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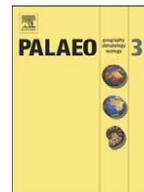
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Seasonal and geographic climate variabilities during the Last Glacial Maximum in North America: Applying isotopic analysis and macrophysical climate models

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ABSTRACT

Climate models provide estimates of climatic change over periods of time in the ancient past. Macrophysical climate models (MCM) differ from the more widely used general circulation models (GCM), in that MCMs provide temporally high-resolution (~100 years) and site-specific estimations of monthly values of climate variables such as temperature and precipitation. In this paper, seasonal changes in climate variables are modeled for six ¹⁴C-dated fossil localities in North America. Five of these localities represent the time of maximum extent of ice during the most recent glacial episode, the Full Glacial (25 + –15 ka), including one at the peak of the Last Glacial Maximum (17–15 ka). The other locality represents the time as the ice began to recede, the Late Glacial (15–11 ka). Seasonal variations in temperature and precipitation modeled by MCM are herein compared with interpretations of seasonal variation based upon oxygen isotopes from serially sampled hypsodont teeth (mostly *Equus* and *Bison*) collected from each of these localities. Additionally, the MCM-modeled seasonal variations are used to predict the expected abundances of different plant functional groups (PFG) during those times, especially C3 and C4 functional groups, using modern relationships. These predictions are compared with carbon isotopic values from the same teeth. The importance of atmospheric $p\text{CO}_2$ for the relative abundance of plants utilizing the C4 metabolic pathway is discussed, given that glacial episodes are known to have been times of lower atmospheric $p\text{CO}_2$. Interpretations of seasonal variability and the relative abundance of C3 versus C4 vegetation based upon isotopes from tooth enamel are in broad agreement with predictions using the MCM and the modern distribution of PFGs with climate variables. The influence of $p\text{CO}_2$ on the distribution of C4 vegetation during glacial times appears to be negligible.

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1. Introduction

Computerized climate models provide insight into ancient and future climate patterns on planet Earth. The most well-known computer models are general circulation models (GCMs), which examine global or continental-scale variations in climate (COHMAP, 1988; Kutzbach et al., 1993). These models begin with the understanding of climate forcing mechanisms (such as Milankovitch cycles) on the seasonality and intensity of solar radiation, the size and distribution of ice sheets, and the size and distribution of land masses during intervals of time (usually 1000+ years) in the past, to provide snapshots of the global climate during these intervals.

More recently, macrophysical climate models (MCMs; Bryson and DeWall, 2007) have been developed to provide a higher resolution (100-year intervals), site-specific glimpse of climate patterns in the past. The MCM models atmospheric physics using 'centers of action,' which include seven sub-tropical highs, five approximations for

intertropical convergences, and seven approximations for jet streams that comprise 19 of 21 modules in the MCM. The other two modules are models for temperature in the northern and southern hemispheres. The positions for each of these centers of action were calculated for the past 40,000 years in 100-year increments (Bryson and DeWall, 2007), using what is in essence a heat-budget model dependent upon "orbital forcing, variations in atmospheric transparency, and the principles of synoptic climatology" (Bryson and DeWall, 2007). Of the 21 modules in the MCM, only four to six are used when determining past conditions at a specific location.

MCMs rely upon the assumption that the local forcing factors, such as the general landscape and proximity to bodies of water, and the position of large-scale atmospheric features, have remained relatively static over the past 40,000 years (Bryson and DeWall, 2007), which is supported by studies employing both GCMs and MCMs (Ruter et al., 2004 and references therein). The MCM utilizes average monthly observations of climate from weather stations located nearest to the locality of interest and assumes that climate at this nearest station is representative of that of the locality. The MCM applies models for seasonality of solar radiation (like the GCM) plus data from volcanic eruptions (which affect atmospheric transmission of solar radiation)

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and back-calculates monthly climatic averages for the same site at 100-year intervals of times in the past. Thus the MCM has the advantages over traditional GCMs because it models climate variation at high temporal resolution and is specific to the particular fossil locality that is of interest. It is also advantageous because it can be run on a personal computer using widely available software. The MCM, however, is only valid for up to 40,000 years BP and depends upon average weather data having been collected near the site.

In recent years, isotopic analysis has developed as another excellent means for reconstructing ancient environments. Isotopes of oxygen are especially important and are frequently used as a proxy of temperature, humidity, or precipitation (Dansgaard, 1964; Rozanski et al., 1993). Isotopes of carbon provide an indication of the types of vegetation present, rates of productivity, and the 'openness' of the habitat (e.g. closed forest canopy or open prairie; Teeri and Stowe, 1976; Dienes, 1980; Ehleringer et al., 1991; Ehleringer et al., 1997; Levin et al., 2006).

Both GCMs and MCMs provide insights into climatic change as glacial climates have changed into interglacial climates. In this paper we present evidence from analysis of stable isotopes of tooth enamel of mammalian herbivores to compare with predictions from MCMs. Additionally, we will explore climatic patterns in North America during Full Glacial and Late Glacial times. Our goals are to address the following three questions:

- Do interpretations of climate based upon serial isotopic analyses of fossil mammal teeth agree with interpretations of climate from computer models (especially MCMs)?
- Is there evidence of more C4 vegetation during periods of low atmospheric $p\text{CO}_2$?
- Can an isotope-based model be derived wherein the general environment in which a mammal lived can be recognized by the range and values of carbon and oxygen isotopes from teeth?

Teeth of large, water-dependent herbivorous mammals were selected for analysis because tooth enamel in these animals mineralizes in isotopic equilibrium with body water, which is in turn in isotopic equilibrium with the surface waters that the mammals drink (Kohn, 1996). The isotopic values of surface water reflect general climate variables like temperature, precipitation, and humidity (Bryant and Froelich, 1995). Carbon isotopes in tooth enamel reflect sources of dietary carbon, and in the case of herbivores this reflects the metabolic pathway (C3 or C4) of the vegetation that is consumed. *Equus* (horse) and *Bison* (bison) were selected for analysis as they are grazers (though *Equus* may browse), they have hypsodont teeth that record at least 18 months of the life of the individual, and are abundant in the fossil record (Fricke and O'Neil, 1996; Passey and Cerling, 2002; Hoppe et al., 2004). Grasses may utilize either the C3 or C4 photosynthetic pathway, and the relative abundance of plants with each pathway should be evident in the diets of these large grazers. *Camelops*, a large browsing mammal, was also selected for analysis (when available) for and opposite end-member comparison with the grazers *Equus* and *Bison*. It is understood that *Equus* is not necessarily a dedicated grazer, and its diet may reflect some input from C3 browse; however its tall teeth are advantageous for the study of annual variations in $\delta^{18}\text{O}$ and thus are still included here. It is assumed that the teeth of *Equus* will show a lower percentage of C4 vegetation consumed than would those of co-occurring *Bison*. Fig. 1 shows the localities from which fossils were sampled for this research.

1.1. Oxygen isotopes, climate, and predictions

First-order variations in oxygen isotope ratios studied from meteoric and surface waters in terrestrial environments have been ascribed to environmental temperature changes, where warmer weather results in higher values of $\delta^{18}\text{O}$ and cooler weather results in lower values of $\delta^{18}\text{O}$ in meteoric water (McCrea, 1950; Bryant et al., 1996; Fricke and O'Neil, 1996; MacFadden et al., 1999; Feranec and

MacFadden, 2000). Another important factor affecting oxygen isotope ratios in meteoric waters, the "Amount Effect," is an important relationship among precipitation and humidity, temperature, and $\delta^{18}\text{O}$ (Dansgaard, 1964). The main result of the Amount Effect is that when environmental temperatures rise above a threshold of $\sim 20^\circ\text{C}$, and there is significant precipitation and/or high humidity, $\delta^{18}\text{O}$ decreases (Rozanski et al., 1993; Bard et al., 2002; IAEA/WMO, 2001; Straight et al., 2004; Higgins and MacFadden, 2004).

With this model for $\delta^{18}\text{O}$ variation, it is possible to predict the spatial arrangement of seasonal $\delta^{18}\text{O}$ values throughout North America during various times in the past. A simple latitudinal gradient is expected, with highest mean $\delta^{18}\text{O}$ values in the southernmost localities, and the lowest $\delta^{18}\text{O}$ values in the northernmost localities (e.g. MacFadden et al., 1999). In more northerly localities, the Amount Effect would be expected to be negligible or absent and a sinusoidal seasonal pattern for annual variation of $\delta^{18}\text{O}$ is predicted (Fig. 1). In more southern localities, temperatures may be warm enough to reach the Amount Effect threshold. Warmer temperatures would cause greater mean $\delta^{18}\text{O}$ in the south relative to more northern localities; however, warm-season rains could cause a decrease in $\delta^{18}\text{O}$ during the hottest times of the year (Rozanski et al., 1993; Higgins and MacFadden, 2004).

1.2. Carbon isotopes, vegetation, and predictions

Stable isotopes of carbon are fractionated in different proportions depending upon the photosynthetic pathway used by different plant species. Three photosynthetic pathways are utilized by plants: C3, C4, and CAM. C3 plants, which photosynthesize carbon using the Calvin Cycle, comprise $\sim 85\%$ of terrestrial plant biomass, and include most trees, shrubs, and high-elevation, high-latitude, and other cool-growing season grasses, have a mean $\delta^{13}\text{C}$ value of -27% , with a wide range from about -32 to -24% (Dienes, 1980; Farquahar et al., 1989; Boutton, 1991). In contrast, C4 plants, which photosynthesize carbon using the Hatch-Slack cycle, comprise about 5–10% of the terrestrial plant biomass and consist predominantly of temperate, sub-tropical, and tropical grasses. C4 vegetation is common in arid regions because such vegetation in general has greater water use efficiency (Ehleringer et al., 1997; Huang et al., 2001). C4 grasses also tend to dominate in regions where proportionally more precipitation falls in summer than in winter (Paruelo and Lauenroth, 1996; Epstein et al., 1997, 2002). C4 grasses characteristically have a mean $\delta^{13}\text{C}$ value of -13% with a narrow range between -15 and -11% . CAM plants, which in terrestrial communities include succulents (Cactaceae) and consist of a minor percentage ($\sim 5\%$) of global plant terrestrial biomass, exhibit a wide range of $\delta^{13}\text{C}$ values that can overlap between those seen in C3 and C4 plants (Dienes, 1980; Farquahar et al., 1989; Boutton, 1991). A general latitudinal gradient in the distribution of C3 and C4 plants, and therefore in $\delta^{13}\text{C}$, is predicted and has been recognized in North America (Teeri and Stowe, 1976; Paruelo and Lauenroth, 1996; Ehleringer et al., 1997), wherein lower $\delta^{13}\text{C}$ values are found at higher latitudes and higher $\delta^{13}\text{C}$ values are found at lower latitudes. The threshold at which C3/C4 plants are equally dominant is at about 35°N latitude (Ehleringer et al., 1997).

It is also known that C4 plants have a physiological advantage over C3 plants with lower atmospheric $p\text{CO}_2$ (Ehleringer et al., 1991, 1997). This advantage is potentially greater than the advantage that C3 plants over C4 with cooler weather (Cowling and Sykes, 1999). A pattern of decreasing atmospheric CO_2 concentration as glaciers advanced and increasing CO_2 concentration as glaciers receded has been noted for at least the last four glacial-interglacial episodes and probably for much of the Pleistocene (Raymo, 1992; Cowling, 1999; Cowling and Sykes, 1999; Olago et al., 1999). With this in mind, one might predict more C4 vegetation during glacial times than would otherwise be expected from temperature and moisture gradients alone. However, recent research has shown that climatic variables such as amount and timing of precipitation may overshadow the

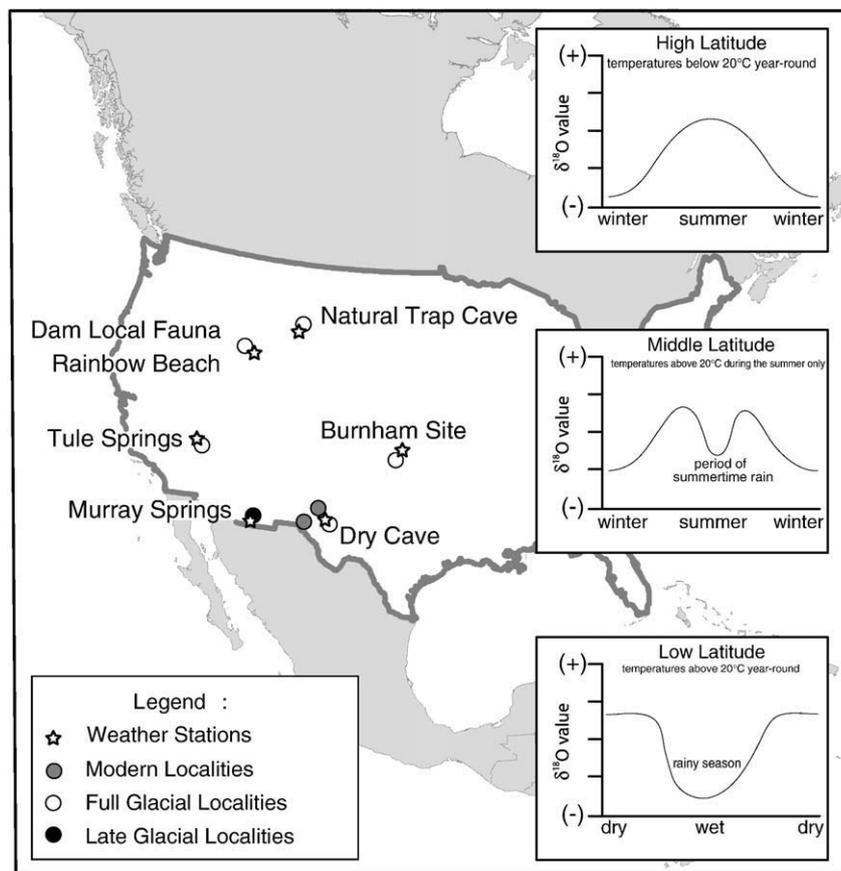


Fig. 1. Map of North America showing localities discussed in this paper. Open circles mark Full Glacial localities; closed circles mark Late Glacial localities; grey circles mark modern localities; stars mark approximate positions of weather stations used for MCM. The three graphs on the right side of the map are models of the seasonal changes in $\delta^{18}\text{O}$ values in meteoric waters depending upon latitude.

advantage of C4 metabolism even during times of low $p\text{CO}_2$ (Huang et al., 2001; Vidic and Montañez, 2004). Also, there are lower temperature and moisture thresholds at which C3 plants prevail over C4 vegetation, regardless of aridity and $p\text{CO}_2$ (Epstein et al., 1997; Zhang et al., 2003; Vidic and Montañez, 2004).

Plants are subdivided into plant functional groups (PFGs), wherein all the members of the group are physiologically and ecologically similar to one another (Paruelo and Lauenroth, 1996). The general distribution of PFGs in a region is related to environmental variables such as mean annual temperature (MAT), mean annual precipitation (MAP), and the seasonality of this precipitation (Paruelo and Lauenroth, 1996; Epstein et al., 1997, 2002). Only three PFGs are considered here when describing the predicted general flora of a region based upon climatic factors: C3 grasses, C4 grasses, and shrubs (which are typically C3). The distribution of other PFGs, such as forbs, graminoid herbs, and succulents, has a much smaller degree of correlation with changing climatic variables (Paruelo and Lauenroth, 1996).

1.3. Considering oxygen and carbon isotopes together

Consideration of both oxygen and carbon isotope data simultaneously, can potentially clarify predictions about climate patterns and expected vegetation. At 1997 levels of $p\text{CO}_2$ (~350 ppmv), a daytime growing-season temperature of ~21 °C or warmer will occur with a predominance of C4 plants (Ehleringer et al., 1997; Fig. 2). The Amount Effect temperature threshold at about 20 °C mean daily temperature (Rozanski et al., 1993) means that if the Amount Effect is evident for any modern site, C4 plants should dominate. During the Full Glacial, when atmospheric $p\text{CO}_2$ was about 195 ppmv (Monnin

et al., 2001), Ehleringer et al. (1997) predicted that C4 would dominate whenever daytime growing-season temperatures reach above ~13 °C, well below the Amount Effect threshold. During the Late Glacial ($p\text{CO}_2$ ~240 ppmv; Monnin et al., 2001), daytime temperatures should be about 17 °C before C4 plants dominate (Ehleringer et al., 1997). Therefore, the interpretation of C4 vegetation in Full Glacial or Late Glacial specimens from stable isotope data of teeth would not necessarily be associated with temperatures warm enough to result in a notable Amount Effect. The discovery of definitive C4 vegetation at places and times when the Amount Effect is not present would lend support to the hypothesis that atmospheric $p\text{CO}_2$ is an important control upon the distribution of C4 vegetation.

1.4. Tooth mineralization

Tooth enamel, dentine, and bone are composed of biogenic apatite often within a matrix of organic connective tissues. Of these tissues, enamel contains the least (<5%; Hillson, 2005) organic component. Teeth in vertebrates typically mineralize incrementally from the occlusal surface toward the root during development. Isotopes of oxygen and carbon, in equilibrium with the animal's environment, are incorporated into the enamel as it mineralizes (Rozanski et al., 1993; Fricke and O'Neil, 1996; Feranec and MacFadden, 2000; Bard et al., 2002; Straight et al., 2004; Higgins and MacFadden, 2004). Once mineralized, the isotopic composition of tooth enamel does not change during the life of the animal; the overall pattern of isotope ratios is even preserved after the animal dies and after the tooth is fossilized. An individual third molar of a horse may preserve a record of as much as three years (Hoppe et al., 2004). In contrast, *Bison* third molars typically record about 18 months of the animal's life (Fricke

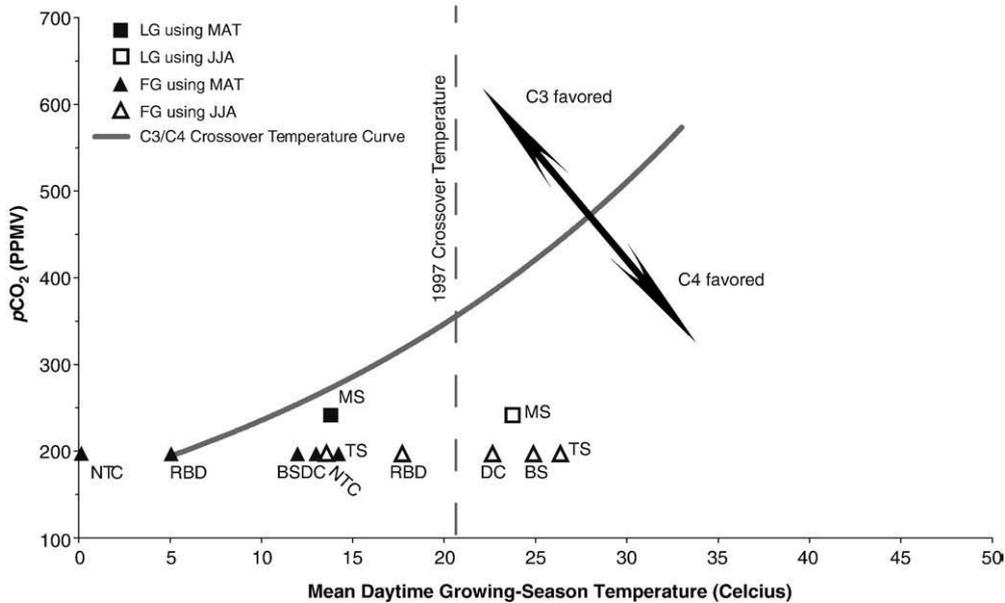


Fig. 2. Plot showing the relationship between the amount of atmospheric carbon dioxide, the mean daytime growing-season temperature, and the relative abundance of C3 and C4 vegetations (Ehleringer et al., 1997). Crossover curve is the NADP-me monocot line of Ehleringer et al. (1997). Plotted on this are each of the fossil localities discussed in this paper. NTC = Natural Trap Cave; DC = Dry Cave; MS = Murray Springs; RBD = Rainbow Beach and Dam localities; BS = Burnham Site; TS = Tule Springs. Open symbols are used where mean June, July, and August temperature is used as a proxy for daytime growing-season temperature. Closed symbols are used when MAT is used to estimate daytime growing-season temperature. The C3/C4 crossover temperature (at about 21 °C) is also shown for 1997 values of atmospheric carbon dioxide (~350 ppm; Ehleringer et al., 1997). If pCO₂ is an important control on the relative abundance of C4 vegetation, we would predict to see evidence for C4 from the localities plotting below the C3/C4 crossover curve and at temperatures less than 21 °C.

and O’Neil, 1996). Seasonal changes in isotopic values for oxygen and carbon preserved along the length of the tooth can be studied using serial analysis. Detailed discussions of the mineralization process in modern hoofed mammals are included in Passey and Cerling (2002), Hoppe et al. (2004), and Higgins and MacFadden (2004).

Oxygen isotopic enrichment from surface water to tooth enamel is a complex system dependent upon the sources of water (drinking vs. getting it from food), the metabolic processes within the animal, and upon how water is lost from the animal (e.g. excretion). For these reasons it is advantageous to use large animals, which: (1) consume most of their water through drinking (Bryant and Froelich, 1995; Kohn, 1996; Kohn et al., 1998; Higgins and MacFadden, 2004); and (2) also have a relatively constant body temperature. Large mammals, like horses, bison, and camels are ideal in this regard.

The carbon isotope signature of plant foods is incorporated into the biological apatite mineral phase of vertebrate teeth (Dienes, 1980; Farquhar et al., 1989; Boutton, 1991). Whereas the mean values of C3 and C4 plants are -27 and -13‰, respectively, the corresponding mean δ¹³C values carbon from tooth enamel for most herbivorous mammals are about 14.1 ± 0.5‰ more positive, as reported for medium sized terrestrial herbivores (Cerling and Harris, 1999). For example, a browser feeding on C3 plants will have a mean δ¹³C tooth enamel carbonate value of ~-13‰ whereas a C4 grazer will have a corresponding δ¹³C value of ~+1‰.

2. Methods

Twenty-one teeth of water-dependent, large-bodied herbivorous mammals (*Equus*, *Bison*, *Bootherium*, and *Camelops*) were selected for this study from Full Glacial through Late Glacial localities in western North America. All localities have associated radiometric dates, which were assumed to reflect calibrated ages if it was not otherwise specified. Seventeen of the 21 teeth were selected from Full Glacial localities. These include the high-latitude Dam Local Fauna (Idaho), high-latitude Rainbow Beach (Idaho), low-latitude mid-continental Burnham Site (Oklahoma), low-latitude mid-continental Dry Cave, Camel Room (New Mexico), low-latitude western Tule Springs

(Nevada), and high-latitude Natural Trap Cave (Wyoming). Only two teeth are from the Late Glacial low-latitude western Murray Springs (Arizona). Though it would have been ideal, it was not possible to find sufficient material from a single locality that spanned the Full Glacial into the Late Glacial. Two modern teeth, one from near Roswell, New Mexico and the other from El Paso, Texas were also analyzed. Approximate latitude and longitude for each locality were used to plot the relative percentages of C3, C4, and shrubby vegetation expected (Paruelo and Lauenroth, 1996).

Annual climate patterns for each locality were modeled using the macrophysical climate model of Bryson and DeWall (2007) and modern climatic data from weather stations nearest to each locality. Data of mean annual temperature and precipitation at the measured radiometric age were used to plot each site within the graph of the distribution of C3 and C4 vegetations according to MAT and MAP of Epstein et al. (1997). Percent C4 grass was also calculated using modeled temperature and precipitation (Bryson and DeWall, 2007) using the following equation from Paruelo and Lauenroth (1996, Fig. 3

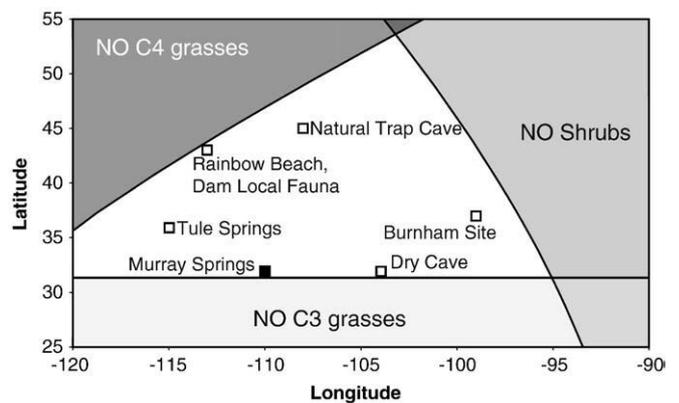


Fig. 3. Modeled distribution of C3 grasses, C4 grasses and shrubs in North America as related to latitude and longitude of Paruelo and Lauenroth (1996). The positions of Full Glacial (filled squares) and Late Glacial (open squares) localities used in this study are plotted.

caption; also in Epstein et al., 2002). Note that this equation does not include a term for pCO_2 :

$$\text{Proportion of C4 grasses} = -0.984 + (0.000594 * \text{MAP}) + (1.35 * \text{JJA} / \text{MAP}) + (0.271 * (\ln \text{MAT})). \quad (1)$$

Higgins and MacFadden (2004) describe the serial sampling and isotopic analysis techniques used here. Powdered samples were chemically treated to ensure that only pure biological apatite was analyzed. Samples were first treated with H_2O_2 , to remove any organic contaminants, and then with weak (0.1 N) acetic acid to remove any surficial carbonate, in preparation for analysis in the mass spectrometer (also see Higgins and MacFadden, 2004). All samples, except those from SBCM L3088-6, were analyzed using the VG Prism isotope ratio mass spectrometer, using a common acid bath, available in the Department of Geological Sciences at the University of Florida. Samples from SBCM L3088-6 were analyzed using a ThermoFinnigan Delta Plus XP mass spectrometer, with a Gasbench inlet device, in the Department of Earth and Environmental Sciences at the University of Rochester. About 1–2 mg of sample is needed for each analysis. Isotopic data are reported in the conventional delta (δ) notation, where $\delta^{18}O$ (parts per mil, ‰) = $(R_{\text{sample}}/R_{\text{standard}}) - 1$ 1000, and $R = {}^{18}O/{}^{16}O$. All data ($\delta^{18}O$ and $\delta^{13}C$) are reported in ‰ V-PDB (Coplen, 1994). Typical 1-sigma error for carbon and oxygen analyses is 0.10‰. Parametric ANOVA and non-parametric Kruskal–Wallis statistics were used to compare similarity of mean isotopic value among different individual teeth, based upon similar age, latitude, or taxon.

Oxygen isotopic results were compared to predicted patterns of isotopic variation based upon modeled temperature and precipitation (Higgins and MacFadden, 2004). Using the mean carbon isotopic values from each tooth, the percent of C4 vegetation consumed by the animal was calculated using the equation from Koch et al. (2004):

$$(100)\delta^{13}C_{\text{fossil enamel}} = (1-X)\delta^{13}C_{\text{pure C3 enamel}} + (X)\delta^{13}C_{\text{pure C4 enamel}} \quad (2)$$

where X is the proportion of C4 vegetation in the diet of the animal and $\delta^{13}C_{\text{pure C3 enamel}}$ and $\delta^{13}C_{\text{pure C4 enamel}}$ represent the isotopic value of enamel if the animal had a pure C3 or pure C4 diet, respectively. Values for $\delta^{13}C_{\text{pure C3 enamel}}$ and $\delta^{13}C_{\text{pure C4 enamel}}$ used in these calculations are those for LGM (Koch et al., 2004, their Table 1) taking into account known differences in the $\delta^{13}C$ of atmospheric carbon dioxide between the modern world and that at the end of the most recent glaciation. These percentages were compared to the predictions of proportions of C4 vegetations made using the model of Bryson and DeWall (2007) and equations of Paruelo and Lauenroth (1996).

3. Results and discussion

A total of 336 individual analyses were made from samples collected from the 21 teeth used in this study (an average of about 16 samples per tooth). Values for each sample, by specimen number and position along tooth, are provided in the Supplementary data. Univariate statistics for each tooth are provided in Table 1.

Different taxa and localities were compared first with parametric (ANOVA) statistics, provided in Table 2. Non-parametric (Kruskal–Wallis) statistics were also calculated and are provided in Table 3. The results are discussed in the following sections.

Table 1
Sample statistics for specimens used in this study.

Specimen number	Taxon	Tooth position	Number of samples (N)	$\delta^{13}C$ V-PDB					$\delta^{18}O$ V-PDB					Corr. coeff. $\delta^{13}C$ to $\delta^{18}O$
				Mean	St dev	Max	Min	Rge	Mean	St dev	Max	Min	Rge	
<i>Glacial sites</i>														
Dam Local Fauna, ID, 43N 113W														
IMNH 52002/27672	Bison	Rm3	16	-10.5	0.3	-10.1	-11.1	1.0	-11.1	2.0	-7.5	-13.9	6.4	-0.37
IMNH 52002/1172	Equus	LM3	20	-10.6	0.3	-9.7	-11.1	1.4	-10.3	1.1	-8.3	-11.9	3.7	0.27
IMNH 52002/2199	Camelops	RM3	19	-5.6	0.7	-4.4	-7.1	2.7	-8.9	1.1	-6.9	-10.9	4.1	0.05
Rainbow Beach, ID, 43N 113W														
IMNH 72003/23772	Equus	Rm3	23	-10.6	0.3	-10.0	-11.0	1.0	-10.9	1.2	-7.7	-12.1	4.5	0.13
IMNH 50001/16939	Camelops	Rm3	23	-8.9	0.3	-8.4	-9.4	1.0	-10.9	0.8	-9.3	-12.2	2.9	0.25
Burnham Site, OK, 36.5N 99W														
UOK 511	Bison	m3	17	-1.1	0.7	0.2	-2.1	2.3	-2.8	0.9	-1.7	-4.2	2.6	0.00
UOK 610b	Equus	m3	29	-5.6	0.5	-4.7	-7.1	2.4	-5.0	1.5	-2.0	-7.7	5.8	0.56
Tule Springs, NV, 36N 115W														
SBCM L3088-6	Bison	M3	9	-5.3	2.2	-2.5	-9.3	6.8	-3.4	1.0	-2.1	-5.0	2.9	-0.79
SBCM L3988-311	Equus		12	-5.9	0.4	-5.4	-6.5	1.1	-6.2	0.4	-5.7	-6.9	1.2	-0.78
SBCM L3988-388C	Camelops		7	-7.8	0.4	-7.4	-8.4	1.0	-6.5	0.5	-5.6	-7.0	1.4	-0.50
Dry Cave, Camel Room, NM, 32N 104W														
UTEP 25-543	Bison	LM3	13	-5.9	0.6	-4.9	-6.8	2.0	-10.9	0.8	-9.4	-12.5	3.0	-0.09
UTEP 25-537	Equus	RM3	15	-3.8	1.7	-1.6	-7.2	5.5	-5.5	1.4	-3.5	-8.7	5.3	0.32
Natural Trap Cave, WY, 45N 108W														
KU 44827	Bison		7	-8.1	0.2	-7.9	-8.3	0.4	-15.3	0.6	-14.5	-16.3	1.8	0.35
KU 52966	Equus	m3	22	-8.8	0.6	-6.6	-9.5	2.9	-13.2	1.8	-7.9	-15.8	7.8	0.10
KU 326	Equus	m3	19	-9.4	0.4	-8.6	-9.8	1.2	-12.5	1.2	-10.1	-14.2	4.1	-0.55
KU 61635	Bootherium		5	-9.3	0.1	-9.1	-9.5	0.4	-14.0	0.8	-12.7	-14.6	2.0	0.20
KU 44029	Camelops		9	-9.1	0.2	-8.7	-9.4	0.7	-12.3	0.9	-11.2	-13.6	2.4	-0.69
<i>Late glacial sites</i>														
Murray Springs, AZ, 32N 110W														
UALP uncatalogued	Bovidae	m3	19	0.3	1.0	1.9	-1.4	3.3	-4.1	1.9	-1.0	-7.2	6.2	-0.32
UALP 3433	Equus	LM3	16	-0.7	0.5	0.3	-1.8	2.1	-3.9	0.7	-2.6	-5.0	2.4	-0.55
<i>Modern sites</i>														
Near Roswell, NM, 33N 105W														
UTEP 6381	Bos	M3	16	-7.3	2.1	-4.1	-10.1	6.1	-4.0	0.7	-3.0	-5.6	2.6	0.02
El Paso, TX, 32N 106W														
UTEP 5167	Equus	M3	20	-8.4	2.1	-5.2	-11.3	6.1	-2.8	2.3	-0.1	-8.8	8.7	0.06

Table 2
Parametric (ANOVA) comparisons of means based on data in Appendix A. SIG = significantly different; NS = not significant, i.e. similar means. B = Burnham Site; DC = Dry Cave; ID = Idaho localities Rainbow Beach and Dam; MS = Murray Springs; NTC = Natural Trap Cave; TS = Tule Springs.

Means compared	$\delta^{13}\text{C}$			$\delta^{18}\text{O}$				
	F obs	p value	F crit	F obs	p value	F crit		
Full Glacial Northern Sites (ID, NTC)								
<i>Bison</i> only	461.00	$p \ll 0.001$	4.32	SIG	29.83	$p \ll 0.001$	4.32	SIG
<i>Equus</i> only	99.34	$p \ll 0.001$	2.72	SIG	20.40	$p \ll 0.001$	2.72	SIG
<i>Camelops</i> only	286.64	$p \ll 0.001$	3.19	SIG	43.81	$p \ll 0.001$	3.19	SIG
Full Glacial vs. Late Glacial Southern Sites (TS, B, MS, DC)								
<i>Bison</i> from all localities	107.89	$p \ll 0.001$	2.78	SIG	111.09	$p \ll 0.001$	2.78	SIG
<i>Bison</i> from TS and MS	91.38	$p \ll 0.001$	4.23	SIG	0.88	$p \sim 0.4$	4.23	NS
<i>Bison</i> from TS and DC	0.70	$p \sim 0.4$	4.35	NS	353.63	$p \ll 0.001$	4.35	SIG
<i>Equus</i> from all localities	124.00	$p \ll 0.001$	2.74	SIG	9.73	$p \ll 0.001$	2.74	SIG
<i>Equus</i> from TS and MS	831.64	$p \ll 0.001$	4.23	SIG	98.67	$p \ll 0.001$	4.23	SIG
<i>Equus</i> from TS and DC	17.22	$p \ll 0.001$	4.24	SIG	2.67	$p \sim 0.1$	4.24	NS
Full Glacial Northern Sites (ID)								
All specimens of all taxa from ID	540.31	$p \ll 0.001$	2.47	SIG	9.47	$p \ll 0.001$	2.47	SIG
All taxa except <i>Camelops</i>	0.78	$p \sim 0.5$	3.16	NS	1.42	$p \sim 0.2$	3.16	NS
<i>Camelops</i> only	413.82	$p \ll 0.001$	4.08	SIG	43.28	$p \ll 0.001$	4.08	SIG
Full Glacial Southern Sites (TS and B)								
All specimens of all taxa	102.44	$p \ll 0.001$	2.51	SIG	27.29	$p \ll 0.001$	2.51	SIG
All specimens from B	588.39	$p \ll 0.001$	4.06	SIG	31.18	$p \ll 0.001$	4.06	SIG
All specimens from TS	9.01	$p \sim 0.001$	3.39	SIG	48.20	$p \ll 0.001$	3.39	SIG
<i>Bison</i> from B and TS	55.19	$p \ll 0.001$	4.26	SIG	2.74	$p \sim 0.1$	4.26	NS
<i>Equus</i> from B and TS	2.99	$p \sim 0.09$	4.09	NS	7.42	$p \ll 0.001$	4.09	SIG
Full Glacial Northern Site (NTC)								
All specimens of all taxa	14.78	$p \ll 0.001$	2.53	SIG	7.11	$p \ll 0.001$	2.53	SIG
All taxa except <i>Bison</i>	6.86	$p \ll 0.001$	2.79	SIG	2.50	$p \sim 0.07$	2.79	NS
<i>Equus</i> only	15.84	$p \ll 0.001$	4.09	SIG	2.22	$p \sim 0.1$	4.09	NS

3.1. Plant functional types modeled by geographic position

Paruelo and Lauenroth (1996) established a basic relationship between latitude, longitude, and general vegetation form (C4, C3, and shrub), for modern environments in North America (Fig. 3). Based upon their criteria, one would expect that the most southern localities would be dominated by C4 and shrubby vegetation, with Dry Cave

having relatively more C4 vegetation than Murray Springs. The most northern localities would be dominated by C3 grasses and shrubs. Localities at middle latitudes (Tule Springs and Burnham Site) would have a mixture of all three vegetation types, with the Burnham Site having proportionately less shrubs, because it lies furthest to the East (Paruelo and Lauenroth, 1996). Paruelo and Lauenroth (1996) showed that the geographical coordinates of any particular site explained

Table 3
Non-parametric (Kruskal–Wallis) comparisons of means based on data in Appendix A. SIG = significantly different; NS = not significant, i.e. similar means. B = Burnham Site; DC = Dry Cave; ID = Idaho localities Rainbow Beach and Dam; MS = Murray Springs; NTC = Natural Trap Cave; TS = Tule Springs.

Means compared	$\delta^{13}\text{C}$			$\delta^{18}\text{O}$				
	H obs	p value	H crit	H obs	p value	H crit		
Full Glacial Northern Sites (ID, NTC)								
<i>Bison</i> only	14.000	$p \sim 0$	3.84	SIG	14.000	$p \sim 0$	3.84	SIG
<i>Equus</i> only	65.615	$p \ll 0.001$	7.81	SIG	40.913	$p \ll 0.001$	7.81	SIG
<i>Camelops</i> only	37.079	$p \ll 0.001$	5.99	SIG	33.470	$p \ll 0.001$	5.99	SIG
Full Glacial vs. Late Glacial Southern Sites (TS, B, MS, DC)								
<i>Bison</i> from all localities	46.186	$p \ll 0.001$	7.81	SIG	32.697	$p \ll 0.001$	7.81	SIG
<i>Bison</i> from TS and MS	19.862	$p \ll 0.001$	3.84	SIG	19.862	$p \ll 0.001$	3.84	SIG
<i>Bison</i> from TS and DC	14.117	$p \sim 0$	3.84	SIG	3.438	$p \sim 0.6$	3.84	NS
<i>Equus</i> from all localities	49.936	$p \ll 0.001$	7.81	SIG	23.167	$p \ll 0.001$	7.81	SIG
<i>Equus</i> from TS and MS	17.690	$p \ll 0.001$	3.84	SIG	0.509	$p \sim 0.5$	3.84	NS
<i>Equus</i> from TS and DC	2.258	$p \sim 0.1$	3.84	NS	15.269	$p \ll 0.001$	3.84	SIG
Full Glacial Northern Sites (ID)								
All specimens of all taxa from ID	78.871	$p \ll 0.001$	9.49	SIG	27.759	$p \ll 0.001$	9.49	SIG
All taxa except <i>Camelops</i>	1.874	$p \sim 0.4$	5.99	NS	3.636	$p \sim 0.2$	5.99	NS
<i>Camelops</i> only	30.488	$p \ll 0.001$	3.84	SIG	21.738	$p \ll 0.001$	3.84	SIG
Full Glacial Southern Sites (TS and B)								
All specimens of all taxa	50.442	$p \ll 0.001$	9.49	SIG	42.383	$p \ll 0.001$	9.49	SIG
All specimens from B	31.470	$p \ll 0.001$	3.84	SIG	20.407	$p \ll 0.001$	3.84	SIG
All specimens from TS	12.632	$p \sim 0.002$	5.99	SIG	18.171	$p \sim 0$	5.99	SIG
<i>Bison</i> from B and TS	17.000	$p \ll 0.001$	3.84	SIG	1.281	$p \sim 0.3$	3.84	NS
<i>Equus</i> from B and TS	4.376	$p \sim 0.04$	3.84	SIG	6.359	$p \sim 0.01$	3.84	SIG
Full Glacial Northern Site (NTC)								
All specimens of all taxa	23.623	$p \ll 0.001$	9.49	SIG	33.579	$p \ll 0.001$	9.49	SIG
All taxa except <i>Bison</i>	10.458	$p \sim 0.02$	7.81	SIG	20.699	$p \sim 0$	7.81	SIG
<i>Equus</i> only	15.379	$p \ll 0.001$	3.84	SIG	2.713	$p \sim 0.1$	3.84	NS

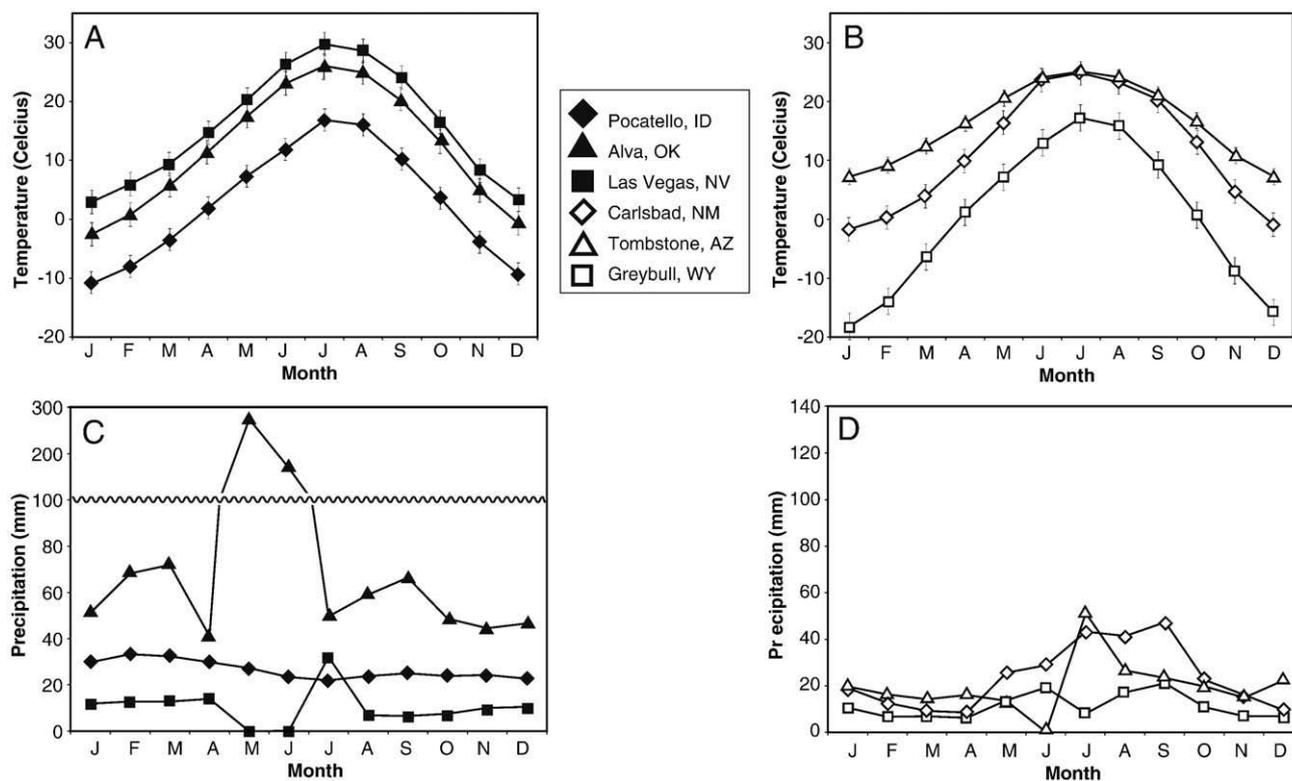


Fig. 4. Modeled temperature and precipitation from the MCM for Full Glacial and Late Glacial sites. Models were compiled using modern long-term weather data for cities and towns near the fossil localities as follows: Rainbow Beach and Dam Local Fauna: Pocatello, ID; Burnham Site: Alva, OK; Tule Springs: Las Vegas, NV; Dry Cave: Carlsbad, NM; Murray Springs: Tombstone, AZ; Natural Trap Cave: Greybull, WY. Error bars plotted for temperature are the Standard Error reported by the MCM. Standard error for precipitation results in error bars much smaller than the symbols used in the plot (refer to Table 4). Symbols representing each locality are the same as in Fig. 8.

about 61% of the variability of C4 grasses (Paruelo and Lauenroth, 1996, Fig. 2 caption):

$$\text{Proportion of C4 vegetation} = 15.9339 - 3.2460 * (\ln(\text{longitude})) - 0.0003072 * (\text{latitude})^2 \quad (3)$$

3.2. Plant functional types estimated by macrophysical climate model

Using published calibrated radiocarbon dates (calibrated years BP), modern historical data from weather stations nearest the locality, and the MCM of Bryson and DeWall (2007), we model mean monthly temperature and mean monthly precipitation for each locality at the point in the past when the sampled mammals were alive (Fig. 4). There are five localities representing Full Glacial times and one locality representing Late Glacial times. The modeled climate for each locality includes some error, which is estimated by the MCM as an R^2 value (indicating the fit of modeled results for the modern to observed modern values) and a standard error (provided in Table 4).

At first glance, it appears that the predicted Late Glacial conditions (from Murray Springs) are generally the same temperature as those from Full Glacial sites, calling to question the correctness of the MCM. However, when one compares the modeled temperatures at each site for the Full Glacial (18,000 years ago) and the Late Glacial (12,000 years ago), the Full Glacial temperatures are always cooler as expected. It appears that earlier in glacial times, the temperatures were warmer than they were at the peak of the LGM (17,000–15,000 calibrated years ago).

The most northerly fossil localities (Natural Trap Cave, Rainbow Beach, and Dam Local Fauna) have modeled temperatures much cooler than the more southerly localities from the same time periods, with mean monthly temperatures low enough that no Amount Effect is predicted. The Late Glacial Northern Site, Natural Trap Cave, appears to have experienced a much greater range of annual temperature than the Full Glacial sites in Idaho. The northerly localities also were fairly dry, experiencing much less than 40 mm of precipitation per month during the year.

The more southerly sites (Tule Springs, Murray Springs, Dry Cave and the Burnham Site) do appear to have had temperatures warm

Table 4

Modeled temperature and precipitation values from the MCM and their associated error for individual localities. Both mean annual temperature (MAT) and mean June, July, and August (JJA) temperatures are provided for reference.

Locality	Weather station	Length of record	Age cal yrs BP	Age bin	Modeled temperature				Modeled precipitation		
					MAT	JJA	R^2	SE	MAP	R^2	SE
Rainbow Beach and Dam	Pocatello, ID	68 years	31,300	FG	5.08	17.68	0.97	1.91	344.23	0.95	0.08
Tule Springs	Las Vegas, NV	70 years	30,000	FG	14.18	26.32	0.96	1.98	126.35	0.95	0.11
Burnham Site	Alva, OK	29 years	27,600	FG	12.00	24.85	0.97	2.04	780.83	0.90	0.30
Dry Cave	Carlsbad, NM	108 years	21,000	FG	13.00	22.59	0.95	2.00	284.06	0.89	0.31
Natural Trap Cave	Greybull, WY	57 years	17,500	FG	-0.51	13.58	0.94	2.19	154.28	0.88	0.22
Murray Springs	Tombstone, AZ	115 years	12,800	LG	13.77	23.69	0.97	1.36	238.53	0.96	0.24

Table 5
Abundances of various plant functional groups (PFG) calculated from average isotopic values of fossil *Bison* teeth and environmental parameters calculated from MCM results. Negative calculated percentages are considered 0%, and percentages calculated to be above 100% are listed only as 100%. Koch et al. (2004) cite potential error of up to 10% for calculations of relative abundance of C4 vegetation using carbon isotopes from tooth enamel. Note that in all cases, tooth enamel isotopes overestimate the amount of C4 grass available.

	Relative abundance of C4	Percent abundance of PFG using MCM results					C4 predictions	
		C3 grass	C4 grass	Shrubs	Total	Interpretation	MAT	JJA
Rainbow Bridge and Dam	14%	56%	2%	40%	99%	C3 grassland	No	Yes
Tule Springs	48%	10%	1%	80%	91%	Shrubland	Yes	Yes
Burnham Site	77%	9%	63%	9%	105%	C4 grassland	Yes	Yes
Dry Cave	45%	23%	42%	28%	93%	C4 grassland	Yes	Yes
Natural Trap Cave	30%	39%	0%	49%	89%	Mixed C3 shrubland/grassland	No	No
Murray Springs	86%	30%	31%	49%	110%	Mixed grassland	No	Yes
References	Koch et al. (2004)	Paruelo and Lauenroth (1996); Epstein et al. (1997)					Ehleringer et al. (1997); Collatz et al. (1998)	

enough for an Amount Effect, if precipitation were to occur at the warmer times of year. The more western sites, Tule Springs and Murray Springs, appear to have been both warmer and drier than the more eastern sites, Dry Cave and the Burnham Site. In fact, the Burnham Site appears to have been much wetter than the other sites, with spring and early summer rains amounting to 200 mm or more of precipitation per month (Fig. 4).

Paruelo and Lauenroth (1996) describe the relationship between abundance of C4 vegetation and MAT, MAP, and the proportion of summertime precipitation (Eq. (1), above). This relationship accounts for 66% of the variability in measured C4 abundance (Paruelo and Lauenroth, 1996). Having proportionately more summer (June, July, and August, abbreviated JJA) rain increases the abundance of C4 vegetation relative to C3 grasses and shrubs (Paruelo and Lauenroth, 1996; Epstein et al., 1997, 2002). Calculated abundances of C4 vegetation, using modeled monthly estimations of precipitation, are in Table 5. Occasionally C4 abundances were greater than 100% or less than 0%. These curious results have two potential origins: 1) the localities studied lie within the 34% of variance not explained by the equation of Paruelo and Lauenroth (1996); and/or 2) the localities have climate variables outside of the range studied by Paruelo and Lauenroth (1996). In Table 4, calculated abundances greater than 100% are listed as 100%. Calculated abundances of less than 0% are listed as 0%. Epstein et al. (1997, 2002) take this one step further and develop relationships between MAT, MAP, the seasonal distribution of precipitation, and the relative and absolute productivities of C3, C4, and shrubby vegetation. Predicted abundances of C3 and C4 vegetation types are illustrated visually in Fig. 5.

3.3. Isotopic data

Isotopic results are provided in Table 1 and Supplementary data. Using only the mean isotopic value from the teeth of *Bison*, an obligate grazer, we calculate the approximate percent C4 vegetation available in the environment (Koch et al., 2004, Eq. (1); Table 5). Koch et al. (2004) note that due to the range of delta values for carbon in C3 and C4 plants, there is an inherent 5–10% error in this calculation. It is also important that we are certain that CAM plants are not being consumed by the mammals being studied. We are confident that the *Equus* and *Bison* studied do not include CAM vegetation in their diets. We also assumed that *Camelops*, when studied, also did not feed on CAM vegetation. However, *Camelops* often yields spurious results compared to coeval *Equus* and *Bison* which leads us to suspect that there is another component to their diet and that this component may be CAM vegetation.

The calculated percentage of C4 vegetation is compared with modeled percentages of C4 (discussed above). The approximate dietary C4 for the other mammal taxa is also calculated, to examine the potential breadth of PFGs in a given area at a given time. The serial oxygen isotopic data will be discussed in terms of annual patterns, especially the predicted presence or absence of the Amount Effect.

3.3.1. Full Glacial Northern Sites: Dam Local Fauna and Rainbow Beach, Idaho (43°N 113°W)

For the highest latitude Full Glacial faunas used in this study (43°N), isotopic $\delta^{13}C$ values are relatively low, about -10.5% for *Bison* (with a total range from -11.1 to -10.1%), indicating a diet of dominantly C3 grasses (Fig. 6_A), comprised of perhaps 14% C4 vegetation (Koch et al., 2004). This is in general agreement with the simple model for PFG according to geographic position (Paruelo and Lauenroth, 1996), calculated abundances using equations in Epstein et al. (1997) which predict 6% or less C4 vegetation. This also agrees with the predicted abundance of C4 at low temperatures and low atmospheric CO_2 (Ehleringer et al., 1997).

Average $\delta^{13}C$ values of *Equus* from the Dam Local Fauna and Rainbow Beach are not significantly different from those of *Bison* (Tables 2 and 3). *Camelops*, however, is significantly different in $\delta^{13}C$ from both *Equus* and *Bison*. The differences between *Camelops*, a browser, and *Bison* and *Equus*, grazers, indicate potential resource partitioning, including preference for any C4 or CAM vegetation that may have been available.

Mean $\delta^{18}O$ values for all Dam Local Fauna and Rainbow Beach specimens range from -11.1 to -8.9% (with a total range from -13.9 to -6.9%). A fairly strong sinusoidal signal of seasonal change is preserved in the teeth, with no obvious evidence of the Amount Effect (Fig. 6_A). This is in accordance with the MCM for Pocatello, ID at Full Glacial times. Mean monthly temperatures only once make it above 20 °C (barely: 21 °C), and precipitation tends to be relatively uniform during the year, so there is no reason to expect an obvious Amount Effect.

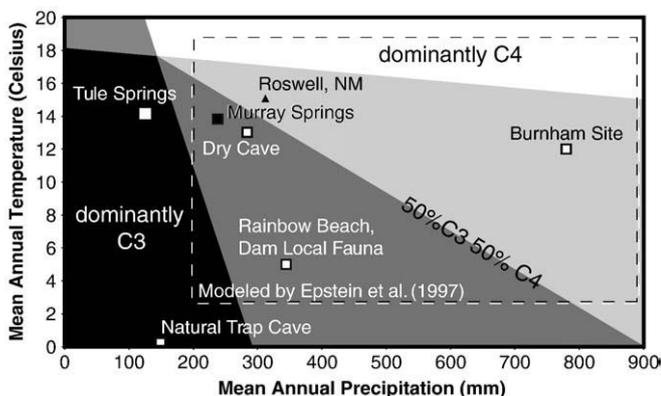


Fig. 5. Simplified diagram from Epstein et al. (1997) showing the distribution of C3 and C4 vegetations with respect to mean annual temperature (MAT) and mean annual precipitation (MAP). Dashed box outlines the ranges of MAT and MAP modeled by Epstein et al. (1997). Each of the fossil localities is plotted based upon modeled ancient values of MAT and MAP using the MCM (Bryson and DeWall, 2007). Open circles mark Full Glacial localities; closed circles mark Late Glacial localities.

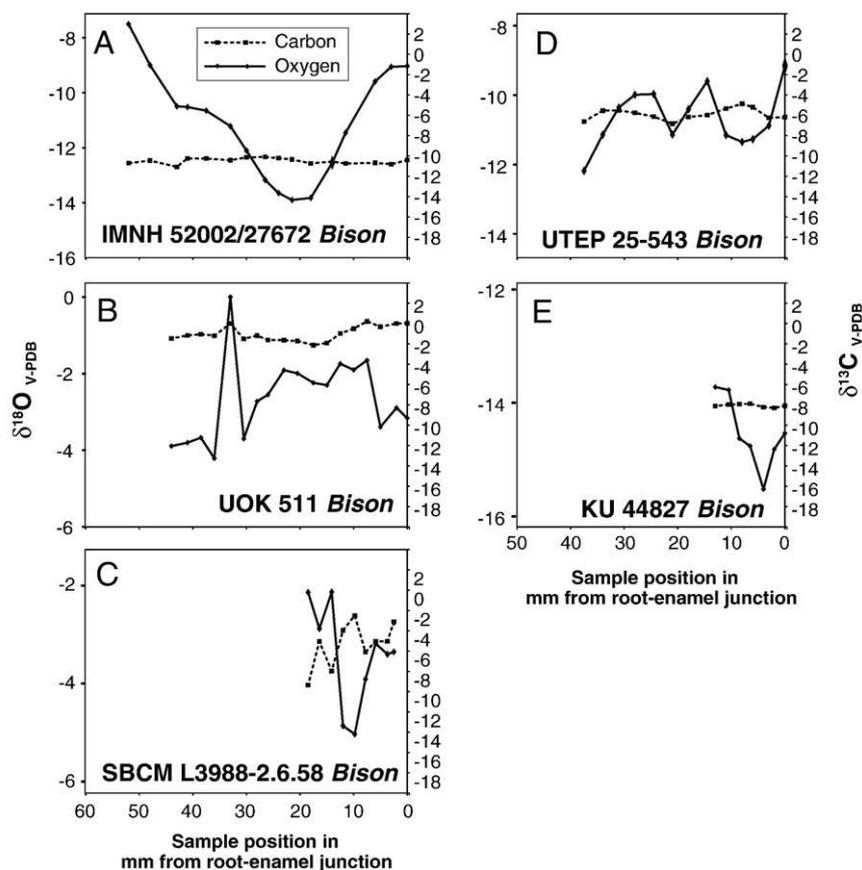


Fig. 6. Serial analyses from *Bison* for all Full Glacial aged sites. Oxygen and carbon data are plotted together with separate y-axes. Left axis is for oxygen data; right axis is for carbon data. A: *Bison* from Dam Local Fauna, ID. B: *Bison* from Burnham Site, OK. C: *Bison* from Tule Springs, NV. D: *Bison* from Dry Cave, NM. E: *Bison* from Natural Trap Cave, WY.

3.3.2. Full Glacial Southeastern Site: Burnham Site, OK (36.5°N 99°W)

C4 grasses clearly dominated the Burnham Site, where *Bison* has an average $\delta^{13}\text{C}$ value of -1.1 (with a range from -2.1 to 0.2% ; Fig. 6_B), meaning the diet of *Bison* was comprised of about 77% C4 vegetation (Koch et al., 2004). The calculated abundance of C4 grasses using modeled climatic data is 63% (Table 5), with essentially the rest of the flora being comprised of C3 grasses (Paruelo and Lauenroth, 1996; Epstein et al., 1997). On the basis of modeled temperature and glacial $p\text{CO}_2$, C4 vegetation is also presumed to be abundant (Ehleringer et al., 1997; Collatz et al., 1998).

Of the six localities examined in this study, the Burnham Site has the greatest modeled annual precipitation, at 778 mm per year. The majority of this precipitation falls during the summer months (May through August) and peaks in June. Mean monthly temperatures for May through September are modeled to fall above the Amount Effect threshold of 20°C . Therefore, an obvious Amount Effect in serial oxygen data is predicted. However, the Amount Effect is not evident in the oxygen isotopic data (Fig. 6_B). This is perhaps due to the fact that the greatest rain occurs only at the very beginning of the hottest part of the summer (Fig. 4), leaving the rest of the summer with lower precipitation and therefore modulating the Amount Effect.

3.3.3. Full Glacial Southwestern Site: Tule Springs, NV (36°N 115°W)

Isotopic results from *Bison* from Tule Springs (SBCM L3088-6), indicate that C4 grasses comprised only about 48% of their diet (Koch et al., 2004; Fig. 6_C). Predicted productivity from C4 vegetation (Paruelo and Lauenroth, 1996; Epstein et al., 1997) is significantly lower, predicting a landscape dominated by shrubby vegetation with little to no C4 grass (Table 5). This discrepancy may be due to *Bison* selectively grazing on what little C4 grass is available, ignoring the shrubby vegetation. Epstein et al. (2002) would predict no C4 grass at

all, however, their modeled results account for only about 91% of the total vegetation. Perhaps the rest is all C4 grass and this is what *Bison* was eating. It is worth noting that carbon isotopic results from *Bison* show a high degree of variation (6.8%; Table 1, Fig. 6_C). The source of this variability is uncertain, but could be due to seasonal changes in plant abundances or dietary preferences, or due to migratory movements of the *Bison*. More work is needed to understand this variation.

It is also informative to examine the diets of other large herbivorous mammals that are not obligate grazers that lived at the same time. *Equus*, capable of browsing and grazing, also shows a strong component of C4 vegetation in its diet. *Camelops* shows much less C4 in its diet, likely reflecting its browsing habits. In all three cases, however, there is some component of C4 vegetation that is not accounted for by models based only on climate or geographic position.

One potential explanation for the presence of C4 vegetation when little to none was predicted is the low $p\text{CO}_2$ postulated to have existed during glacial events (Ehleringer et al., 1991; Raymo, 1992; Ehleringer et al., 1997; Cowling, 1999; Cowling and Sykes, 1999; Olago et al., 1999; Fig. 2). Tule Springs during the Full Glacial was definitely warm enough to support C4 vegetation (Ehleringer et al., 1997; Collatz et al., 1998), but conditions were very dry with only a small spike of increased precipitation occurring in summer (32 mm in July), according to the MCM of Bryson and DeWall (2007; Fig. 4). Perhaps the better water use efficiency of C4 plants also played an important role in their dominance at Tule Springs (Huang et al., 2001). Modeled climate variables for Tule Springs plot in part of the graph (high MAT and low MAP) of Epstein et al. (1997) that was not well represented by real floras in that study.

Our specimen of *Equus* appears to have preserved part of the annual cycle of oxygen isotopes that might include the summer, but

the range in variation of $\delta^{18}\text{O}$ is only 1.1‰ for the whole tooth. Looking at modern data from Waco Texas (see Fig. 9 in Higgins and MacFadden, 2004) a change of at least 2‰ occurring over the span of what would be only a few months (10 to 20 mm along a *Bison* m3; Higgins and MacFadden, 2004) would be a more compelling argument for an obvious Amount Effect. This is what we observe from the *Bison* m3 sampled from Tule Springs (Fig. 6_C). There appear to be two peak times for precipitation recorded in this tooth. Comparing this with the MCM, we correlate one with precipitation in the late spring (May) and the next with the return of late summer and winter precipitation in August. So at least during the lifetime of this *Bison*, there may have been sufficient summertime precipitation to support a more dominant C4 plant population, and perhaps we do not need to call on decreases in atmospheric $p\text{CO}_2$ to explain the abundance of C4 plants at that time.

3.3.4. Full Glacial Southeastern Site: Dry Cave, NM (32°N 104°W)

The fauna near Dry Cave experienced warm temperatures which seldom fell below freezing and moderate amounts of summertime rain (JJA ~70 mm). We therefore might expect a recognizable amount of C4 grass in the plant biomass. Using the modern distribution of PFGs as a guide (Paruelo and Lauenroth, 1996), we would expect to see essentially no C3 grasses in an environment dominated by C4 grasses and shrubby vegetation. Using the results of the MCM with the work of Epstein et al. (1997, 2002), we can estimate that about 42% of the plant biomass was probably C4 grass. Equations in Epstein et al. (2002) can be used to further estimate that there should have been about 28% shrubs and 23% C3 grasses (the rest of the flora presumably being comprised of other PFGs). Average carbon isotopic values from a *Bison* tooth (UTEP 25-543; -5.9‰), suggest that 45% of the *Bison* diet was comprised of C4 vegetation. An average of -3.8‰ from the tooth of *Equus* (UTEP 25-537), indicates that the horse ate about 56% C4 forage.

Because of the warm temperatures and summertime rain, an obvious Amount Effect is expected. Given also that most of the predicted precipitation occurs during the hottest point of the year, one might expect the $\delta^{18}\text{O}$ pattern to appear “scalped,” with the values of $\delta^{18}\text{O}$ decreasing during the summer, due to higher levels of precipitation, rather than increasing due to warmer temperatures. In *Bison*, a pattern of increasing and decreasing $\delta^{18}\text{O}$ is observed, with approximately twice the frequency that would be expected based upon mineralization rates and a simple sinusoidal pattern due to annual temperature variation (Fig. 6_D). We assert that the oxygen isotopic signal representing a year is comprised of two minima in the $\delta^{18}\text{O}$ pattern. One represents the cool weather of winter, and the other represents the rainy summer season.

3.3.5. Last Glacial Maximum Northern Site: Natural Trap Cave, WY (45°N 108°W)

As with the northernmost Full Glacial sites, $\delta^{13}\text{C}$ values from teeth from Natural Trap Cave indicate a dominance of C3 vegetation. The average value from the *Bison* tooth is -8.1‰ (ranging from -8.3‰ to -7.1‰) which suggests a diet incorporating about 30% C4 vegetation. Calculations from Paruelo and Lauenroth (1996) and Epstein et al. (2002) predict the complete absence of C4 vegetation from Natural Trap Cave. However, the much simpler model of C4 abundance according to geographic position (Paruelo and Lauenroth, 1996) indicates the possibility of C4 vegetation (and predicts more than that from the Full Glacial northerly sites) in a landscape dominated by C3 vegetation and shrubs. Other herbivorous taxa analyzed from Natural Trap Cave also suggest the presence of C4 vegetation, comprising between 21 and 30% of the animal's diet. Predicted temperatures from the MCM are too low to explain the presence of C4 vegetation in terms of lower $p\text{CO}_2$ and crossover temperature (Ehleringer et al., 1997; Collatz et al., 1998; Fig. 2).

Given the northern location of Natural Trap Cave, and the modeled cool temperatures and low precipitation, it is expected that no Amount Effect would be observed from serial oxygen isotopic data, which is what

is observed (Fig. 6_E). One might expect a more pronounced sinusoidal pattern than that from Full Glacial sites in Idaho, due to the much colder monthly means during the winter months using the MCM. However, with much of the winter experiencing temperatures below freezing, combined with low amounts of precipitation (Fig. 4), this might not be the case. The isotopic results from the teeth of five large mammalian herbivores have a lower average $\delta^{18}\text{O}$ than those from the Full Glacial Idaho sites, but do not appear to exhibit a larger range of variation. Mean annual temperatures were cooler, but not necessarily the annual range in temperature variability.

3.3.6. Late Glacial Southwestern Site: Murray Springs, AZ (32°N 110°W)

The fauna at Murray Springs lived at a time of warm temperatures and relatively small annual changes in temperature (Fig. 4). There was a small peak in precipitation in summer (JJA ~70 mm), from which we might predict an abundance of C4 vegetation. The geographic position also leads to a prediction of abundant C4 vegetation (Paruelo and Lauenroth, 1996). Examination of Fig. 5 also suggests that there should be a domination of C4 grasses at Murray Springs (Epstein et al., 1997). However, calculations of biomass (Epstein et al., 2002) based upon predictions of the MCM suggest that only about 60% of the biomass be grasses, and of those, only about 31% should be C4 grasses. Isotopic data from carbon from mammalian herbivores suggest that C4 grasses dominated the diets of both *Bison* and *Equus* (with mean $\delta^{13}\text{C}$ values of 0.3 and -0.7‰ , respectively). As with the results from Tule Springs, this could again be due to the fact that the Late Glacial environment of Murray Springs was characterized by high MAT and low MAP.

Modeled monthly precipitation is generally constant throughout the Late Glacial year at Murray Springs, at about 20 mm per month, with notable deviations from this in June, where no precipitation was predicted, and August, when about 51 mm of precipitation was predicted (Fig. 4; Table 5). Given this, there is a slight potential for a visible Amount Effect due to late summer rain, but it may be difficult to recognize due to low amounts of rain and the short duration of the potential “rainy” season. One would predict this to appear to a small dip in the $\delta^{18}\text{O}$ values on the side of the part of the sinusoidal curve associated with fall cooling. This pattern is, in fact, what we see. Fig. 7_A illustrates a roughly sinusoidal pattern for oxygen, with a

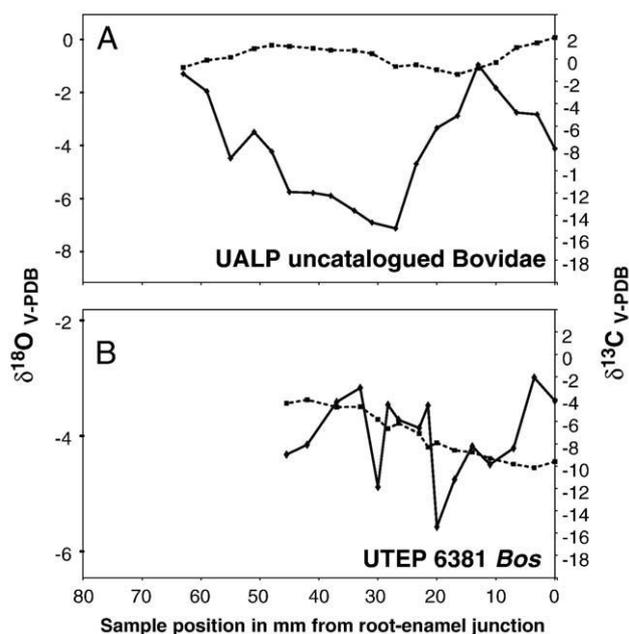


Fig. 7. Serial analyses from *Bison* or other *Bos* Late Glacial and modern sites. Oxygen and carbon data are plotted together with separate y-axes. Left axis is for oxygen data; right axis is for carbon data. A: Bovidae indet. from Murray Springs, AZ. B: Modern *Bos* from near Roswell, NM.

slight deviation from a more perfect sinusoid by a few data points on the part of the sinusoid correlated with spring.

3.4. Differences in C4 plant abundances based upon MCM data or isotope-calculations

One important observation that can be made from observing the data summarized in Table 5 is that in all cases, C4 plant abundance is much greater when estimated using the two end-member mixing model of tooth enamel isotopes (Koch et al., 2004) than it is when calculated using modeled values from the MCM. This relationship holds true for both *Bison* and *Equus*. One potential source for this discrepancy is that animals may have been feeding selectively on C4 vegetation (specifically C4 grasses) whereas much of the plant biomass may have been composed of C3 plants like shrubs. The MCM provides a complete estimation for C4 vegetation from the complete biomass, whereas the estimation calculated from teeth reflects primarily the dietary preferences of the herbivore. This could be further tested through isotopic analysis of soil carbonates (if available) from the localities in question, which should also provide a more complete picture of the entire plant biomass. Until this hypothesis can be tested, caution should be taken when using isotopic values from teeth to estimate C4 biomass, as it is likely to overestimate (potentially greatly) the amount of C4 vegetation in a region.

3.5. Atmospheric $p\text{CO}_2$ and C4 plant abundance

Ehleringer et al. (1997) described how variations in the concentration of carbon dioxide in the atmosphere can affect the proportion of C4 vegetation. The simple hypothesis is that the C4 photosynthetic pathway is advantageous during periods of lower atmospheric carbon dioxide, such as is known to be the case during glacial episodes (Indermöhle et al., 1999; Smith et al., 1999; Monnin et al., 2001).

Low atmospheric $p\text{CO}_2$ has been cited as an important causative factor in the post glacial expansion of C4 plants (Ehleringer et al., 1991, 1997). Recent research suggests that $p\text{CO}_2$ is not always an important factor, and that climatic variables such as amount and timing of precipitation and overall temperature may also be important (Muhs et al., 1999; Zhang et al., 2003; Vidic and Montañez, 2004).

Using estimations of past atmospheric $p\text{CO}_2$ (Indermöhle et al., 1999; Smith et al., 1999; Monnin et al., 2001), crossover temperatures (where C4 vegetation would be favored over C3) were estimated for the times represented by the various fossil localities in this study (Fig. 2; Ehleringer et al., 1997; Collatz et al., 1998). The crossover temperature as defined by Ehleringer et al. (1997) is based upon mean daytime growing-season temperature. This crossover temperature was compared with climate modeled using the MCM to make predictions about dominant PFGs expected if $p\text{CO}_2$ were a major control on the distribution of C4 vegetation. Since the MCM does not explicitly define mean daytime growing-season temperature, we estimate by using the modeled average daily temperature for the summertime months (June, July, and August) or by using the MAT (Fig. 2).

When using MAT as a proxy for growing-season temperature, the Full Glacial sites except for the northern sites in Idaho, are predicted to have favored C4 vegetation (provided that there was enough summertime precipitation; Paruelo and Lauenroth, 1996; Fig. 2). The Late Glacial Murray Springs site was also too cool for a dominance of C4 vegetation, though it came close to the crossover temperature. When mean daily temperature for the summertime months is used, all localities would be predicted to have had proportionately more C4 vegetation than C3.

During Full Glacial times, the crossover temperature is thought to have been around 10 °C (Ehleringer et al., 1997; Collatz et al., 1998). Only the Burnham Site has ample summertime precipitation which would also favor C4 vegetation. Isotopic results from Burnham Site teeth indicate the presence of C4 vegetation. However, these same

teeth show the Amount Effect, i.e. temperatures exceeded 20 °C meaning that the presence of C4 vegetation may have equally been due to warm summers with ample rain as due to low $p\text{CO}_2$. Results from teeth from Tule Springs and Dry Cave show a great deal of variation and evidence for mixed C3 and C4 diets. Here again, lower $p\text{CO}_2$ is not necessary to explain the presence of C4 vegetation, because there is also evidence for the Amount Effect from teeth from both localities.

The crossover temperature during Late Glacial times was higher than that of the Full Glacial, at approximately 18 °C (Collatz et al., 1998). Murray Springs was warm enough to have potentially favored C4 vegetation. Still Murray Springs is modeled to have had very low amounts of precipitation, a range of climate variables not well constrained by Epstein et al. (2002). Nevertheless, Murray Springs appears to have had a slight increase of precipitation during the summer months, and concurrently, the carbon isotopes indicate that C4 vegetation was a dominant component in the diet of mammalian herbivores. A very weak Amount Effect is evident from the teeth collected from Murray Springs, suggesting that while perhaps the atmospheric $p\text{CO}_2$ was important in explaining why C4 vegetation was dominant, it is just as likely that the dominance of C4 vegetation could be explained by climatic variables.

If $p\text{CO}_2$ were the most important factor controlling the abundance of C4 vegetation, we would predict proportionally more C4 vegetation (detected by more positive $\delta^{13}\text{C}$ values) during Full Glacial times than at Late Glacial times in areas of the same temperature. When we compare Full Glacial sites that lie between 43° and 45°N latitude, in general C3 plants dominate. The proportions of C3 and C4 grasses may need only be explained in terms of climatic variables such as MAT and MAP, and the distribution of precipitation throughout the year, although further work is needed to understand the relative proportions of PFGs in environments of high MAT and low MAP to assess this more fully. It does not appear that changes in the amount of atmospheric $p\text{CO}_2$ are the singular control on the distribution of C4 vegetation in North America during the Last Glacial Maximum. Our data indicate that temperature and aridity are at least as important as the effect of $p\text{CO}_2$ in controlling the distribution of C4 vegetation during the shift from Full Glacial to Late Glacial times.

4. Conclusions

4.1. The utility of climate interpretation using isotopes from fossil teeth and MCMs

Measured values and patterns for $\delta^{18}\text{O}$ from the tooth enamel of fossil mammals are consistent with predicted patterns based upon MCMs. The values and patterns for $\delta^{13}\text{C}$ using MCMs and calculations based upon equations in Epstein et al. (2002) notably differ from those calculated from isotopes of teeth such that C4 abundance estimates from tooth enamel isotopes are always greater than those estimated from the MCM only. These deviations are especially notable when climate is predicted to be warm and relatively dry for a region, in part because the equations of Epstein et al., do not include such end-members. The models of Epstein et al. (2002) applied to MCM models for the studied sites seem to predict relative abundance of C4 grasses in the plant biomass as a whole, whereas tooth enamel isotopes predict the dietary preferences of the animal. Since the MCMs do a good job of predicting annual patterns in $\delta^{18}\text{O}$, we suggest that MCMs are generally a good tool for understanding past environments, provided that caution is used when interpreting C4 plant abundance for warm and relatively dry regions.

4.2. Plant functional types estimated by atmospheric carbon dioxide

An original goal of this research project was to determine if decreased atmospheric carbon dioxide ($p\text{CO}_2$) during the Full Glacial

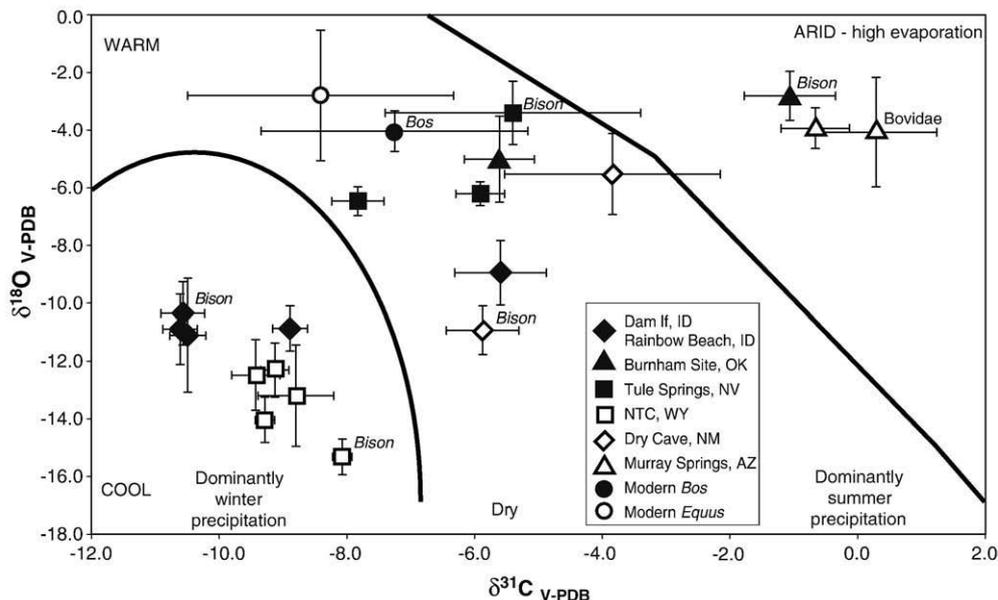


Fig. 8. Plot of mean isotopic values of carbon versus oxygen for each specimen from each locality in this study. Error bars show the range of variability of multiple samples collected from a single tooth. Results tend to group into three major categories: cool with dominantly winter precipitation; warm and dry; and warm with dominantly summer precipitation. Symbols representing each locality are the same as in Fig. 4.

could result in increased proportions of C4 vegetation under climatic conditions that would otherwise predict a lack of C4 vegetation. Unfortunately, in this data set all localities that showed evidence of C4 vegetation also showed evidence of the Amount Effect, meaning that environmental conditions were suitable for C4 vegetation without the necessity of reduced $p\text{CO}_2$. Further research on a new suite of fossil localities is necessary to address this important question. These localities might best be selected from latitudes between 36 and 43°N in North America, where temperatures might not be so cold to preclude C4 vegetation, but not so warm to result in the Amount Effect.

4.3. The environment and isotopes from tooth enamel

Fig. 8 represents a bivariate plot of all the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic results from this study. Generalizations about the modeled climates from the MCM, specifically a general sense of temperature and the amount and seasonality of precipitation, for each site are used to map out different general climate regimes in carbon versus oxygen space. The general pattern is that more positive $\delta^{18}\text{O}$ values reflect warmer temperatures, and more positive $\delta^{13}\text{C}$ values reflect shifts from conditions with dominantly winter or year-round precipitation to drier conditions or to wetter conditions where precipitation occurs primarily in the summer.

The results from this study (Fig. 8) suggest that it is possible to use a simple plot of carbon versus oxygen isotopic data from large, water-dependent mammals as a first-order proxy for climate of the past. The examples used here represent only a small range in the possible carbon and oxygen isotopic combinations obtainable from mammal teeth and are limited to taxa that been studied previously using isotopic methods, a geographic area for which the modern climate is adequately documented, and from a period of time that is readily modeled using the MCM. Further work is needed to show whether this simple proxy can be applied to different continents and for biomes other than the relatively open interior of North America.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.palaeo.2009.08.015](https://doi.org/10.1016/j.palaeo.2009.08.015).

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