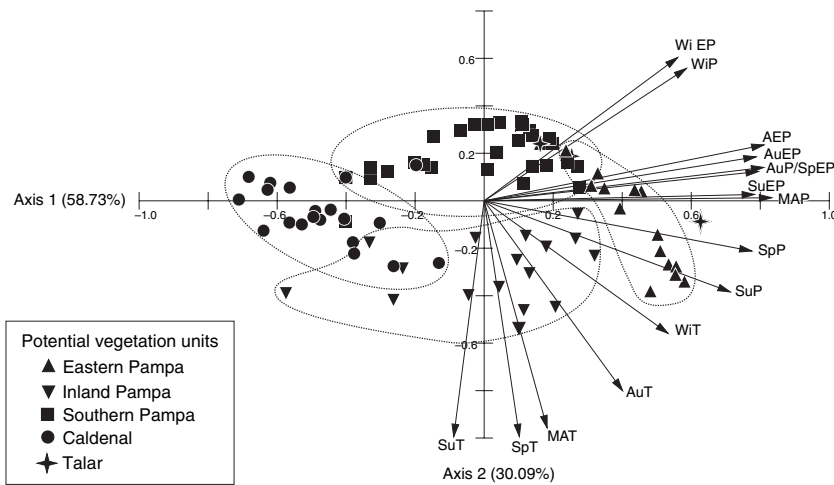


Figure 5 Principal components analysis showing the first two PCA axes. Climatic variables: mean annual temperature (MAT), mean annual precipitation (MAP), annual effective precipitation (AEP), winter temperature (WiT), winter precipitation (WiP), winter effective precipitation (WiEP), spring temperature (SpT), spring precipitation (SpP), spring effective precipitation (SpEP), summer temperature (SuT), summer precipitation (SuP), summer effective precipitation (SuEP), autumn temperature (AuT), autumn precipitation (AuP), autumn effective precipitation (AuEP). Each symbol represents the potential vegetation units.

The Inland and Southern Pampa are separated on the second axis. These units have the same physiognomy, although some floristic differences are associated with the temperature gradient. The Inland and Southern Pampa belong to the subhumid–dry climate type (Fig. 2a).

According to these results, the moisture regime is the dominant climatic characteristic in Pampa grasslands and xerophytic woodlands. The precipitation gradient constrains the vegetation distribution, but the water available to vegetation is different from the total rainfall. Effective precipitation is used as an approximation to water balance and allows identification of areas with water excess and water deficit. Water balance or incipient water excess characterizes the humid climate types, while water balance or water deficit characterizes the drier climate types. According to Lemcoff (1991), the classification into humid, subhumid–humid, subhumid–dry and semi-arid climatic types is the most suitable to define native vegetation units.

Pollen–climate relationships

The correlation coefficients between pollen types and selected climatic variables (MAP, AEP and SuT) are presented in Table 1. Twelve pollen types show statistically significant relationships with MAP and AEP, while nine pollen types are significantly correlated with SuT, but with low correlation coefficients. We present and comment only on a portion of this analysis to illustrate the relationships between some pollen types and MAP (Fig. 6) (others are presented in Appendices S1 and S2 in Supplementary Material). Pollen–climate relationships are discussed only for pollen types with high correlation coefficients (> 0.40) and/or for those with ecological relevance.

Table 1 Pearson's correlation coefficients between pollen types and selected climatic variables (summer temperature, SuT; mean annual precipitation, MAP; annual effective precipitation, AEP). Marked correlations (bold) are significant at $P < 0.05$, $n = 103$.

| Pollen type | SuT | MAP | AEP |
|--------------------------------|--------------|--------------|--------------|
| Poaceae | −0.18 | 0.03 | 0.08 |
| Chenopodiaceae | 0.35 | −0.50 | −0.56 |
| Asteraceae subf. Asteroideae | 0.03 | −0.30 | −0.27 |
| Asteraceae subf. Cichorioideae | −0.39 | 0.24 | 0.32 |
| Apiaceae | −0.20 | 0.36 | 0.39 |
| Cyperaceae | −0.07 | 0.68 | 0.66 |
| Aquatic-type | −0.15 | −0.25 | −0.28 |
| Psammophytic-type | −0.32 | 0.09 | 0.15 |
| Other herbs | −0.22 | 0.10 | 0.05 |
| <i>Prosopis</i> | 0.22 | −0.61 | −0.63 |
| <i>Schinus</i> | 0.24 | −0.40 | −0.43 |
| <i>Condalia microphylla</i> | 0.21 | −0.59 | −0.61 |
| <i>Ephedra</i> | 0.23 | −0.57 | −0.59 |
| Other xerophytic taxa | 0.18 | −0.42 | −0.43 |
| <i>Celtis tala</i> | −0.08 | 0.19 | 0.18 |
| <i>Sambucus australis</i> | 0.08 | −0.11 | −0.12 |
| <i>Jodina rhombifolia</i> | 0.00 | 0.22 | 0.20 |

Poaceae

This pollen type is not significantly correlated with any of the climatic variables tested, probably because grasses are widespread along the whole climatic gradient (Table 1; Fig. 6a). However, the Poaceae show a consistent regional pattern (group C, Fig. 3). Cabrera (1976) proposed a relationship between the distribution of Poaceae and the precipitation gradient on the basis of the fact that mesic grasses are dominant in the northern sector of Pampa grasslands, while xerophytic grasses are dominant in the west and south.

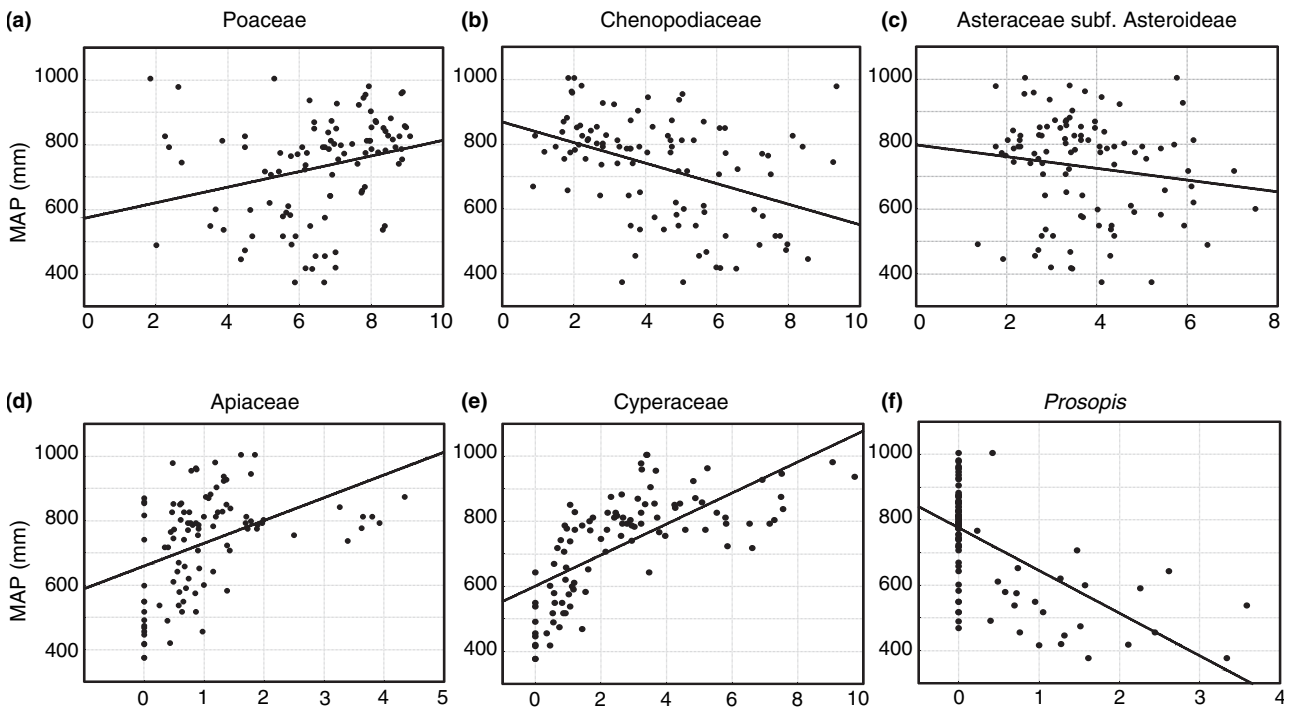


Figure 6 Scatter diagrams of pollen type (square root-transformed percentages) vs. mean annual precipitation (MAP).

Vegetation heterogeneity analysis carried out in the Eastern Pampa has shown a latitudinal pattern in the abundance of Poaceae genera correlated with grasses belonging to megameso and microthermic groups (Perelman *et al.*, 2001). Neither this heterogeneous pattern nor the differences in distribution of mesic versus xerophytic grasses are recorded in the Poaceae pollen spectra, probably due to the limited taxonomic resolution.

Chenopodiaceae

This pollen type shows negative correlation coefficients with mean annual precipitation and annual effective precipitation (Table 1). The Chenopodiaceae show a negative linear trend with these climatic variables, although higher pollen values are widespread (Fig. 6b). This taxon is positively correlated with summer temperature with a low correlation coefficient (Table 1). Despite a wide climatic and edaphic tolerance, Chenopodiaceae can be used as an indicator of regional moisture regimes.

Asteraceae subf. Asteroideae

This pollen type shows significant but low negative correlation coefficients with mean annual precipitation and annual effective precipitation, but does not show any relationship with temperature (Table 1). Low pollen values are associated with high precipitation values, with a slight negative linear trend (Fig. 6c). This pollen type is represented by species of different growth forms (herbs and shrubs) that cannot be identified from pollen. Taxa in this sub-family have wide

climatic tolerances that could suppress a clear relationship with climatic variables.

Apiaceae

This pollen type shows significant correlation coefficients with selected climatic variables (Table 1). The scatter diagram shows a positive correlation of high pollen values with high precipitation values (Fig. 6d). Apiaceae pollen is present in grassland samples along the whole climatic gradient. The significant relationship with the moisture regime is based on samples with high pollen values from local communities in humid areas.

Cyperaceae

This pollen type has high positive correlation coefficients with mean annual precipitation and annual effective precipitation (Table 1). High pollen values are associated with high precipitation values (Fig. 6e). The pollen–climate relationship shows a linear trend up to a maximum point where edaphic conditions are the main factors that influence pollen abundance. Cyperaceae pollen does not have a significant relationship with temperature, being widely distributed along the temperature gradient.

Prosopis

Several pollen taxa characteristic of the Caldenal vegetation, except for other xerophytic taxa, show similar relationships with climatic variables: high negative correlation coefficients

with mean annual precipitation and annual effective precipitation, and low positive correlation with summer temperature (Table 1). We have selected one, *Prosopis*, to illustrate the group (Fig. 6f). The other pollen types are *Schinus*, *C. microphylla*, *Ephedra* and other xerophytic taxa.

The scatter diagrams showed pronounced linearity for some pollen types in their relationships with climatic variables. In some cases, this linearity can reflect a unimodal curve that will appear monotonic when a limited range of the climatic variable is sampled. In other cases, pollen types (e.g. Cyperaceae and Apiaceae) could be showing an exponential relationship. Different responses of pollen type to environmental variables should be considered carefully in the choice of statistical methods for quantitative environmental reconstructions. For other types, no clear relationship to climate is evident.

The relationships between individual pollen types and MAP are illustrated in Fig. 7.

All Caldenal pollen taxa are related to low precipitation, being good indicators of subhumid–dry and semi-arid climatic conditions. However, more pollen data from the *Prosopis* woodland region are needed to improve the model so that it can be used for palaeoclimatic reconstructions from fossil records. Pollen taxa from the Talar vegetation are outliers in

the pollen–precipitation model, confirming the edaphic characteristics of this vegetation unit. These pollen types do not provide climatic information at regional scales, but constitute potential modern analogues for past vegetation dynamics during the Holocene. Fossil pollen records document the presence of *C. tala* for the last c. 7200 years in the Eastern Pampa (Stutz *et al.*, 2006) and, according to these pollen records, its geographical distribution has not changed since the mid-Holocene.

A previous modern pollen study in the Pampa grasslands showed that Poaceae pollen is positively related to precipitation, while that of Chenopodiaceae and Asteraceae was inversely related (Prieto, 2000). In the present study, neither Poaceae nor Asteraceae subf. Asteroideae shows a relationship with precipitation. This finding may be due to the limited taxonomic resolution, or to the fact that both taxa are widely distributed along the climatic gradient. The Poaceae pollen type does not permit reliable identification beyond the family level, hence this pollen type is treated as a single unit in modern and fossil pollen studies. While Asteraceae subf. Asteroideae, if identified to the genus level, can reveal a correlation with precipitation, fossil pollen types are generally not resolved at that level. According to these results, Poaceae and Asteraceae subf. Asteroideae should not be used as

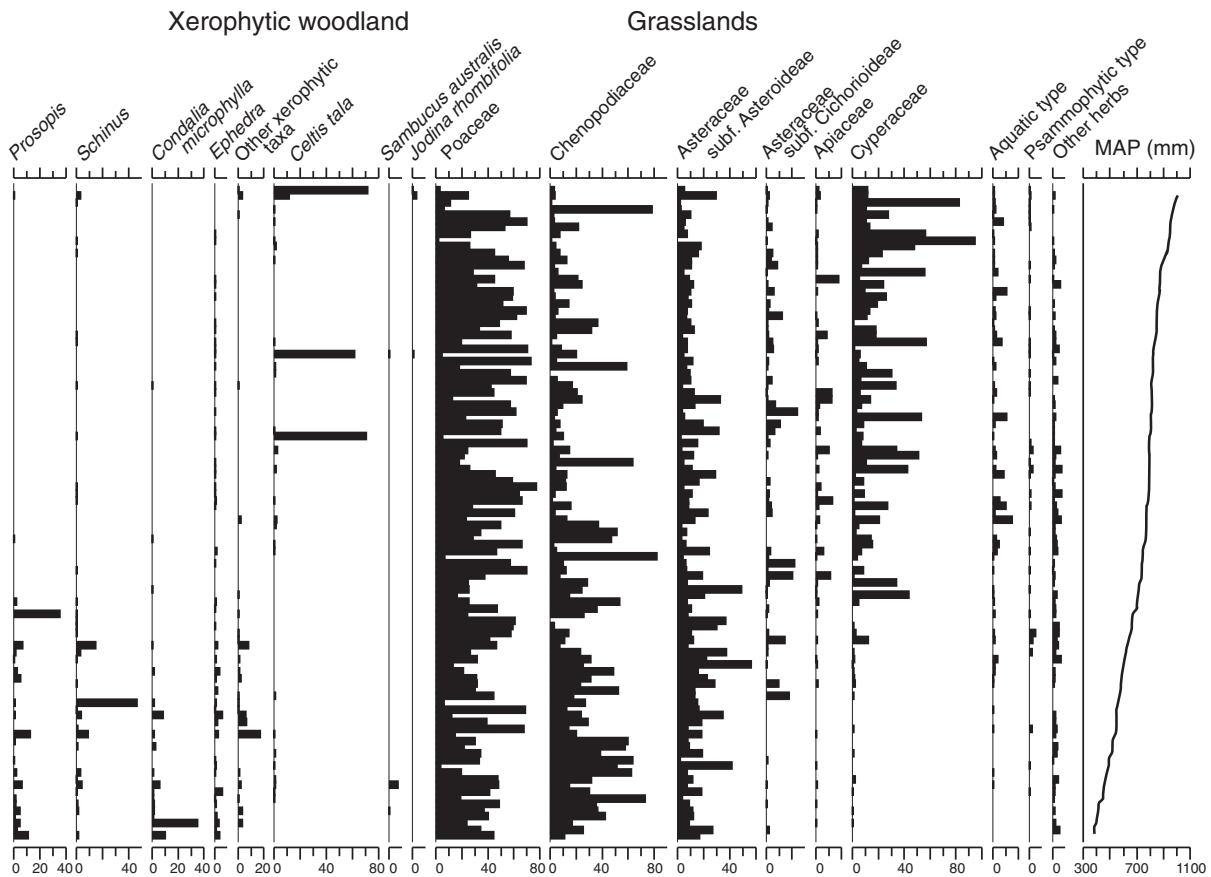


Figure 7 Selected pollen percentages. Modern pollen samples are arranged from highest to lowest values of mean annual precipitation (MAP).

indicators of precipitation in fossil pollen records from the Pampa grasslands.

As noted previously, Chenopodiaceae pollen exhibited an inverse relationship with precipitation, rendering this taxon a good indicator for dry conditions at a regional scale. Samples strongly dominated by Chenopodiaceae (up to 80%) that represent edaphic communities are easy to recognize along the precipitation gradient (Fig. 7).

Cyperaceae pollen is positively related to precipitation. This supports the inclusion of this pollen type in modern pollen–climate analysis in Pampa grasslands. At present, extensive inundated areas during rainy years are colonized by Cyperaceae communities. This situation has been used as a modern analogue to interpret fossil records in Pampa grasslands.

CONCLUSIONS

We present the first quantitative analysis of the relationships between modern pollen assemblages and climate variables for the Pampa grasslands. This region, like other grass-dominated biomes, presents two problems: (1) the human impact, and (2) the limited taxonomic resolution of some pollen types. Human transformations of landscape, plant introductions and altered fires regimes can result in misleading modern pollen rain signatures. Particularly in the Pampa grasslands, human activities have caused changes in floristic composition, and most of the native and introduced species are impossible to separate on the basis of pollen. However, the most important families are represented primarily by native species, for example, the Poaceae comprises about 190 native species and only 40 introduced species (León, 1991).

Despite these problems, our results show strong relationships between modern vegetation distribution, pollen assemblages and climate variables. The ability to relate modern pollen to environmental settings is partly due to the existing pollen data base, the strong climatic gradient, and the vegetation distribution related to this gradient. The consistency of the pollen data base is the result of the wide and uniform spatial coverage, systematic sampling from undisturbed or minimally disturbed sites, and the fact that 70% of modern pollen samples are from similar sedimentary environments.

The combined analysis of the pollen diagram, isopoll maps and potential natural vegetation units allows us to distinguish grasslands from xerophytic woodland and from edaphic communities. The vegetation distribution patterns are influenced by the strong northeast–southwest gradient of mean annual precipitation and effective precipitation. The analysis of the relationships between vegetation units and climate variables showed that this gradient is the dominant climatic characteristic of the region.

Individual pollen types, such as Chenopodiaceae, Cyperaceae, Apiaceae, *Prosopis*, *Schinus*, *C. microphylla*, *Ephedra* and other xerophytic taxa, are good indicators of the moisture regime. However, neither Poaceae nor Asteraceae subf. Asteroideae can be used for reconstructing precipitation changes. Few pollen types are significantly correlated with

summer temperature, mainly due to the low temperature range in the region, which in turn is related to the oceanic influence.

This study provides meaningful insights into the vegetation–pollen–climate relationships at a regional scale in Pampa grasslands and adjacent xerophytic woodland. Our data also provide new modern analogues for the interpretation of fossil assemblages. The quantitative analysis between individual pollen types and climatic variables provides the information for more accurate palaeoclimatic interpretations from fossil pollen data. The results indicate that mean annual precipitation and effective precipitation can be reconstructed from Holocene fossil pollen records from Pampa grasslands and from the grassland–xerophytic woodland (Caldenal) ecotone.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1 Scatter diagrams between abundance of pollen types (square root-transformed percentages) and summer temperature (SuT) and annual effective precipitation (AEP) for Poaceae, Chenopodiaceae, Asteraceae subf. Asteroideae, Apiaceae, Cyperaceae and *Prosopis*.

Appendix S2 Scatter diagrams between abundance of pollen types (square root-transformed percentages) and summer temperature (SuT), mean annual precipitation (MAP) and annual effective precipitation (AEP) for *Schinus*, *C. microphylla*, *Ephedra* and other xerophytic taxa.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01854.x>

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BIOSKETCHES

Marcela S. Tonello is a post-doctoral researcher from CONICET working at the Universidad Nacional de Mar del Plata, Argentina. Her research interests are centred on pollen–climate relationships and palaeoclimatology, particularly focused on quantitative palaeoclimatic reconstructions based on pollen data over the late Quaternary.

Aldo R. Prieto is a geologist and Quaternary palaeoecologist at the Universidad Nacional de Mar del Plata and an independent researcher for CONICET, Argentina. His research interests are centred on late Quaternary environmental reconstruction using pollen analysis and geology as well as quantitative palaeoecology, particularly in the Pampa and Patagonia regions.

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