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Late Pleistocene C_4 Plant Dominance and Summer Rainfall in the Southwestern United States from Isotopic Study of Herbivore Teeth

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Patterns of climate and C_4 plant abundance in the southwestern United States during the last glaciation were evaluated from isotopic study of herbivore tooth enamel. Enamel $\delta^{13}C$ values revealed a substantial eastward increase in C_4 plant consumption for *Mammuthus* spp., *Bison* spp., *Equus* spp., and *Camelops* spp. The $\delta^{13}C$ values were greatest in *Bison* spp. (−6.9 to +1.7‰) and *Mammuthus* spp. (−9.0 to +0.3‰), and in some locales indicated C_4-dominated grazing. The $\delta^{13}C$ values of Antilocaprids were lowest among taxa (−12.5 to −7.9‰) and indicated C_3 feeding at all sites. On the basis of modern correlations between climate and C_4 grass abundance, the enamel data imply significant summer rain in parts of southern Arizona and New Mexico throughout the last glaciation. Enamel $\delta^{18}O$ values range from +19.0 to +31.0‰ and generally increase to the east. This pattern could point to a tropical or subtropical source of summer rainfall. At a synoptic scale, the isotope data indicate that interactions of seasonal moisture, temperature, and lowered atmospheric pCO_2 determined glacial-age C_4 abundance patterns.

Key Words: **quantum yield; atmospheric CO_2; plant macrofossils; climate model; C and O isotopes; herbivore teeth; global change; American Southwest; paleoclimate; monsoon.**

INTRODUCTION

Patterns of rainfall and C_4 plant dominance in the southwestern United States during the late Quaternary are controversial. Community Climate Model (CCM) simulations and plant macrofossil data point to winter rainfall and C_3 (most dicotelydenous plants and temperate grasses) dominance across the region during the late Pleistocene (Van Devender and Spaulding, 1979; Thompson *et al.*, 1993; Bartlein *et al.*, 1998). Recent carbonate isotope studies, however, indicate at least local C_4 (tropical grasses and some herbs and shrubs) dominance in southern deserts after 18,000 ^{14}C yr B.P. (Cole and Monger, 1994; Monger *et al.*, 1998; Liu *et al.*, 1996), which may reflect lowered pCO_2 levels (Cole and Monger, 1994; Cerling *et al.*, 1997), summer rainfall (Liu *et al.*, 1996), or other environmental factors (Boutton *et al.*, 1994).

Iterative comparisons of CCM climate simulations and paleoenvironmental data provide a qualitative check for model design and further understanding of climate–biosphere interactions relevant to forecasting global change (Bartlein *et al.*, 1998). Disagreements over the ecological significance and past extent of C_4 plant dominance could point to errors in late Pleistocene climate reconstructions for North America, as well as other continents (Street-Perrott, 1994). Such errors may, in turn, reduce the diagnostic sensitivity of "model-data comparisons" necessary to assess CCM capabilities. In this study, we identify patterns of C_4 plant distribution in the southwestern United States during the last glaciation from the diets of megaherbivores. The data are derived from isotope values of tooth enamel and provide a unique interpolation of relative C_4 abundance across regional climate gradients and physiographic settings from ca. 40,000 to 10,000 ^{14}C yr B.P.

Our primary objectives were to: (1) delineate synoptic patterns in late Pleistocene C_4 plant abundance across the southwest from $\delta^{13}C$ values of herbivore enamel, and (2) evaluate the data in the context of a quantum yield model for photosynthesis (Ehleringer *et al.*, 1997) and surface moisture conditions inferred from enamel $\delta^{18}O$ values and other paleoproxy records.

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BACKGROUND

Climate and C_4 Plant Distributions

C_3 and C_4 plant abundance can be predicted from surface energy and moisture balance characteristics (Lloyd and Farquhar, 1994). This results from the fact that C_4 plants have a competitive advantage over C_3 plants under conditions of high light intensity and moisture stress due to more efficient CO_2 capture at high leaf temperatures and low stomatal conductance (Ehleringer, 1978). C_4 plants are, in fact, most common today in desert and subtropical regions with warm season rainfall (Chazdon, 1978; Hattersley, 1983; Paruelo and Lauenroth, 1996).

Warm-season grasses comprise the largest component of C_4 plant cover in the southwestern United States, with smaller contributions from dicots (e.g., *Atriplex* spp.) and more mesic monocots (e.g., *Cyperus* spp.). Patterns of C_4 grass diversity in North America indicate a strong positive relationship with growing season temperatures (Teeri and Stowe, 1976), while C_4 dicot diversity increases with aridity (Stowe and Teeri, 1978). Similar to C_4 grasses, the diversity of C_4 species of the Cyperaceae increases with growing-season temperatures, as well as with summer precipitation (Teeri *et al.*, 1980). However, some C_4 Chenopodiaceae (*Atriplex* spp.) are relatively cold tolerant and display substantial photosynthetic capacity at temperatures as low as 4–10°C (Caldwell *et al.*, 1977).

Competitive indices of C_3 and C_4 grass distribution highlight the importance of average climatic conditions, as well as rainfall seasonality. In the Great Plains, both relative and absolute C_4 grass abundances correlate with mean annual temperature (MAT) and mean annual precipitation (MAP) (Epstein *et al.*, 1997); the annual proportion of summer precipitation covaries with MAP over this region. Paruelo and Lauenroth (1996) also report an increase in C_4 grass abundance within the western United States at southern latitudes and eastern longitudes—increasing with MAT, MAP, and the proportion of summer precipitation falling from June to August (JJA/MAP). In contrast, C_3 grass abundance decreases with MAT and JJA/MAP, while in areas with high MATs but low MAP and JJA/MAP (e.g., Mojave Desert) C_3 shrubs predominate (Paruelo and Lauenroth, 1996).

Quantum Yield Differences and Plant Competition

The quantum yield for plant CO_2 uptake describes photosynthetic efficiency as a function of temperature and atmospheric pCO_2 level, providing a mechanistic basis to predict distributions of C_3 and C_4 plants (Ehleringer, 1978). The quantum yield (mol CO_2 photon^{-1}) is lower in C_4 than C_3 plants due to the higher energetic costs of C_4 photosynthesis. However, net-carbon gains in C_3 plants are reduced at higher leaf temperatures due to photorespiration. C_4 plants do not exhibit photorespiration, such that temperature has little influence on net-carbon gain. As a result, crossover temperatures for C_3/C_4 superiority are constrained by the influence of atmospheric pCO_2 levels on the quantum yield, with C_4 plants favored under lowered pCO_2 levels and elevated temperature (Ehleringer *et al.*, 1997).

Quantum yield estimates point to C_4 dominance in grassland habitats under current pCO_2 levels (350 p.p.m.v.) where daytime growing season temperatures exceed 30°C and soil moisture is adequate to support production. A balance in C_3/C_4 production should occur at temperatures in the range of 22–30°C (Ehleringer *et al.*, 1997). On this basis, Ehleringer (1987) predicted a transition from C_4 to C_3 grass dominance in the Great Plains north of 45°N. This is consistent with a C_3/C_4 "crossover latitude" of 43°N estimated from regional productivity measurements (Epstein *et al.*, 1997).

C and O Isotopes in Tooth Enamel

In wild herbivores, $\delta^{13}C$ values of the carbonate apatite in tooth enamel correlate with bulk diet (DeNiro and Epstein, 1978) offset by a diet-tissue fractionation of ~14‰ (Cerling *et al.*, 1997). The average $\delta^{13}C$ value of C_4 plants (−12‰) is distinct from that of C_3 plants (−26‰) (O'Leary, 1988), and within photosynthetic types, $\delta^{13}C$ values of plants growing under closed canopy environments, low light intensity, or high humidity are generally more negative (Farquhar *et al.*, 1982). Additionally, angiosperm trees are on average ~1.1 to 1.4‰ more depleted in ^{13}C than gymnosperm trees (Leavitt and Newberry, 1992).

In warm regions, modern C_4 feeders have enamel $\delta^{13}C$ values of approximately +1–3‰ on average, whereas C_3 feeders have average values of approximately −12 to −13‰ (Cerling *et al.*, 1997; Bocherens *et al.*, 1996). Cerling *et al.* (1997) recently proposed a cutoff of −8‰ for $\delta^{13}C$ values of pure C_3 feeders to prevent a "false positive" signal for C_4 biomass in herbivore diets. However, $\delta^{13}C$ values may be ~1–2‰ greater in fossil material due to modern release of ^{13}C depleted CO_2 from burning of fossil fuels. This would imply a more positive C_3/C_4 cutoff (approximately −7‰) for prehistoric herbivores. On this basis, contributions of C_4 plants to herbivore diets have been discerned from enamel material up to 16 myr old (Morgan *et al.*, 1994) and have, in turn, been used to infer past changes in relative C_3/C_4 abundance (Cerling *et al.*, 1997; Quade *et al.*, 1992). Our study provides the first application of this technique to infer regional-scale climate and vegetation patterns specific to the last glaciation.

Oxygen isotope values of structural carbonate apatite in tooth enamel ($\delta^{18}O_{sc}$) are linked to those of local precipitation ($\delta^{18}O_{mw}$) (Longinelli, 1984) and, in turn, local average surface temperatures (Dansgaard, 1964). A consistent relationship exists between $\delta^{18}O_{sc}$ and $\delta^{18}O$ values of body water ($\delta^{18}O_{bw}$) in homeotherms (Bryant *et al.*, 1996). For large herbivores, $\delta^{18}O_{bw}$ is largely determined by the ^{18}O balance of drinking water ($\delta^{18}O_{dw}$) and plant water ($\delta^{18}O_{pw}$), with the proportional influence of $\delta^{18}O_{dw}$ increasing with body mass (Bryant and Froelich, 1995). In general, $\delta^{18}O_{dw}$ is well correlated with the average $\delta^{18}O_{mw}$ (Longinelli, 1984) such that $\delta^{18}O_{sc}$ values can be used as a climate proxy. However, $\delta^{18}O_{sc}$ values of biogenic apatite are more sensitive to post-depositional diagenetic processes than corresponding $\delta^{13}C$ values (Wang and Cerling, 1994), which lends caution to interpreting $\delta^{18}O_{sc}$ data from some fossil assemblages.

METHODS

Study Area

The study region encompasses portions of the Great Basin (NV), southeastern Mojave Desert (NV, CA), northern Sonoran (AZ) and Chihuahuan deserts (NM), and Southern High Plains (NM), from ca. 40° to 30°N and 120°–103°W (Fig. 1). Elevations range from <600 m along the Colorado River Valley to ~3700 m in some mountain ranges. Strong orographic controls on temperature and precipitation are apparent within these regions. In general, however, average July (and January) temperatures decrease from $>30°C$ (~10–20°C) in the Mojave Desert and Lower Colorado River Valley to ~20–30°C (~0–10°C) in the eastern deserts, Southern High Plains, and Great Basin (Meigs, 1957). Cooler average temperatures occur at the highest elevations.

Patterns of MAP are more variable but generally increase from <120 mm in the southeastern Mojave Desert to ~120–240 mm in the Great Basin and to ~240–490 mm in the eastern deserts and Southern High Plains; MAP can be >600 mm at the highest elevations (Meigs, 1957). The proportion of annual rainfall occurring in summer months increases with decreasing latitude and longitude, reflecting summer monsoon circulation patterns. These contributions are as little as 10–30% of the MAP in the southeastern Mojave Desert and as great as 60% in southeastern Arizona and southwestern New Mexico (Fig. 2).

Participating Institutions, Material Selection, Dietary Patterns, and Dating

Fossil tooth enamel was gathered from paleontological collections at San Bernardino County Museum, University of California at Berkeley, Nevada State Museum, University of Arizona, New Mexico Museum of Natural History and Science, Blackwater Draw Site Museum, and University of Texas at El Paso. Additional samples were collected in the field by the authors. At several locales, tusks were collected for isotope analysis. Taxa selected included *Mammuthus* spp., *Bison* spp., *Equus* spp., *Camelops* spp., and members of the Antilocapridae (*Capromeryx* spp., *Stockocerus* spp., and *Antilocapra* spp.) Of the species examined, only *Antilocapra americana* and some members of *Bison* survived the late Pleistocene extinction.

Previous paleo-dietary studies and inferences based on feeding habits of surviving genera indicate that *Bison* spp. and *Mammuthus* spp. were preferential, though not obligate, grazers (O'Gara, 1978; Mead *et al.*, 1986; Akerston *et al.*, 1988). In contrast, *Camelops* spp. and *Equus* spp. likely consumed greater proportions of browse, C_4 *Atriplex* spp., and succulent CAM plants (Hansen, 1980; Koch, in press). CAM species have $\delta^{13}C$ values intermediate between C_3 and C_4 plants (O'Leary, 1988), which would produce $\delta^{13}C$ values of ca. −6‰ in herbivore enamel. Antilocaprid species are predominantly browsers (O'Gara, 1978).

Enamel was collected from fossils with known geological and chronological provenance. The latter was based on ^{14}C dates of associated sediment fractions (e.g., shells, carbonate, charcoal, soil organic matter), bone (collagen and carbonate), or tusk collagen. As a consequence, the ^{14}C ages reported here are presented as the possible time range represented by associated ^{14}C dates. We adopt this approach in order to reduce the possibility for erroneous age assignments, but also note that it reduces the overall temporal resolution of our data. Care was also taken to avoid fossil materials that may have been reworked from older or younger sediments. In some cases, ^{14}C ages were inferred by interpolating between dated strata.

Laboratory Pretreatment and Measurement

Fossil enamel was removed from the base of teeth using a small Dremel™ drill. Every attempt was made to select enamel from teeth formed after weaning (e.g., P2–P4, M3), as weaning has been linked to isotopic enrichment in the phosphate-apatite enamel phase (Fricke and O'Neil, 1996). Unfortunately, it was frequently necessary to use tooth fragments of either unknown position or M1 and M2. Enamel was prepared for isotope analysis following a modified method of Quade *et al.* (1992). Briefly, the enamel was cleaned of adhering material and dentine with a dental drill under continuous water flow, dried, and then crushed. Resultant powders were reacted (24 h) with 5% NaOCl to remove organic C, rinsed and centrifuged 2× with 50 ml deionized water, reacted with 1.0 M acetic acid under vacuum (24 h) and then in a sonicator (1 h) to remove nonstructural carbonate. The remaining material was then rinsed and centrifuged 3× with 50 ml deionized water, dried, and stored for analysis.

Isotope values of carbonate apatite were determined from cryogenically purified CO_2 following sample reaction with 100% H_3PO_4 at 50°C (~4 h) after the method of McCrea (1950). Sulfur contamination was indicated for several samples during gas transfer by the formation of a "red" ring on the vacuum line under a liquid-nitrogen trap. The contaminant was subsequently removed by refreezing the gas with Ag_3PO_4 and then warming to room temperature. This does not appear to fractionate the oxygen isotopes. The purified CO_2 was then measured manometrically to determine percentage of carbonate. The isotopic ratios for carbon and oxygen were measured on a Finnigan delta S gas source mass spectrometer at the Department of Geosciences, University of Arizona.

The $\delta^{13}C$ values of enamel carbonate are given relative to the Vienna Pee Dee Belemnite (VPDB) standard (Coplen, 1994) in δ (per mil) notation, where δ (per mil) =

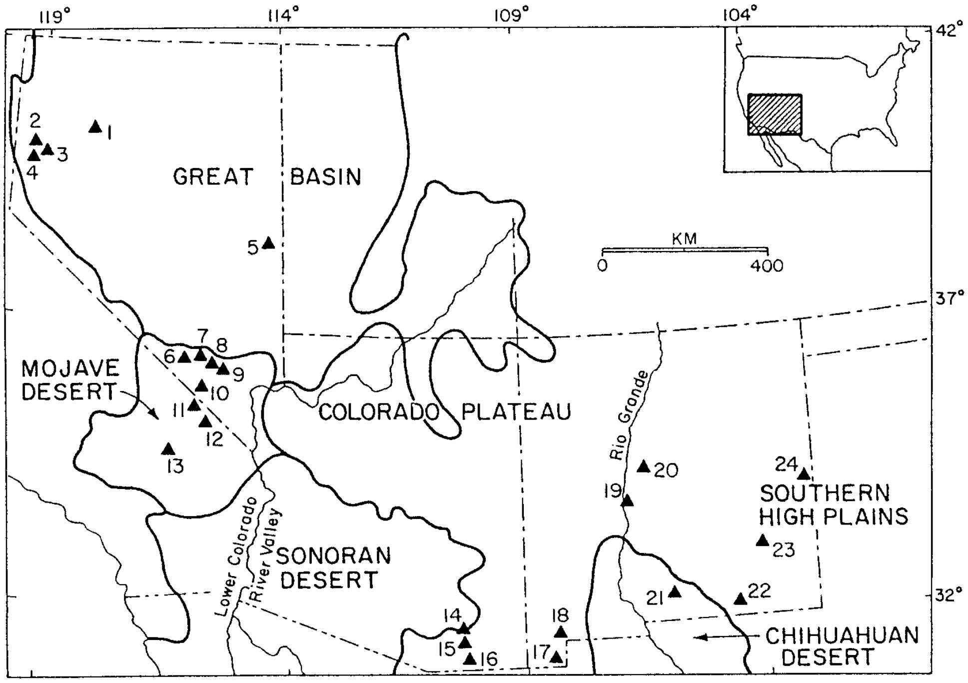

FIG. 1. Map of the Great Basin and American Southwest showing: late Pleistocene fossil localities, (1) Rye Patch 40°28′N 118°18′W; Pyramid Lake Sites, 39°28′N 119°04′W, (2) Crypt Cave, (3) Fishbone Cave, (4) Wizards Beach; (5) Sunshine Lake 39°30′N 115°18′W; SE Mojave Sites, (6) Lathrop Wells 36°42′N 116°24′W, (7) Cactus Springs 36°32′N 115°44′W, (8) Corn Creek 36°21′N 115°18′W, (9) Tule Springs 36°19′N 115°11′W, (10) Pahrump Valley 36°7′N 116°0′W, (11) Valley Wells 35°30′N 115°38′W; (12) Kokoweef Cave 25°25′N 115°29′W; (13) Mojave River Sites 34°35′N 116°47′W, Calico Lakes, Solar 1; San Pedro River Valley, (14) Seff 31°58′N 110°18′W, (15) Murray Springs 31°34′N 110°10′W, (16) Naco 31°20′N 109°57′W; (17) U-Bar Cave 31°29′N 108°26′W; (18) Howell's Ridge Cave 31°55′N 108°30′W; (19) Isleta Cave 34°53′N 106°52′W; (20) Sandia Cave 35°15′N 106°24′W; (21) Pendejo Cave 32°22′N 105°53 W; (22) Dry Cave 32°8′N 104°43′W; (23) Roswell 33°24′N 104°32′W; (24) Blackwater Draw 34°26′N 103°12′W.

$((R_{\mathrm{sample}}/R_{\mathrm{standard}})-1) \cdot 1000$ and R_{sample} and R_{standard} refer to the $^{13}C/^{12}C$ or $^{18}O/^{16}O$ ratios of sample and standard, respectively. The $\delta^{18}O$ values are reported relative to Vienna Standard Mean Ocean Water (VSMOW) (Coplen, 1994). Repeated measurement of the NBS-19 calcite standard yielded a precision (± one standard deviation, SD) for $\delta^{13}C$ and $\delta^{18}O$ of ±0.1‰ and ±0.2‰, respectively. Variation within a single enamel sample (Cat. No. vwb87-1; $n = 8$) was ±0.02‰ ($\delta^{13}C$) and ± 0.09‰ ($\delta^{18}O$). The percentage of structural CO_3^{2-} in fossil enamel following pretreatment was 4 ± 1% by mineral weight, similar to fresh enamel (~4%).

Statistical Analyses

We used the Pearson product-moment correlation to measure the association between enamel $\delta^{13}C$ and $\delta^{18}O$ values. Statistical analyses were made using the SAS statistical package (SAS, 1987). All measures of variation for enamel data are reported as 1SD from the mean of individual samples.

Calculations

To estimate values of modern C_4 productivity in proximity to our fossil localities, and seasonal contributions of precipitation to glacial-age C_4 plant distributions, we used a response function developed by Paruelo and Lauenroth (1996), which relates modern climate parameters and percent C_4 grass abundance (C_4G): $C_4G = -0.9837 + 0.000594\mathrm{MAP} + 1.3528\mathrm{JJA/MAP} + 0.2710\ln\mathrm{MAT}$ ($r^2 = 0.66$, $F = 44$, $P < 0.0001$). It is important to note that precipitation amounts used in our comparison (from nearest climate stations) may vary from actual rainfall at the sites, particularly in mountainous terrain. Similar variations in MAT owing to elevation differences should be small <2°C (Meyer, 1992).

Our own examination of the model based on the error of residuals indicates that analytical uncertainty of modern C_4G at individual locations varies by ≤10% (±2SD). However, we found that the model predicts negative values for C_4G where MAP and JJA/MAP are very low. Consequently, climate-C_4 relationships must be treated cautiously in portions of the Great Basin and Mojave Desert. Assumptions and limitations pertaining to our use of the model for paleoenvironmental reconstruction are discussed later in the paper.

RESULTS

Enamel $\delta^{13}C$ Values

Enamel $\delta^{13}C$ values generally increased with decreasing longitude for all taxa except the Antilocapridae (Table 1, Fig.

TABLE 1
Stable Isotope and Radiocarbon Age Range Assignments for Fossil Tooth Enamel

Local source[a,b] (approximate elevation in m)	Species (strata)[c]	Catalog number	Estimated ^{14}C age (10^3 yr B.P.)	Material[d] dated	Tooth[e]	δ^{13}C (‰)	δ^{18}O (‰)
California							
Kokoweef Cave, SBCM(1,2) (1950)	*Equus* spp.	na	>9.0	c	F	−9.5	22.0
	Equus spp.	na	>9.0	c	F	−11.6	26.0
	Equus spp.	na	>9.0	c	F	−11.9	23.7
Mojave River Valley							
Calico Lakes, SBCM (3) (1910)	*Equus* spp.	na	13.0–10.0	bca, c	F	−10.6	24.2
	Equus spp.	na	13.0–10.0	bca, c	1	−9.6	24.6
	Equus spp.	6.21.1	13.0–10.0	bca, c	F	−9.8	24.6
	Equus occidentalis	17.18.6	13.0–10.0	bca, c	F	−9.0	23.7
	Camelops spp.	3.20.2	13.9–10.0	bca, c	M2	−11.0	26.2
	Camelops spp.	3.27.2	13.0–10.0	bca, c	F	−5.6	25.0
	Camelops spp.	3.27.19	13.0–10.0	bca, c	F	−8.2	25.4
	Camelops spp.	3.6.3	13.0–10.0	bca, c	F	−6.5	25.1
Solar 1, SCBM[93] (1940)	*Equus occidentalis*	10.32.2	13.0–10.0	bca, c	M1/2	−10.8	26.2
S.E. Mojave							
Valley Wells (1100)	*Mammuthus* spp. (E1)	A.4898	14.0–11.5	so, c, f	F	−7.2	21.9
Nevada							
S.E. Mojave							
Corn Creek, A (4) (881)	*Equus* spp. (E1)	A.4861	14.0–11.5	so, c, f	F	−7.7	24.9
	Camelops spp. (E1)	A.4901	14.0–11.5	so, c, f	F	−8.7	27.7
Pahrump Valley, A (4) (860)	*Mammuthus* spp. (E1)	A.5494	14.0–11.5	so, c, f	F	−8.9	24.9
	Mammuthus spp. (E1)	A.4592	14.0–11.5	so, c, r	F	−7.9	27.7
Lathrop Wells, A (4) (850)	*Equus* spp. (D)	na	22.0–17.0	ms	F	−9.8	25.4
Cactus Springs, A (4) (950)	*Mammuthus* spp. (E1)	na	14.0–11.5	so, c, f	F	−8.9	23.2
Tule Springs, UCMB (5,6) (970)	*Antilocapridae* (E1)	64929	14.0–11.5	so, c, f	F	−10.8	29.5
	Tetrameryx spp. (E1)	64536	14.0–11.5	so, c, f	P	−10.9	24.2
	Tetrameryx spp. (E1)	64533	14.0–11.5	so, c, f	F	−9.9	28.4
	Equus spp. (E1)	na	14.0–11.5	so, c, f	P	−6.3	25.1
	Equus spp. (E1)	64252	14.0–11.5	so, c, f	F	−8.8	24.0
	Camelops spp. (E1)	64525	14.0–11.5	so, c, f	P	−9.6	24.8
	Camelops spp. (E1)	64268	14.0–11.5	so, c, f	M1/2	−8.0	25.8
	Mammuthus spp. (E1)	64393	14.0–11.5	so, c, f	M3	−8.3	20.6
	Mammuthus spp. (E1)	64393	14.0–11.5	so, c, f	P	−9.0	20.6
	Mammuthus spp. (D)	64501	22.0–17.0	ms	M3	−6.4	22.8
	Bison spp. (B2)	64692	≥40.0	ms	P	−4.9	20.3
	Bison spp. (B2)	64692	≥40.0	ms	P2	−3.4	25.0
	Mammuthus spp. (B2)	na	≥40.0	ms	M	−6.4	19.3
	Equus spp. (B2)	64250	≥40.0	ms	M3	−1.6	22.5
Pyramid Lake							
Crypt Cave, NSM (7) (1250)	*Camelops* spp.	941	13.0–10.0	gc	F	−11.6	27.3
	Equus spp.	191	13.0–10.0	gc	F	−10.5	21.3
Fishbone Cave, NSM (8) (1255)	*Camelops* spp.	936	13.0n10.0	w	M2	−6.5	22.8
	Camelops spp.	943	13.0–10.0	w	F	−2.7	21.4
Wizards Beach, NSM (9) (1180)	*Equus pacificus*	14	22.0–25.0	gc	F	−10.0	21.1
	Camelops hesturnus	na	23.0–27.0	beo	P2	−6.7	20.9
Rye Patch, NSM (10) (1260)	*Mammuthus columbi*	na	22.9–29.0	bca	F	−10.7	18.8
	Camelops hesturnus	na	22.9–29.0	bca	F	−10.3	19.0
	Bison spp.	na	22.0–29.0	bca	M2	−9.5	19.8
	Equus spp.	na	22.0–24.0	bca	P2	−8.4	18.6
Sunshine Lake, NSm (11) (1880)	*Camelops* spp.	na	10.0–12.0	c	M3	−3.9	23.8

TABLE 1—*Continued*

Local source^{a,b} (approximate elevation in m)	Species (strata)^{c}	Catalog number	Estimated 14C age (10^3 yr B.P.)	Material^{d} dated	Tooth^{e}	δ^{13}C (‰)	δ^{18}O (‰)
	Arizona						
San Pedro River Valley							
Naco,							
UALP (12,13) (1380)	*Equus.* spp.	2550	10.0–12.0	so	F	1.1	29.4
	Bison spp.	2215	10.0–12.0	so	F	0.6	30.7
Seff, A (12, 13) (1130)							
	Mammuthus spp.	na	10.0–12.0	gc	F	−0.9	27.1
	Equus spp.	na	10.0–12.0	gc	F	−2.3	29.4
Murray Springs,							
UALP (13) (1270)	*Bison* spp. (F2/F1)	na	11.5–10.2	ca	M	1.1	27.0
	Bison spp. (F2/F1)	15137	11.5–10.2	ca	F	1.7	28.5
	Bison spp. (F2/F1)	2162	11.5–10.2	ca	P	1.0	27.1
	Bison spp. (F2/F1)	na	11.5–10.2	ca	F	0.9	26.7
	Equus spp. (F2/F1)	3427	11.5–10.2	ca	M	−7.1	25.6
	Equus spp. (F2/F1)	3430	11.5–10.2	ca	M	−2.7	26.8
	Equus (F2/F1)	3481	11.5–10.2	ca	F	−1.9	28.2
	Equus spp. (F2/F1	63-2381	11.5–10.2	ca	F	−5.2	24.6
	Equus spp. (F2/F1)	na	11,5–10.2	ca	F	−1.2	25.2
	Mammuthus spp. (F2/F1)	63-2389	11.5–10.2	ca	F	−1.7	27.2
	Mammuthus spp. (F2/F1)	na	11.5–10.2	ca	F	−2.3	26.0
	Camelops spp. (F2/F1)	15120	11.5–10.2	ca	F	−0.9	31.2
	Camelops spp. (F2/F1)	na	11.5–10.2	ca	M	−1.0	27.7
	Camelops spp. (F2/F1)	63-2389	11.5–10.2	ca	F	−1.4	31.0
	Camelops spp. (F2/F1)	na	11.5–10.2	cc	F	−3.7	29.2
	Equus spp. (E/D1)	63-270	28.5–26.0	ca	F	−2.7	23.6
	Equus spp. (E/D1)	63-2351	28.5–26.0	ca	M	−3.2	25.6
	Equus spp. (E/D1)	63-2390	28.5–26.0	ca	F	−1.4	28.9
	Equus spp. (E/D1)	63-2371	28.5–26.0	ca	F	−2.6	26.9
	Equus spp. (E/D1)	14883	28.5n26.0	ca	F	−9.2	26.7
	Equus spp. (E/D1)	CVH105	28.5–26.0	ca	M	−.1	24.9
	Camelops spp. (E/D1)	63-2386	28.5–26.0	ca	M	−1.0	29.4
	Camelops spp. (E/D1)	na	28.5–26.0	ca	F	−1.5	29.6
	Camelops spp. (E/D1)	14880	28.5–26.0	ca	M3	−0.6	28.9
	Camelops spp. (E/D1)	63-2413	28.5–26.0	ca	F	−0.1	29.9
	Bison spp. (E/D1)	63-2382	28.5–26.0	ca	M	0.3	25.0
	Equus spp. (D)	63-2353	31.0–27.0	ca	M	−6.7	26.2
	Equus spp. (D)	63-2352	31–27.0	ca	M3	−6.1	24.7
	Equus spp. (D)	63-2378	31.0–27.0	ca	F	−1.8	26.9
	New Mexico						
Pendejo Cave,							
UTEP (14) (1400)	*Equus* spp. (D/E1)	G837.1	20.0–15.8	c	F	−2.1	26.7
	Equus spp. (H)	G2209.001	28.0–27.5	c, w	F	−4.9	27.5
	Equus spp. (H/L)	G2209.001	38.0–28.4	c	F	−1.8	26.7
	Equus spp. (M/M1)	G2207.001	51.0–29.2	c, w	F	−4.6	25.2
	Equus spp. (M/M1)	G475.001	51.0–29.2	c, w	F	−0.3	28.0
	Equus conversidens (M/M1)	G124.001	51.0–29.2	c, w	F	−4.3	25.1
	Equus spp. (N)	1095.0001	55.00–29.0	w	F	−0.7	27.0
Isleta Cave, UTEP (15) (1720)							
	Equus niobrensis	41-58	16.0–18.0	bco	1	−12.5	16.5
	Equus niobrensis	46-139	16.0–18.0	bco	M2/3	−11.1	24.6
	Antilocapridae	46-A2528	16.0–18.0	bco	M2/3	−7.9	26.1
Howell's Ridge Cave,							
UTEP (15,16) (1680)	*Camelops* spp.	32-141	14.0–12.0	c,w, h	F	−1.7	30.1
	Mammuthus spp.	32-504	14.0–12.0	c,w, h	F	−5.6	22.9

TABLE 1—*Continued*

Local source[a,b] (approximate elevation in m)	Species (strata)[c]	Catalog number	Estimated ^{14}C age (10^3 yr B.P.)	Material[d] dated	Tooth[e]	δ^{13}C (‰)	δ^{18}O (‰)
			New Mexico				
Dry Cave, UTEP (15, 17) (1280)	*Stockoceros* spp.	3-41	14.0–10.0	gc	M3	−11.0	27.8
	Bison spp.	54-1268	10.9–10.5	bco	M3	−2.6	20.9
	Bison spp.	54-1267	10.9–10.5	bco	M2	−2.9	27.2
	Bison spp.	54-1252	10.9–10.5	bco	F	−6.9	20.1
	Equus spp.	54-1310	10.9–10.5	bco	F	−0.1	26.0
	Equus conversidens	23-64	12.2n11.6	c	F	−7.7	24.2
	Equus conversidens	31-47	12.2–11.6	c	F	−6.9	25.3
	Camelops spp.	23-47	12.2–11.6	c	F	−7.8	29.5
	Equus spp.	25.538	13.0–12.0	gc	F	−6.8	25.2
	Equus conversidens	4-827	14.0–11.0	gc	M2	−1.1	26.6
	Bison antiquus	4-1266	14.0–11.0	gc	M2	−3.6	20.8
	Equus spp.	6-813	14.7–14.2	f	F	−5.2	25.3
	Equus conversidens	22-1627	15.2–14.8	bco	F	−2.3	27.8
	Equus niobrensis	22-1645	20.0–11.0	gc	F	−6.8	24.3
	Camelops spp.	22-295	24.0–23.0	gc	P4	−5.5	26.6
	Camelops spp.	5-54	26.7–23.3	bco	F	−11.0	27.2
	Antilocapriidae	5-67	30.4–28.2	bco	F	−12.5	27.8
	Capromeyrc spp.	1-1095	30.4–28.2	bco	M3	−10.9	27.5
	Antilocapra americana	1-1193	30.4–28.2	bco	M1/2	−11.0	29.9
	Camelops spp.	1-48	30.4–28.2	bco	M1	−7.9	28.5
	Equus spp.	26-645	38.1–35.1	bco	F	−2.2	27.7
	Equus spp.	27-271	38.1–35.1	bco	F	−7.0	21.2
U-Bar Cave, UTEP (18,19) (1570)	*Stockoceros* spp.	5689.88.2	>31.0	gu	F	−12.2	32.1
	Equus spp.	5689.54.2	42.3–39.3	so	F	−2.0	25.1
Roswell, NMMNH (20) (1680)	*Mammuthus* spp.	P25508	10.0–12.0	tco	Tusk	−3.1	29.2
Sandia Cave, NMMNH (21) (2220)	*Mammuthus* spp.	L-1585	14.0–11.0	bb	F	−5.0	22.8
Blackwater Draw, BDM (6,22) (1280)	*Bison bison* (G2)	na	0.9–0.7	so	F	0.3	26.8
	Bison bison (G1)	9816	4.8–3.5	bb, so	F	−1.3	26.4
	Bison spp. (F)	814A	8.8–6.5	bb, cw	F	0.8	24.8
	*Bison*spp. (F)	na	8.8–6.5	bb, so	M	1.8	27.3
	Bison spp. (F)	na	8.8–6.5	bb, so	F	0.9	25.6
	Bison spp. (F)	na	8.8–6.5	bb, so	F	−1.9	20.8
	Bison spp. (E)	na	10.5–8.8	so	M	0.9	29.7
	Bison spp. (E)	na	10.5–8.8	so	F	−0.8	28.1
	Bison spp. (C)	na	11.5–11.1	so	F	−1.3	28.0
	Bison spp. (C)	na	11.5–11.1	so	M	0.4	26.2
	Mammuthus spp. (C)	#4	11.5–11.1	so	F	0.3	24.2
	Mammuthus spp. (C)	na	11.5–11.1	so	F	−1.9	29.9
	Mammuthus spp. (C)	na	11.5–11.1	so	M	−0.8	27.6
	Mammuthus spp. (C)	na	11.5–11.1	so	M	−1.6	29.8
	Bison spp. (B)	9789	13.0–11.5	so	F	1.1	25.2
	Equus spp. (A/B)	na	20.0–15.0	gc	F	−1.3	27.5

[a] Sources for fossil enamel: SBCM (San Bernardino County Museum); A (Authors); UCMB (University of California Museum of Paleontology, Berkeley); NSM (Nevada State Museum); UALP (University of Arizona Laboratory of Paleontology); UTEP (University of Texas, El Paso); NMMNH (New Mexico Museum of Natural History); BWD (Blackwater Draw Site Museum).

[b] Primary sources for ^{14}C age assignments: (1) Jefferson (1991); (2) R. Reynolds (personal communication, 1997); (3) Reynolds and Reynolds (1985); (4) Quade (1986); (5) Haynes (1967); (6) V. Haynes (personal communication, 1997); (7) Orr (1952); (8) Orr (1956); (9) Dansie *et al.* (1988); (10) Firby *et al.* (1987); (11) Jones *et al.* (1996); (12) Haynes (1968); (13) Haynes (1987); (14) Chrisman *et al.*, (1966); (15) A. Harris (personal communication, 1997); (16) Emslie (1987); (17) Harris (1980); (18) Harris (1985); (19) Harris (1987); (20) M. O'Neil (personal communication, 1997); (21) Haynes and Agogino (1986); (22) Haynes (1995).

[c] Strata are nomenclature for individual depositional horizons reported in the primary literature. We report these where appropriate to facilitate future use of the data.

[d] These are: bco (bone collagen); bb (burned bone); bca (bone carbonate); c (charcoal); ca (carbonaceous earth); cw (carbonized wood); f (feces); gc (geological context); gu (guano); h (hair); ms (mollusc shell); so (soil organic matter), tco (tusk collagen); w (wood).

[e] F (fragment); I (incisor); M (molar); P (premolar). Numerical suffixes designate the relative position of individual teeth; more than one number indicates uncertainty in position assignment.

3a). This trend was particularly evident for *Mammuthus* spp. and *Bison* spp., and may highlight a coincident shift from browsing to grazing or from a C_3 to C_4 grass diet. For example, $\delta^{13}C$ values of *Mammuthus* spp. increased ~88% from southeastern Mojave sites ($-8.4 \pm 0.8‰$) to Blackwater Draw ($+1.0 \pm 1.0‰$) ca. 12,000–10,000 ^{14}C yr B.P., and $\delta^{13}C$ values of *Bison* spp. increased similarly from Rye Patch ($-9.54‰$, ca. 15,000–10,000 ^{14}C yr B.P.) to Blackwater Draw ($+0.1 \pm 1.2‰$, ca. 12,000–10,000 ^{14}C yr B.P.). A C_4-dominated diet is indicated by $\delta^{13}C$ values $\geq -5.0‰$ (Cerling *et al.*, 1997). Lower $\delta^{13}C$ values and greater inter-site variability were generally evident in *Equus* spp. and *Camelops* spp. The $\delta^{13}C$ values of the Antilocaprids were lowest among co-occurring taxa, varying from $-11.5 \pm 0.9‰$ at Dry Cave (ca. 25,000–20,000 ^{14}C yr B.P.) to $-7.9‰$ at Isleta Cave (ca. 20,000–15,000 ^{14}C yr B.P.), consistent with C_3 feeding.

Not all taxa were equally represented at each site or time, which precludes any meaningful statistical treatment of the data. However, temporal variation in $\delta^{13}C$ values of taxa within sites was relatively small. Average $\delta^{13}C$ values within genera differed by $<2.0‰$ when compared across 5000 and 10,000 yr intervals. Variation among co-occurring specimens of single genera was similar ($\pm 2.8‰$ or less).

Enamel $\delta^{18}O$ Values

Enamel $\delta^{18}O$ values were generally lowest in Great Basin sites and highest east of the lower Colorado River Valley (Table 1; Fig. 3b). Several deviations from this trend were apparent in *Equus* spp. (Isleta Cave) and *Mammuthus* spp. (Howell's Ridge Cave and Sandia Cave). Unfortunately, lack of consistent sample replication over space and time makes it difficult to evaluate such discrepancies. Isotopic differences compared between samples of single genera/locales from 15,000–10,000 ^{14}C yr B.P. and older were small, typically $\leq 2.0‰$, although samples $>15{,}000$ ^{14}C yr B.P. tended to be slightly more negative. In general, isotopic variability within genera was greatest in cave sites, perhaps reflecting local topographic controls on $\delta^{18}O_{mw}$. Such variation may also reflect temporal mixing within established ^{14}C age ranges. Where present, *Camelops* spp. and the Antilocaprids generally exhibited the highest $\delta^{18}O$ values among coeval taxa, although average differences were $<2.0‰$.

DISCUSSION

The spatial patterning of enamel $\delta^{13}C$ values (Fig. 3a) is remarkably similar to modern C_4G predicted for these locales (Table 2) using the vegetation–climate model of Paruelo and Lauenroth (1996). These observations are surprising and challenge most current conceptions of the glacial-age environment in the region. Specifically, the data imply a strong interaction between rainfall seasonality, temperature, and lowered atmospheric pCO_2 levels as controls on regional C_4 plant production—with summer rainfall patterns across the southern deserts similar to modern patterns. To illustrate the significance of these findings, we will review previous reconstructions of the late-glacial climate as inferred from CCM simulations, plant macrofossil records, and isotopic studies.

Late Pleistocene Climate Solutions and Plant Macrofossil Records

CCM simulations for the American Southwest reveal a climate unfavorable to C_4 plants. Model reconstructions for the last glacial maximum (LGM) ca. 18,000 ^{14}C yr B.P. indicate departures in atmospheric circulation (relative to modern) across North America due to continental glaciation (Thompson *et al.*, 1993; Bartlein *et al.*, 1998). The results point to a sharp thermal gradient across the southern edge of the Laurentide ice sheet that produced a strengthened jet stream aloft. Upper air flow divergence displaced the jet stream, producing a southern branch ca. 20°C south of the present winter (January) position (45°N); the displacement was also evident, although weaker, during summer (July). This displacement, coupled with a weakened East Pacific Subtropical High, would have produced prevailing westerlies that enhanced winter (reduced summer) precipitation during the LGM.

Evidence for cooler and wetter conditions across the Southwest during last glaciation are supported by paleoenvironmental data. Noble gas measurements of late-Pleistocene groundwater indicate a ~5–6°C decrease in MAT relative to modern values (e.g., Stute *et al.*, 1992), while estimates of treeline and snowline depression suggest cooling of 5–10°C (Thompson *et al.*, 1993). Precipitation estimates vary from decreased MAP and seasonality similar to today (Johnson, 1977) to doubled MAP, with reduced summer (monsoonal) contributions (Spaulding and Graumlich, 1986). Greater effective moisture is apparent from the occurrence of pluvial lakes throughout the Great Basin and southern deserts (Thompson *et al.*, 1993). However, the relative contributions and seasonality of temperature and precipitation to the paleohydrologic balance remain unresolved.

Late Pleistocene vegetation reconstructions for the Southwest are generally consistent with the CCM climate simulations. Plant macrofossil data record an expansion of the lower and southern limits of pinyon-juniper woodlands in areas now dominated by desert scrub, and a similar replacement of modern woodlands by mixed-conifer and boreal communities (Van Devender and Spaulding, 1979). Evidence for winter-dominated precipitation in late Pleistocene midden records includes: (1) the prevalence of winter annuals in what are now the southern deserts; (2) the near absence of C_4 grasses in middens from the Colorado Plateau (L. Toolin, personal communication, 1997); and (3) the absence of ponderosa pine (*Pinus ponderosa*) from most of the Pleistocene landscape. The latter has been variously attributed to pronounced summer drought, reduced fire activity, and anomalously cool tempera-

TABLE 2
Climate Station Summaries and Predicted C_4 Grass Abundance (Modern) in Proximity to Fossil Localities

Climate station	Station elevation (m)	Fossil locale(s)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Summer precipitation (mm)	Predicted C_4 abundance
Barstow, CA	659	Mojave River	16.0	105.0	10.0	−4.0
Searchliglht, NV	1079	SE Mojave	17.0	168.0	48.0	27.0
Rye Patch Dam, NV	1260	Rye Patch	10.0	182.0	38.0	3.0
Lahontan Dam, NV	1268	Pyramid Lake	12.0	106.0	21.0	2.0
Ruby Lake, NV	1830	Sunshine Lake	8.0	317.0	55.0	−3.0
Benson, AZ	1097	San Pedro River	17.0	298.0	164.0	71.0
Animas, NM	1346	Ubar/Howel’s Ridge	15.0	263.0	128.0	53.0
Orogrande, NM	1280	Pendejo Cave	17.0	224.0	111.0	59.0
Carlsbad Caverns, NM	1352	Dry Cave	17.0	363.0	153.0	57.0
Roswell, NM	1112	Roswell	15.0	269.0	116.0	40.0
Albuquerque, NM	1619	Isleta Cave	14.0	197.0	82.0	41.0
Sandia Ranger Sta., NM	1920	Sandia Cave	10.0	364.0	143.0	33.0
Clovis, NM	1293	Blackwater Draw	14.0	197.0	82.0	41.0

Note. Predictions were calculated from the model of Paruelo and Lauenroth (1996) based on climate data reported in Meigs (1957). The northwest-to-southeast increase in C_4G reflects a similar gradient of increasing summer moisture. Climate data were taken from United States Department of Commerce (1973).

tures forestalling seed germination in the fall (Betancourt *et al.*, 1990).

Some summer precipitation is indicated during full glacial conditions by the presence of evergreen oak (*Quercus* spp.) and C_4 grasses in middens from the northern Chihuahuan Desert (south of ∼34°N), albeit in low frequency (Van Devender, 1990). C_4 grasses are also found in middens from the Tinajas Mountains (AZ) and Whipple Mountains (CA) as early as 15,000 and 13,000 ^{14}C yr B.P., respectively. However, their presence may reflect the ability to respond, at low elevations, to available moisture at relatively cool temperatures (Van Devender, 1995). The midden records further indicate that extensive C_4 grasslands only formed in the southwestern United States following postglacial warming and a shift to summer-dominated precipitation ca. 8000 ^{14}C yr B.P. (Van Devender and Spaulding, 1979).

Revised Late Pleistocene Climate and C_4 Plant Distributions in the American Southwest

Our data provide the first clear evidence for C_4 plant dominance during the late Pleistocene, across areas of the Southwest where such species are common today. These observations are consistent with C_4 plant distributions predicted for the late Pleistocene based on the quantum-yield model for photosynthesis (Cerling *et al.*, 1997). Our results also indicate that summer rainfall was significant in portions of the Southwest throughout the late Pleistocene, and that its distribution was an important determinant of regional C_4 plant abundance. In this context, the $\delta^{13}C$ record presented here promotes a view of C_4 paleobiogeography overlooked by plant macrofossil records and CCM simulations. Support for our interpretation is drawn from previous paleo-dietary research and isotopic studies of pedogenic carbonate.

Cerling *et al.* (1997) provide evidence for a global expansion of C_4 plants at low to intermediate latitudes (0–40° lat) ca. 8–6 myr ago, from $\delta^{13}C$ values of herbivore tooth enamel. They attribute this expansion to a decline in atmospheric pCO_2 levels below a threshold affording photosynthetic advantage to C_3 grasses relative to C_4 grasses. Interestingly, the shift from a C_3- to C_4-based diet in some taxa (e.g., equids) appeared earlier in the warmer tropics than in the cooler intermediate latitudes; diets of all genera remained C_3-dominated above 45°N. These observations were attributed to differences in the temperature dependence of the quantum yield for C_3 and C_4 species (Cerling *et al.*, 1997). For similar reasons, an expansion of C_4 plants at low and middle latitudes during the atmospheric pCO_2 minima (∼190 p.p.m.v.) of the LGM is not surprising (Ehleringer *et al.*, 1997; Cerling *et al.*, 1997).

Evidence for C_4 expansion during the last glaciation is recorded in the isotopic chemistry of soils and peat at several tropical sites (Street-Perrott, 1994). Isotopic studies of pedogenic carbonate also reveal the presence of C_4-dominated communities in southern Arizona (Liu *et al.*, 1996) and New Mexico (Cole and Monger, 1994; Monger *et al.*, 1998) ca. 20,000–10,000 ^{14}C yr B.P. A subsequent shift to C_3 dominance in these latter sites (ca. 9000 ^{14}C yr B.P.) has been attributed to a postglacial increase in atmospheric pCO_2 (Cole and Monger, *et al.*, 1994). However, this interpretation does not explain the opposite shift to C_4 dominance in central Texas (ca. 9000–5000 ^{14}C yr B.P.) indicated by $\delta^{13}C$ values of organic carbon in paleosols (Nordt *et al.* 1994).

The diets of late Pleistocene herbivores inferred from our analyses provide evidence for widespread C_4 dominance in the Southwest east of ∼114°W and south of ∼35°N. In this context, C_4 plants probably occurred within basin grassland, savanna, and wetland communities. In the latter case, *Cyperus* spp. may have been common. This, and woodrat preference for woody perennials, might account for the poor representation of grasses recorded in midden records, which are largely collected from rocky upland environments (Betancourt *et al.*, 1990). Scant evidence of C_4 species in the diets of *Mammuthus* spp. on the Colorado Plateau (Davis *et al.*, 1984) suggests that C_4 dominance was restricted to the southern deserts and Southern High Plains, similar to today.

A cause of the transition from C_3- to C_4-based diets east of the Mojave Desert (below 35°N) is not obvious from the quantum-yield model. For example, current growing-season temperatures decrease east of the Mojave, which would favor slightly higher quantum yields in C_3 than C_4 plants. Nonetheless, modern C_4G increases significantly from the Mojave Desert to the northern Sonoran and Chihuahuan deserts and Southern High Plains (Fig. 2). This is attributable to a coincident transition from winter- to summer-dominated rainfall (Paruelo and Lauenroth, 1996). Provided a similar regional temperature gradient occurred during the LGM (Thompson *et al.*, 1993), the dietary data indicate a similar seasonal distribution of rain across the Southwest during the late Pleistocene.

Past C_4 distributions may also reflect patterns of soil moisture during summer that were dependent on spring precipitation. For example, greater-than-present spring rainfall has been inferred for full-glacial time in the Southwest (Bartlein, *et al.*, 1998) and could account for significant levels of C_4 production during summer. Summer rains would, however, seem necessary to sustain C_4 productivity at levels consistent with nearly pure C_4 feeding, as inferred for some *Bison* spp. and *Mammuthus* spp.

Initial Estimates of Summer Rainfall during the Late Pleistocene

Inferences concerning past C_4 abundance in the Southwest have lacked regional synthesis, quantitative rigor, and consideration of the range of synoptic features that would influence summer circulation and precipitation. To initiate such discussion, we present a preliminary estimate of summer rainfall in southeastern Arizona for the LGM from isotopic evidence of herbivore diets and modern climate–C_4 grass distributions. The limitations of our approach are also discussed.

A C_4-dominated diet is demonstrated by $\delta^{13}C$ values of enamel from *Mammuthus* spp. and *Bison* spp. collected along the San Pedro Valley of southeastern Arizona (Table 1, Fig. 3a). It is probable that actual C_4G on the landscape (at similar elevation) during full glaciation was ca. 70–80%. Using the model of Paruelo and Lauenroth (1996), and selecting ~70% C_4G, a decrease in MAT from modern of 5–7°C, and a MAP 1–2 times modern, we estimate that summer rainfall comprised ~48–65% of the MAP at these localities.

We make three primary assumptions in the use of this model: (1) physiological requirements of modern and glacial-age C_3 and C_4 grasses are similar; (2) C_4-based diets largely reflect the consumption of grasses; and (3) enamel $\delta^{13}C$ values provide an accurate record of C_4G on the local landscape integrated over the period of enamel formation. The first assumption is difficult to test but is probably sound. The second assumption is supported by the similar spatial distributions of enamel $\delta^{13}C$ values and modern C_4G. However, it may be best applied to *Bison* spp. and *Mammuthus* spp. (Mead *et al.*, 1986; Jefferson, G. T., unpublished data; Koch, in press).

The third assumption overlooks the possibility of feeding selectivity and migration. Selection for C_4 grasses has been documented in some modern herbivores (Tieszen *et al.*, 1979). Consequently, estimates of C_4G from enamel $\delta^{13}C$ data should consider intra-taxa isotopic variation, which we have done. Migratory behavior is more difficult to confirm or negate. Seasonal migration of extinct *Bison antiquus* has been inferred from fossil population age structure at Rancho La Brea, CA (Jefferson and Goldin, 1989) and may reflect a response to forage production patterns (G. T. Jefferson, personal communication, 1997). However, little information is available for other extinct genera or for other regions of the Southwest. We believe the overall spatial and temporal consistency in our $\delta^{13}C$ data among taxa lends support to relatively local feeding behavior.

Our model estimate does not account for interacting effects of lowered pCO_2 on plant competition, specifically, the presence (or absence) of oxygen inhibition in C_3 (C_4) photosynthetic types. Given a full-glacial growing season temperature of 20°C for the San Pedro Valley (i.e., 6°C less than modern) and an atmospheric pCO_2 level of ~190 p.p.m.v., C_4 plants would be competitively favored (Cerling *et al.*, 1997). Low pCO_2 could, therefore, facilitate C_4 plant production under decreased summer precipitation during the late Pleistocene, such that we overestimate C_4 requirements for summer rain in the San Pedro Valley. However, recent regional-scale climate model simulations have indicated amounts of summer rainfall in southeastern Arizona during the LGM similar to those of today (S. Hostetler, personal communication, 1997).

Additional research is needed to understand C_4G distributions in Texas during the late Pleistocene. Stafford *et al.* (1994) inferred a C_3 to C_4 plant transition after ca. 8000 yr B.P. on the Southern High Plains (Lubbock, Texas) based on *Bison* spp. diets, as reconstructed from $\delta^{13}C$ values of bone collagen. The $\delta^{13}C$ values of soil organic matter in central Texas also suggest C_3 dominance prior to the Holocene (Nordt *et al.*, 1993). Our data indicate high levels of C_4 production during full glacial time at Blackwater Draw, which lies only ~100 km west of Lubbock, that were maintained throughout the Holocene (Table 1). Provided the data are properly interpreted, a steep gradient from summer- to winter-dominated rainfall could have occurred across the western portion of the Southern High Plains. Alternatively, these differences represent methodological inconsistencies.

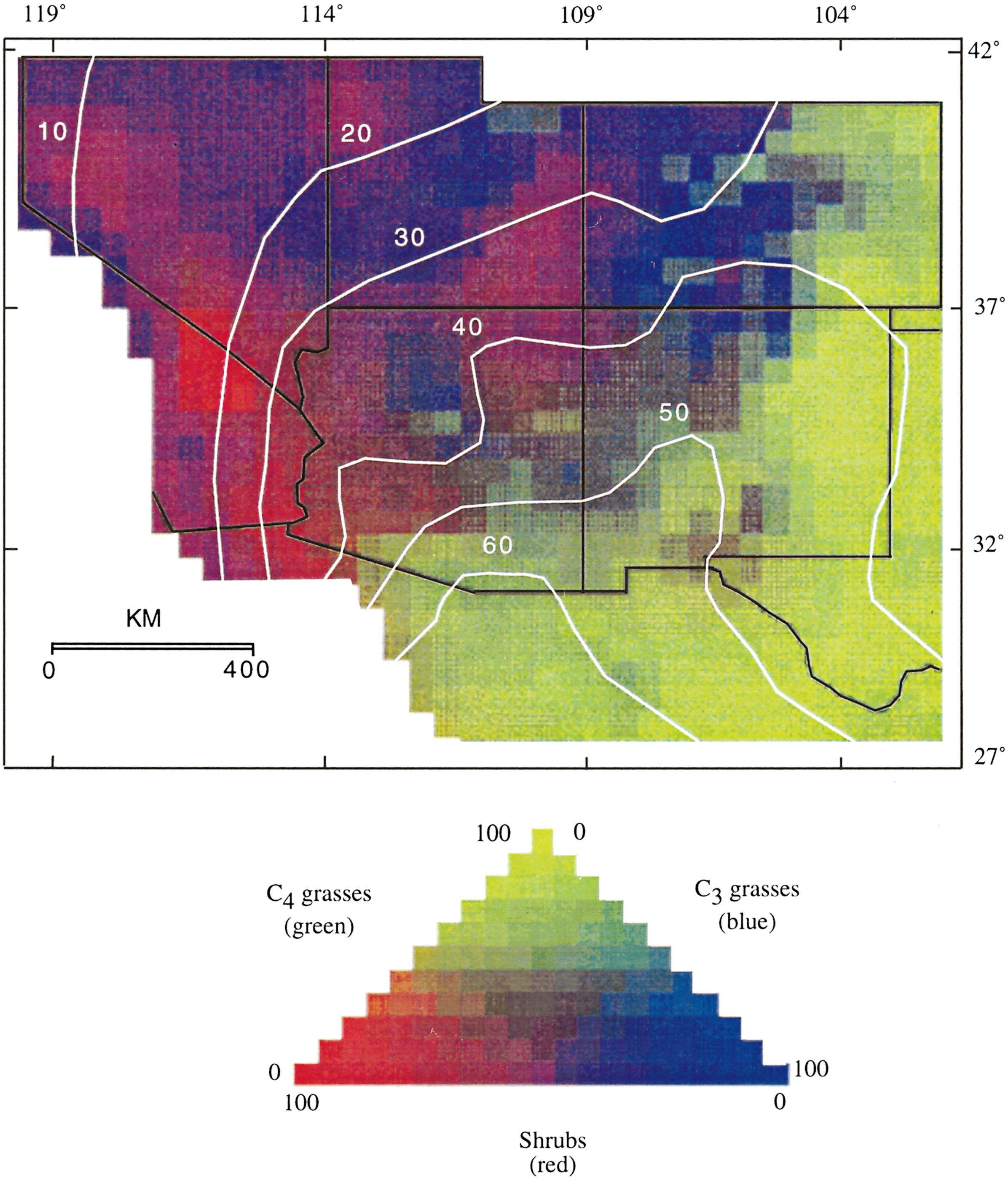

FIG. 2. Relative abundance patterns of C_4 grasses, C_3 grasses, and C_3 shrubs across the Great Basin and American Southwest as modeled by Paruelo and Lauenroth (1996). Annual proportions of rainfall in summer months (JJAS) are indicated by isolines.

Source Waters for Summer Rainfall in the Southern Deserts

Full-glacial CCM simulations for the Southwest indicate rainfall associated with westerly air flow from the Pacific coast (Thompson *et al.*, 1993). In contrast, an overall increase in enamel $\delta^{18}O_{sc}$ values from the northwest to southeast is similar to trends in modern $\delta^{18}O_{mw}$ and may indicate a tropical or subtropical source of summer rain. Oxygen isotope values of modern rainfall and surface spring waters (at equivalent elevations) increase from the Pacific Coast across the southwestern deserts (Sheppard *et al.*, 1969; C. J. Eastoe, personal

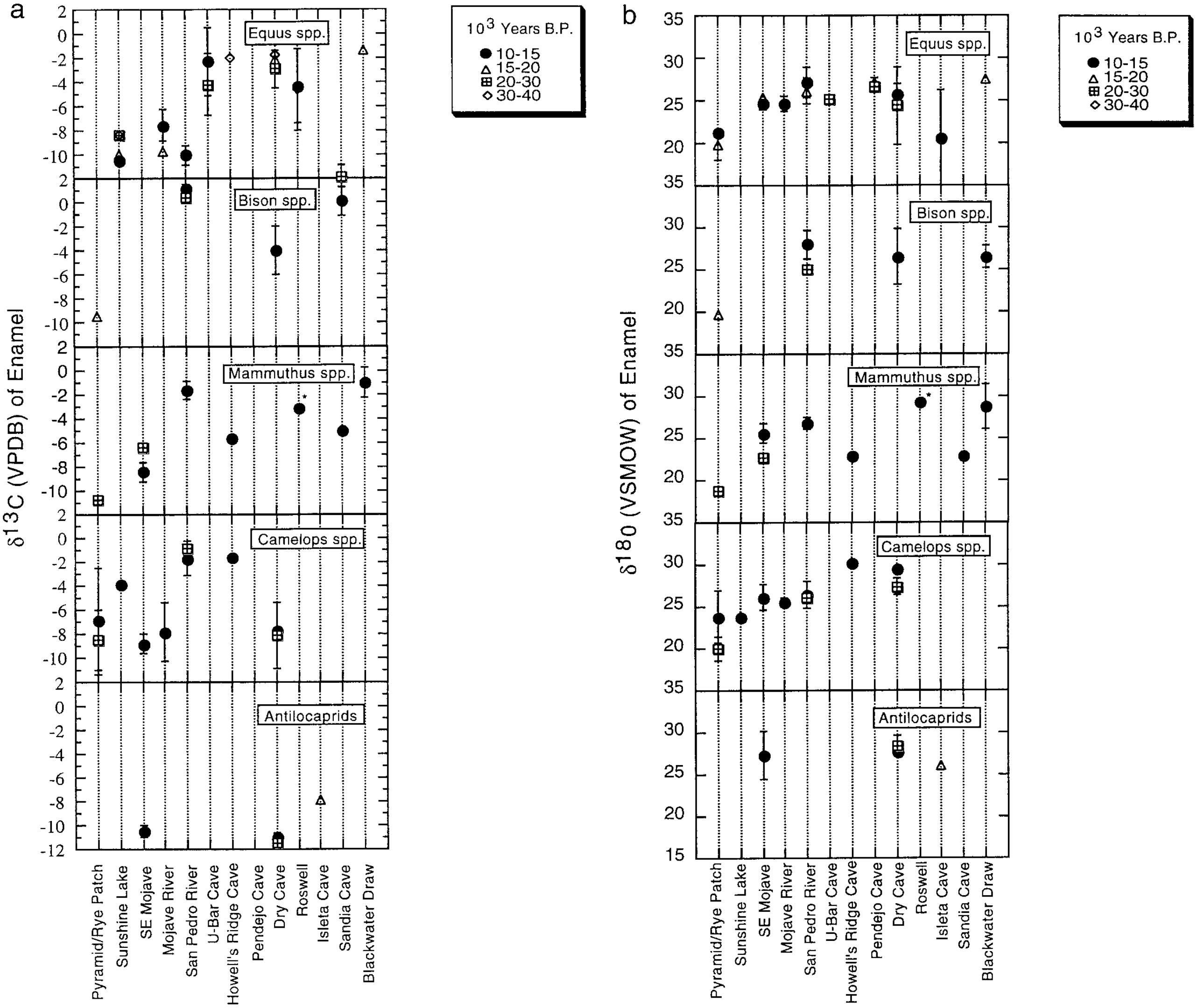

FIG. 3. (a) Carbon isotope values and (b) Oxygen isotope values of late Pleistocene herbivore enamel. Error bars represent 1 SD or σ of individual samples for the included time range. Asterisk indicates isotopic measurement of tusk.

communication, 1997), reflecting a coincident increase in monsoonal summer rains from the warm waters of the Gulf of California and the Gulf of Mexico. In general, $\delta^{18}O_{mw}$ values decrease with the condensation temperature, distance from source, and increasing rainfall amount (Dansgaard, 1964). If summer rains were derived primarily from western sources at latitudes above ~33°N, the $\delta^{18}O_{mw}$ ($\delta^{18}O_{sc}$) pattern should be reversed.

Two important questions pertinent to paleoclimate modeling arise from these observations: (1) could other phenomena account for spatial patterns observed in our $\delta^{18}O_{sc}$ data, and (2) could summer monsoon circulation patterns exist in the Southwest under a glacial-age climate? In the first case, herbivore feeding preferences might have influenced the spatial and temporal patterning of enamel $\delta^{18}O_{sc}$ values. It is worth noting that $\delta^{18}O_{pw}$ values of C_4 plants are typically greater than those of co-occurring C_3 plants in dry environments (Sternberg *et al.*, 1984). Enamel $\delta^{13}C$ and $\delta^{18}O_{sc}$ values were weakly correlated ($r=0.44$; $P>0.013$) in our study, which might indicate a dietary influence of $\delta^{18}O_{pw}$ on enamel chemistry (Fig. 4). However, similar correlation can result from climate-C_4 plant relationships and it is more likely that enamel $\delta^{18}O_{sc}$ values of "megafauna" were determined by those of drinking water (Bryant and Froelich, 1995).

The modern southwestern monsoon is a large-scale circulation system forced by differential heating of the North American continent and by tropical/subtropical source waters during summer months (Carleton, 1987). In effect, wet summers are associated with the development of a thermally induced low-pressure trough over the Southwest, northward displacement of the Pacific and Bermuda highs, formation of southerly low-level jets over the Gulf of California and Gulf of Mexico, and

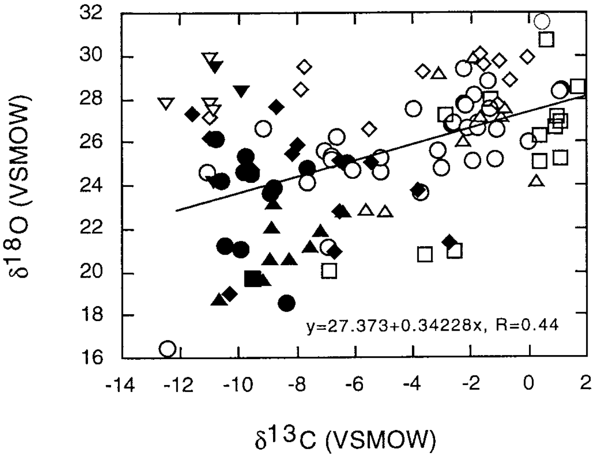

FIG. 4. Correlation between δ^{13}C and δ^{18}0 values of fossil tooth enamel from ca. 40,000 to 10,000 MC yr B.P. Shaded symbols represent sites from California and Nevada. Open symbols represent sites from Arizona and New Mexico. Circles, *Equus* spp.; squares, *Bison* spp.; upright triangles, *Mammuthus* spp.; diamonds, *Camelops* spp.; down-turned triangles, *Antilocaprids.*

increases in eastern Pacific sea surface temperature gradients (Higgins *et al.*, 1997). Provided a comparable thermal gradient between land and sea was maintained in summer months during the last glaciation, it is plausible that vapor was similarly advected into the region. Stute *et al.* (1992) report that gradients in MAT across the Southwest were probably similar to those of today, which may lend support to this hypothesis.

Several physical reasons suggest weakened monsoonal circulation during full glaciation. Greater and less-variable precipitation in the winter, coupled with cooler summers, would have prolonged snowcover in the southern Rocky Mountains and Colorado Plateau, thereby suppressing the continental heating that typically drives monsoonal flow (Gutzler and Preston, 1997). The Gulf of Mexico and Gulf of California may also have been less effective conduits for tropical air masses due to lowered sea level and reduced surface areas. At a synoptic scale, cooling of tropical waters (Guilderson *et al.*, 1994) would have weakened Hadley circulation patterns and further constrained monsoonal circulation. Based on these arguments, monsoonal rains are difficult to envision for the Southwest under full-glacial conditions.

In the absence of monsoonal circulation, other processes for summer moisture transport must be considered. One source of summer precipitation may have been tropical storms formed off the southwestern coast of Mexico, from ca. 11–15°N and 95–109°W (Reyes and Mejia-Trejo, 1991). This region now spawns more tropical storms than any area in the world, most of which travel west to northwest. During full-glacial time, a weak subtropical high and southern displacement of the jet stream (to 35°N) could have produced cutoff low pressure cells over the Southwest, and enhanced steering of extratropical and tropical moisture into the region throughout spring and summer months. To our knowledge there has been no research to test this hypothesis for LGM conditions.

Multiple environmental, behavioral, and physiological factors contribute to variability in enamel $\delta^{18}O_{sc}$ values. We have attempted to minimize the possibility of climatic misinterpretation by selecting herbivores of large body mass and by reporting geographic patterns in $\delta^{18}O_{sc}$ data by genera (Bryant and Froelich, 1995). However, spatial and temporal patterns observed in our $\delta^{18}O_{sc}$ data may be biased by the limited number of samples, time ranges, and locales currently available for this study. In this context, additional research will be necessary to establish firmly the patterns and processes of summer moisture transport to the Southwest during the late Pleistocene.

CONCLUSION

This study provides the first regional measurement of C_4 plant distribution and relative productivity during a glacial age. Isotopic measurements of late Pleistocene herbivore tooth enamel reveal abundant C_4 plants in the arid Southwest, with geographic distributions similar to modern C_4 grasses. On the basis of modern correlations between climate and C_4 plant distributions, our data indicate significant proportions of summer rainfall in areas of Arizona and New Mexico during the last glaciation. This view is supported by oxygen isotope values of enamel which generally increase across taxa to the east. A tropical or subtropical source of summer precipitation is suggested by these patterns, although further research is needed to confirm this. Our work complements previous comparisons of the quantum yield model for photosynthesis with past C_4 distributions, but emphasizes the additional role of summer precipitation as a determinant of regional C_4 abundance in the Southwest during the late Pleistocene.

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