

Vegetation invasions into absolute desert: A 45 000 yr rodent midden record from the Calama–Salar de Atacama basins, northern Chile (lat 22°–24°S)

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ABSTRACT

Plant macrofossils, percentage abundance of grass taxa, fecal-pellet $\delta^{13}\text{C}$, and plant-cuticle contents from 49 fossil rodent middens dated by ^{14}C record changes in local vegetation and precipitation since 45 ka (calibrated or measured to thousands of calendar years before present) in the central Atacama Desert (lat 22°–24°S) of northern Chile. The midden sites are along the hyperarid upper margin (2400–3100 m) of the “absolute desert,” in an extreme environment sparsely vegetated by annual herbs and halophytic shrubs. Conditions between 40 and 22 ka may have been at least intermittently dry, and possibly cooler, as implied by four middens with low species richness. We infer a large increase in summer rainfall between 16.2 and 10.5 ka on the basis of the lowering of steppe grasses by as much as 1000 m, prominence of C_4 grasses and summer annuals, high species richness, and displacement of northern species at least 50 km south of their modern ranges. The precipitation increase was greatest for a cluster of middens between 11.8 and 10.5 ka. Abrupt drying, evident in a dramatic decrease in grass abundance, occurred after 10.5 ka at all four midden localities. Increased percentages of

grass, higher species richness, and extralocal taxa record slightly wetter conditions between 7.1 and 3.5 ka. The present hyperarid conditions were established after 3 ka.

Present-day variability of summer precipitation in the central Atacama Desert and adjacent Altiplano is related to the intensity and position of upper air circulation anomalies, which in turn respond to Pacific sea-surface temperature anomalies. Summer insolation over the central Andes (lat 20°S) was at its minimum during the latest glacial to early Holocene transition, so regional insolation forcing cannot account for intensified pluvial conditions in the central Atacama. Summer precipitation collapsed abruptly between 10.5 and 10 ka, indicating either nonlinear relationships with seasonal insolation or a change in intensity of upper air circulation over the Altiplano, effectively blocking moisture transport to the Atacama Desert. Here, we suggest that precipitation variations on millennial time scales in the central Atacama are the result of extraregional forcing of the South American Summer Monsoon through intensified Walker Circulation (stronger easterlies) and La Niña-like conditions operating through insolation anomalies (i.e., departures in insolation values) directly over central Asia and the equatorial Pacific.

Keywords: Atacama Desert, late Quaternary, middens, monsoons, northern Chile, paleoecology.

INTRODUCTION

Paleoclimate research has accelerated in the central Andes in response to the need for tropical land records to better resolve leads and lags associated with high-latitude versus low-latitude climate forcing. Ice-age cooling (5–6 °C) in the tropics of South America is now evident from multiple records including $\delta^{18}\text{O}_{\text{ice}}$ in the central Andes (Thompson et al., 1995, 1998; Thompson, 2000), mixing of temperate and tropical pollen floras in Amazonian sediment records (Colinvaux et al., 2000; Van der Hammen and Hooghiemstra, 2000), and noble-gas concentrations in ^{14}C -dated Amazonian groundwaters (Stute et al., 1995). Fluctuations in the areal extent of tropical wetlands, driven by changes in temperature and precipitation (and perhaps sea level), are thought to drive the CH_4 variations seen in polar ice cores (Chappellaz et al., 1990, 1993; Severinghaus and Brook, 1999; Raynaud et al., 2000). Other notable records in the central Andes include evidence for glacial fluctuations in the Cordillera Real, Bolivia (Seltzer, 1990, 1992), the Andes of Ecuador and Peru (Rodbell, 1993; Rodbell and Seltzer, 2000), and at Salar de Uyuni, Bolivia (Clapperton et al., 1997; Clayton and Clapperton, 1997). Lake-level histories are now available for Salar de Uyuni (Servant and Fontes, 1978; Wirmann and Mourguiart, 1995; Servant et al., 1995; Sylvestre et al., 1999; Baker et al., 2001a), Lake Titicaca (Wirmann and Mourguiart, 1995; Seltzer et al., 1998; Cross et al.,

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2000; Baker et al., 2001b), and the Pacific slope of the Andes (Grosjean and Nuñez, 1994; Grosjean et al., 1995, 1997b; Valero-Garcés et al., 1996; Geyh et al., 1999; Schwab et al., 1999; Bobst et al., 2001).

In many of these glacial and lake records, lack of suitable material or hard-water effects may complicate dating, and interpreting glacial and lake-level histories may also be difficult because of problems in discriminating temperature from precipitation effects. These shortcomings can be overcome through reconstructing a detailed vegetation history for the central Atacama Desert, where summer storms spill over from the Altiplano. The lower limits of plants in this hyperarid environment are governed primarily by seasonal precipitation, and temperature causes only a secondary effect. Hyperaridity also affords excellent preservation of organic vegetal remains that can be dated with ^{14}C techniques. Although past pluvial phases in the Atacama have been recognized since the 1950s (Brüggen, 1950), there is little indication of how these episodes affected former plant and animal distributions, specifically whether vegetation has ever invaded what is now "absolute desert," a broad expanse of the Atacama Desert now completely devoid of precipitation and vascular plants. The boundaries of the absolute desert are assumed to have remained the same throughout the Quaternary, with absolute desert imposing a permanent barrier to north-south migration of plants and animals (Villagrán et al., 1983; Arroyo et al., 1988; Marquet, 1994).

The Atacama Desert harbors few sites suitable for pollen deposition and preservation. Even where pollen is preserved, taxonomic resolution is poor, as pollen of the dominant grasses (Poaceae) and composites (Asteraceae) are seldom distinguishable to the species level. The prospects for reconstructing Atacama vegetation improved with the discovery of fossil rodent deposits similar to North American packrat (*Neotoma*, Sigmodontinae) middens (Betancourt et al., 1990, 2000). In the Atacama, middens rich in plant macrofossils are ubiquitous; they are produced by four different families of rock-dwelling rodents (Betancourt et al., 2000). Here, we present a midden record spanning the past 45 000 yr from the edge of the absolute desert in the Calama and Salar de Atacama basins in northern Chile (Fig. 1). We use the resulting vegetation history to infer variations in monsoonal circulation and precipitation over the central Atacama Desert and the central Andes.

The Study Area—Climate

Constituting one of the harshest environments on Earth, the Atacama and Peruvian

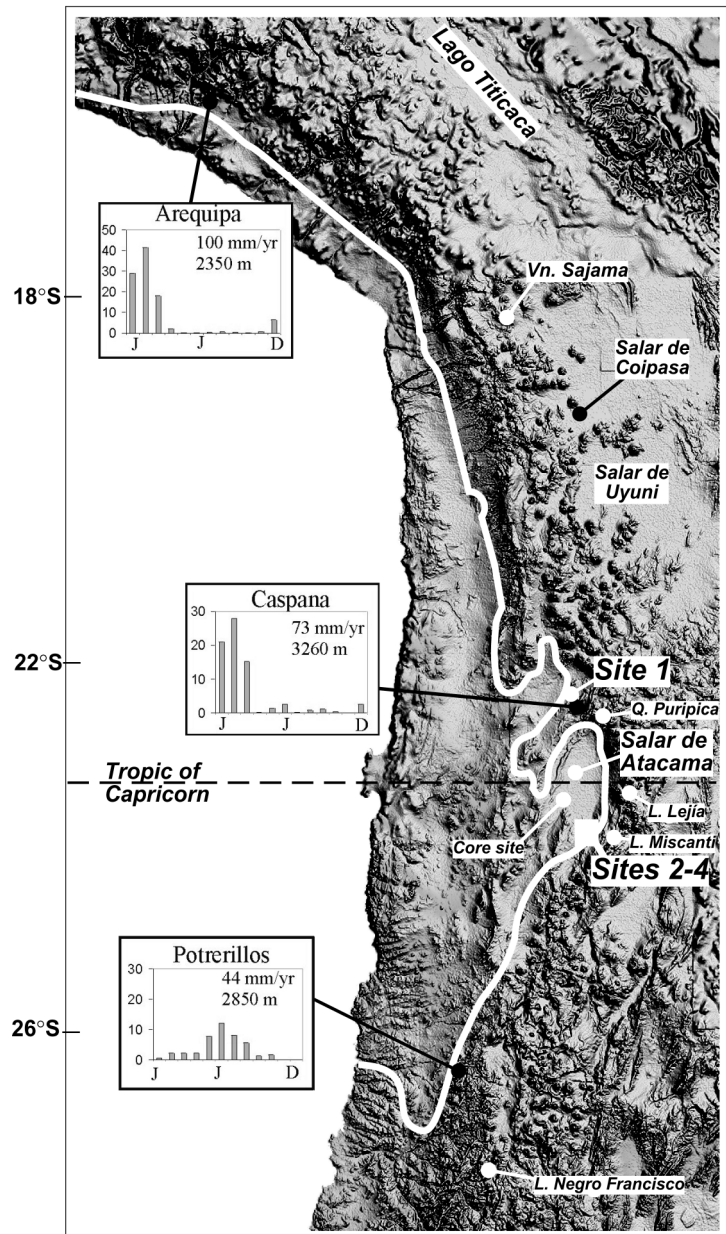


Figure 1. Physiography of the Andes Cordillera and Altiplano, with Quaternary records discussed in the text. Precipitation gradients shift from summer- to winter-dominated rainfall within 200 km south of the Salar de Atacama basin. The white line denotes the approximate eastward extent of absolute desert, defined by the absence of vegetation except in a few scattered oases and intermittent and perennial streams. The small white rectangle (labeled sites 2–4) indicates the approximate extent of Figure 2. Insets show rainfall distribution (in mm/yr; J–J–D—January, June, December), mean annual rainfall, and elevation for three locations.

Coastal Deserts extend $>25^\circ$ from the Ecuador-Peru border (lat 5°S) to La Serena, Chile (lat 30°S) (Rundel et al., 1991). These deserts encompass vast areas that receive virtually no rain and harbor no vegetation, i.e., these vast areas are considered absolute deserts (Fig. 1). Arid conditions, which may have begun as

early as the Eocene, evolved into hyperarid conditions by the middle Miocene (Mortimer, 1973; Stoertz and Ericksen, 1974; Alpers and Brimhall, 1988). Factors contributing to hyperaridity include (1) the extreme rain shadow of the high Andes, which blocks the advection of tropical and subtropical moisture from the

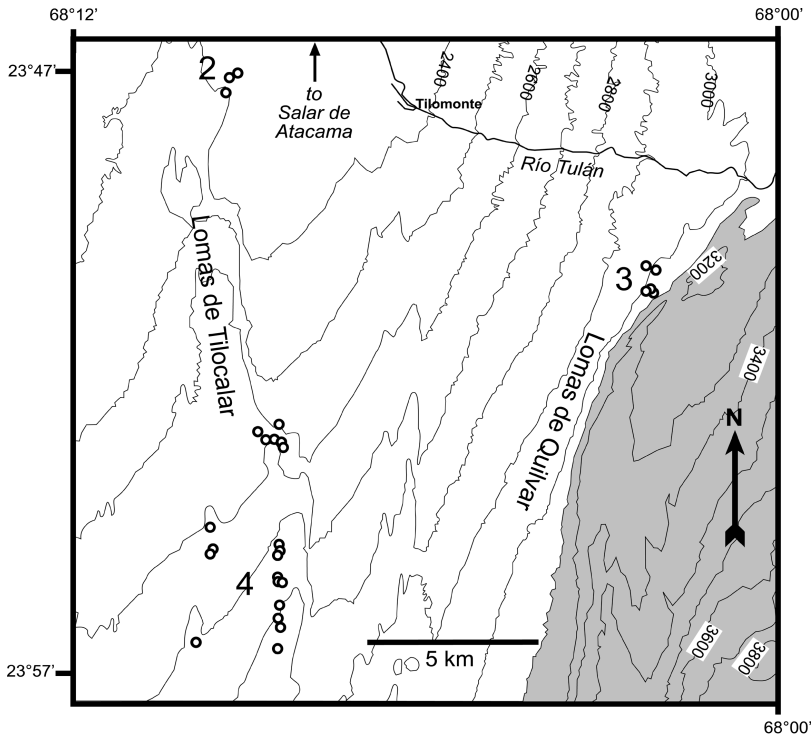


Figure 2. Locality map for sites 2–4 indicating distribution of rodent midden sites (circles). The shaded area shows where vegetation is present today. Plant cover is <1% for the rest of the area. Numbers indicate midden localities: 2—Vegas de Tilocalar, 3—Lomas de Quilvar, 4—Lomas de Tilocalar. Elevations are given in meters; contour interval is 100 m.

southern Amazon basin; (2) the blocking influence of the semipermanent South Pacific Anticyclone, which limits winter storm tracks to south of lat 28°S; and (3) the presence of cold, upwelling waters associated with a subduction zone and the north-flowing Humboldt Current off the northern Chilean coast (Borgel, 1973; Caviedes, 1973; Alpers and Brimhall, 1988).

We focused our midden survey in the Calama and Salar de Atacama basins (Figs. 1, 2), the midpoint of an ongoing study spanning the entire length of the Atacama Desert. The Calama and Salar de Atacama basins (lat 22–24°S) lie 100–200 km north of the transition from winter-rainfall dominance in the southern Atacama (lat 25–30°S) to summer-rainfall dominance in the central (lat 20–25°S) and northern (lat 16–20°S) Atacama (Fig. 1). This abrupt transition in rainfall seasonality makes the central Atacama Desert an ideal region for studying past shifts and intensities of both tropical and extratropical rainfall belts.

Convective summer storms commonly occur north of lat 25°S on the Pacific slope of the Andes, as a result of the spilling over of moisture from the Amazon basin. Known locally as *Invierno Boliviano* (“Bolivian win-

ter,” in reference to the precipitation that falls as snow on the Altiplano), the magnitude and frequency of these episodic storms reflect the intensity of the South American Summer Monsoon (SASM) (Zhou and Lau, 1998). This seasonal pattern is produced by continental heating over the Altiplano and Gran Chaco during the Austral spring and summer; the pattern’s intensity is linked to the upper tropospheric circulation known as the Bolivian High (Lenters and Cook, 1995, 1997, 1999; Zhou and Lau, 1998). South of lat 25°S, incursions of westerly winds become more frequent, and winter precipitation increases in importance (Miller, 1976) (Fig. 1). Winter snowfalls can occur as far north as lat 19°S owing to very infrequent cutoff lows (Vuille and Baumgartner, 1998).

The El Niño–Southern Oscillation (ENSO) phenomenon affects interannual precipitation variability on the Altiplano (Aceituno, 1988). The eastern and western Cordilleras, however, exhibit different levels of sensitivity to ENSO (Garreaud, 1999; Vuille et al., 2000). A negative Southern Oscillation index or warm ENSO phase (El Niño) is characterized by high-altitude westerly wind anomalies that inhibit convection over the western edge of the

Altiplano. This phenomenon causes sustained dry conditions by limiting moist air advection from the eastern Cordillera across the Altiplano (Garreaud, 1999). Conversely, positive or cold ENSO phases (La Niña) are characterized by a southward displacement of the Bolivian High and enhanced easterly circulation that produces greater advection and increased precipitation (Vuille, 1999). These synoptic circumstances seem to explain why precipitation over the entire Altiplano occurs coherently in time and space but correlates poorly with adjacent moisture-source lowlands to the east (Garreaud, 2000).

In the central and northern Atacama Desert, >80% of the mean annual precipitation occurs in the summer months (December–March). Absolute precipitation amounts depend on elevation and distance from the crest of the Andes, which controls rainout from spillover storms (Fig. 3A). Precipitation data from five weather stations in our study area exhibit only a modest correlation ($R^2 = 0.29$) with the Southern Oscillation index (SOI) for the period between 1980 and 1993 (Fig. 3B). Whereas precipitation increased at all stations during the strong La Niña episodes of 1984 and 1989, precipitation peaks have also happened during El Niño years (e.g., 1987). Spatial and temporal coverage (few records longer than 25 yr) is inadequate, yet records from different altitudes (and latitudes) show good agreement after 1980 (Fig. 3B). Less agreement before 1980 may reflect problems in the original Dirección General de Aguas (DGA) monthly precipitation data, which underestimate winter snowfall (Vuille and Ammann, 1997; Vuille and Baumgartner, 1998). The extreme aridity of the region accelerates sublimation of light snowpack, however, rendering runoff, infiltration, and soil moisture negligible in winter (Vuille and Ammann, 1997).

The Study Area—Vegetation

The strong north-south and east-west climatic gradients in the Atacama form pronounced gradients in plant distribution (Fig. 4). Five major physiognomic vegetation belts characterize northern Chile (Villagrán et al., 1981, 1983; Arroyo et al., 1982; Gajardo, 1993). A low-lying fog zone, extending up to 800–1000 m above sea level (masl), forms discontinuous Lomas (“hill”) fog-adapted plant communities along the Coastal Range (Rundel et al., 1991). In the study area, the absolute desert extends 200 km inland from the Coastal Range to the western flanks of the Domeyko and Andes Cordilleras at 2700–3000 masl, close to its maximum extent in

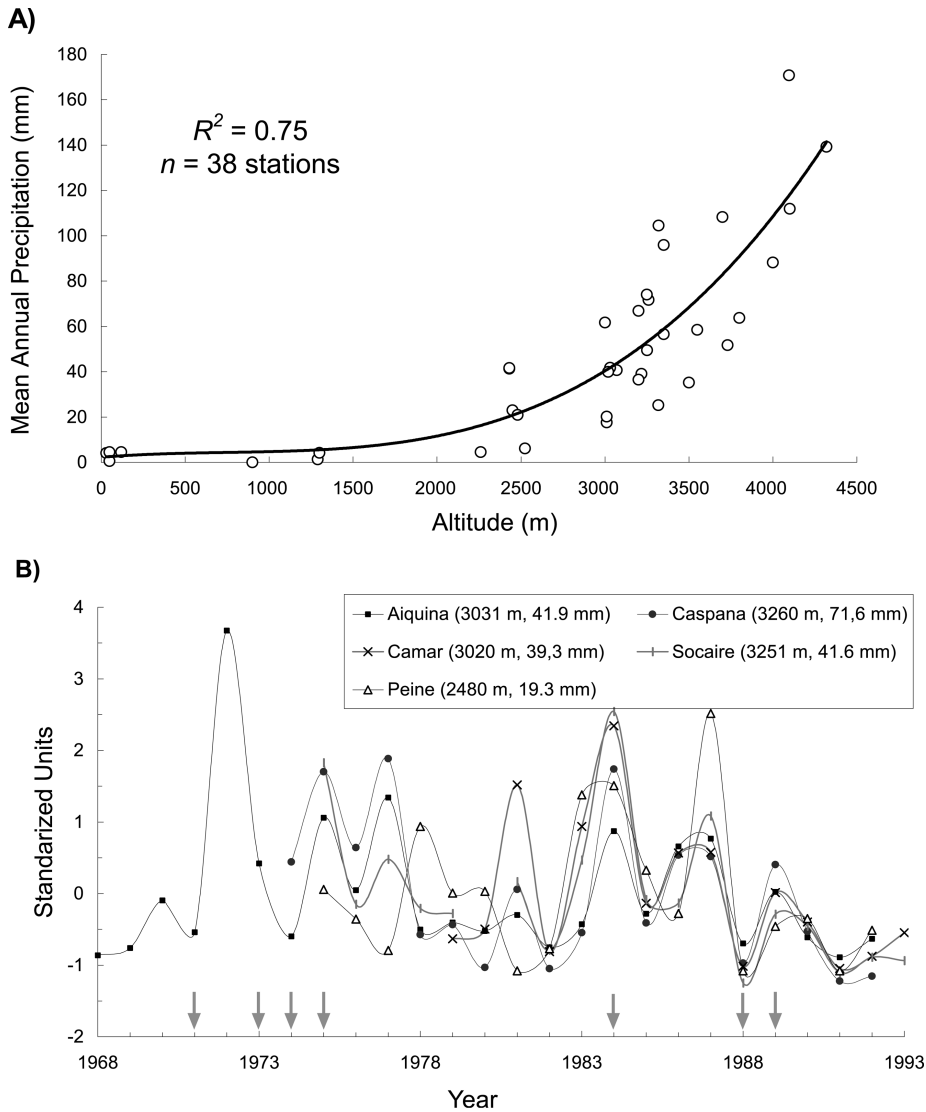


Figure 3. (A) Relationship between mean annual precipitation (MAP) and altitude for 38 stations in Chile between latitudes $21^{\circ}13'$ and $25^{\circ}24'S$ based on monthly DGA (Dirección General de Aguas) measurements. A second-order polynomial was fitted to the data (black line). (B) Standardized time series of precipitation records from select stations bordering the Salar de Atacama and Calama basins. Gray arrows along the x-axis indicate strong La Niña years. Lack of pre-1980 coherence between records may be due to errors in source data (source: Dirección General de Aguas, Ministerio de Obras Públicas, Santiago, Chile).

northern Chile. The edge of the absolute desert is defined by the Prepuna, a transitional zone (<30 mm MAP [mean annual precipitation]) between 3000 and 3300 masl with sparse ($<5\%$ cover) shrubs and succulent annuals. Common plants include *Cistanthe celosioides* and *C. salsoloides* (Portulacaceae), *Lycopersicon chilense* and *Exodeconus integrifolius* (Solanaceae), *Cristaria* spp. and *Tarasa operculata* (Malvaceae), and *Cryptantha* spp. (Boraginaceae). Halophytic shrubs (*Atriplex imbricata*: Chenopodiaceae), cushion cacti (*Opuntia camachoii*), and Boraginaceae

(*Tiquilia atacamensis*) are the only perennials. The shrubs *Acantholippia deserticola* (Verbenaceae) and *Ephedra breana* (Ephedraceae) are common in dry washes and places that collect runoff.

The Andean tolar zone (or Puna belt, e.g., Ruthsatz, 1977) extends from 3200 to ~ 4000 m, with MAP averaging between 50 and 100 mm. This diverse, shrub-dominated zone has the highest species richness and total plant cover values (20%–30%) in transects spanning the entire gradient at this latitude (Villagrán et al., 1981, 1983). Most extensive is

the *Fabiana* tolar, characterized by *Fabiana denudata* and *F. ramulosa* (Solanaceae), which are commonly found in association with *Baccharis boliviensis* (Asteraceae) between 3300 and 3500 masl (Armesto and Villagrán, 1987). At higher elevations (3700–4000 masl), the upper tolar zone (or Transition zone) is dominated by the species *Parastrephia quadrangularis* and *P. lepidophylla* (Asteraceae). Many C_4 annual and perennial grasses are found in the tolar, including *Aristida adscensionis*, *Bouteloua simplex*, *Enneapogon desvauxii*, and *Munroa decumbens*. Other annuals include *Tagetes multiflora* and *Schkuhria multiflora* (both Asteraceae) as well as *Hoffmannseggia doelli* (Caesalpiniaceae). The *Echinopsis* tolar zone is dominated by the columnar cacti *E. atacamensis* and *Oreocercus leucotrichus* and is geographically restricted to areas north of the Salar de Atacama (lat $23^{\circ}S$). Other common shrubs in the tolar are *Junellia seriphioides* (Verbenaceae) and *Chiquiraga atacamensis* (Asteraceae).

The high Andean steppe zone, from 4000 to 4500 masl, receives between 100 and 200 mm MAP. Perennial bunch grasses—*Stipa chrysophylla*, *Festuca chrysophylla*, *Anatherostipa venusta*, and *Deyeuxia cabrerai*—and other grasses (*Nassella nardoides*) dominate the Andean steppe. Many of these grasses are restricted to high elevations, but *Stipa chrysophylla* occurs as low as 3500 masl on south-facing slopes and shady canyons. Cushion plants like *Azorella compacta* (Apiaceae) and *Pycnophyllum bryoides* (Caryophyllaceae) are common along rocky outcrops. Above the steppe, between 4500 and ~ 4800 masl, small perennials and flat cushion plants form a sparsely vegetated alpine zone.

METHODS

Fossil rodent middens are amalgamations of rodent feces and plant, insect, and vertebrate remains encased in hardened urine (amberat) and commonly preserved in rock shelters, caves, and crevices. Middens were extracted by using a hammer and chisel, cleaned in the field for weathering rinds and surface contaminants, and split along clear stratigraphic units when recognizable. Possible contamination can occur along cracks in the indurated deposits or by inadvertent mixing of different stratigraphic units. AMS (accelerator mass spectrometry) ^{14}C dating of suspect plant remains, though costly, is the only means of detecting temporal mixing. Middens in both North and South America are discontinuous in nature and represent “snapshots” of flora through time (Betancourt et al., 1990, 2000).

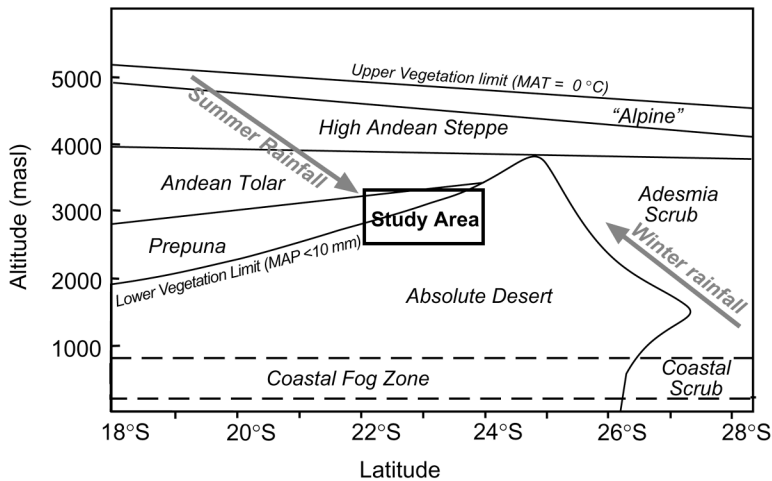


Figure 4. Simplified diagram of the major vegetation zones found in northern Chile (modified from Villagrán et al., 1983). The study area (rectangle) is located near the maximum inland penetration of the absolute desert. Numerous disjunct Lomas communities inhabit the coastal fog zone (see Rundel et al., 1991).

Midden fecal-pellet sizes and shapes are the means for distinguishing the midden-forming agents. Four rodent families produce fossil middens in the Atacama Desert: vizcachas (*Lagidium viscacia*, Chinchillidae), leaf-eared mice (*Phyllotis* spp., Sigmodontinae), chinchilla rats (*Abrocoma cinerea*, Abrocomidae), and brushy-tailed rats (*Octodontomys gliroides*, Octodontidae). *Phyllotis* (average mass of an individual mouse is 50 g—all rodent masses from Redford and Eisenberg, 1989) middens are easy to identify by pellet size and morphology. *Abrocoma* and *Octodontomys* are similar in mass (150–300 g), and their middens are segregated on the basis of pellet shape. The larger (1–2 kg) and gregarious *Lagidium* (Pearson, 1948) produces middens of considerable size. *Octodontomys* is uncommon in the central Atacama and is not considered here.

Foraging areas for these rodents are usually <100 m (Pearson, 1948; Pearson and Ralph, 1978), though individual vizcachas may stray farther from the colony in search of food. Peruvian species of *Lagidium* and *Phyllotis* (also found in northern Chile) have been reported as dietary generalists (Pearson, 1948; Pizzimenti and De Salle, 1980), which ensures that midden floras are fairly representative of local vegetation.

For this study, 49 rodent middens were collected in the field; their locations spanned ~800 m in elevation between 2400 and 3200 masl, along the upper margin between the absolute desert and Prepuna. Middens were soaked in 10 L buckets of water for two to three weeks to dissolve urine (amberat), wet-

sieved with a no. 20 (0.825 mm) mesh, and placed in a drying oven at 50–60 °C for three days. Dried middens were weighed, quantified for grass abundance, and sorted for plant macrofossils as described in Betancourt et al. (1990).

Between 3 and 10 g of feces from 47 middens were submitted for bulk dates at Geochronology Laboratories, Inc., Boston, Massachusetts. Accelerator mass spectrometry (AMS) was used in cases where insufficient material was available for bulk dates or when temporal mixing of macrofloras was a concern. AMS targets were pretreated on a vacuum line at the University of Arizona Desert Laboratory in Tucson, and then measured by a tandem accelerator mass spectrometer at the University of Arizona–National Science Foundation Accelerator Facility. Radiocarbon ages were calibrated (by applying a 24-yr Southern Hemisphere correction) with method A (ranges with intercepts) from Calib 4.3 (Stuiver and Reimer, 1993), using the Intcal98 calibration curve. Calib 4.3 was also used in generating a summed probability distribution of midden ages. Thousands of calendar years before 1950 (ka) is used here to facilitate comparisons across records. Fecal-pellet $\delta^{13}\text{C}$ values obtained along with bulk ^{14}C dates indicate the proportions of $\text{C}_3/\text{CAM}/\text{C}_4$ plants in the rodent's diet based on the isotopic difference between C_3 and C_4 plant end members.

Grass abundance was measured as point occurrence on a 120-cell rectangular grid overlaid on a sorting tray. A sediment matrix splitter was used to randomly segregate 100 mL of plant debris from each washed and dried

midden. Midden debris was then spread uniformly across a 120-cell rectangular grid (each cell is ~6.45 cm² or 1 inch × 1 inch). The percentage abundance of grass taxa was calculated from the number of cells in which grass blades, florets, or seeds were identified (i.e., “hits” on the grid) divided by 120, and then multiplied by 100%.

Dried middens were sieved into size classes and hand sorted for three hours under a binocular microscope (8–35×) for plant macrofossils, including leaves, seeds, wood, grass blades, and florets. Insects, vertebrate bones, and teeth were also sorted. Plant macrofossils were identified to the highest taxonomic level possible either by direct comparison with our extensive reference collection of modern flora or by reference to specialists. Each taxon was quantified by using a relative abundance index (RAI) where 0 = absent, 1 = rare, 2 = common, and 3 = dominant. The RAI is a quick method for estimating past variations in vegetation composition (Spaulding et al., 1990). Alternate methods, such as absolute counts or pooled weights of individual species, are time consuming and ultimately biased by midden size and dietary preferences. These difficulties are compounded in the Atacama, where several families of rodents produce middens. We used Tilia 2.0 and Tiliagraph (Grimm, 1991–1993) to plot macrofossil abundance and a constrained incremental sum of squares (CONISS) cluster analysis (Grimm, 1987) to group these assemblages into midden local floras.

Additional fecal pellets were sorted from 41 middens for cuticle analyses (5–6 pellets for *Lagidium* and 10–20 for *Phyllotis*). These were ground with a mortar and pestle, treated with 5% sodium hypochlorite (NaOCl), and wet-sieved by using mounted 200 and 100 μm meshes. A small fraction from the 100 μm mesh was then mounted on a slide with silicone oil and viewed at 200× under an optical microscope. Samples were compared with our reference collection of >100 taxa. Cuticle identifications are based mostly on shape and size of stomata guard cells, seed testae patterns, and the presence and shape of glandular hairs and trichomes (Metcalf and Chalk, 1950; Dilcher, 1974). Several genera (i.e., *Cryptantha*, *Cistanthe*, and *Atriplex*) and families (Brassicaceae, Poaceae) could not be resolved to species. Quantification was performed by using line transects of two slides from each midden with a total of 50 fields of view counted. The total number of counts for each taxon is expressed as a percentage of the total fields counted.

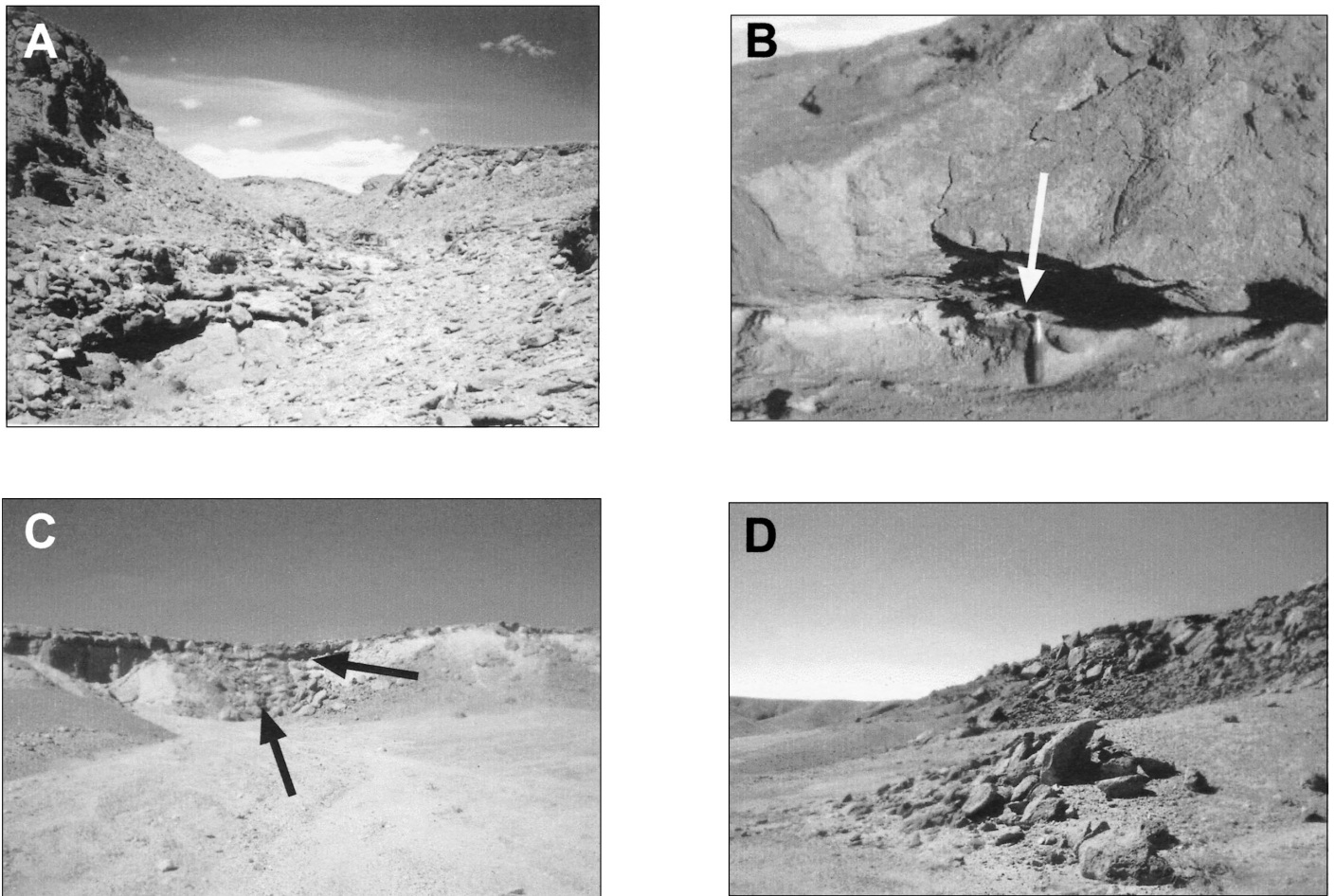


Figure 5. Photographs of midden localities sampled on the edge of the absolute desert. (A) View looking upstream (southeast) of Quebrada Aiquina A, a dry, hanging-canyon tributary of the perennial Río Salado. Middens come from small cavities and rock shelters along the late Miocene ignimbrite cliffs. (B) A large, exposed 35 ka midden (VdT 419A and VdT 419B, white arrow) found underneath an ignimbrite boulder at Vegas de Tilocalar. VdT 419C was found farther back and to the right of 419A and 419B (note rock hammer for scale). Located at 2400 masl and within a few hundred meters of the edge of the Salar de Atacama, Vegas de Tilocalar sites are mostly east-facing slopes on a low ridge defined by eroded Pliocene ignimbrite boulders. (C) A view of the Lomas de Tilocalar locality at 2800 masl, showing lack of plants in the foreground or on top of the west-facing Pliocene ignimbrite scarp. Arrows indicate where middens were found. (D) Lomas de Quilvar, 3100 masl, looking northeast. As with Lomas de Tilocalar, plants are almost absent and are represented by a few dried annuals of *Cryptantha* and *Cristaria*.

RESULTS

Interpretations of midden assemblages are based on modern vegetation transects (Villa-grán et al., 1981, 1983). We obtained two middens from one locality along the eastern edge of the Calama basin (site 1, Figs. 1, 5) and 47 middens from three localities south of Salar de Atacama (sites 2–4, Figs. 2, 5). The age probability distribution obtained from the total sum of 45 calibrated ^{14}C midden dates shows that the largest cluster was formed between 14.0 and 8.6 ka (Fig. 6). Three other clusters were formed in the intervals 8.2–6.5, 6.0–4.4, and 3.0–0.5 ka. Discernible gaps in the distribution are apparent in the intervals 20–16.8,

8.6–8.2, 6.5–6.0, 4.4–3.8, and 0.5–0 ka (i.e., to the present). Limitations of Calib do not allow for calibration of middens older than 22 ka. Of the four middens that were dated as older than 35 ka, the results for two should be treated as minimum ages (LdQ 396: >45 000 ^{14}C yr B.P. and VdT 419B: >36 000 ^{14}C yr B.P.; see Table 1). None was dated between 35 and 22 ka, and only one was dated to the Last Glacial Maximum (LGM) (LdT 465, 22 ka).

Fecal Pellet $\delta^{13}\text{C}$ and Grass Abundance

Fecal-pellet $\delta^{13}\text{C}$ values from 47 middens (Fig. 7A) show a large spread in values rang-

ing from -24.0‰ (VdT 416, 10.46 ka; LdT 472A, 11.54 ka) to -16.4‰ (LdT 462B, 0.66 ka). Samples older than 14 ka average -20.5‰ , excluding the oldest midden LdQ 396 (>44.5 ka), which has a $\delta^{13}\text{C}$ value of -23.2‰ . The most striking feature of the $\delta^{13}\text{C}$ record is the midden cluster between 13.8 and 10.2 ka, with values that average -22.3‰ . In samples dated from 9.7 to 6.9 ka, $\delta^{13}\text{C}$ values increase to an average of -20.0‰ . For samples dated between 5.9 and 3.5 ka, fecal-pellet $\delta^{13}\text{C}$ values average -20.5‰ . A prominent decrease in $\delta^{13}\text{C}$ occurred at 4.4 ka (LdT 434C2), reflected by a $\delta^{13}\text{C}$ value of -23.2‰ . The greatest increase in ^{13}C sequestration occurred between 2.7 and 0.7 ka, and $\delta^{13}\text{C}$ val-

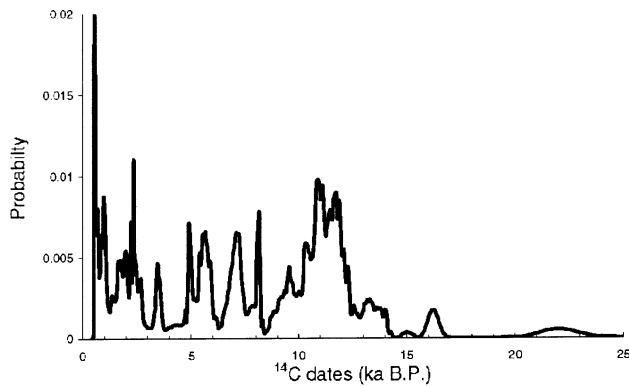


Figure 6. Sum probability distribution of 45 calibrated ^{14}C dates on central Atacama Desert middens. Deviations from exponential decay are either due to midden sampling biases or changes in ecosystem productivity. Note large cluster of dates at 14–8.5 ka. The sum probability distribution was calculated with CALIB 4.3 (Intcal98) (Stuiver and Reimer, 1993).

ues for that period range between -19.6% and -16.4% .

Grass abundance percentages (Fig. 7B) show a similar pattern with low percentages before 16.2 ka. However, the midden LdQ 396 (>44.5 ka) has high grass abundance (88%) and is one exception to this pattern. Three 45–22 ka middens have $<10\%$ grass. Grass abundance rises to 66% in a midden dated at 16.2 ka. A cluster of 14 middens between 11.8 and 10.5 ka has grass abundances that average $>50\%$. Sharp reductions in grass abundance occurred between 11.9 and 10.2 ka at Quebrada (“canyon”) Aiquina, after 10.5 ka at Vegas de Tilocalar, after 11.7 ka at Lomas de Quilvar, and between 10.7 and 9.5 ka at Lomas de Tilocalar (Table 1). Grass abundances remained at $<5\%$ until 7 ka when they rose to $\sim 10\%$, although these abundances entailed modest increases in summer grasses (discussed subsequently). Grass abundance dropped after 4 ka and remained $\sim 0\%$ until 0.9 ka, with values $>5\%$ at 2 ka and 0.7 ka.

Plant Macrofossils and Cuticle Assemblages

Forty-seven middens were analyzed for plant macrofossils. In total, 49 taxa were identified, the majority to the species level (Table 2). The number of taxa identified per midden ranges from a minimum of 7 (VdT 419B, >36 ka) to a maximum of 29 (LdT 436, 11.7 ka) (Fig. 8, Table 1). A CONISS cluster analysis on midden macrofloras from sites 2–4 generated six distinct vegetation zones based on species-richness similarities sorted by physiognomic (vegetation units defined by their general aspect, i.e., shrubland, grassland, etc.) affinity and life form (Ti or Tilocalar zones,

Fig. 8). A similar pattern was obtained from a CONISS analysis of the species’ RAI obtained from these same localities (Fig. 9). These patterns of similarity were divided into midden local-flora (MLF) zones, which are summarized in Table 3.

Fecal pellets from 41 middens (from sites 2–4) were processed for cuticles to characterize rodent diets (Fig. 10). The proportion of *Phyllotis* to *Lagidium* middens remained the same throughout the entire record (Table 1). Dietary changes likely reflect habitat changes rather than selective preference by particular rodents. Results from the cuticle analysis are summarized in Table 4. Twenty-eight taxa were identified, the majority to genus, although in some cases, highly digested cuticles permitted identification only to family (e.g., Poaceae). This analysis added paleoenvironmental information that was otherwise unavailable (e.g., taxa evident in rodent diets were not found as plant macrofossils in the same middens, such as *Fabiana* and *Baccharis* cf. *boliviensis*).

DISCUSSION

Sum probability distributions of ^{14}C dates, along with fecal-pellet $\delta^{13}\text{C}$ data, grass abundance, plant species richness, and composition of midden macrofloras and rodent diet constitute several independent climate proxies obtained from a single midden record. Agreement between these paleoenvironmental proxies implies common causes.

The largest cluster of ^{14}C dates occurs between 14 and 8.6 ka (Fig. 6). Because the probability of midden occurrence decreases exponentially with age, this clustering is either due to sampling biases (“the lure of the Pleis-

tocene”) or temporal variability in rodent population size and midden formation because such data track ecosystem productivity (Webb and Betancourt, 1990). We collected middens in the Atacama more or less randomly without bias for age or appearance, so we attribute the late glacial–early Holocene cluster to heightened productivity.

Most of the late glacial–early Holocene middens (16.2–10.5 ka) contained large quantities of annual and perennial grasses (Fig. 7B). Because grasses do not occur today at any of our midden sites and are usually found at higher elevations (in the tolar or Andean steppe zones) or in valleys with perennial rivers and wetlands, we interpret grass abundance as a proxy for precipitation and productivity (Betancourt et al., 2000). The average fecal-pellet $\delta^{13}\text{C}$, -22.0% , from late glacial–early Holocene middens reflects an almost pure C_3 diet, though some enriched values in this period may reflect feeding on heavy annual blooms of C_4 grasses.

Midden macrofloras and cuticles reveal several prominent patterns (Figs. 8–10). Prepuna and summer annuals are scarce (2–3 taxa) in the few middens older than 22 ka, in contrast with dominance of these taxa (6–8 taxa) during the late glacial and Holocene (Fig. 8). Few middens, few annuals particularly sensitive to low temperatures (Arroyo et al., 1988), and the dominance of Prepuna shrubs such as *Ephedra* suggest cold and hyperarid conditions.

Starting at 16.2 ka and most notably between 13.8 and 10.5 ka, a mixed plant community of steppe grasses, many summer annuals, and tolar taxa expanded across the margin of what is now absolute desert in the southern Salar de Atacama basin (Figs. 8, 9). Species richness and macrofossil assemblages indicate that this unique period of plant invasions peaked between 11.8 and 10.5 ka and ended abruptly after 10.5 ka. The presence of steppe grasses, particularly *Anatherostipa venusta* and *Nassella nardoides* (found today at >3900 masl), implies a displacement of at least 800 m. On the basis of precipitation data from the region (Fig. 3A), this spreading of the vegetation must have entailed more than a threefold increase in MAP from 30–50 mm to ~ 150 mm.

Other steppe grasses in the late glacial–early Holocene middens include *Stipa chrysophylla* and *Nassella arcuata*, a common species in the Altiplano of northernmost Chile and Bolivia but now rare in the central Atacama (Matthei, 1965; Marticorena et al., 1998). The numerous C_4 grasses—including *Munroa decumbens*, *Aristida adscensionis*, *Bouteloua simplex*, *Enneapogon desvauxii*, and

TABLE 1. GECHRONOLOGIC AND BIOLOGICAL DATA FOR THE 49 MIDDENS USED IN THIS STUDY

Midden field number	Radiocarbon lab number*	Radiocarbon age (¹⁴ C yr B.P.)	δ ¹³ C _{PDB} [†] (‰)	Calendar age (yr B.P.) [§]	Intercept or midpoint ^{**} (masl)	Elevation (masl)	Number of taxa	Grass (%)	Midden agent	Slope aspect
Quebrada Alquina A (S 22°17.5'; W 68°21.1')										
1	QA-A 349	9140 ± 130	-22.4	10470 (10240) 10190	10240	2986	N.D.	1	Phyllotis	N
2	QA-A 352	10110 ± 380	-20.9	12610 (11640, 11610, 11580) 11170	11890	2986	N.D.	35	Phyllotis	N
Vegas de Tilocalar (S 23°47'; W 68°09')										
3	VdT 417	6050 ± 260	-18.9	7250 (6860, 6820, 6810) 6550	6900	2360	10	3	Lagidium	SE
4	VdT 416	9250 ± 250	-24.0	10730 (10400, 10315, 10310, 10300, 10290) 10180	10460	2360	12	20	Phyllotis	E
5	VdT 419C	13500 ± 90	-17.0	16440 (16190) 15950	16190	2400	17	66	Phyllotis	NE
6	VdT 419A	13330 ± 960	-19.0	17122 (15990) 14307	15990	2400	17	66	Phyllotis	NE
7	VdT 419B	35100 ± 700	-20.0	Uncalibrated	Uncalibrated	2400	13	2	Lagidium	NE
8	VdT 418	>36060	-20.8	Uncalibrated	Uncalibrated	2400	7	1	Lagidium	NE
9	VdT 418	40900 ± 1400	-20.5	Uncalibrated	Uncalibrated	2400	9	0	Lagidium	NE
Lomas de Quilvar (S 23°50.6'; W 68°02.4')										
9	LdQ 395B1	GX-25059	2560 ± 320	2950 (2720) 2160	2720	3050	13	1	Phyllotis	NW
10	LdQ 399	AA-32650	4340 ± 65	4960 (4860) 4830	4860	3050	9	0	Lagidium	W
11	LdQ 400	GX-24831	10120 ± 150	12095 (11690, 11680, 11640, 11605, 11600) 11260	11680	3087	25	100	Lagidium	W
12	LdQ 397A	GX-24877	11270 ± 220	13450 (13160) 13000	13160	3110	27	100	Phyllotis	W
13	LdQ 398A	GX-25250	11860 ± 180	14080 (13830) 13510	13830	3050	21	14	Abracoma, Phyllotis	W
14	LdQ 396	GX-25249	>44560	Uncalibrated	Uncalibrated	3100	10	88	Lagidium	W
Lomas de Tilocalar (S 23°53'; to S 23°58'; W 68°08'; to W 68°10')										
15	LdT 470	AA-36773	530 ± 35	542 (527) 513	527	2954	14	0	Phyllotis	W
16	LdT 462B	GX-25258	725 ± 70	680 (660) 560	660	2875	11	7	Phyllotis	W
17	LdT 464B	GX-24023	990 ± 75	950 (920) 790	920	2820	10	0	Lagidium	E
18	LdT 425B	GX-25037	1095 ± 70	1060 (970) 930	970	2650	9	0	Lagidium	SE
19	LdT 432	GX-25038	1485 ± 175	1810 (1350, 1340, 1330) 1190	1360	2840	12	1	Phyllotis	E
20	LdT 464A	GX-25259	1805 ± 75	1820 (1710) 1570	1710	2350	9	0	Lagidium	E
21	LdT 439	GX-25040	2035 ± 75	2040 (1985, 1980, 1970, 1960, 1950) 1880	1960	2650	16	8	Lagidium	E
22	LdT 444	GX-25253	2330 ± 55	2350 (2340) 2210	2340	2600	11	0	Phyllotis	E
23	LdT 437A	GX-24932	2400 ± 125	2710 (2350) 2210	2350	2600	10	1	Lagidium	E
24	LdT 437B	GX-24974	3250 ± 95	3570 (3460) 3360	3460	2825	14	0	Lagidium	W
25	LdT 434C2	GX-24976	3940 ± 400	4860 (4410) 3730	4410	2840	19	11	Phyllotis	W
26	LdT 463	GX-25043	4670 ± 190	5590 (5440, 5420, 5320) 5050	5320	2950	9	0	Phyllotis	W
27	LdT 462A	GX-25257	4820 ± 150	5660 (5590, 5500, 5490) 5323	5490	2875	15	12	Phyllotis	W
28	LdT 422	GX-25062	4920 ± 160	5860 (5610) 5470	5610	2650	12	0	Lagidium	SE
29	LdT 453	GX-25042	5140 ± 160	6170 (5910) 5660	5910	2675	14	11	Lagidium	E
30	LdT 446A	GX-25255	6170 ± 280	7410 (7140, 7130, 7010) 6670	7020	2640	13	10	Phyllotis	N
31	LdT 461A	GX-24977	6240 ± 120	7430 (7180, 7170, 7160, 7110, 7100) 6680	7050	2780	15	7	Phyllotis	E
32	LdT 478	GX-25260	6260 ± 120	7270 (7200, 7190, 7180, 7170, 7160, 7110, 7100) 6950	7110	2910	11	0	Phyllotis	W
33	LdT 446B	GX-24933	7060 ± 250	8150 (7920, 7900, 7840) 7610	7880	2640	13	0	Phyllotis	N
34	LdT 468	AA-39721	7341 ± 54	8177 (8157, 8136, 8131, 8119, 8112, 8078, 8061) 7979	8060	2785	17	N.D.	Phyllotis	W
35	LdT 442	GX-24975	8140 ± 210	9400 (9030) 8650	9030	2950	13	3	Lagidium, Phyllotis	W
36	LdT 464C	GX-24024	8460 ± 340	9890 (9470) 9010	9470	2820	13	1	Lagidium	E
37	LdT 471	GX-24936	8590 ± 150	9690 (9530) 9440	9530	2954	13	5	Lagidium	E
38	LdT 449A	GX-24934	9470 ± 530	11340 (10690, 10650, 10640) 9980	10660	2610	19	34	Phyllotis	E
39	LdT 438B	GX-25039	9570 ± 320	11230 (11055, 11050, 11040, 11020, 11000, 10960, 10760) 10300	10760	2825	19	66	Phyllotis	W
40	LdT 433	GX-24931	9600 ± 450	11550 (11060, 10940, 10850, 10830, 10790) 10240	10890	2840	26	53	Phyllotis	E
41	LdT 438A	GX-25063	9610 ± 170	11180 (11070, 10940, 10860, 10820, 10810, 10800, 10790) 10600	10870	2825	19	49	Lagidium	W
42	LdT 434A	AA-39272	9610 ± 59	11116 (11067, 10940, 10857, 10825, 10807, 10798, 10792) 10690	10900	2825	11	N.D.	Phyllotis	W
43	LdT 472C	GX-24879	9710 ± 140	11200 (11160) 10760	11160	3030	22	50	Lagidium	W
44	LdT 472A	GX-24876	10000 ± 150	11880 (11340, 11320, 11300, 11260) 11200	11540	3030	14	30	Lagidium	W
45	LdT 436	GX-25026-PR1	10150 ± 150	12270 (11690) 11260	11690	2825	29	98	Lagidium	W
46	LdT 441	GX-25041	10160 ± 150	12280 (11730, 11720, 11700) 11300	11790	2950	18	61	Lagidium	W
47	LdT 460	AA-29273	10183 ± 70	12099 (11900, 11856, 11839, 11823, 11750, 11707, 11703) 11579	11840	2850	17	N.D.	Phyllotis	NE
48	LdT 447	GX-25256	10730 ± 440	13150 (12840) 11960	12840	2610	16	11	Phyllotis	N
49	LdT 465	GX-24978	18550 ± 680	22860 (22000) 21150	22000	2825	9	11	Phyllotis	W

Note: N.D.—not determined.

*GX—Geochron Labs; AA—Arizona—NSF Accelerator Facility. Geochron dates were performed on bulk (3–10 g) fecal pellet samples; Arizona dates were performed on plant macrofossils or fecal pellets. All standard deviations are at 1 σ .

[†]PDB—Pee Dee belemnite isotope standard.

[§]Calibrated ages are in calendar years before 1950 at 1 σ , and where obtained using Method A of the Calib 4.1.3 (Intcal98 data set) software. A Southern Hemisphere deduction of 24 yr was applied to all calibrated dates.

^{**}In case of more than one intercept, a range midpoint (at 1 σ) was calculated.

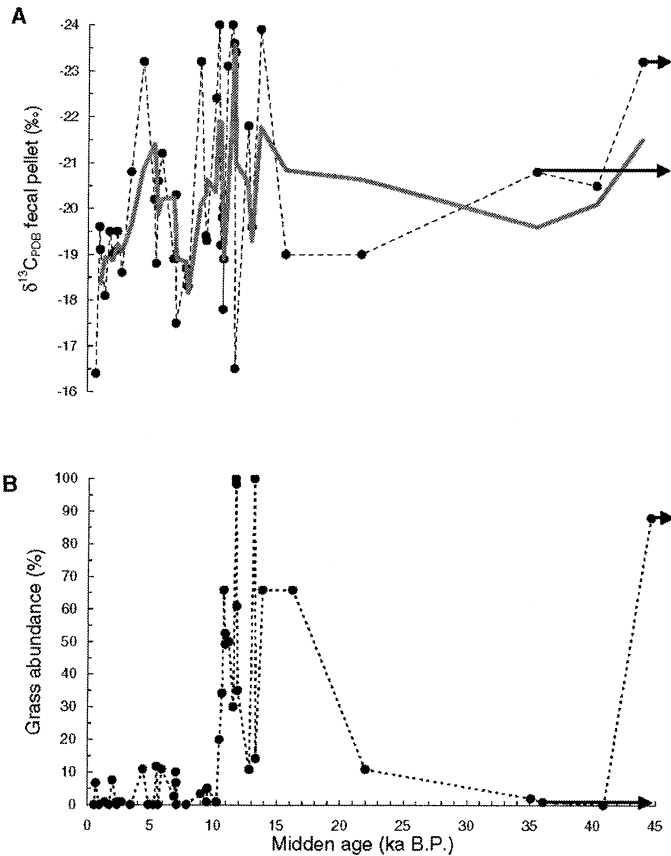


Figure 7. (A) $\delta^{13}\text{C}_{\text{PDB}}$ values obtained from bulk- ^{14}C -dated fecal pellets of 45 middens (PDB—Peedee belemnite isotope standard). The bold gray line is a smoothing curve generated from a three-point running average. Note reversed scale on ordinate. In general, rodents consumed more C_3 plants (shrubs and steppe grasses) between 13.8 and 9 ka. More positive $\delta^{13}\text{C}_{\text{PDB}}$ values during the Holocene indicate consumption of *Atriplex* and cacti, as well as C_4 grasses. (B) Total grass abundance (%) calculated from point occurrences of grasses obtained from 47 middens. Total grass abundance represents a generalized productivity index for both annual and perennial grasses. Grasses are not found near midden sites at the present. (Note: Arrows on samples denote minimum ages).

Pappophorum caespitosum—indicate that the precipitation increase occurred in summer. *P. caespitosum* has never been collected in Chile despite 30 yr of intensive collecting efforts (O. Matthei, 2000, personal commun.), but is common in southern Peru and northwestern Argentina (Nicora and Rúgolo de Agrasar, 1987; Tovar, 1993). Tolar shrubs and cacti such as *Junellia seriphioides* and *Echinopsis atacamensis* are well represented in the macrofloras, as well as *Fabiana* in most cuticle samples (Fig. 10). Taken together, these data indicate that 11.8–10.5 ka was the wettest period in the central Atacama Desert for possibly the past 45 000 yr.

The onset of hyperaridity is recorded by the abrupt extirpation of vegetation. Hyperaridity is evidenced by more positive $\delta^{13}\text{C}$ values (i.e., ^{13}C enrichment) and low grass percent-

ages between 11.8 and 10.2 ka at the northern midden site and between 10.5 and 9.5 ka at the southern sites (2–4). The discontinuity typical of midden series prevents better resolution of this desiccation event, but must have been complete by 9.5 ka, when grass abundance dropped to $\leq 3\%$ at all sites. Starting at 9.5 ka, the midden record has diminished species richness and lacks steppe and tolar elements. Prepuna elements, such as *Atriplex imbricata* and *Opuntia camachoi*, are dominant until 7.1 ka. *Cistanthe* and *Exodeconus integrifolius*, both Prepuna annuals, are also common. Cuticle samples indicate prevalence of *Atriplex*, *Hoffmannseggia*, and *Cistanthe* in rodent diets, although the latter increases in importance throughout the Holocene, whereas *Hoffmannseggia* percentages decrease dramatically during the early Holocene.

Moisture increased slightly during the middle Holocene (7.1–3.5 ka), with a modest increase in grass abundance and a decrease in fecal-pellet $\delta^{13}\text{C}$ values. A prominent increase in C_3 plant content occurred at 4.4 ka as indicated by a $\delta^{13}\text{C}$ of -23.2% . This change coincides with a large increase of *Fabiana* (a C_3 shrub) cuticles in fecal pellets. Grass percentages hovered at $\geq 10\%$ during much of this period and decreased after 4.4 ka. Tolar shrubs *Junellia* and *Krameria* and the cactus *Echinopsis* reappear briefly during the middle Holocene, starting at 7.1 ka. This change was accompanied by the presence of wetlands near the Salar de Atacama, as indicated by seeds of *Scirpus* cf. *californicus* at Vegas de Tilocalar (VdT 417, 6.9 ka). A few C_4 grasses and summer annuals (*Munroa decumbens*, *Aristida adscensionis*, and *Euphorbia amandi*) in middens between 7.1 and 3.5 ka point to increases in summer rainfall. Although cuticle samples are dominated by high percentages of *Atriplex* and *Cistanthe*, they also indicate the presence of Poaceae and *Fabiana*. The latter could not have survived, let alone become established, at such low elevations without some rainfall every year, arguing against a disproportionate influence of the occasional storm and so-called annual bloom once every few decades.

In contrast, late Holocene grass percentages are $< 2\%$ throughout except for two middens at 2 and 0.7 ka with values slightly above 5%. These samples could represent very brief surges in summer rainfall, causing local annual blooms. The late Holocene $\delta^{13}\text{C}$ record is remarkably uniform and characterized by higher isotopic values, indicating strong C_4 and CAM plant influences in rodent diets. The highest percentages of *Atriplex* and *Cistanthe* in cuticle samples occur during the late Holocene, however, especially after 3.5 ka (Fig. 10). Midden macrofloras indicate low species richness and abundance of Prepuna shrubs and annuals (Figs. 8, 9). Only the youngest midden at 0.5 ka shows evidence for a slightly more humid climate, as evinced by the presence of single seeds of *Junellia seriphioides*, *Krameria lappacea*, and the annuals *Munroa decumbens* and *Euphorbia amandi*. These taxa represent a more diverse assemblage than indicated by a one-day survey of the modern landscape. This discrepancy might be explained by accumulation over several decades in a single midden, generating higher diversity than is found at the site today.

REGIONAL PALEOCLIMATOLOGY

To facilitate comparisons with other records, we have established a relative paleo-

TABLE 2. LIST OF PLANT SPECIES IDENTIFIED FROM RODENT MIDDEN MACROFOSSILS

Taxa	Family	Life form	Phytogeography	Plant part identified
<u>Gymnospermae</u>				
<i>Ephedra breana</i> Phil.	Ephedraceae	Shrub	Prepuna and Tolar	Seeds, bark
<u>Angiospermae-Dicotyledoneae</u>				
<i>Ambrosia artemisioides</i> Meyen and Walp.	Asteraceae	Shrub	Prepuna	Fruits
<i>Helogyne macrogyne</i> (Phil.) B.L.Rob.	Asteraceae	Shrub	Tolar	Achenes
<i>Schkuhria multiflora</i> Hook. and Arn.	Asteraceae	Summer annual	Tolar	Achenes
<i>Tagetes multiflora</i> Kunth	Asteraceae	Summer annual	Tolar	Achenes
<i>Cryptantha diffusa</i> (Phil.) I.M. Johnst.	Boraginaceae	Annual	Prepuna	Nutlets
<i>Cryptantha hispida</i> (Phil.) Reiche	Boraginaceae	Annual	Prepuna	Nutlets
<i>Cryptantha limensis</i> (A.DC.) Reiche	Boraginaceae	Annual	Prepuna	Nutlets
<i>Cryptantha phaceloides</i> (Clos) Reiche	Boraginaceae	Annual	Prepuna	Nutlets
<i>Cryptantha</i> spp.	Boraginaceae	Annuals	Prepuna	Leaves, fruits
<i>Pectocarya linearis</i> (Ruiz and Pavón) DC.	Boraginaceae	Perennial herb		Nutlets, leaves
<i>Tiquilia atacamensis</i> (Phil.) A.T. Richardson	Boraginaceae	Subshrub	Prepuna	Nutlets, leaves
<i>Sysimbrium</i> spp.	Brassicaceae	Subshrub to annual	Prepuna and Tolar	Siliques, pedicels, leaves
<i>Opuntia camachoii</i> Espinosa	Cactaceae	Perennial herb	Prepuna and Tolar	Seeds
<i>Opuntia</i> cf. <i>ignescens</i> Vaupel	Cactaceae	Perennial herb	Tolar	Seeds
<i>Opuntia</i> cf. <i>sphaerica</i> C.F. Först.	Cactaceae	Perennial herb	Prepuna	Seeds
<i>Echinopsis</i> cf. <i>atacamensis</i> (Phil.) Friedrich and G.D. Rowley	Cactaceae	Tree	Tolar	Seeds
<i>Hoffmannseggia</i> sp.	Caesalpinaceae	Perennial herb	Prepuna and Tolar	Seeds, leaves
<i>Atriplex imbricata</i> (Moq.) D. Dietr.	Chenopodiaceae	Shrub	Prepuna and Tolar	Leaves, fruits
cf. <i>Chenopodium quinoa</i> Willd.	Chenopodiaceae	Annual	Cultivated	Seeds
<i>Euphorbia amandi</i> Oudejans	Euphorbiaceae	Annual	Tolar	Seeds, fruits
<i>Phacelia</i> sp.	Hydrophyllaceae	Perennial herb to annual	Prepuna and Tolar	Seeds
<i>Krameria lappacea</i> (Dombey) Burdet and B.B. Simpson	Krameriaceae	Shrub	Tolar	Leaves, fruits
<i>Huidobria fruticosa</i> Phil.	Loasaceae	Shrub	Prepuna	Seeds, bark
<i>Dinemandra ericoides</i> A. Juss.	Malpighiaceae	Shrub	Prepuna	Fruits
<i>Cristaria</i> sp1	Malvaceae	Annual	Prepuna and Tolar	Seeds
<i>Cristaria</i> sp2	Malvaceae	Annual	Prepuna and Tolar	Seeds
<i>Tarasa</i> cf. <i>operculata</i> (Cav.) Krapov.	Malvaceae	Subshrub	Prepuna	Leaves, seeds
<i>Nolana</i> cf. <i>tarapacana</i> (Phil.) I.M. Johnst.	Nolanaceae	Perennial herb	Prepuna	Mericarps, leaves
<i>Allionia incarnata</i> L.	Nyctaginaceae	Perennial herb		Seeds
<i>Adesmia</i> cf. <i>erinacea</i> Phil.	Papilionaceae	Shrub	Tolar	Spines
<i>Adesmia</i> cf. <i>spinosissima</i> Meyen	Papilionaceae	Shrub	Tolar	Spines
<i>Chorizanthe commisuralis</i> J. Remy	Polygonaceae	Annual	Prepuna and Tolar	Fruits, stems
<i>Cistanthe</i> spp.	Portulacaceae	CAM annuals	Prepuna	Seeds, leaves
<i>Exodeconus integrifolius</i> (Phil.) Axelius	Solanaceae	Annual	Prepuna	Seeds
<i>Lycopersicon chilense</i> Dunal	Solanaceae	Shrub	Prepuna	Seeds, leaves
<i>Acantholippia deserticola</i> (Phil. ex F. Phil.) Moldenke	Verbenaceae	Shrub	Prepuna and Tolar	Seeds, wood
<i>Junellia seriphoides</i> (Gillies and Hook.) Moldenke	Verbenaceae	Shrub	Tolar	Seeds
<u>Angiospermae-Monocotyledoneae</u>				
<i>Scirpus</i> cf. <i>californicus</i> (C.A. Mey.) Steud.	Cyperaceae	Perennial herb	Wetlands	Seeds
<i>Anatherostipa venusta</i> (Phil.) Peñail.*	Poaceae	C ₃ perennial herb	Steppe	Florets
<i>Aristida adscensionis</i> L.	Poaceae	C ₄ summer annual	Tolar	Florets
<i>Bouteloua simplex</i> Lag.	Poaceae	C ₄ summer annual	Tolar	Florets
<i>Enneapogon desvauxii</i> P. Beauv.	Poaceae	C ₄ perennial herb	Tolar	Florets
<i>Munroa decumbens</i> Phil.	Poaceae	C ₄ summer annual	Tolar	Florets
<i>Munroa</i> sp2	Poaceae	C ₄ summer annual	Tolar	Florets
<i>Nassella arcuata</i> (R.E. Fries) Torres*	Poaceae	C ₃ perennial herb	Steppe	Florets
<i>Nassella</i> cf. <i>nardooides</i> (Phil.) Barkworth	Poaceae	C ₃ perennial herb	Steppe	Florets
<i>Pappophorum caespitosum</i> R.E. Fries	Poaceae	C ₄ perennial herb	Tolar	Florets
<i>Stipa chrysophylla</i> E. Desv.*	Poaceae	C ₃ perennial herb	Steppe	Florets, awns

*Identified by O. Matthei, Departamento de Botánica, Universidad de Concepción, Chile.

productivity curve (Fig. 11) by using two independent parameters—plant species richness and grass abundance. This curve is based on the strong correlation between modern plant cover, plant species richness, and precipitation in northern Chile (Meserve and Glanz, 1978). We calculated an anomaly (departure) curve for productivity and precipitation by using statistical normalization methods based on the mean from three middens spanning the past 1000 yr. Positive departures indicate increased precipitation with respect to the past 1000 yr, whereas negative departures indicate increased aridity. We limit our paleoproductivity curve to the past 22 k.y., for which we have adequate coverage.

The Late Glacial Period

Most late Quaternary geologic records of climate change in the Atacama are derived from lake sediments on the Chilean Altiplano (Messerli et al., 1993; Grosjean, 1994; Grosjean and Nuñez, 1994; Grosjean et al., 1995; Valero-Garcés et al., 1996; Geyh et al., 1999). Other records include wetland deposits at Quebrada Puripica (Grosjean et al., 1997a) and a 106 ka halite core obtained from the deepest part of the Salar de Atacama (Bobst et al., 2001). By using ¹⁴C dates on terrestrial macrofossils from Laguna Lejía, organic sediments at Laguna Tuyajto, diatomites at Salar de Punta Negra, and peat beds in the Salar de

Atacama, all sites between 23°S and 25°S (see Fig. 1B), Geyh et al. (1999) identified a wet phase between ca. 15 and 9.2 ka that agrees with our midden record. On the basis of a simple hydrologic model, Kull and Grosjean (1998) concluded that precipitation must have doubled to account for increased lake levels at 4300 masl on the Chilean Altiplano. Our vegetation record suggests more than threefold precipitation increases on the margin of the absolute desert at 2400–3000 masl. A 22 ka pollen record (¹⁴C) from Laguna Miscanti (4140 masl, Grosjean et al., 2001; Fig. 1) indicates dry conditions during the LGM and a strong lake transgression during the late glacial, as evidenced by high levels of aquatic

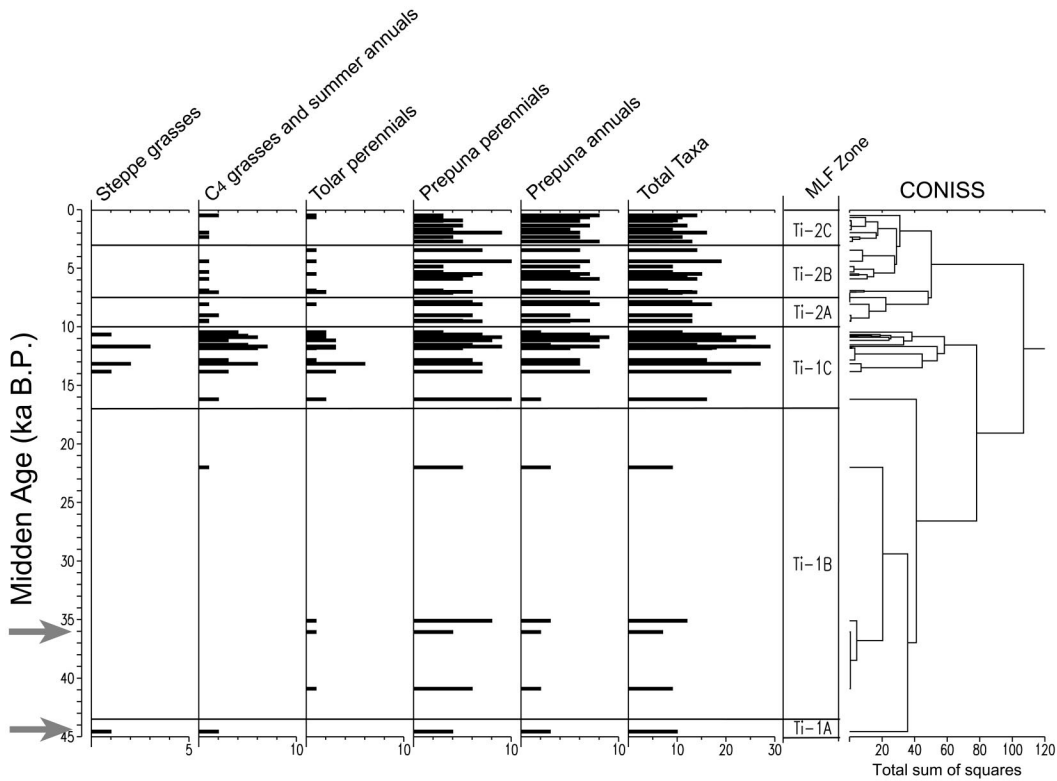


Figure 8. Summary diagram indicating the number of taxa obtained from 47 fossil rodent middens from the Tilocalar and Quilvar localities, ordered by life form and phytogeographic category (see Table 2). Midden local-flora zones were partly defined by using a cluster analysis (CONISS) as well as other floristic similarities. Gray arrows next to age scale indicate middens with minimum ages. Ti—Tilocalar zone.

pollen. A sharp increase in pollen concentrations ca. 11–9 ka (corrected for reservoir effects from 17 to 14 ka) at Laguna Miscanti may correspond to grassland expansion evident in our midden record from lower elevations. A record of past regional fluctuations of groundwater levels reconstructed from paleowetland deposits in the central Atacama also indicates a major increase in discharge between 16 and 9 ka (Betancourt et al., 2000; Rech et al., 2002).

Paleoclimate records from the Altiplano typically have older dates for the wet phases. Ice cores spanning the past 25 000 yr from the summit of Nevado Sajama indicate above-average ice accumulation, temperatures 8–12 °C colder than those of today, and low atmospheric dust concentrations synchronous with Altiplano paleolake highstands during the intervals 25–22, 19–15.5, and 14–9.5 ka (Thompson, 2000). A recent study using U-series dating and validation of ¹⁴C dates on shoreline tufas in the Uyuni-Coipasa basin (Sylvestre et al., 1999) identified two wet phases: one major event between 18.9 and 14.0 ka (Tauca phase) and a minor event between 10.8 and 9.5 ka (Coipasa phase), separated by a dry phase (Ticaña event) between 14.0 and 10.8 ka. These highstands are younger than those inferred from a ¹⁴C-dated sediment core in the center of the Salar de Uyuni,

which indicates wet phases at >42, 33.4–31.8, 30.8–28.2, and 26.1–14.9 ka, followed by a minor lake stand at ca. 12.5 ka (Baker et al., 2001a). Possible conflicts can arise from U-Th dating of lakeshore carbonates in the Altiplano, which incorporate a considerable detrital correction (Sylvestre et al., 1999) or large reservoir effects on ¹⁴C dates. ¹⁴C dates on terrestrial organic matter and macrofossils preserved in wetland deposits found downslope from the Uyuni and Coipasa basins, however, show a rise in the water table in the intervals 15–9 and 8–3 ka that concurs with our record (Rech et al., 2002).

Sedimentologic changes in a U-series-dated core from the Salar de Atacama (Bobst et al., 2001) indicate wet phases at 75.8–60.7, 54–15.2, 11.2–10.3, and 5.3–3.5 ka. Subaqueous halite formed between 26.7 and 16.5 ka is interpreted as the maximum wet phase at Salar de Atacama. Despite good agreement between midden evidence and the late glacial wet phases on the Altiplano (and middle Holocene for the Salar de Atacama core), we found only one midden between 26.7 and 16 ka, which indicates arid conditions at 22 ka (low grass abundance and absence of steppe and tolar taxa). We remain cautious about overinterpreting full glacial aridity from negative evidence or incomplete coverage, but suggest that at the very least it was intermittently dry.

Records from the Andes of Peru and Bolivia indicate older dates for the end of the late glacial humid phase. Glaciers retreated in the Cordillera Blanca of Peru before 12.8 ka (Rodbell and Seltzer, 2000) and were apparently synchronous with glacier retreat and Lake Tauca desiccation at Salar de Uyuni (Clayton and Clapperton, 1997).

The Holocene

Lakes on the Chilean Altiplano disappeared completely after 8.9 ka (Grosjean, 1994; Geyh et al., 1999), >600 yr after our vegetation records indicate abrupt drying (9.5 ka). The inference from these lakes is that conditions drier than today persisted throughout the middle Holocene. The evidence includes gypsum beds at Laguna Miscanti (Valero-Garcés et al., 1996), lower lake levels at Laguna Negro Francisco (Grosjean et al., 1997b), Lago Titicaca (Seltzer et al., 1998; Cross et al., 2000; Baker et al., 2001b), and Lago Taypi Chaka Kkota in the Cordillera Real of Bolivia (Abbott et al., 2000). The onset, duration, and persistence of middle Holocene aridity are poorly documented and vary from site to site. Local hard-water effects confound radiocarbon dating of the Laguna Negro Francisco and Miscanti records (Grosjean et al., 1997b), but low lake levels (85 m below present) inferred from

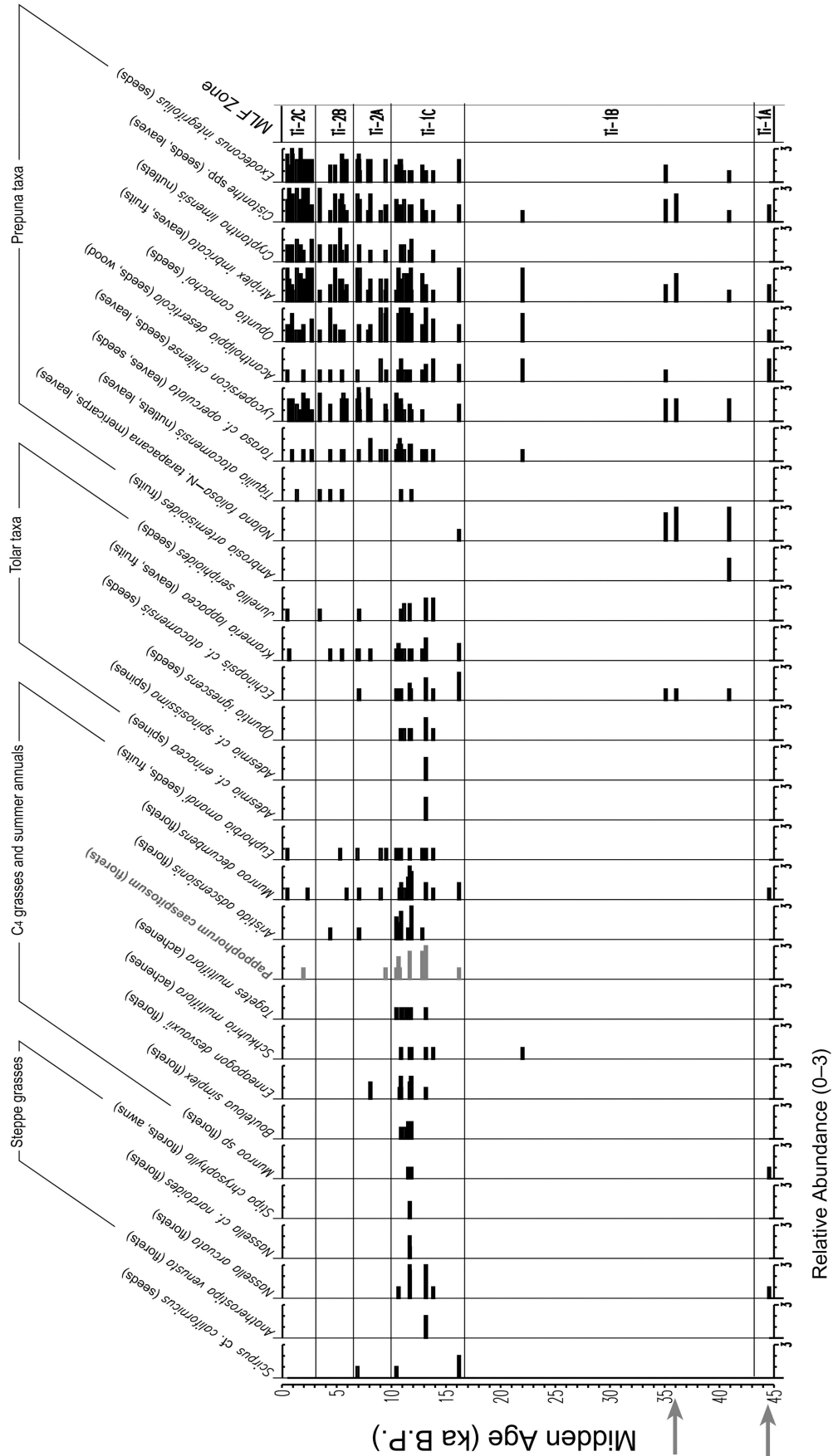


Figure 9. Relative abundance diagram for 19 taxa obtained from 47 fossil rodent middens at the Tilocalar and Quilvar localities. Relative abundance scale: 0 = absent, 1 = rare, 2 = common, 3 = dominant. MLF zones are the same as those in Figure 8. Gray arrows next to age scale indicate middens with minimum ages. *Pappophorum caespitosum* (in gray) has never been collected in Chile and may be locally extinct. Ti—Tilocalar zone.

VEGETATION INVASIONS INTO ABSOLUTE DESERT, NORTHERN CHILE

TABLE 3. MACROFLORAS OF 47 MIDDENS FROM THE CENTRAL ATACAMA DESERT

Midden local flora zone	Age (ka B.P.)	Number of middens analyzed	Description	Inferred Paleoclimate
Ti-2C	0.5–2.7	10	Modern floras. Species richness averages 12 taxa. Prepuna shrubs and annuals are dominant. Last appearance of <i>Pappophorum caespitosum</i> at 2.0 ka. Youngest midden indicates rare occurrence of two summer annuals (<i>Aristida</i> and <i>Euphorbia amandi</i>).	Modern hyperarid climate. Slight increase in precipitation may have occurred at 0.5 ka.
Ti-2B	3.5–7.1	10	Average species richness increases to 14 taxa. Tolar cacti and shrubs (<i>Echinopsis</i> and <i>Junellia</i>), C ₄ annuals and perennials, and <i>Scirpus cf. californicus</i> appear in several middens.	Moderate increase in summer rainfall. Proximity of wetlands at Vegas de Tilocalar.
Ti-2A	7.1–9.5	6	Dramatic drop in species richness and absence of steppe and tolar taxa. Cactaceae (<i>Opuntia camachoii</i>), <i>Atriplex imbricata</i> , and <i>Ephedra</i> are common shrubs. Prepuna annuals abundant as well.	Conditions arid to hyperarid with floras resembling those of present-day middens.
Ti-1C	10.5–16.2	16	Highly distinctive macrofloras and elevated species richness. <i>Scirpus cf. californicus</i> present at Vegas de Tilocalar. First appearance of <i>Pappophorum caespitosum</i> . Average species richness between 13.8 and 10.5 ka is 21 species, the highest in the record. Four species of Andean steppe grasses present in most middens. Several tolar species present as well as abundant C ₄ grasses and summer annuals. Prepuna shrubs and annuals rare to common.	Wettest period in the record. Descent of <i>Anatherostipa venusta</i> and <i>Nassella nardoides</i> (both steppe grasses) imply rainfall 3–5 times greater than today. Precipitation from tropical sources is indicated by C ₄ grasses and southward migration of several species.
Ti-1B	22–40.9	4	Low species richness in all four samples (7–13 species). <i>Atriplex</i> , <i>Cistanthe</i> , and <i>Nolana</i> abundant. <i>Ambrosia artemisioides</i> (absent from the rest of the record) and <i>Echinopsis atacamensis</i> present at Vegas de Tilocalar (~50 km south of their current distribution). Very few annuals.	Middens represent conditions that are drier than those of today, as indicated by abundance of Prepuna vegetation and lack of steppe grasses. Few annuals may indicate possibly colder temperatures.
Ti-1A	>44.5	1	<i>Atriplex imbricata</i> and <i>Sisymbrium</i> sp. are dominant, presence of <i>Nassella arcuata</i> and two species of C ₄ grasses (<i>Munroa</i>)	Wetter than today; summer storms present.

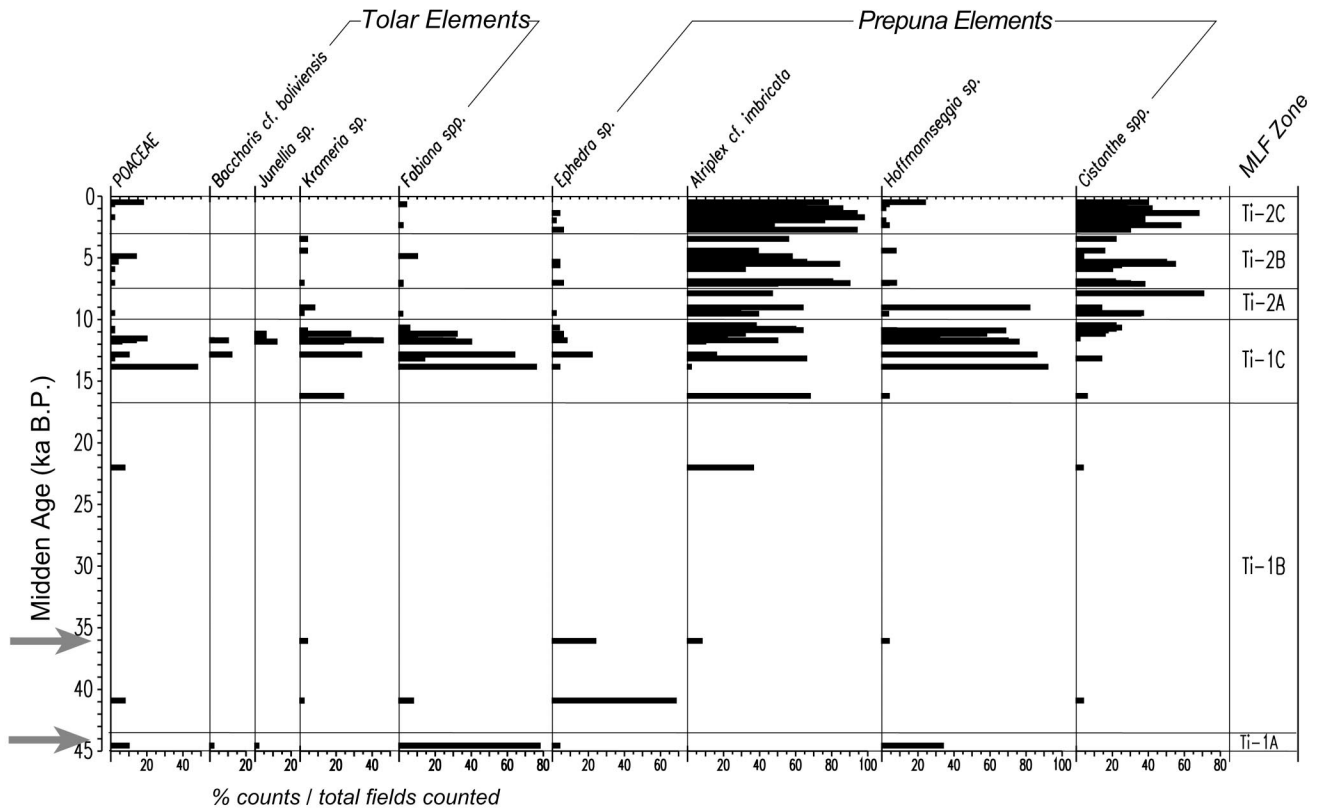


Figure 10. Percentage diagram of plant taxa based on rodent diets from 41 middens from the Tilocalar and Quilvar localities. Note presence of the genus *Fabiana*, a tolar shrub absent from the macrofossil record. MLF zones are identical to those in Figures 8 and 9. Gray arrows next to age scale indicate middens with minimum ages.

TABLE 4. RODENT FECAL PELLET CONTENTS OF 41 MIDDENS FROM THE CENTRAL ATACAMA DESERT

Midden local flora zone	Age (ka B.P.)	Number of middens analyzed	Description	Comments
Ti-2C	0.5–2.7	9	<i>Atriplex</i> (>60%) and <i>Cistanthe</i> (>30%) are present in most samples. <i>Ephedra</i> is present in trace amounts at the beginning of this zone; is absent after 1.5 ka. A slight increase in <i>Fabiana</i> spp. (4%) occurred at 0.7 ka. A large increase in <i>Hoffmannseggia</i> (up to 24%) and Poaceae (18%) occurred at 0.5 ka.	Rodent diets are similar in composition to scant vegetation found today at several midden sites. Climate has been hyperarid since 2.7 ka, although the presence of Poaceae and <i>Fabiana</i> implies very slight increases in local precipitation at 0.5 and 0.7 ka, respectively.
Ti-2B	3.5–7.1	9	High percentages of <i>Atriplex</i> and <i>Cistanthe</i> along with minor increases (>10%) in Poaceae and <i>Fabiana</i> cuticles between 4.9 and 4.4 ka. Very low percentages (<10%) of <i>Krameria</i> and <i>Hoffmannseggia</i> were also present in rodent diets.	Generally the same assemblages are present as in zone Ti-2C, but larger increases in <i>Fabiana</i> and Poaceae at 4.9–4.4 ka could only have been supported by a significant increase in rainfall.
Ti-2A	7.1–9.5	5	<i>Atriplex</i> cuticles remained at high values (>40%); and <i>Cistanthe</i> increased to over 50% at the end of this zone. Percent of <i>Hoffmannseggia</i> sharply diminishes after 8.5 ka.	Diets indicate assemblages similar to modern-day vegetation, which implies a hyperarid climate.
Ti-1C	10.5–16.2	14	Abrupt appearance of unique cuticle assemblages. Up to 50% Poaceae epidermis and a maximum of 80% <i>Fabiana</i> (not recorded in macrofossils). <i>Atriplex</i> and <i>Cistanthe</i> also present, but in lower percentages.	Diets indicate that a diverse and unique plant community was present at the midden sites. High percentage of Tolar shrubs and Poaceae indicate substantial precipitation increases relative to the present.
Ti-1B	22–40.9	3	High percentages of <i>Ephedra</i> and <i>Atriplex</i> . Tolar elements found only in trace values. <i>Cistanthe</i> appeared at 40.9 ka. Poaceae fell to <10%.	Diets dominated by <i>Prepuna</i> plants and <i>Ephedra</i> . Coupled with few trace amounts of grasses, these plants imply a hyperarid habitat.
Ti-1A	>44.5	1	Samples contained 80% <i>Fabiana</i> and small amounts of Tolar shrubs, <i>Junellia</i> , and <i>Baccharis boliviensis</i> . Also 10% Poaceae and 35% <i>Hoffmannseggia</i> were counted.	Diets compatible with the midden macroflora and indicate climate wetter than today's.

a core drilled in the deepest part of Lago Titicaca are well dated between 8.0 and 5.5 ka (Baker et al., 2001b).

In contrast, midden macrofloras show modest increases in precipitation (relative to modern) during the middle Holocene relative to the hyperaridity in the early and late Holocene. Summer annuals, C₄ grasses, *Fabiana* (in rodent diet), and *Echinopsis* in middens between 7.1 and 3.5 ka suggest rainfall increases from tropical, not extratropical, sources. Other evidence for a middle Holocene wet phase comes from wetland records at Tilomonte, Río Salado, and Río Loa, which indicate high regional water tables between 7 and 3 ka (Betancourt et al., 2000; Rech et al., 2002). Río Desaguadero ¹⁴C-dated river terrace deposits, formed by either Lake Titicaca spillover or changes in local precipitation budgets, suggest highstands between 4.5 and 3.9 and between 2.2 and 2.0 ka (Baucom and Riggsby, 1999). A brief increase in moisture between 5.7 and 4.4 ka is also documented at the Laguna Seca pollen site, only 200 km south of Lago Titicaca and northwest of the Salar de Uyuni (Baied and Wheeler, 1993). Lake levels were also higher during the middle Holocene at Lago Aricota (lat 17°S), a moderate-sized lake on the Pacific slope of the Andes in southern Peru (Placzek et al., 2001). An extensive series of rodent middens between 2350 and 2750 m near Arequipa, Peru (lat 16°S), shows that vegetation was relatively stable during the middle Holocene (Holmgren et al. 2001).

Contrasting interpretations for the middle Ho-

locene bear directly on interpretation of the region's archaeological record. Sustained hyperaridity has been invoked to explain the paucity of middle Holocene human occupation in the Atacama basin, the so-called *Silencio Arqueológico* or Archaeological Hiatus (Grosjean and Nuñez, 1994; Nuñez and Grosjean, 1994). Middle Holocene human occupation was apparently limited to springs and wetlands. At Quebrada Puripica, a steep canyon northeast of Salar de Atacama, 30-m-thick stacks of diatomite are interbedded with alluvium and archaeological materials dating between 6.8 and 3.2 ka. The diatomite beds are perched high up above the present streambed and local groundwater table. Grosjean et al. (1997a), who studied the site in 1993, interpreted the diatomite beds as lake deposits dammed behind a side-canyon debris flow, which could not be breached by main-stem low flow conditions during a hyperarid middle Holocene. Quebrada Puripica was reexamined by our group in 2000, who came to a different conclusion. The presence of diatomite for several kilometers above and below the suggested side-canyon dam suggests that the diatomite actually formed in springs fed by a higher groundwater table, not a lake. The diatomite at Quebrada Puripica is contemporaneous with other perched wetland deposits indicating higher groundwater levels in the central and northern Atacama (Betancourt et al., 2000; Rech et al., 2002; Quade et al., 2001). Grosjean (2001) suggested that these wetland deposits and locally elevated water tables result from alluviation in canyons during low-flow

conditions. Middle Holocene wetland deposits indicating higher groundwater levels, however, are not confined to deep, erosive canyons in the central and northern Atacama (lat 18–24°S). They crop out in small channels and interfluvies outside of main-stem channels, in open, marshy environments, and around spring vents on hillslopes (Betancourt et al., 2000; Rech et al., 2002; Quade et al., 2001). Contrary to Grosjean's (2001) assertions, middle Holocene and late glacial–early Holocene spring deposits, the latter that he accepted as evidence for wetter conditions, occur in the same geomorphic settings. We infer that wetland deposits in the central and northern Atacama imply wetter conditions and pose a challenge to the conventional assumption of middle Holocene aridity on the Pacific slope of the Andes. Finally, we agree with Grosjean et al. (1997a) that Early Archaic (13–9 ka) occupation of the Atacama was disrupted by the end of the late glacial–early Holocene pluvial. We suggest, however, that the resettlement of the Atacama later in the Holocene might have been complex, involving not just climatic variations but also diffusion of technologies from other areas, such as domestication of camelids at ca. 7–6 ka in Peru.

What Drives the Intensity of the South American Summer Monsoon

Summer and seasonal insolation forcing of Amazon basin convection has been used to explain millennial time-scale variations in

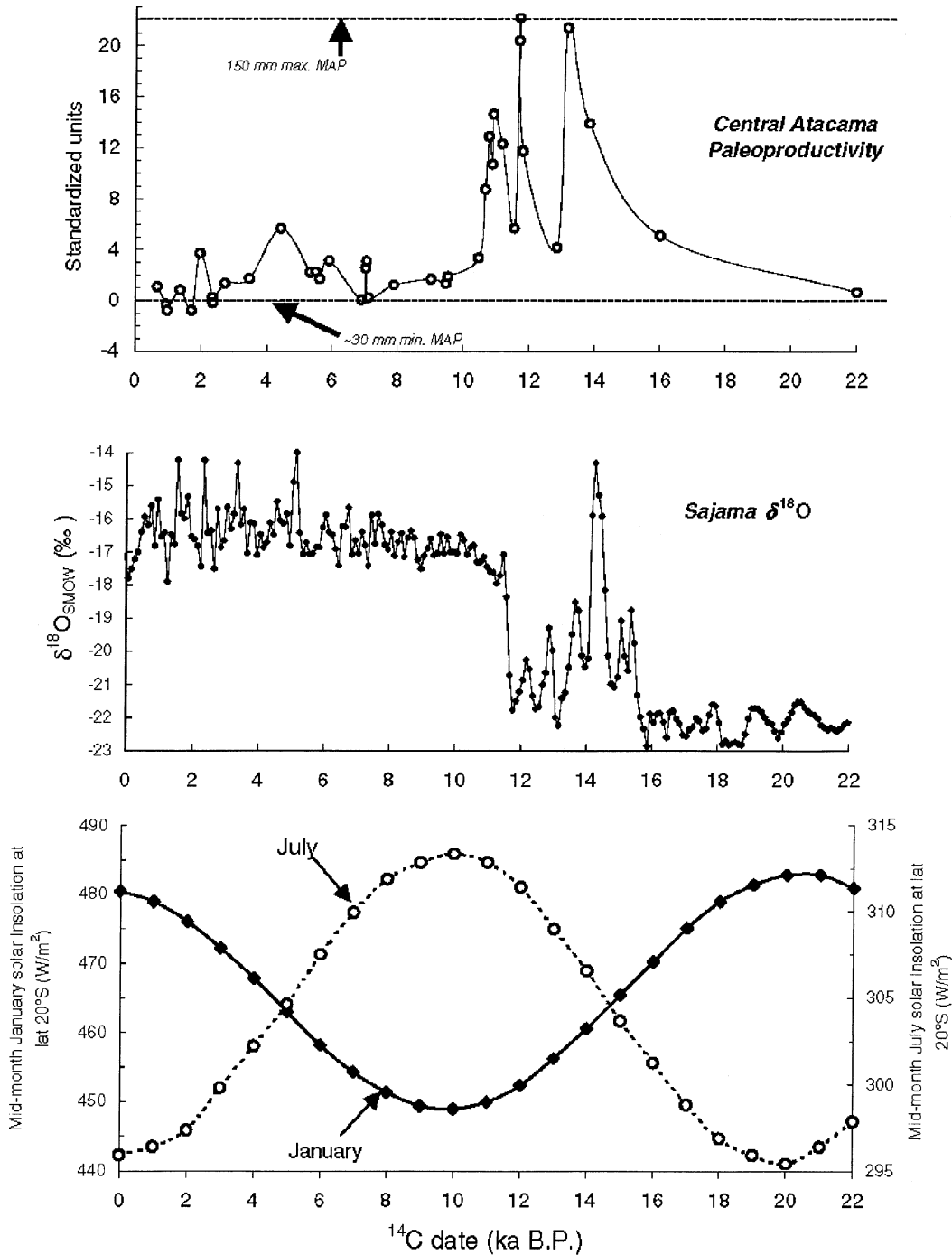


Figure 11. Paleoproductivity curve for the past 22 000 yr based on grass-abundance and species-richness departures with respect to the past 1000 yr. Positive departures indicate increased precipitation, whereas negative departures indicate increased aridity. The precipitation minimum is based on mean annual precipitation (MAP) at midden sites today. Steppe grasses today grow in areas with MAP of ~150 mm and set the past precipitation maximum at the end of the Pleistocene. Solar insolation at lat 20°S and the Sajama $\delta^{18}O$ ice-core record (Thompson et al., 1998) are plotted for comparison to the midden record.

central Andes lake records (Martin et al., 1997; Seltzer et al., 2000; Baker et al., 2001a, 2001b). Limited adiabatic heating over the South American tropics during periods of minimal summer and seasonal insolation

would lead to reductions in precipitation over the central Andes. An 18 000 ka record of $\delta^{18}O_{\text{calcite}}$ from Lago Junín, central Peruvian Andes (lat 11°S), implies low lake levels during the late glacial–early Holocene transition

that matches the January (summer) insolation minimum at lat 10°S (Seltzer et al., 2000). Lago Titicaca levels, as reconstructed from several climate proxies (Baker et al., 2001b), fell after 11.5 ka. Amazon River discharge re-

cords, however, conflict regarding increased or reduced moisture budgets during the late glacial–early Holocene. Variations in terrigenous mineral content during the past million years in a marine sediment core from Ceara Rise, east of the Amazon fan, indicate increased discharge and precipitation in the Amazon basin during glacial to interglacial transitions (Harris and Mix, 1999). Evidence from planktic foraminiferal $\delta^{18}\text{O}$ values (Showers and Bevis, 1988) point to increased discharge during the Younger Dryas, whereas a recent record using the isotopic difference between foraminiferal $\delta^{18}\text{O}$ values and global ice volume indicates decreased discharge (Maslin and Burns, 2000). The Atacama pluvial phase between 16.2 and 10.5 ka described here, however, suggests that, at the tail end of the tropical rainfall belt, the wettest episode in the past 45 000 yr occurred at a time of minimum summer insolation and insolation seasonality at lat 20°S (Berger and Loutre, 1991) (Fig. 11). This paradox leads us to look elsewhere for explanations of the intensity of the SASM on millennial time scales.

Our record indicates that maximum rainfall in the central Atacama Desert was achieved between 11.8 and 10.5 ka, with a lesser pluvial phase between 7.1 and 3.5 ka. Modern precipitation over the Bolivian Altiplano occurs during the mature phase (midsummer) of the SASM (Zhou and Lau, 1998). As previously stated, regional variations in precipitation spillover onto the highlands of the Atacama Desert are strongly dependent on upper air conditions favorable for moisture transport across the Altiplano and independent of fluctuations in lowland moisture-source areas (Garreaud, 2000; Vuille et al., 1998, 2000). Thus, any relationship between the past intensity of the SASM and the wet phases that occurred over the central Andes and the Atacama Desert should incorporate forcing other than warming of the continental interior or variations in source areas for moisture.

Strong easterlies during La Niña conditions produce a southward displacement and intensification of the Bolivian High, favoring convection and moisture transport across the Altiplano. The reverse occurs during El Niño, when upper-level westerly winds suppress convection (Vuille et al., 2000). Thus, remote forcing by variations in Walker Circulation is capable of modifying SASM intensity. Research with coupled ocean-atmosphere models (Cane and Clement, 1999) suggests that variations in orbital insolation produced nonlinear effects in tropical Pacific sea-surface temperature gradients. Recent climate modeling (Liu et al., 1999) also links maximum summer in-

solation in the Northern Hemisphere to an intensified Asian monsoon, strengthened Pacific trades, and intensified Walker Circulation, producing La Niña-like conditions during the early Holocene. We propose that such linkage would have also increased precipitation over the central and northern Atacama Desert and the western Altiplano through an intensification of the SASM. Conversely, abrupt drying by 9.5 ka may have been caused by strengthened westerlies over the Altiplano, inhibiting convection and precipitation similar to an onset of sustained El Niño-like conditions. A cold tropical Pacific during the middle Holocene, indicated by several marine and terrestrial proxies (Cole, 2001), would have intensified upper-level circulation, enhancing the transport of tropical moisture across the Altiplano and onto the central Atacama.

PALEOBIOGEOGRAPHY IN THE CENTRAL ATACAMA DESERT

Biogeographers have traditionally referred to present and past biotic distributions in the Atacama Desert as the outcome of a “natural experiment” (Arroyo et al., 1988; Marquet, 1994; Villagrán et al., 1983). Low diversity and a high degree of endemism, the result of pronounced climatic and biological barriers, are key features of the modern Atacama (Rundel et al., 1991; Marquet et al., 1998). Climate change plays a pivotal role among the many hypotheses proposed to account for these distributions. The decrease in vegetation as the absolute desert is approached presumably formed filters or corridors for north-south dispersal from northern into central Chile during the Pleistocene (Moreno et al., 1994), whereas sustained desiccation would have imposed formidable barriers (Villagrán et al., 1983; Arroyo et al., 1988).

Latest Pleistocene plant communities on the margin of the absolute desert in the Atacama were more diverse and probably occupied a much larger area than today, forming extensive mixed tolar-steppe grasslands. Prepuna communities were enriched by an 800 m descent of Andean steppe species at the peak of the wettest phase, between 11.8 and 10.5 ka. This brief interlude of increased moisture is in strong contrast with sustained hyperaridity, probably during the full glacial and certainly for the early and late Holocene. Although plant invasions into the absolute desert were likely extensive, lowland biogeographic corridors during the late glacial–early Holocene were probably short-lived. Indeed, low affinity between Puna (northern Chile) and Mediterranean (central Chile) Andean floras suggests

that isolation predates the Quaternary (Villagrán et al., 1983). Sustained hyperaridity (and very low bioproductivity) would also explain the lack of reliably dated latest Pleistocene extinct “megafauna” sites (Moreno et al., 1994) in the Atacama Desert. For Early Archaic cultures in the Atacama, however, the late glacial–early Holocene pluvial apparently stimulated a population explosion evident in numerous sites dated between 13 and 10.2 ka (Nuñez and Grosjean, 1994) (these sites are actually coeval with Paleindian cultures elsewhere).

As witnessed in the present study, the sudden loss of steppe grasses at the end of the Pleistocene reveals that plant species in the Atacama are subject to constant “local” extinctions or extirpations. Such extirpations occurred throughout the Holocene, including the northerly retreat of *Echinopsis* and *Ambrosia artemisioides* and the disappearance from northern Chile of the perennial *C₄* grass *Pappophorum caespitosum* ~2000 yr ago.

Finally, we point out that the central Atacama presents a unique natural experiment in that life and water overrun lifeless landscapes at known times in the past, leaving an organic lag and a host of fluvial landforms. There is no other comparable circumstance on Earth, save for the early Holocene expansion of tropical savannas into the hyperarid core of the eastern Sahara Desert (Ritchie et al., 1985; Ritchie and Haynes, 1987).

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