

Vegetation and climate change since 14,810 ^{14}C yr B.P. in southeastern Uruguay and implications for the rise of early Formative societies

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Abstract

This article presents a combined pollen and phytolith record of a 1.70-m sediment core from the wetlands of India Muerta (33° 42' S, 53° 57' W) in the lowland Pampa (grasslands) of southeastern Uruguay. Six ^{14}C dates and the pollen and phytolith content of the samples permitted the recognition of four distinct climatic periods between 14,850 ^{14}C yr B.P. and the present. The Late Pleistocene period (between ca. 14,810 and ca. 10,000 ^{14}C yr B.P.) was characterized by drier and cooler conditions indicated by the presence of a C3-dominated grassland. These conditions prevailed until the onset of the warmer and more humid climate of the Holocene around 9450 ^{14}C yr B.P. The early Holocene (between around 10,000 and 6620 ^{14}C yr B.P.) was characterized by the establishment of wetlands in the region as evidenced by the formation of black peat, the increase in wetland taxa, and the replacement of C3 Pooideae by C4 Panicoideae grasses. During the mid-Holocene, around 6620 ^{14}C yr B.P., began a period of environmental change characterized by drier climatic conditions, which resulted in the expansion of halophytic communities in the flat, low-lying areas of the wetlands of India Muerta. About 4020 ^{14}C yr B.P. a massive spike of *Amaranthaceae/Chenopodiaceae* coupled with a radical drop in wetland species indicates another major and more severe period of dryness. After ca. 4000 ^{14}C yr B.P., a decrease of halophytic species indicates the onset of more humid and stable climatic conditions, which characterized the late Holocene.

The findings reported in this article substantially improve our knowledge of the late Glacial and Holocene climate and vegetation in the region. The data provide a detailed record of the timing and severity of mid-Holocene environmental changes in southeastern South America. Significantly, the mid-Holocene drying trend coincided with major organizational changes in settlement, subsistence, and technology of the pre-Hispanic populations in the region, which gave rise to early Formative societies. This study also represents the first combined pollen and phytolith record for southeastern South America reinforcing the utility of phytoliths as significant indicators of long-term grassland dynamics.

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Introduction

The dynamic interactions between human populations and their environments have played a major role in the development of early Formative societies in the Americas during the mid-Holocene (e.g., Blake, 1999; Piperno and Pearsall, 1998a; Zárte and Neme, 2005). Sandweiss et al.

(1999) review of mid-Holocene climatic changes suggests that worldwide this was a period of environmental flux when compared with the preceding and succeeding millennia. The differences in timing and severity of these mid-Holocene environmental changes in Central Brazil (Alexandre et al., 1999; Ledru et al., 1998), the Pantanal (Peixoto et al., 2001), and southeastern South America (Behling et al., 2004, 2005; Iriarte and Garcia, 1993; Manzini et al., 2005; Prieto, 1996, 2000) caution researchers that the study of the human–environment relationships need to be addressed in case-by-case studies with high temporal

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resolution and precise dating at a local scale. Until recently, climate reconstructions for southeastern Uruguay were interpolated from records located in southeastern Brazil and the Chaco-Pampa plains of Argentina (Bracco et al., 2000). The multidisciplinary paleoecological study presented in this article was designed to fill in this vacuum of information. This article presents a combined pollen and phytolith record covering the period since 14,810 ^{14}C yr B.P. obtained from the analysis of a sediment core extracted from the wetlands of India Muerta, northern Rocha Province, southeastern Uruguay (Figs. 1 and 2). It expands upon our previously published summary paper (Iriarte et al., 2004) to show the detailed pollen and phytolith vegetation history, to correlate it with other paleoclimatic records from different vegetation types in southern Brazil and the Chaco-Pampa plains of Argentina, and to discuss the implications of these findings to the rise of early Formative societies in the region. This study also has implications for the study of the peopling of southeastern South America, which in Uruguay took place by at least 11,200 ^{14}C yr B.P. (Suárez and López, 2003). The vegetation and climatic sequence presented in this study will now allow for a better understanding of human–environment interactions associated with the end of the Pleistocene and the transition to the Holocene, their significance for the peopling of the region, and later developments throughout the Holocene.

Study area and its vegetation

The study area comprises a coastal plain along the Atlantic ocean characterized by slight elevations (maximum 200 m above sea level), generated by the Late Pleistocene and Holocene marine oscillations (Montaña and Bossi,

1995; Tomazelli and Vilwock, 1996). The climate of the area is subtropical humid with high average temperatures of 21.5°C during the summer and low average temperatures of 10.8°C during the winter. Total annual rainfall averages 1123 mm (PROBIDES, 2000). The region corresponds to the phytogeographic province of the Pampa (Cabrera and Willink, 1973) and is located in the boundary between the northern subregional divisions of the Rio de la Plata grasslands (RPG), defined by Leon (1992) as “southern campos” and “northern campos” (Fig. 1). Campos are characterized by the abundance of subtropical grass genera such as *Andropogon*, *Axonopus*, *Panicum*, *Paspalum*, *Schizachyrium*, and *Bothriochloa*, among others, and in turn by the lower presence of *Stipa*, *Piptochaetum*, and *Aristida*, which are more abundant in the southern subdivisions of the RPG (Arrarte Amonte, 1969; Leon, 1992; Rosengurt et al., 1949, 1970).

Southeastern Uruguay consists of a patchwork of closely packed environmental zones including wetlands, wet prairies, upland prairies, riparian forest, and palm forest. The area stands out for its high biodiversity and supports a great variety of flora and fauna. Wetlands occur in the low floodplains, which remain covered with shallow water most of the year, cover an area of about half a million hectare (Fig. 2). Today, much of them have been drained and are under rice cultivation or used for cattle grazing. They present deep, poorly drained, clayey, or peat superficial horizons and its vegetation is characterized by diverse groups of emergent, hydrophytic vegetation (Table 1). Wet prairies occur in areas slightly higher than wetlands, which are characterized by flat and poorly drained soils that remain waterlogged during the winter months. Upland prairies located in hills and knolls are

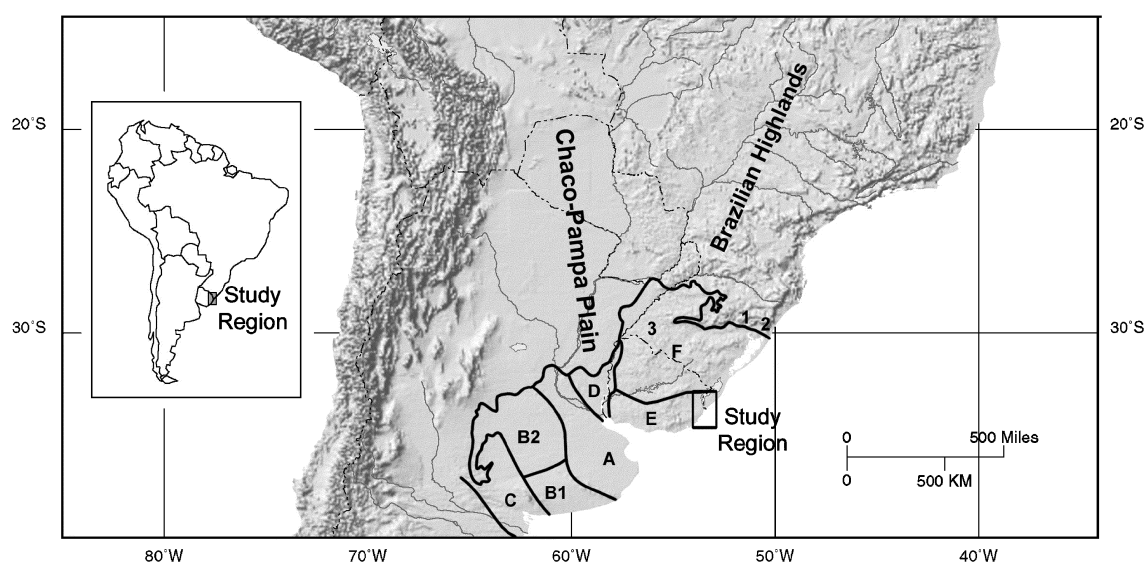


Figure 1. Map of southeastern South America showing the location of the study region, the regional subdivisions of the Rio de la Plata grasslands, the extension of the Chaco-Pampa plain (which also includes de Rio de la Plata grasslands), and the sites mentioned in the text. Key to regional subdivision of the Rio de la Plata grasslands: (A) humid Pampa; (B) dry Pampa, (B1) southern Pampa, (B2) inland Pampa; (C) xerophytic woodland ecotone; (D) mesopotamic Pampa; (E) southern campos; (F) northern campos. Key to sites mentioned in the text: (1) São Francisco de Paula; (2) Cambará do Sul; (3) São Francisco de Assis.

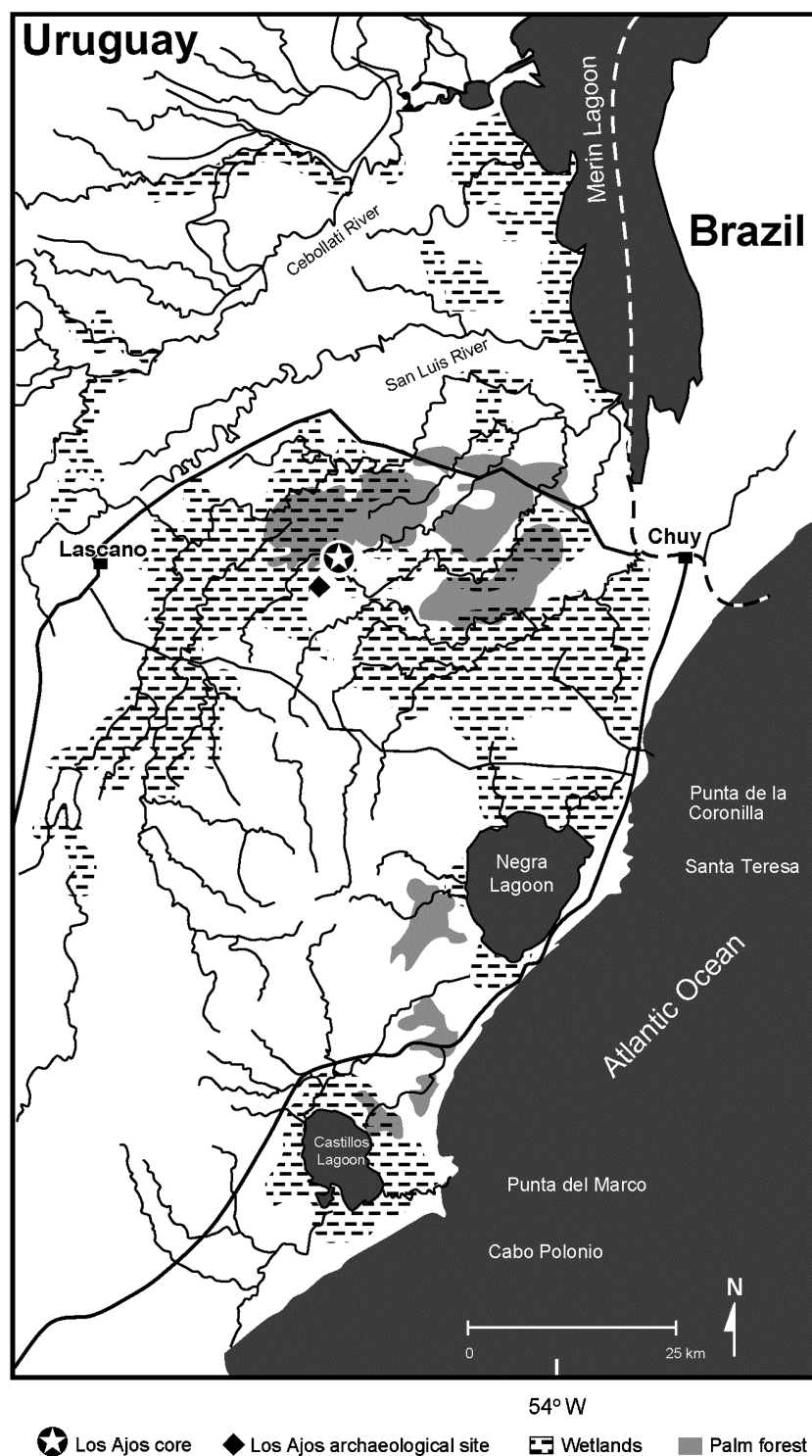


Figure 2. Map of southeastern Uruguay showing the location of Los Ajos core and Los Ajos multi-mound archaeological site.

characterized by well-drained superficial soils, which suffer from a hydric deficit during the summer months. Halophytic communities proliferate in the saline wetlands that occur mainly below 5 m above sea level terrace that borders Merin Lake and are mainly composed by saline-tolerant grasses and other halophytic herbs (Table 1). Riparian forests comprise a narrow strip bordering the

main streams and are mainly composed by species from Anacardiaceae, Euphorbiaceae, Myrtaceae, and Ulmaceae. The palm forest of *Butia capitata* is characteristic of southeastern Uruguay and southern Brazil. In Uruguay, it covers more than 70,000 ha, constituting the world's largest population of *Butia* palms (*Butia capitata*), which may attain a density of up to 452 individuals per hectare

Table 1

Vegetation associations from southeastern Uruguay and their dominant plant species and families

| Wetlands | Wet prairies | Upland prairies | Salt marshes | Riparian forest | Palm forest |
|------------------------------------|--------------------------------|----------------------------|---------------------------------|-----------------------------------|---------------------------|
| <i>Rhynchospora corymbosa</i> | <i>Eryngium</i> spp. | <i>Paspalum notatum</i> | <i>Distichlis spicata</i> | <i>Lithraea brasiliensis</i> | <i>Butia capitata</i> |
| <i>Zizaniopsis bonaerensis</i> | <i>Axonopus affinis</i> | <i>Setaria geniculata</i> | <i>D. scoparia</i> | <i>Schinus longifolius</i> | <i>Axonopus affinis</i> |
| <i>Schoenoplectus californicus</i> | <i>A. suffultus</i> | <i>Axonopus compressus</i> | <i>Spartina coarctata</i> | <i>Sapium</i> spp. | <i>Panicum gounii</i> |
| <i>Typha</i> spp. | <i>Stenotaphrum secundatum</i> | <i>Paspalum dilatatum</i> | <i>S. densiflora</i> | <i>Sebastiania</i> spp. | <i>Sporobolus indicus</i> |
| <i>Ludwigia</i> spp. | <i>Paspalum notatum</i> | <i>Aristida</i> spp. | <i>S. longispica</i> | <i>Blepharocalyx salicifolius</i> | |
| Alismataceae | <i>Luziola peruviana</i> | <i>Stipa</i> spp. | <i>Polypogon</i> spp. | <i>Celtis</i> spp. | |
| Solanaceae | <i>Paspalum</i> spp. | <i>Briza</i> spp. | <i>Puccinellia glaucescens</i> | <i>Syagrus romanzoffiana</i> | |
| Ranunculaceae | <i>Echinochloa</i> spp. | <i>Chloris</i> spp. | <i>Atriplex</i> spp. | | |
| <i>Leersia hexandra</i> | <i>Panicum prionitis</i> | <i>Eragrostis</i> spp. | <i>Chenopodium macrosperrum</i> | | |
| <i>Luziola peruviana</i> | <i>Paspalum quadrifarium</i> | Apiaceae | <i>Salicornia ambigua</i> | | |
| <i>Echinochloa helodes</i> | <i>Cortadeira selloana</i> | Asteraceae | Asteraceae | | |
| <i>Paspalum</i> spp. | Asteraceae | Convolvulaceae | Cyperaceae | | |
| <i>Paspalidium paludivagum</i> | Alismataceae | Cyperaceae | Juncaceae | | |
| <i>Glyceria</i> spp. | Cyperaceae | Iridaceae | | | |
| | Juncaceae | | | | |
| | Ranunculaceae | | | | |
| | Solanaceae | | | | |

(Table 1, Fig. 2). Table 1 shows the most abundant species of each vegetation association. More detailed descriptions of the vegetation associations in this region could be found in the literature (Alonso, 1997; PROBIDES, 2000).

Methods

The studied site (33° 42' S, 53° 57' W) is an abandoned meander of the middle sector of the Los Ajos stream located in the wetlands of India Muerta, northern Rocha Province, southeastern Uruguay (Fig. 2). A 1.70-m core was extracted from the deepest section of the peat using a Wildco hand corer. Pollen samples were extracted every 5 cm and processed following standard methods of analysis (Faegri and Iversen, 1975). Additional samples were taken at 62.5, 77.5, 83.5, and 89 cm in order to obtain a better resolution for the mid-Holocene period. Claudia Listopad (Florida Institute of Technology) extracted and identified the pollen from the sediment samples. Pollen preparations were examined under magnifications of 1000×. Prior to processing, *Lycopodium* tablets were added to each sample for calculation of pollen concentration. Pollen concentration of the core subsamples varied between 640 and 13,545 grains/cm³. A minimum of 200 grains was counted per slide. The pollen percentage diagram display in Figure 3 consists of 23 samples and present the most abundant (>1%) taxa from 97 pollen types identified. Percentages of all taxa were calculated from the total pollen sum.

Phytolith samples were taken every 10 cm, and at 5 cm intervals in the early and mid-Holocene sections of the core. The extraction and slide preparation of phytoliths followed the standard procedures described by Piperno (2005) and were carried out at the Smithsonian Tropical Research Institute (STRI) in Panama. Slides were scanned using an Olympus B2 light microscope (400–1000×). The number of phytoliths counted varied from 203 to 308 per

slide and includes at least 200 short-cells for each sample. Given the dominance of Poaceae morphotypes in most of the samples, and in order to emphasize the variability of short-cell phytoliths, percentages of phytoliths from the Panicoideae, Chloridoideae, Pooideae, and Oryzoideae subfamilies of grasses (GPWG, 2000; Judziewicz et al., 2000) were calculated on the sum of the short-cell phytolith types alone. Percentages of non-grass phytoliths were calculated on the basis of the total sum of phytoliths.

Phytolith identifications were made by comparison with our modern plant reference collection (Iriarte, 2003b; J. Iriarte and E. Alonso, unpublished data), the extensive studies of Poaceae from the RPG (e.g., Zucol, 2000), the Cerrados of Central Brazil (e.g., Sendulsky and Labouriau, 1966), and the phytolith comparative collection curated at STRI. For the classification of the Poaceae, the three-partite morphological classification related to grass taxonomy (Panicoideae–Chloridoideae–Pooideae) first proposed by Twiss et al. (1969) and refined through extensive studies of grasses from North America (e.g., Fredlund and Tieszen, 1994), and the Neotropics (Piperno, 2005; Piperno and Pearsall, 1998b) was used. The pollen and phytolith percentage diagrams (Figs. 3 and 4) were plotted using TILIA and TILIA-GRAPH software (Grimm, 1987).

Results

Core stratigraphy and chronology

Six radiocarbon dates provide chronological control for the core indicating a fairly continuous sequence of sedimentation beginning during the Late Pleistocene and extending into the modern era. Four 1-cm-thick Holocene peat samples were submitted for AMS radiocarbon dating. The gray silty clay underlying the organic peat

is organic poor and thus susceptible to be contaminated by younger materials like soluble humic acids that appear to percolate through sequences such as these and cause sediment dates to be too young (e.g., Vandergoes and Prior, 2003). Because the plant carbon occluded by phytoliths provides a suitable substrate for radiocarbon dating (Kelly et al., 1991; Mulholland and Prior, 1993), which is protected from post-depositional contamination, both a conventional ^{14}C determination on bulk sediment (158–165 cm) and a phytolith date (158–167 cm) from the basal levels of the core (Table 2) were run. When compared with the phytolith date, the bulk sediment sample gave a much younger age (about 4000 yr) suggesting that this sector of the core was probably contaminated by downward infiltration of relatively young carbon into older strata. Thus, the phytolith date was accepted and the bulk sediment sample was discarded for chronological purposes.

The sediments from Los Ajos core can be described as follows. Between 170 and 102 cm there is a zone of gray (2.5 YR 6/1) silty clay with olive yellow (5 YR 6/6) mottles of sand corresponding to the Late Pleistocene. From 102 to 84 cm the sediment is composed of black compact, completely decomposed peat, which marks the establishment of wetlands in the region. An estimated date for the bottom of this zone is around 9450 ^{14}C yr B.P. based on an average sedimentation rate of 0.066 mm/yr calculated for the Holocene period using calibrated dates. Between depths of 83 and 72 cm, sediments consist of a black compact, completely decomposed peat intercalated with four gray clayey bands (5 YR 6–7/1) at 75 (0.5 cm wide), 77.5 (0.5 cm wide), 80 (0.5 cm wide), and 83.5 cm (1.5 cm wide). Between 72 and 22 cm, there is a black compact, completely decomposed peat interrupted by a 1-cm clayey gray (10 YR 5/1) band at 48 cm, and a very dark brown (7.5 YR 2.5/2), 5 cm wide, compact peat band between 57 and 62 cm. Between 22 cm and the surface there is a black weakly decomposed peat with plant remains, abundant roots and rootlets of grasses.

Description of the pollen and phytolith diagrams

The diagrams (Figs. 3 and 4) are divided in four local zones based on significant changes in the pollen, phytoliths, and sediment characteristics.

Zone I. Late Pleistocene (170–102 cm) $>14,810 \pm 250$ to ca. 10,000 ^{14}C yr B.P.

The sediment consists of gray silty clay with sand mottles. Due to the poor preservation of pollen grains, only two samples (105 and 115 cm) from the upper part of Zone I had countable pollen and were incorporated into the pollen diagram (Fig. 3). Phytolith representation was good throughout the entire sedimentary sequence.

In comparison with the early Holocene period, the upper part of the Late Pleistocene zone shows markedly greater percentages and concentrations of the Poaceae (38–41%), Asteraceae (13–14%), and Amaranthaceae/Chenopodiaceae (4–11%). In contrast, percentages of pollen from wetland species like the Cyperaceae and *Myriophyllum* are lower during the Pleistocene. Arboreal pollen is present in minor amounts, with some taxa like Bignoneaceae, Phytolacaceae, and Arecaceae being better represented during the Late Pleistocene, while others like *Celtis*, *Forsteronia*, and Urticaceae/Moraceae are reduced. Ferns are only present in trace amounts.

The Poaceae phytolith assemblage is dominated by morphotypes that are diagnostic of the subfamily Pooideae, which reach percentages of 26% to 45%. In contrast, phytoliths diagnostic of the Panicoideae and Chloridoideae subfamilies of grasses are represented in minor proportions (from 3–9% to 7–10%, respectively).

During the Pleistocene, there is an absence of woody phytolith morphotypes (rugose spheres). Cyperaceae phytoliths are less common, corroborating the presence of fewer Cyperaceae pollen grains at this time.

Zone II. Early Holocene (102–85 cm) ca. 10,000 to 6620 ± 40 ^{14}C yr B.P.

Major sedimentary changes mark the beginning of this interval. The Late Pleistocene gray, silty clay changes to a black, completely decomposed peat indicating fundamentally different depositional environments in these two periods. This major transition marks the establishment of wetlands in the region accompanied by progressive and significant changes in the local flora, which include (1) a dramatic shift in the composition of the grass flora, from C3 Pooideae grasses to C4-dominated Panicoid grass taxa; (2) declining frequencies of Chloridoideae grasses, which are

Table 2
Radiocarbon dates from Los Ajos cores

| Depth (cm) | Laboratory number | Dated material | Conventional ^{14}C yr B.P. | 2-sigma cal yr B.P. | $\delta^{13}\text{C}/^{12}\text{C}$ (‰) |
|------------|-------------------|------------------|--------------------------------------|---------------------|---|
| 62 | Beta 180947 | peat (AMS) | 4020 ± 40 | 4510–4445 | –26 |
| 71 | Beta 155022 | peat (AMS) | 4680 ± 40 | 5580–5530 | –26.2 |
| 85 | Beta 156071 | peat (AMS) | 6620 ± 40 | 7580–7440 | –24.5 |
| 98 | Beta 155023 | peat (AMS) | 8840 ± 40 | 10,150–9730 | –26.7 |
| 158–165 | Beta 156970 | peat (AMS) | $10,790 \pm 40$ | 12,740–12640 | –25.2 |
| 158–167 | Beta 161406 | phytoliths (AMS) | $14,810 \pm 250$ | 18,580–16,910 | N.A. |

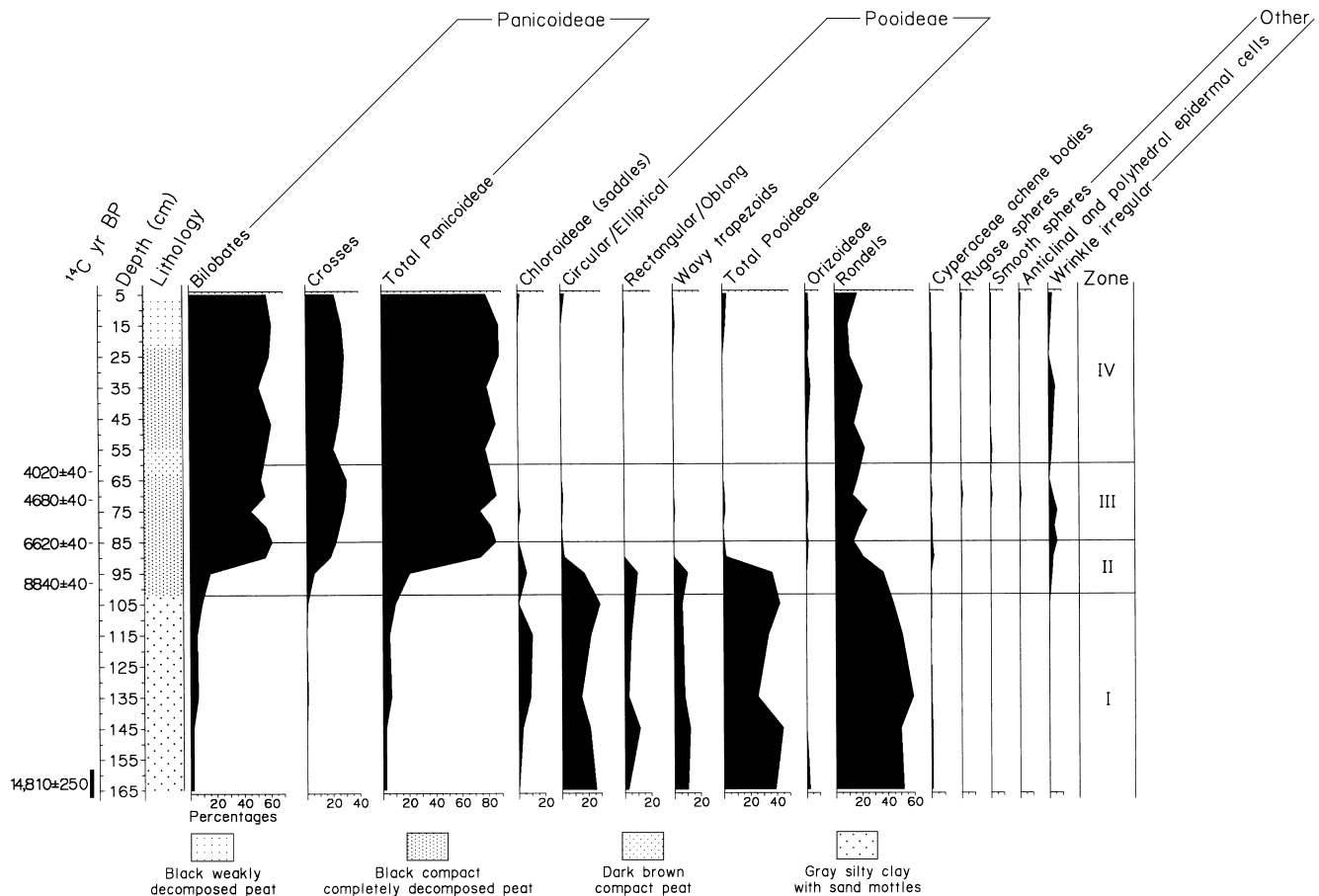


Figure 4. Phytolith percentage diagram from Los Ajos core.

more tolerant of arid climates than are Panicoid grasses; (3) an increase in the wetland taxon *Myriophyllum*; and (4) an increase of anticlinal and polyhedral silicified epidermal cells, which are abundant in modern wetland analogs (J. Iriarte and E. Alonso, unpublished data).

Zone III. Mid-Holocene (85–60 cm) 6620 ± 40 to 4020 ± 40 ¹⁴C yr B.P.

This period is characterized by dynamic oscillations in some of the plant taxa. One of the most significant patterns is the alternation of peaks of *Amaranthaceae/Chenopodiaceae* with synchronous declines in wetland species, in particular, the *Cyperaceae* and *Myriophyllum*. *Amaranthaceae/Chenopodiaceae* pollen fluctuate (1–76%) with major peaks at 83 (58%), 80 (38%), 75 (42%), 62 (64%), and 60 cm (76%), which are correlated with the deposition of thin clayey gray bands within the peat. Significant declines in *Amaranthaceae/Chenopodiaceae* are synchronous with increases in *Cyperaceae* at 89 (54%), 85 (31%), 77.5 (32%), and 65 cm (29%), and *Myriophyllum*, in particular, at 100 (20%) and 70 cm (27%). Concomitant with the major peaks of *Amaranthaceae/Chenopodiaceae* at 83.5 and 60 cm, both the percentage and the

concentration of wetland taxa also decrease indicating that the decline in *Cyperaceae* during these periods is not an artifact of the major increase in *Amaranthaceae/Chenopodiaceae* percentage.

A massive spike of *Amaranthaceae/Chenopodiaceae* occurs at 62.5–65 cm dated to ca. 4020 ¹⁴C yr B.P., which reaches 76% of the total pollen sum, is paralleled by a major drop both in percentage and concentrations in wetland species and *Poaceae*. This sector of the core is also correlated with a distinct change to lighter peat from black to very dark brown, indicating the presence of drier conditions.

Zone IV. Late Holocene (60–5 cm) 4020 ± 40 ¹⁴C yr B.P. to present

This period is characterized by a major increase in wetland taxa, an increase of *Poaceae*, and a major decline in *Amaranthaceae/Chenopodiaceae*. The *Cyperaceae* attains its strongest representation during this period (25–52%). Pollen from the *Poaceae* also attain their highest percentage in the upper part of this period (46%), and the *Asteraceae*, *Apiaceae*, *Polygonum*, *Rubiaceae*, and fern/spores are better represented during this period than throughout the preceding early and mid-Holocene. The total arboreal sum

shows a slight increase, in particular in the upper 30 cm of the core.

Panicoid Poaceae phytoliths are continuously predominant (78–89%), while Chloridoid and Poooid morphotypes are rare or absent. The slight increase in the woody dicot phytolith morphotypes (rugose spheres) and the increase in anticlinal and polyhedral silicified epidermal cells phytolith category (abundant in wetlands) also supports the inferred more humid conditions that appear to have prevailed during the late Holocene.

Interpretation and comparison with other records

Late Pleistocene ($>14,810 \pm 250$ to ca. 10,000 ^{14}C yr B.P.)

The predominance of Poooid grasses, adapted to cool climates, indicates that a much cooler Late Pleistocene climate characterized the wetlands of India Muerta region. Similar conditions during the Late Pleistocene in the temperate grasslands of Great Plains of North America have been inferred by Kelly et al., (1991) and Fredlund and Tieszen (1997) from a dominance of C3 grasses. The climate of the wetlands of India Muerta was also probably substantially drier before around 9450 ^{14}C yr B.P., as is evidenced by relatively low percentages of the Cyperaceae, *Myriophyllum*, and other wetland taxa. Highest percentages of Chloridoid phytoliths during the Late Pleistocene also point to a climate drier than today's, as this subfamily of grasses can tolerate very dry conditions. The low percentages of Cyperaceae and arboreal pollen, together with the absence of woody dicot phytolith morphotypes, suggest the presence of isolated trees or shrubs mainly limited to a narrow belt accompanying the major water courses during the Late Pleistocene. The formation of gallery forest along rivers may have been prevented by the dry and cool climate conditions prevailing during the Late Pleistocene.

Our results are in agreement with Prieto's (1996, 2000) palynological studies from several sites in the southern regional subdivisions of the RPG in Argentina (humid, dry, and xerophytic woodland) (Fig. 1), which characterized the Late Pleistocene vegetation as a psammophytic steppe indicating subhumid-dry to semiarid climatic conditions. Similarly, stratigraphic studies across the Chaco-Pampa plain of Argentina by Iriando (1993, 1999) and Iriando and García (1993) indicate that the Late Pleistocene climate was cool and dry and the resulting vegetation was a dry steppe. In the southeastern Brazilian Highlands, the dominance of campos (grassland) vegetation during the Late Pleistocene in what at present is *Araucaria* forest was also attributed to the dry and cold climates that prevailed during this period (Behling, 1997, 2002; Behling et al., 2004). In the lowland campos (grasslands) of southern Brazil, the absence of gallery forest along rivers also indicates that the climate was dry and cool during this period (Behling et al., 2005).

Early Holocene (ca. 10,000 to 6620 ± 40 ^{14}C yr B.P.)

The early Holocene appears to have been substantially warmer and wetter than the preceding 5000 yr. At the beginning of this period, around an estimated date of 9450 ^{14}C yr B.P., the replacement of the silty clay sediment by black peat indicates that the site was subjected to permanent flooding. This is corroborated by the significant increase of phytoliths and pollen from wetland taxa after around 9450 ^{14}C yr B.P. and the near loss of phytoliths from cool-adapted Pooideae together with a very significant increase in Panicoid grasses during the early Holocene. The phytolith record for this zone is very similar to the modern wetland analog as indicated by the presence of the following: (a) very high percentages of Panicoid morphotypes; (b) Oryzoid morphotypes; (c) Cyperaceae achene phytoliths; (d) high percentages of polyhedral and anticlinal silicified epidermal cells; and (e) absence of Asteraceae opaque platelets (J. Iriarte and E. Alonso, unpublished data).

The early Holocene evidences the formation of wetlands and the onset of a climate very similar to the present conditions. The increase in precipitation associated to the Pleistocene/Holocene transition and probably also the rising Holocene sea levels played key roles in the expansion of wetlands over previously exposed river margins and flood-plains in the region.

The onset of the humid conditions of the early Holocene around 9450 ^{14}C yr B.P. in southern Uruguay demonstrates considerable regional variability when compared with the records of the Chaco-Pampa plain of Argentina and southern Brazil. In the southern regional subdivisions of RPG in Argentina, Prieto (1996, 2000) based on five terrestrial pollen records inferred the replacement of the Late Pleistocene dry steppe by different humid grassland environments associated to the establishment of pond environments by around 10,500 ^{14}C yr B.P. Iriando and García (1993), based on stratigraphic studies in the Chaco-Pampa plain, argue that the early Holocene was dry and cold until 8500 ^{14}C yr B.P., after which it was replaced by the warm and humid conditions characteristic of the Hypsithermal. Syntheses of Late Quaternary pollen records from south and southeastern Brazil by Ledru et al. (1998) and Behling (2002) indicate that the early Holocene after ca. 10,000 ^{14}C yr B.P. was characterized by warm and dry climates. The timing and climates of the early Holocene in the region appear to be highly complex showing considerable variability. Further investigations and additional records are required to establish with more precision the climatic conditions of the Late Pleistocene–early Holocene transition in each location.

Mid-Holocene (6620 ± 40 to 4020 ± 40 ^{14}C yr B.P.)

Starting at ca. 6620 ^{14}C yr B.P. and lasting until shortly after ca. 4020 ^{14}C yr B.P., unstable climates and dynamic fluctuations in the local and regional vegetation appear to

have affected the study region. Four major peaks of *Amaranthaceae/Chenopodiaceae* occur between ca. 6620 and 4020 ^{14}C yr B.P., which alternate with mark increases in *Myriophyllum*. There is no modern counterpart in the area for the very high pollen percentages of *Amaranthaceae/Chenopodiaceae*. These high peaks probably indicate relatively brief periods during which a precipitation regime that is more strongly seasonal and drier than today's prevailed in the study area, and halophytic vegetational communities expanded at the expense of wetlands and grasslands.

During the same period, pollen from *Myriophyllum*, an important taxon of the modern wetland environment, demonstrates marked increases during intervals when the percentages of *Amaranthaceae/Chenopodiaceae* pollen are decreasing or low, a factor which suggests conditions that were wetter and/or less seasonal than today's. These drier periods appear to have alternated with relatively brief periods of climates wetter than today's, which are marked by sudden rises of *Myriophyllum* pollen.

A possible alternative explanation, that the *Amaranthaceae/Chenopodiaceae* peaks are indicative of the presence of a local salt marsh upon regional rises in sea level, is much less compelling. Due to their topographical location at ca. 15 m above sea level, the wetlands of India Muerta were not directly affected by the marine highstands of the mid-Holocene at ca. 5000 ^{14}C yr B.P., which reached to only 5 m above sea level. The coring locale is located 30 km west of the marine terrace left by this marine highstand, and ca. 50 km from the present Merin Lake shore. Furthermore, unlike the wetlands that occur below 5 m above sea level, which are saline and whose extension primarily depends on overflows of Merin Lake, the wetlands of India Muerta are freshwater and their extension depends on rainfall. Finally, the major *Amaranthaceae/Chenopodiaceae* peaks are not temporally correlated either with the major mid-Holocene marine highstand at ca. 5000 ^{14}C yr B.P. or another that is dated to ca. 3000 ^{14}C yr B.P. (Bracco et al., 2000, 2005; Montaña and Bossi, 1995).

The phytolith record supports this reconstruction. If the *Amaranthaceae/Chenopodiaceae* peaks represented the proliferation of a salt marsh in the area, the *Poaceae* phytolith assemblage should have been dominated by Pooid and Chloridoid morphotypes, since the most abundant grasses in salt marshes in the region are *Distichlis spicata*, *D. scoparia*, *Spartina coarctata*, *S. densiflora*, *S. longispica*, *Polypogon maritimus*, *P. monspeliensis*, and *Puccinellia glaucescens* (Alonso, 1996; Cabrera, 1970; Rosengurt et al., 1970). *D. spicata* produces non-sinuous, short trapezoids with both straight and mixed ends, as well as plateau and ridge tops (Brown, 1984). *Polypogon elongatus* (*Polypogon* genus) produces wavy trapezoids phytoliths (Piperno and Pearsall, 1998b), and *Puccinellia airoides* (*Puccinellia* genus) produces non-sinuous short trapezoids with round ends and ridged tops (Brown, 1984). *Spartina coarctata* produces saddle-shape (Chloridoid) dominated phytolith assemblages (Mulholland, 1989). Unlike of what

should be expected from a salt marsh, the Holocene phytolith assemblage is dominated by Panicoid grasses with a near absence of Chloridoid (saddle-shaped) and Pooid morphotypes indicating that though reduced in extent, the locality continued to be a freshwater wetland. Modern conditions similar to those inferred by the *Amaranthaceae/Chenopodiaceae* peaks between ca. 6620 and 4020 ^{14}C yr B.P. are found at present in the dry Pampa and the xerophytic woodland-grassland ecotone of Argentina (Prieto, 2000) (Fig. 1). These southern regional subdivisions of the RPG present a drier climate (800–500 mm/yr and >500 mm/yr, respectively) and suffer from a water deficit. Similar to the inferred drier conditions of the mid-Holocene, modern pollen data from these RPG subdivisions are characterized by relatively higher percentages of *Amaranthaceae/Chenopodiaceae* (mean 28–29%; range 0 to >80%) and low percentages of *Cyperaceae* and *Poaceae* (Prieto, 2000). In sum, the evidences show that these drier climatic episodes cause a decrease in the surface water recharge to the inland wetlands that were reduced in extent and the desiccation of grasslands with the consequent expansion of halophytic communities in the area.

Late Holocene (4020 \pm 40 ^{14}C yr B.P. to present)

The Late Holocene period is characterized by sharp decrease in *Amaranthaceae/Chenopodiaceae* pollen and a major increase in *Cyperaceae* pollen. The climate appears to have become wetter and less variable, and a flooded system like the one that characterized the earliest Holocene period appears to have been back in place. Two *Amaranthaceae/Chenopodiaceae* spikes that are less pronounced than before 4020 ^{14}C yr B.P. and a decrease of the *Myriophyllum* between 40 and 30 cm may represent less intensive, brief drier periods. Nonetheless, the period from 4020 ^{14}C yr B.P. until the present was marked by more humid and stable climatic conditions than prevailed during the mid-Holocene.

The mid- and late-Holocene climates in southeastern Uruguay are different from other areas of southeastern South America. In the Chaco-Pampa plain of Argentina, stratigraphic studies carried out by Iriando and his colleagues (Iriando, 1993, 1999; Iriando and Garcia, 1993; Kröhling, 1999; Kröhling and Iriando, 1999) recorded a humid tropical climate between 8500 and 3500 ^{14}C yr B.P. evidenced by widespread pedogenesis and the development of fluvial deltas. According to these authors (op. cit.), this was succeeded by a dry period characterized by the extensive deposition of wind-deflated silt and sand and the formation of dune fields in the region, which began at 3500 ^{14}C yr B.P. and lasted until 1400 ^{14}C yr B.P. Prieto (1996) inferred a more arid climate between 5500 and 3000 ^{14}C yr B.P. based on several pollen records from the southern regional subdivisions of the RPG. A review of palynological records of southern and central Brazil by Ledru et al. (1998) suggests that climatic conditions during the early Holocene until 7000 ^{14}C yr B.P. have been dry and were later replaced by

progressively moister climatic conditions during the mid- and late-Holocene when the forest and gallery forest began to expand. For the south and southeast grasslands of Brazil, Behling (2002) indicates that a change to wetter climatic conditions as evidenced by the expansion of *Araucaria* forest took place between 6000 and 3000 ^{14}C yr B.P.

The shift to a more humid climate after ca. 4000 ^{14}C yr B.P. in Los Ajos appears to be well-correlated with more recent and well-dated pollen sequences from Rio Grande do Sul studied by Behling et al. (2004). Changes to wetter conditions were recorded by Behling et al. (2004) in the site of Cambará do Sul on the highlands of northeastern Rio Grande do Sul State, Brazil, at around 3950 ^{14}C yr B.P. evidenced by the expansion of *Araucaria* forest. In São Francisco de Assis on the lowland campos (grassland) region in western Rio Grande do Sul State, more humid conditions took place at 4620 ^{14}C yr B.P. as indicated by the expansion of gallery forest (Behling et al., 2005). Similar conditions were recorded by Behling et al. (2001) in the São Francisco de Paula site where pollen was only preserved after 4000 ^{14}C yr B.P. The mid- to late-Holocene period of dryness proposed by Bombin and Klamt (1976) in southern Brazil between 3500 and 2400 ^{14}C yr B.P. based on the presence of calcic horizons in hydromorphic soils from Formación Hormiga is not supported by our findings nor by the study carried out by Behling et al. (2004, 2005).

Recently, Bracco et al. (2005) carried out a multiproxy paleoenvironmental reconstruction of the Negra lagoon in the study region covering the last four millennia (Fig. 2). The gastropod and diatom records show that the lagoon was a brackish water body between around 4000 and 2000 ^{14}C yr B.P. and a freshwater one between 2000 ^{14}C yr B.P. and the present. Using Twiss (1992) generalizations about the global distribution of C3 and C4 grasses, Bracco et al. (2005) inferred regional climatic changes in temperature and humidity based on the percentages of C4 Chloridoid – characteristic of warm and dry climates – vs. C3 Pooid phytoliths – common in cool and humid conditions. Based on the high percentages of C4 Chloridoid phytoliths between around 4000 and 2000 ^{14}C yr B.P., Bracco et al. (2005) inferred that this period was arid or highly seasonal with respect to the following two millennia before present. This interpretation contrasts with the results presented in this study and the pollen records from southern Brazil (Behling et al., 2004, 2005), which indicate that a more humid period started after 4000 ^{14}C yr B.P.

The interpretations of Bracco et al. (2005) should be treated with considerable caution. As detailed above, salt marshes in the region are dominated by particular Poaceae taxa specifically adapted to saline conditions that render a distinctive phytolith signature dominated by Chloridoid and Pooid phytolith morphotypes in an otherwise Panicoid dominated subtropical grasslands characteristic of the region. The presence of Chloridoid and Pooid phytolith morphotypes in Bracco et al. (2005) study simply reflects the local dynamics of a salt marsh between 4000 and 2000

^{14}C yr B.P. in the Negra lagoon and should not be used as evidence for broader climatic reconstruction in the region in terms of temperature and humidity. Therefore, their conclusions about regional landscapes derived from the phytolith record should be revised.

Overall, the records from southeastern Uruguay and southeastern Brazil (Rio Grande do Sul State) indicate that after a fluctuating and increasing drier mid-Holocene climate, wetter climatic conditions similar to the present were established between ca. 4620 and shortly after 4000 ^{14}C yr B.P.

Human responses to mid-Holocene climate changes

The associated archaeological data from our investigations at the multi-mound site, called Los Ajos, indicate that the changing climate of the mid-Holocene coincided with the emergence of early Formative societies in the region (Iriarte, 2003a; Iriarte et al., 2004). The mid-Holocene drying trend acted as a catalyst for major organizational changes in settlement, subsistence, and technology in the pre-Hispanic populations who inhabited the region. The maximum drying episode that took place around 4020 ^{14}C yr B.P. likely caused a decrease in the surface water recharge to the inland wetlands and waterways, which resulted in the desiccation of grasslands. This caused increasing diminishing returns from grasslands, deepening the resource gradient between wetlands and grasslands. Although reduced in extent, wetlands became attractive places for pre-Hispanic populations by providing abundant, now more highly circumscribed plant and animal resources and a stable source of water. The upper (15 m above sea level) freshwater wetlands of the region, like the wetlands of India Muerta, which were not directly affected by the mid-Holocene marine highstands (Bracco et al., 2000; Montaña and Bossi, 1995), had more favorable conditions during the mid-Holocene and promoted the aggregation of populations along these restricted and limited resource-rich areas. Archaeological investigations at the multi-mound site, called Los Ajos (Iriarte, 2003a; Iriarte et al., 2004) (Fig. 2), indicate that during this period, local pre-Hispanic populations did not disperse (e.g., disaggregate into smaller groups and increased mobility) or out-migrate to other regions but opted for orienting their settlement towards the upper freshwater wetlands where they established more permanent communities in strategic locations. Increased sedentism appears to have been a response to local resource abundance in wetland areas in the face of regional resource scarcity produced by the drying trend of the mid-Holocene. Large and more permanent communities, geometrically arranged in circular, elliptical, and horseshoe formats surrounding a central communal space, began to be established in more stable sectors of the landscape, such as the flattened spurs of hills that project into the wetlands and on the topographical prominences in the wetland floodplains. These locations are secure from seasonal flooding, have

immediate access to the rich-resource and fertile wetlands areas, and are ecotones, which encompass a mosaic of wetlands, wet prairies, upland prairies, riparian, and palm forest (Iriarte, 2003a; Iriarte et al., 2004). Similar cultural responses to mid-Holocene drying trends have been documented in Midwestern U.S. (e.g., Brown, 1985; Brown and Vierra, 1983; Jefferies, 1987).

The community-focused archaeological investigations carried out at Los Ajos reveal that during the Preceramic Mound Period (ca. 4190 to ca. 3000 ^{14}C yr B.P.) the inhabitants of Los Ajos began to live in a circular village partitioning the site into functionally discrete domestic and public areas. During this time, Los Ajos witnessed the creation of an open plaza area flanked by accretional, circular, dome-shaped residential mounds closely arranged in a circular format. This initial stage of village formation evidences the incorporation and centralization of a clearly demarcated communal space into the overall geometric village layout of Los Ajos. Preceramic Mound Period people also practiced a mixed economy by incorporating the earliest domesticated plants recorded in southeastern South America. Shortly after the beginning of the Preceramic Mound Period, Los Ajos phytolith and starch grain data indicate the adoption of two domesticated crops in the region: *Zea mays* and *Cucurbita* spp. (Iriarte, 2003a; Iriarte et al., 2004). Wetlands provided an ideal context for the adoption and intensification of agriculture (cf. Pope et al., 2001; Siemens, 1999). Larger preceramic mound complexes are situated along fertile wetland floodplains, suggesting that PMP people engaged in wetland margin horticulture during late spring and early fall when the water table is at its lowest and the organic, fertile, and easy-to-till superficial peat horizon is readily exposed.

Conclusions

The findings reported in this article substantially improve our knowledge of the Late Quaternary climate and vegetation history in southeastern South America. They provide us with a detailed reconstruction of the Pleistocene/Holocene transition, which will now allow for a broader consideration of the role that human–environment interactions played in the peopling of Uruguay and later developments throughout the Holocene. Along with other records in southeastern South America, the record from southern Uruguay shows that the mid-Holocene was a time of profound environmental changes. In the region, this period of environmental flux was associated to cultural transitions involving permanent mounded settlements situated within resource-rich, circumscribed wetlands by people who subsisted on mixed economies and adopted major crop plants such as maize (*Z. mays* L.) and squash (*Cucurbita* spp.) around 4000 ^{14}C yr B.P. (Iriarte, 2003a; Iriarte et al., 2001; Iriarte et al., 2004).

This study also reinforces the utility of using phytoliths as significant indicators of vegetation dominated by grasses and

non-grasses alike. Like in many other grass-dominated and -forested regions of the world (i.e., Bush et al., 1992; Denham et al., 2003; Kealhofer and Penny, 1998; Piperno and Jones, 2003), multiproxy studies combining phytolith and pollen data will allow researchers to obtain finer-grained and more complete reconstructions from archaeological and paleoecological contexts. Moreover, the resilience of phytoliths in conditions detrimental to pollen preservation, like the oxidized Late Pleistocene sediments from Los Ajos core, allows us to reconstruct vegetation based on phytolith alone (cf. Kealhofer and Penny, 1998; Piperno and Jones, 2003). This is also a common case for the Late Quaternary terrestrial records in the Pampa grasslands, where for example none of the individual records studied by Prieto (1996, 2000; Prieto et al., 2004) provided a complete vegetational history based on pollen. The systematic incorporation of phytolith analyses for paleoenvironmental reconstruction in the region will fill the lacunae in these records by providing empirical data on grassland dynamics.

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