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A 16,000 ¹⁴C yr B.P. packrat midden series from the USA–Mexico Borderlands

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Abstract

A new packrat midden chronology from Playas Valley, southwestern New Mexico, is the first installment of an ongoing effort to reconstruct paleovegetation and paleoclimate in the U.S.A.–Mexico Borderlands. Playas Valley and neighboring basins supported pluvial lakes during full and/or late glacial times. Plant macrofossil and pollen assemblages from nine middens in the Playas Valley allow comparisons of two time intervals: 16,000–10,000 and 4000–0 ¹⁴C yr B.P. Vegetation along pluvial lake margins consisted of open pinyon–juniper communities dominated by *Pinus edulis*, *Juniperus scopulorum*, *Juniperus* cf. *coahuilensis*, and a rich understory of C₄ annuals and grasses. This summer-flowering understory is also characteristic of modern desert grassland in the Borderlands and indicates at least moderate summer precipitation. *P. edulis* and *J. scopulorum* disappeared or were rare in the midden record by 10,670 ¹⁴C yr B.P. The late Holocene is marked by the arrival of Chihuahuan desert scrub elements and few departures as the vegetation gradually became modern in character. *Larrea tridentata* appears as late as 2190 ¹⁴C yr B.P. based on macrofossils, but may have been present as early as 4095 ¹⁴C yr B.P. based on pollen. *Fouquieria splendens*, one of the dominant desert species present at the site today, makes its first appearance only in the last millennium. The midden pollen assemblages are difficult to interpret; they lack modern analogs in surface pollen assemblages from stock tanks at different elevations in the Borderlands.

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Introduction

More than 2000 packrat middens have been dated and analyzed to reconstruct late Quaternary vegetation changes across western North America, but several key areas remain unexplored. One such gap is the U.S.A.–Mexico Borderlands, the region near the continental divide where the states of Arizona and New Mexico intersect with each other and the Mexican states of Chihuahua and Sonora. The Borderlands occupy the broad transition between the Chihuahuan and Sonoran Deserts, are a hotspot for plant and animal diversity, and are of special concern due to recent woody plant encroachment into desert grasslands (Bahre and Web-

ster, 2001). The packrat midden record from the Borderlands has been previously overlooked for mostly physical reasons. The area is generally wetter and has fewer rock outcrops suitable for midden preservation than adjacent regions.

Here we report on a series of nine middens from the eastern Playas Valley in southwestern New Mexico spanning the past 16,000 ¹⁴C yr. This series represents the first effort to answer several key biogeographic and paleoclimatic questions about the Borderlands. For example, where did glacial woodlands dominated by two-needled pinyons to the east give way to those dominated by single-needled pinyons to the west? What was the importance of C₄ grasses and summer annuals in these glacial woodlands, and hence the extent of summer rainfall? And did creosote bush (*Larrea tridentata*) recently expand from populations long established, or is the current expansion associated with an

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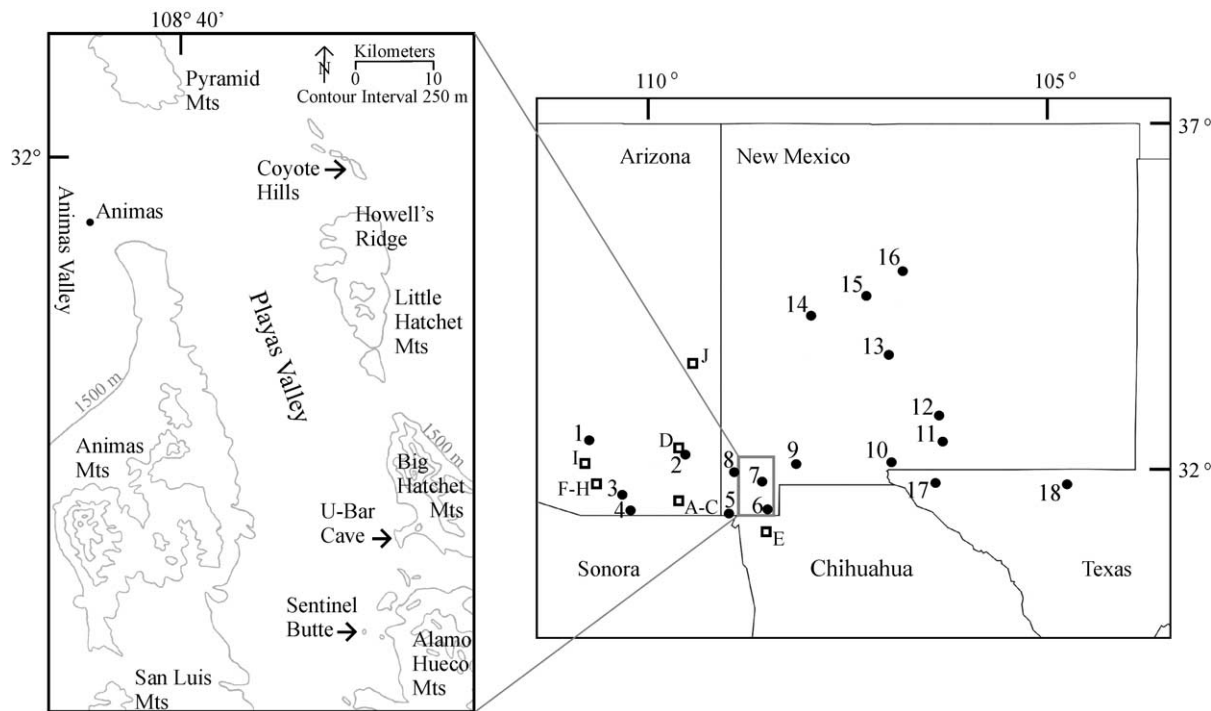


Fig. 1. Map of the Playas Basin and sites mentioned in text: (1) Tucson, AZ; (2) Willcox Playa/Paleolake Cochise; (3) Murray Springs; (4) Lehner Ranch; (5) Paleolake Cloverdale; (6) Sentinel Butte; (7) Coyote Hills; (8) Paleolake Animas; (9) Florida Mountains; (10) Bishop's Cap; (11) Rough Canyon/Otero Mesa; (12) Sacramento Mountains; (13) San Andreas Mountains; (14) Paleolake San Agustin; (15) Sevilleta LTER; (16) Paleolake Estancia; (17) Hueco Mountains; (18) Guadalupe Mountains. Open squares correspond to pollen sites in Fig. 5: (A) 1220 m; (B) 1280 m; (C) 1260 m; (D) 1270 m; (E) 1380 m; (F) 1420 m; (G) 1460 m; (H) 1520 m; (I) 1580 m; (J) 1880 m.

ongoing late Holocene migration of creosote bush across the Borderlands?

Study area

The Borderlands, part of the Mexican Highland section of the Basin and Range Province, are characterized by several northwest–southeast trending and tilted fault-block ranges separated by closed topographic basins (*bolsons*). These basins now contain ephemeral playas, but held pluvial lakes (Animas, Cloverdale, Cochise, Good sight, Hachita, Palomas, Playas) during the Pleistocene. Playas Valley is just north of the Mexican border and ~50 km south of Lordsburg, New Mexico (Fig. 1). Playas Valley is flanked by the Alamo Hueco Mountains and the Little and Big Hatchet Mountains to the east and the San Luis and Animas Mountains on the west. Elevations range from 1300 m on the valley floor to ~2600 m in the Big Hatchet and Animas Mountains. In the late Pleistocene, Playas Valley held a lake ~10 m deep and 65 km² in area with the highstand at ~1311 m elevation (Hawley et al., 2000; Schwennesen, 1918). The packrat middens reported here were collected from two prominent features, Sentinel Butte and Coyote Hills, at the southern and northern end of Playas Valley, respectively. Sentinel Butte is an isolated hill of Cretaceous limestone just west of the Alamo Hueco Mountains. The

Coyote Hills are a low range consisting of Oligocene ash-flow tuff and volcanoclastic rocks.

Average annual temperatures are ~22.5°C in the lowlands, with daily highs/lows averaging 32°C/16°C in summer (June–August) and 14°C/–4°C in winter (December–February). The valleys receive an annual average of 240–380 mm of precipitation, roughly half of which occurs during summer. Winter precipitation contributes <20% of the annual average precipitation. Seasonal and interannual precipitation variability is evident in a three-dimensional graph of historical monthly precipitation for Animas, New Mexico near the northern end of Playas Valley (Fig. 2). Precipitation is more abundant and less variable from year to year in summer than in winter. Winter precipitation results from large Pacific frontal systems that migrate inland from the west; the high year-to-year variability in winter and spring is modulated primarily by tropical sea surface temperature variations and associated teleconnections with the subtropical jet and upper-air westerlies. Summer precipitation variability is less well understood.

In the Playas Valley and surrounding mountains, vegetation zonation with elevation varies widely with substrate and position on the landscape (i.e., slope aspect and degree, hillslope vs. canyon bottom). For example, oaks are both diverse and abundant, while *Pinus discolor* occurs sporadically in the igneous Animas and Alamo Hueco Mountains. The reverse is true in the Big Hatchet Mountains, which are

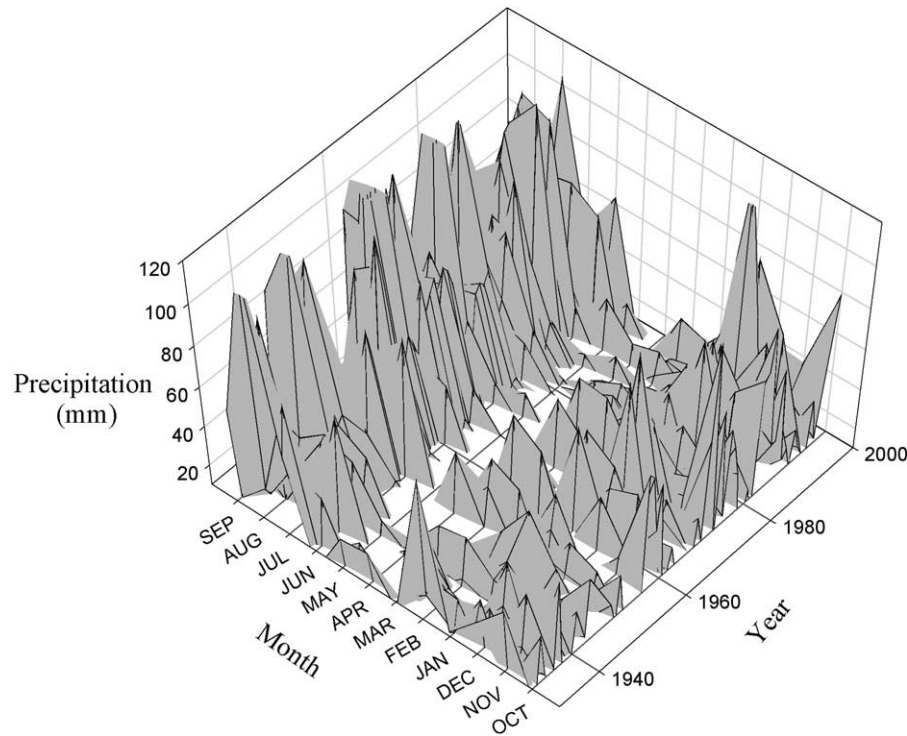


Fig. 2. Three-dimensional graph of monthly precipitation for Animas, NM. Values <10 mm were omitted to increase clarity of graph.

mostly limestone. Here we follow Wagner's (1977) classification for the Animas Mountains, which encompasses desert scrub (1300–1500 m), grassland (1400–1700 m), lower encinal ("encina" is Spanish for "oak") (1700–2600 m), upper encinal (~1900–2600 m), and forest (~2200–2400 m). For each zone, the highest elevations are reached on dry, south- and west-facing slopes and the lowest elevations on north-facing slopes and canyon bottoms.

Deserts scrub communities on the basin floor are dominated by *L. tridentata* and *Flourensia cernua* interspersed with patches of *Bouteloua eriopoda* and *Hilaria mutica*. In the piedmonts, desert grassland includes a variety of grasses (*B. gracilis*, *B. curtipendula*, *B. hirsuta*, *Eragrostis intermedia*, *Setaria macrostachya*) and a mixture of shrubs (*Agave*, *Aloysia*, *Atriplex*, *Calliandra*, *Celtis*, *Dasyllirion*, *Ephedra*, *Fouquieria*, *Juniperus*, *Koeberlinia*, *Mimosa*, *Nolina*, *Opuntia*, *Prosopis*, *Rhus*, *Yucca*, *Ziziphus*). Lower encinal communities begin near the first abrupt rise in the mountain slope and are dominated by semi-evergreen oak and small conifers, principally *Quercus arizonica* and *Q. emoryi*, with lower abundances of *Q. hypoleucoides*, *Juniperus deppeana*, and *Pinus discolor*. Upper encinal is an oak-dominated, dense chaparral growing on rocky slopes with *Q. hypoleucoides*, *Q. rugosa*, *J. deppeana*, and *P. cembroides* becoming more important with elevation. Taller pines (*P. leiophylla*, *P. strobiformis*, and *P. engelmannii*) first appear in canyons at ~1980 m and contribute to the ecotonal pine–oak woodland more characteristic of the Chiricahua Mountains to the west. On deeper soils at higher elevation, open stands of either *P. ponderosa* var. *arizonica*

on drier sites or *Pseudotsuga menziesii* on more mesic sites dominate, in association with *Q. gambelii*.

The vegetation along the base of the limestone cliff at Sentinel Butte (Fig. 3) is dominated by *L. tridentata*. Also present are *Parthenium incanum*, *Prosopis glandulosa*, *Aloysia wrightii*, *Cheilanthes* sp., *Fendlera rupicola*, *Abutilon* sp., *Krascheninnikovia lanata*, *Nicotiana obtusifolia*, *Brickellia* sp., *Aristida* sp., *Muhlenbergia* sp., *Bouteloua curtipendula*, *Elymus elymoides*, *Gutierrezia sarothrae*, *Dasyllirion wheeleri*, *Fouquieria splendens*, *Opuntia engelmannii*, *Datura* sp., *Rhus microphylla*, *Stephanomeria* sp., *Sphaeralcea* sp., and *Heterotheca subaxillaris*. No pinyons or junipers grow within 100 m of the midden sites, although a few isolated junipers occur at the base of Sentinel Butte. The Coyote Hills site includes *L. tridentata*, *J. cf. coahuilensis*, *Flourensia cernua*, *Parthenium incanum*, *Dasyllirion wheeleri*, *Fouquieria splendens*, *Atriplex canescens*, *Gutierrezia sarothrae*, *Hilaria* sp., *Brickellia scabra*, *Eriogonum* sp. and *Senecio* sp.

Methods

Seven middens were collected from the base of the limestone cliff (1490 m) on Sentinel Butte. Two additional middens were collected from 1500 m in the Coyote Hills. Middens were processed and analyzed according to standard procedures (Spaulding et al., 1990). Macrofossil abundances were quantified using a relative abundance scale of 1 to 5, where 0 = 0 fragments, 1 = 1 fragment, 2 = 2–25,

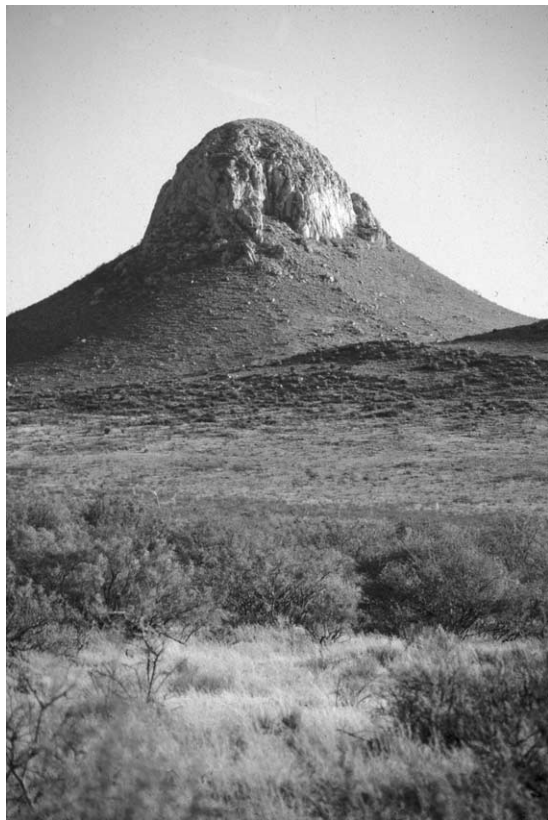


Fig. 3. Photograph looking east toward Sentinel Butte.

2.5 = 26–50, 3 = 51–75, 3.5 = 76–100, 4 = 101–150, 4.5 = 151–200, and 5 \geq 200 fragments. Midden material was screened through both 2-mm (No. 10) and 1-mm (No. 18) sieves to facilitate sorting plant remains. The 1-mm portion of Sentinel Butte #2B was lost and is not included in the results. The possibility of bias against taxa represented by smaller macrofossils has been taken into account in the interpretation of the record for this sample.

Pollen samples were extracted from all middens. A small indurated subsample (~10 g) was soaked in distilled water, disaggregated, and screened through a 500 μ m (No. 35) mesh screen. A 10% KOH solution was added to remove humic acids. HCl was used to remove carbonates and to dissolve the matrix of *Lycopodium* spore tablets added to quantify differences in pollen concentration between middens. The residue was treated with HF to eliminate silica, acetolyzed, and then mounted in glycerine. More than 300 pollen grains were counted in all but one midden (mean = 379 pollen grains/sample; range = 266 to 501). After 300 grains, the rest of the slide was scanned for poorly represented types. Spores (except *Lycopodium*) were included in the pollen sum.

Results

Nine middens span the last ~16,000 ^{14}C yr in the Playas Valley (Table 1). Two middens date from the Pleistocene

(>11,000 ^{14}C yr B.P.), two from the early Holocene (11,000–8000 yr B.P.), two from the boundary between the middle and late Holocene (~4000 ^{14}C yr B.P.), and three from the late Holocene (<4000 ^{14}C yr B.P.). No middens dated between 10,630 and 4100 ^{14}C yr B.P. All dates are reported as corrected, uncalibrated radiocarbon ages. A list of plant taxa appears in Table 2.

Plant macrofossil assemblages are summarized in Fig. 4. Pleistocene middens are dominated by *P. edulis* and *J. spp.* The midden from Sentinel Butte (16,040 ^{14}C yr B.P.) contains a toothed juniper that we tentatively identify as *J. coahuilensis* based on stomate position and morphology. The identification of toothed junipers in southern New Mexico is problematical and is discussed elsewhere in detail (Betancourt et al., 2001). The midden from Coyote Hills (13,830 ^{14}C yr B.P.) contains *J. scopulorum*, a smooth-margined juniper, and a toothed juniper with unusual sunken stomates that we believe may be a separate morphotype of *J. coahuilensis*. *Berberis cf. haematocarpa* and *Mirabilis oxybaphus*, both typically found above ~1500 m, are also found only in Pleistocene middens.

In the case of Sentinel Butte 2C, temporal mixing explains the presence of *Prosopis glandulosa* and a single *L. tridentata* leaf in the 16,040 ^{14}C yr B.P. sample containing abundant *P. edulis* and *Juniperus*. An AMS date of 17,020 ^{14}C yr B.P. from a *P. edulis* needle falls within the 2σ range of the original date (16,040 ^{14}C yr B.P.), while a date of 4179 ^{14}C yr B.P. from *Prosopis glandulosa* indicates that it is indeed a younger contaminant. The *Larrea* leaf was too small to date even via AMS dating. However, given the absence of *L. tridentata* from other northern Chihuahuan Desert middens before the late Holocene (Betancourt et al., 2001; Van Devender, 1990a; Van Devender and Toolin, 1983; Van Devender et al., 1984), the fact that it is represented by a solitary leaf, and the abundance of *Larrea* surrounding Sentinel Butte, we believe it is almost certainly a modern contaminant.

Some plants found in Pleistocene-aged middens were also found in late Holocene middens. These include *Artemisia ludoviciana* Asteraceae, *Atriplex canescens*, *Boerhaavia sp.*, *Kallstroemia sp.*, *Opuntia polyacantha-phaeacantha* type, and the grasses *Bothriochloa cf. barbinodis*, *Aristida sp.*, *Bouteloua gracilis*, *Digitaria californica*, *Elymus elymoides/arizonicus*, and *Setaria sp.* These species are present today and probably persisted at the site throughout the Holocene.

By the early Holocene, *P. edulis* had disappeared from Sentinel Butte (10,670 ^{14}C yr B.P.) and was rare at Coyote Hills (10,635 ^{14}C yr B.P.), where it is represented by a single pinyon shell, possibly the result of long-distance dispersal by birds. Likewise, *J. scopulorum* had disappeared from Coyote Hills, although toothed junipers persisted at both sites. The only record of *Quercus* in the Playas series is from the early Holocene at Coyote Hills.

Several plants characteristic of Chihuahuan desert scrub

Table 1
Site location and radiocarbon dates from Sentinel Butte and Coyote Hills packrat middens

| Midden designation | Latitude (°N) | Longitude (°W) | Elevation (m) | Material dated | ¹⁴ C age (¹⁴ C yr B.P.) | Standard deviation ¹⁴ C yr | δ ¹³ C (‰) | Calibrated (2σ) age range (cal yr B.P.) | Lab No. |
|--------------------|---------------|----------------|---------------|----------------|--|---------------------------------------|-----------------------|---|---------|
| Sentinel Butte 1 | 31°26.460 | 108°37.080 | 1488 | fecal pellets | 2190 | 125 | -23.5 | 2477–1873 | GX21641 |
| Sentinel Butte 2A | 31°26.460 | 108°37.080 | 1488 | fecal pellets | 4040 | 100 | -22 | 4828–4280 | GX21642 |
| Sentinel Butte 2B | 31°26.460 | 108°37.080 | 1488 | fecal pellets | 10670 | 330 | -22.2 | 13,201–11,547 | GX21208 |
| Sentinel Butte 2C | 31°26.460 | 108°37.080 | 1488 | fecal pellets | 16040 | 660 | -22.7 | 20,771–17,540 | GX21209 |
| Sentinel Butte 3A | 31°26.460 | 108°37.080 | 1488 | fecal pellets | 885 | 115 | -25.2 | 997–648 | GX21643 |
| Sentinel Butte 3B | 31°26.460 | 108°37.080 | 1488 | fecal pellets | 4095 | 145 | -24.2 | 4888–4220 | GX21644 |
| Sentinel Butte 4 | 31°26.460 | 108°37.080 | 1488 | fecal pellets | 220 | 105 | -24.7 | 462–0 | GX21645 |
| Coyote Hills 1A | 32°00'10" | 108°30'15" | 1502 | fecal pellets | 10635 | 340 | -24.4 | 13,190–11,333 | GX19992 |
| Coyote Hills 1B | 32°00'10" | 108°30'15" | 1502 | fecal pellets | 13830 | 165 | -24.8 | 17,204–16,012 | GX19993 |

or desert grassland were present by 4000 ¹⁴C yr B.P. These include *Dasyilirion wheeleri*, *Nicotiana obtusifolia*, *Parthenium incanum*, *Prosopis glandulosa*, *Bouteloua hirsuta*, and *Viguiera* sp. *L. tridentata*, a dominant species of Chihuahuan desert scrub, first appears in the macrofossils from Sentinel Butte at 2190 ¹⁴C yr B.P. *Fouquieria splendens* and *Senna* sp. do not appear until 885 ¹⁴C yr B.P.

A total of 49 different pollen types were identified in the middens (Fig. 4). For *Pinus*, an attempt was made to differentiate the pollen grains at the species level, but distinctive characters could not be observed in most grains. The few pine pollen grains in which we could observe the distal membrane indicate the presence of both *P. edulis* and *P. ponderosa* types at 16,040 ¹⁴C yr B.P., *P. ponderosa*-type at 10,635 and 220 ¹⁴C yr B.P., and *P. edulis*-type at 10,670 and 2190 ¹⁴C yr B.P. The taxon Cupressaceae probably represents *Juniperus*, since this is the only genus present in the macrofossil record.

In the 16,040 ¹⁴C yr B.P. midden, *Juniperus* dominates (71.86%) with very low Asteraceae, Poaceae, and Chenopodiaceae pollen. *Pinus* percentages are <10%, which contrasts with the abundant *P. edulis* macrofossils in the sample. However, the underrepresentation of pine pollen in middens, compared both to macrofossils (Thompson, 1985) and to the modern pollen rain (Anderson and Van Devender, 1991; Martin, 1963), has been noted previously. Therefore, low pine pollen frequencies do not exclude the local presence of *Pinus*. This may be especially true for *P. edulis* with poorly dispersed pollen, while the well-dispersed *P. ponderosa* pollen may come from distant populations. *Quercus* shows even lower pollen percentages although it produces abundant pollen. Low *Quercus* percentages were obtained from modern pollen samples in open environments (Martin, 1963, and see Fig. 5), suggesting that low percentages may represent long-distance transport, in accordance with the absence of macrofossils.

Late Pleistocene–early Holocene middens include the 13,830, 10,670, and 10,635 ¹⁴C yr B.P. samples. Main taxa include Cupressaceae, *Pinus*, *Quercus*, *Artemisia*, Chenopodiaceae, *Poaceae*, and Asteraceae Tubuliflorae (characteristic of the desert pollen spectra). The 10,635 ¹⁴C yr B.P.

midden shows slightly higher Cupressaceae values, lower Poaceae and Asteraceae values, and the only Rosaceae pollen in the record. Traces of *Potamogeton* pollen are found in the 13,830, 10,635, 4040, and 885 ¹⁴C yr B.P. samples. This aquatic species lives in ponds and slow-moving rivers; its presence in the middens may indicate that ephemeral ponds existed during wet years or it may be derived from older, reworked Pleistocene playas.

The middens at 4095 and 4040 ¹⁴C yr B.P. are characterized by high Asteraceae, Poaceae, and Chenopodiaceae and very low Cupressaceae, *Pinus*, and *Quercus* pollen values. *Prosopis*, *Mimosa*, and *Larrea* have intermediate values. Sporadic pollen grains of *Prosopis*, *Mimosa*, and *Larrea* are seen before this time, but probably represent contamination. The 4040 ¹⁴C yr B.P. midden also contains five pollen grains that appear to be cereal based on their large (>70-μm) diameter.

In the 2190 ¹⁴C yr B.P. midden *Prosopis*, *Mimosa*, *Larrea*, Asteraceae, and Poaceae are dominant, suggesting essentially modern vegetation. *Fouquieria splendens* and *Opuntia* first occur in this zone, as well as the only pollen grain of *Zea mays* identified with certainty in the record. *Z. mays* had appeared at least a millennium earlier in New Mexico and Arizona (Shackley et al., 1999; Tagg, 1996; Upham et al., 1987; Wills, 1988). The 885 and 220 ¹⁴C yr B.P. samples are characterized by very high pollen values for *Larrea* and very low pollen values for *Pinus*, *Quercus* and other desert taxa.

Fig. 5 compares midden pollen and macrofossil assemblages with surface pollen samples collected from stock ponds at various elevations in the Borderlands (see Martin, 1963, for original descriptions of the surface pollen data). Many of the differences between these types of assemblages were to be expected from previous comparisons (Anderson and Van Devender, 1991; Davis and Anderson, 1987; Thompson, 1985). Midden pollen assemblages tend to be more locally variable than surface pollen samples due to the diverse modes of pollen transport into middens and greater heterogeneity in habitat and flora of cliffs compared to more open landscapes. Pollen may be incorporated into middens by wind or plant parts or via the packrat's body, and locally

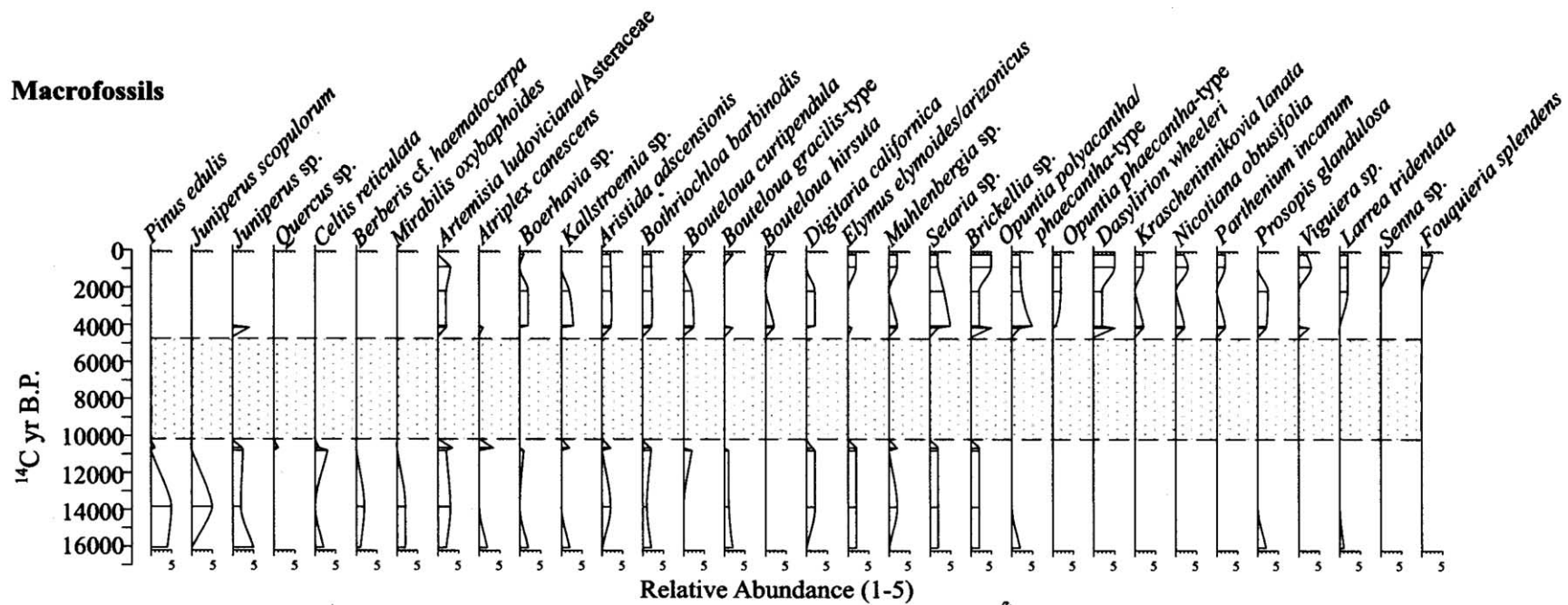
Table 2
Scientific and common names of plant taxa mentioned in text

| Scientific name | Common name | Scientific name | Common name |
|---------------------------------|-------------------------|--|-------------------------|
| Agavaceae | | Nyctaginaceae | |
| <i>Agave</i> spp. | Agave | <i>Boerhavia</i> sp. | Spiderling |
| <i>Yucca</i> spp. | Yucca | <i>Mirabilis oxybaphus</i> | Four-o'clock |
| Anacardiaceae | | Pinaceae | |
| <i>Rhus microphylla</i> | Littleleaf sumac | <i>Pinus cembroides</i> | Mexican pinyon |
| Asteraceae | | <i>Pinus discolor</i> | Border pinyon |
| <i>Artemisia ludoviciana</i> | Louisiana wormwood | <i>Pinus edulis</i> | Colorado pinyon |
| <i>Brickellia scabra</i> | Rough Brickelbush | <i>Pinus engelmannii</i> | Arizona longleaf pine |
| <i>Flourensia cernua</i> | Tarbush | <i>Pinus leiophylla</i> | Chihuahua pine |
| <i>Gutierrezia sarothrae</i> | Broom snakeweed | <i>Pinus monophylla</i> var. <i>fallax</i> | Singleleaf pinyon |
| <i>Heterotheca subaxillaris</i> | Telegraph plant | <i>Pinus ponderosa</i> var. <i>arizonica</i> | Arizona yellow pine |
| <i>Parthenium incanum</i> | Mariola | <i>Pinus ponderosa</i> | Ponderosa Pine |
| <i>Senecio</i> sp. | Groundsel | <i>Pinus remota</i> | Papershell pinyon |
| <i>Stephanomeria</i> sp. | Wire lettuce | <i>Pinus strobiformis</i> | Southwestern white pine |
| <i>Viguiera</i> sp. | Goldeneye | <i>Pseudotsuga menziesii</i> | Douglas fir |
| Berberidaceae | | Poaceae | |
| <i>Berberis haematocarpa</i> | Red barberry | <i>Aristida</i> sp. | Threeawn |
| Cactaceae | | <i>Bothriochloa barbinodis</i> | Cane beardgrass |
| <i>Opuntia engelmannii</i> | Engelman's prickly pear | <i>Bouteloua curtipendula</i> | Sideoats grama |
| <i>Opuntia phaeacantha</i> | Variable prickly pear | <i>Bouteloua eripoda</i> | Black grama |
| <i>Opuntia polyacantha</i> | Plains prickly pear | <i>Bouteloua gracilis</i> | Blue grama |
| Chenopodiaceae | | <i>Bouteloua hirsuta</i> | Hairy grama |
| <i>Atriplex canescens</i> | Fourwing saltbush | <i>Digitaria californica</i> | Arizona cottontop |
| <i>Krascheninnikovia lanata</i> | Winterfat | <i>Elymus elymoides</i> | Squirreltail grass |
| Cupressaceae | | <i>Eragrostis intermedia</i> | Plains lovegrass |
| <i>Juniperus scopulorum</i> | Rocky Mountain juniper | <i>Hilaria mutica</i> | Tobosa grass |
| <i>Juniperus deppeana</i> | Alligator bark juniper | <i>Muhlenbergia</i> sp. | Muhly |
| <i>Juniperus coahuilensis</i> | Coahuila juniper | <i>Zea mays</i> | Corn |
| Ephedraceae | | <i>Setaria macrostachya</i> | Plains bristlegrass |
| <i>Ephedra</i> sp. | Joint fir | Polygonaceae | |
| Fabaceae | | <i>Eriogonum</i> sp. | Wild buckwheat |
| <i>Calliandra</i> sp. | Fairy duster | Potamogetonaceae | |
| <i>Senna</i> sp. | Senna | <i>Potamogeton</i> sp. | Pondweed |
| <i>Mimosa</i> spp. | Mimosa | Pteridaceae | |
| <i>Prosopis glandulosa</i> | Honey mesquite | <i>Cheilanthes</i> sp. | Lip fern |
| Fagaceae | | Rhamnaceae | |
| <i>Quercus arizonica</i> | Arizona white oak | <i>Celtis reticulata</i> | Netleaf hackberry |
| <i>Quercus emoryi</i> | Emory oak | <i>Ziziphus obtusifolia</i> | Graythorn |
| <i>Quercus gambelii</i> | Gambel oak | Saxifragaceae | |
| <i>Quercus hypoleucoides</i> | Silverleaf oak | <i>Fendlera rupicola</i> | Cliff Fendlerbush |
| <i>Quercus rugosa</i> | Netleaf oak | Solanaceae | |
| Fouquieriaceae | | <i>Datura</i> sp. | Jimsonweed |
| <i>Fouquieria splendens</i> | Ocotillo | <i>Nicotiana obtusifolia</i> | Desert tobacco |
| Koeberliniaceae | | Verbenaceae | |
| <i>Koeberlinia spinosa</i> | Allthorn | <i>Alyosia wrightii</i> | Spicebush |
| Malvaceae | | Zygophyllaceae | |
| <i>Abutilon</i> sp. | Indian mallow | <i>Kallstroemia</i> sp. | Caltrop |
| <i>Spharalcea</i> sp. | Globemallow | <i>Larrea tridentata</i> | Creosotebush |
| Nolinaceae | | | |
| <i>Dasyilirion wheeleri</i> | Sotol | | |
| <i>Nolina microcarpa</i> | Beargrass | | |

occurring taxa tend to be better represented than in surface pollen samples. Midden pollen assemblages frequently include zoophilous species rarely recorded in surface samples, and some wind-pollinated species tend to be underrepresented, while others are overrepresented. For example, pines (*Pinus*) and grasses (Poaceae) tend to be underrepresented in midden pollen relative to midden macrofossils and surface pollen samples, while juniper (*Juniperus*) pollen can

be overrepresented in middens due to the occasional incorporation of male cones. Cheno-Am pollen, on the other hand, is overrepresented in modern surface samples, probably an artifact of chronic disturbances near stock tanks and overgrazed grasslands (Martin, 1963). Overall, we found no analogs between the midden pollen assemblages at different times and the surface pollen samples from different elevations.

Macrofossils



Pollen

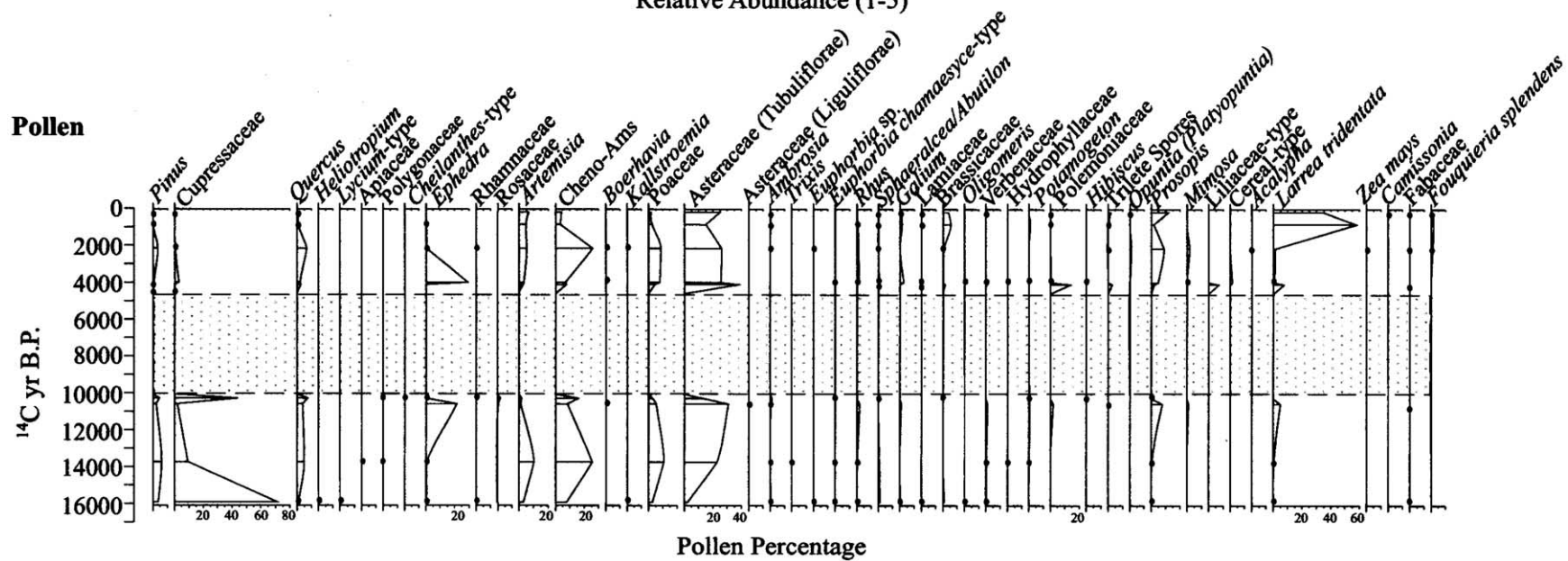


Fig. 4. Plant macrofossil abundance (top graph) and pollen percentage (bottom graph) through time for select species from Sentinel Butte and Coyote Hills, NM. Stippled area indicates period from which no middens were found.

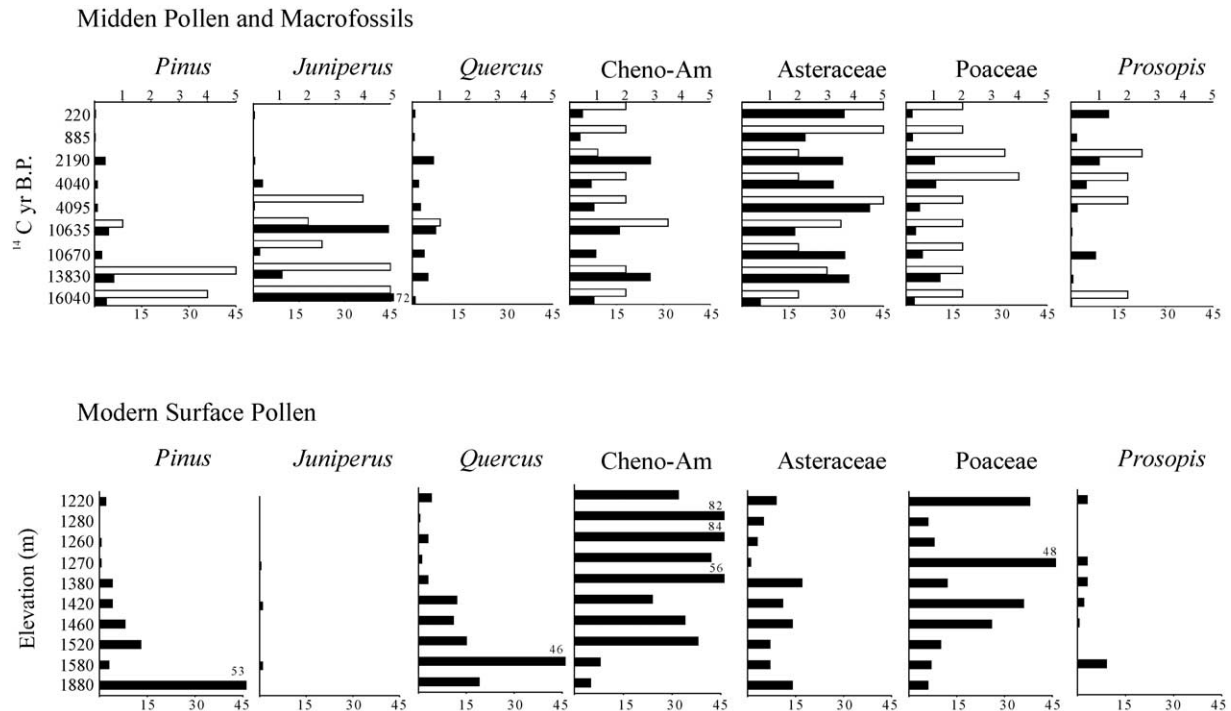


Fig. 5. Comparison of midden macrofossils and pollen (top graph) with modern surface pollen samples (bottom graph). Open bars are for macrofossil abundances (1–5), closed bars for pollen percentages (1–100%). The modern surface pollen data are from Martin (1963, Table 1).

Discussion

The Borderlands midden record indicates that pinyon–juniper woodlands with a rich C_4 understory bordered pluvial lakes that formed in Playas Valley and neighboring basins. The lake-level histories of these basins are not necessarily in phase, with some basins registering full-glacial highstands and others late glacial ones. Lake Cloverdale in southernmost Animas Valley filled between 20,000–18,000 ^{14}C yr B.P. (Krider, 1998), similar to highstands in the San Agustin Plains (Markgraf et al., 1984; Phillips et al., 1992) and Estancia Basin (Allen and Anderson, 2000) to the north, but fails to record the late glacial highstand seen in Lake Cochise.

There are two lake chronologies for pluvial Lake Cochise. The first was based on ^{14}C dates from secondary carbonates in two lacustrine green clay units that reached 1290 m, above the prominent 1274-m shoreline above Willcox Playa. Long (1966) proposed that lake levels were significantly higher than the 1274-m beach ridge from 30,000 to 13,000 ^{14}C yr B.P., dropped between 13,000 and 11,500 ^{14}C yr B.P., and rose again to near the 1274-m level between 11,500 and 10,500 ^{14}C yr B.P. Later, Waters (1989) used a series of backhoe trenches to map and date the shoreline stratigraphy just below 1274 m. Radiocarbon dates from charcoal in beach deposits overlying the green clay suggest that lake levels were at 1274 m from at least 13,750 to 13,400 ^{14}C yr B.P. (Waters, 1989). This implies that the highstand associated with the underlying green clays formed prior to 13,750 ^{14}C yr B.P. and the carbonate

dates from the clays are too young. Dates from humates and organic carbon also indicate that after a period of dessication, Lake Cochise again filled to slightly below the 1274 m shoreline three times during the Holocene, once around or before 8900 ^{14}C yr B.P. and again at \sim 5400 and \sim 4000–3000 ^{14}C yr B.P. (Waters, 1989).

Pluvial Lake Animas experienced a high stand sometime between 24,000 and 8000 ^{14}C yr B.P. (Fleishhauer and Stone, 1982), but inadequate dating precludes precise comparison with other pluvial lakes. Suffice it to say that the climatic conditions for development of pinyon–juniper woodland at \sim 1400–1500 m at 16,000 and 13,800 ^{14}C yr B.P. were also conducive to pluvial lake expansion in the Borderlands.

Late Pleistocene vegetation is marked by expansion of woodlands dominated by *P. edulis* and *J. coahuilensis* at Sentinel Butte and *P. edulis* and *J. coahuilensis* plus *J. scopulorum* at Coyote Hills. This is consistent with other regional records that indicate pinyon–juniper woodlands in what is currently Chihuahuan desert scrub (Betancourt et al., 2001; Lanner and Van Devender, 1981; Van Devender, 1990a; Van Devender et al., 1984; Van Devender and Everitt, 1977; Van Devender and Toolin, 1983). *Pinus* pollen from Willcox Playa in southeastern Arizona reached 99% during the late Pleistocene (22,000 ^{14}C yr B.P.), indicating expansion of pines (Martin and Mehringer, 1965). These high pine percentages were previously attributed to pine forest expansion (*P. ponderosa* var. *arizona*, *P. leiophylla*, *P. strobiformis*, and *P. engelmannii*) (Martin, 1963). The high pine pollen in lake sediments, however, could instead

represent the cumulative effect of pine pollen dispersal from widespread pinyon–juniper woodlands in the vast lowlands upwind of Willcox Playa to the Gulf of California.

The Playas Valley middens add further detail to the glacial-age biogeography of pinyons. Dominant species included *P. monophylla* var. *fallax* in the Sonoran Desert, *P. remota* in the Chihuahuan Desert, and *P. edulis* in what are now desert grasslands in New Mexico and eastern Arizona (Lanner and Van Devender, 1981). In the Catalina Mountains near Tucson, *P. discolor* was sympatric with a *P. monophylla edulis* hybrid (Van Devender, 1990a). The Playas Valley middens indicate that *P. edulis* was the dominant pinyon across all of southern New Mexico. This begs the question of whether present populations of *P. monophylla* var. *fallax* in the Florida Mountains northeast of Playas Valley represent Holocene dispersals instead of Pleistocene relicts.

The presence of *J. scopulorum* at Coyote Hills indicates it descended to ~1500 m on igneous substrates during the late Pleistocene, while its absence at Sentinel Butte at least locally may be due to more xeric limestone substrate. *J. scopulorum* was also common, however, in other Pleistocene middens at ~1500 m from limestone in the Los Pinos, Guadalupe, Sacramento, and Hueco Mountains. An isolated population was also found at 975 m in Pleistocene middens from Organ Pipe National Monument along the Arizona–Sonora border (Van Devender, 1990b). The presence of *J. scopulorum* in the Playas Valley middens further suggests that *J. deppeana*, the dominant juniper at mid to high elevations in the Borderlands today, must have been displaced south into the Sierra Madre Occidental of northern Mexico (Betancourt et al., 2001).

Although both lake and pinyon–juniper expansion across the lowlands have been attributed to greater winter precipitation, the Pleistocene middens from Playas Valley contain several summer rainfall indicators, including the midsummer annuals *Kallstroemia* and *Boerhavia* sp. and the C₄ grasses *Bouteloua* cf. *gracilis*, *Bothriochloa barbinodis*, and *Digitaria californica*. Vertebrate remains from U-Bar Cave (1570 m), only a few km north of Sentinel Butte imply woodland with a well-developed grassy understory (Harris, 1987). Carbon isotope values from soil carbonates elsewhere in the Borderlands (Buck and Monger, 1999; Liu et al., 1996; Monger et al., 1998) and tooth enamel from megaherbivores at U-Bar Cave, also indicate C₄ dominance in woodland understories and grasslands during the full to late glacial (Connin et al., 1998).

Extirpation of pinyon–juniper woodlands must have occurred by 10,600 ¹⁴C yr B.P., when *P. edulis* and *J. scopulorum* disappeared from the lowlands of the Playas Valley. This extirpation may have occurred abruptly during what Haynes (1991) has termed the “Clovis-age Drought.” At Murray Springs in the San Pedro Valley of southern Arizona, the water table began to decline after 14,000 ¹⁴C yr B.P. and dropped to unusually low levels just before 10,900 ¹⁴C yr B.P., corresponding to the disappearance of Rancho-

labrean megafauna. Groundwater levels quickly rebounded by 10,800 ¹⁴C yr B.P., depositing black organic mats (Haynes, 1991). New AMS dates bracket the black mats within the Younger Dryas cold event from ~11,000 to 10,000 ¹⁴C yr B.P. (Jull et al., 1998). At most sites in the northern Chihuahuan desert, the disappearance of pinyon and change to more xeric oak–juniper woodland also occurred around 11,000 ¹⁴C yr B.P. (Van Devender, 1990a), although earlier departures are also reported (Betancourt et al., 2001). Pollen records from Lehner Ranch in the San Pedro (Mehring and Haynes, 1965) and Sulfur Springs valleys (Martin, 1963) also indicate that *Pinus* had decreased drastically and desert grassland was established by 11,000 ¹⁴C yr B.P.

Although woody species changed dramatically in the early Holocene, changes in understory vegetation were less noticeable. Faunal stratigraphy from Howell’s Ridge Cave in the Little Hatchet Mountains suggests well-developed grasslands in the early Holocene (Van Devender, 1995; Van Devender and Worthington, 1977), while a shift from C₄ grasses to C₃ desert scrub is indicated by soil carbonates at lower, drier sites in the Southwest (Buck and Monger, 1999; Liu et al., 1996; Monger et al., 1998). The hillslope understory seen in early Holocene Playas Valley middens was remarkably stable with no noticeable changes in grass composition or abundance.

No middens in our series dated from the middle Holocene (8000–4000 ¹⁴C yr B.P.), a period during which middens are scarce across the Southwest. One possible explanation for this scarcity is that a pervasive winter drought during the middle Holocene led to a decline in woody perennials, which predominantly depend on winter moisture, and in packrat populations and midden production (Betancourt, 1993; Spaulding, 1991). Because our series consists of only nine samples, however, the lack of middens during this period may be due to small sample size. Studies using larger numbers of middens should help resolve this issue.

The Playas Valley middens record progressive arrivals of desert scrub species from ~4000 ¹⁴C yr B.P. onwards. The first occurrence of *L. tridentata* macrofossils at 2190 ¹⁴C yr B.P. is later than in other regional midden records, although a small peak in *Larrea* pollen at 4095 ¹⁴C yr B.P. could indicate an earlier arrival. *Larrea* is found in Chihuahuan Desert middens from Otero Mesa by 4750 ¹⁴C yr B.P., from the San Andres Mountains by 4340 ¹⁴C yr B.P., and from the Sacramento Mountains by 3300 (Betancourt et al., 2001; Van Devender, 1990a; Van Devender et al., 1984; Van Devender and Toolin, 1983). Earlier records of *Larrea* from the Sonoran desert suggest that dispersal from the north and west was also possible. The closest record in the Sonoran desert is from the Waterman Mountains west of Tucson, Arizona where *Larrea* was present in middens by 6195 ¹⁴C yr B.P. (Anderson and Van Devender, 1991; Van Devender, 1990b). Although the diploid race ($2n = 26$) of *Larrea* occurs primarily in the Chihuahuan desert and the tetraploid

race ($2n = 52$) in the Sonoran desert, ploidy level cannot be used to determine the source of the diploid macrofossils present at Sentinel Butte. Diploid isolates are found in regions of the Sonoran desert dominated by tetraploids, including the Waterman Mountains, where the *Larrea* macrofossils identified in 6195 ^{14}C yr B.P. and 1320 ^{14}C yr B.P. middens are diploid (Hunter et al., 2001). Thus, the diploid *Larrea* at Sentinel Butte could be derived from diploid populations in either the Chihuahuan or Sonoran Desert.

The arrival of *Fouquieria splendens* was also later than in surrounding areas. *Fouquieria* was present at Rough Canyon, New Mexico by 6295 ^{14}C yr B.P. (Betancourt et al., 2001) and in the Waterman Mountains, Arizona by 2600 ^{14}C yr B.P. (Anderson and Van Devender, 1991). The late arrival of *Fouquieria splendens* at 885 ^{14}C yr B.P. is similar to that at the Sevilleta LTER site south of Albuquerque (Betancourt et al., in preparation) and suggests that vegetation was essentially modern by this time.

The midden sequence indicates that pinyon–juniper woodland with a C_4 understory expanded downslope to the margins of pluvial lakes in Playas Valley and surrounding basins during the late Pleistocene, suggesting increased effective moisture with at least moderate summer rainfall. The timing of pinyon–juniper woodland extirpation conforms to other regional records, although little change is seen in the understory. By about 4000 ^{14}C yr B.P., desert scrub elements begin to appear, marking the transition to present-day vegetation. Development of more extensive midden series from the Borderlands could help resolve lingering questions regarding precipitation seasonality, understory dynamics, mid-Holocene climate, and the exact timing of desert scrub arrivals in the area.

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