Carbon isotopes from fossil packrat pellets and elevational movements of Utah agave plants reveal the Younger Dryas cold period in Grand Canyon, Arizona

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ABSTRACT

Carbon isotopes in rodent fecal pellets were measured on packrat (*Neotoma* spp.) middens from the Grand Canyon, Arizona. The pellet samples reflect the abundance of cold-intolerant C4 and Crassulacean acid metabolism (CAM) plant species relative to the predominant C3 vegetation in the packrat diet. The temporal sequence of isotopic results suggests a temperature decline followed by a sharp increase corresponding to the Bølling/Allerød–Younger Dryas–early Holocene sequence. This pattern was then tested using the past distribution of Utah agave (*Agave utahensis*). Spatial analyses of the range of this temperature-sensitive CAM species demonstrate that its upper elevational limit is controlled by winter minimum temperature. Applying this paleotemperature proxy to the past elevational limits of Utah agave suggests that minimum winter temperatures were ∼8 °C below modern values during the Last Glacial Maximum, 4.5–6.5 °C below modern during the Bølling/Allerød, and 7.5–8.7 °C below modern during the early Younger Dryas. As the Younger Dryas terminated, temperatures warmed ∼4 °C between ca. 11.8 ka and 11.5 ka. These extreme fluctuations in winter minimum temperature have not been generally accepted for terrestrial paleoecological records from the arid southwestern United States, likely because of large statistical uncertainties of older radiocarbon results and reliance on proxies for summer temperatures, which were less affected.

Keywords: Younger Dryas, Grand Canyon, ^{13}C, packrat middens, *Agave utahensis*, Pleistocene-Holocene transition.

INTRODUCTION

The Grand Canyon Arizona, United States, with nearly 2000 m of vertical relief, is an ideal laboratory for studying the past elevational shifts of plant species. Because elevation mimics latitude for many climate variables, this extreme elevational range stacks many climatic zones in close proximity. As a result, potential migrational lags in plant response to rapid climatic shifts are minimized.

The Grand Canyon also has an abundance of late Quaternary plant records. More than 200 fossil packrat middens have been radiocarbon dated from this area (Phillips, 1977; Mead and Phillips, 1981; Cole, 1985, 1990). Each midden contains macrofossils of 10–30 plant species that grew close enough to the site to be collected by a foraging packrat (Betancourt et al., 1990). Because individual plant macrofossils can be radiocarbon dated, these deposits are ideal for documenting the presence or absence of a plant species close to a specific location in the past (Nowak et al., 2000). In this paper we compare records of fossil Utah agave (*Agave utahensis*) from these packrat middens with the results of carbon isotopic analyses from the same deposits.

δ^{13}C AND ^{14}C METHODS AND RESULTS

Plant species photosynthesize using one of three physiological pathways, known as C3, C4, and Crassulacean acid metabolism (CAM). These metabolic pathways all fractionate carbon isotopes in different ways, producing characteristic carbon isotope ratios (Farquhar et al., 1989). The δ^{13}C ratios of plant tissues resulting from the pre-dominant C3 pathway are much lower than those produced through the C4 or CAM pathways.

Packrats sample a diverse diet from around their home den and must ingest succulent plant species to maintain their hydrological balance (Vaughn, 1990). In the middle desert elevations, packrats consume succulent CAM species, such as prickly pear cactus (*Opuntia* spp.) and agave (*Agave* spp.). In woodland or forest at higher elevations, packrat diets include abundant amounts of C3 conifers, such as species of juniper (*Juniperus* spp.).

Packrat fecal pellets should integrate the isotopic balance of the plants in their diet. The disparity in packrat diets, primarily C3 trees, shrubs, and grasses at high elevations, and a mixture of C3 shrubs, C3 and C4 grasses, and CAM species at middle to low elevations, should result in fecal pellets with higher δ^{13}C values at lower elevations.

In order to test this relationship, the δ^{13}C of packrat pellets from 92 middens was determined. These samples consisted of either 50 pellets ground to dust and analyzed using a gas isotope ratio mass spectrometer, or a subsample of the CO_2 gas produced during combustion of ∼50–100 pellets during radiocarbon analysis.

Radiocarbon ages were converted to a calendar year scale using Calib version 5.01 (Stuiver and Reimer, 1993) (see Data Repository).[1] In this paper, these calendar year conversions are noted in thousands of calendar years before present (ka), while ages on the radiocarbon

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[1]GSA Data Repository item 2005130, isotopic results, calendar year conversions, and agave content for midden samples, is available online from www.geosociety.org/pubs/ft2005.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

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Figure 1. Comparison of carbon isotope and Utah agave chronologies from Grand Canyon with oxygen isotope chronology from Greenland. Younger Dryas period is shown in gray. A: δ13C values from packrat pellets from low- to mid-elevation middens (450–1200 m; gray squares), high-elevation middens (1450–2250 m; open circles), and late Holocene hyperarid desert middens (<550 m, <2.5 ka; triangles) graphed by age of midden samples. Ranges of possible calendar year ages (at 1σ) are indicated by error bars. B: Concentration of Utah agave in fossil packrat middens in Grand Canyon graphed by median probable calendar year age and elevation. Open circles = agave absent; gray circles = agave present; circles are sized to reflect logarithm of concentration/kg from Cole (1985, 1990, and this report), or semiquantitative abundance rank of 1–5 from Phillips (1977) or Mead and Phillips (1981) (most samples <650 m and >10 ka). Dashed line shows departure below late twentieth century mean minimum January temperatures inferred from upper limit of Utah agave (scale at right). C: δ18O isotope values from the Greenland Ice Sheet Project 2 ice core (modified from Grootes and Stuiver, 1997).
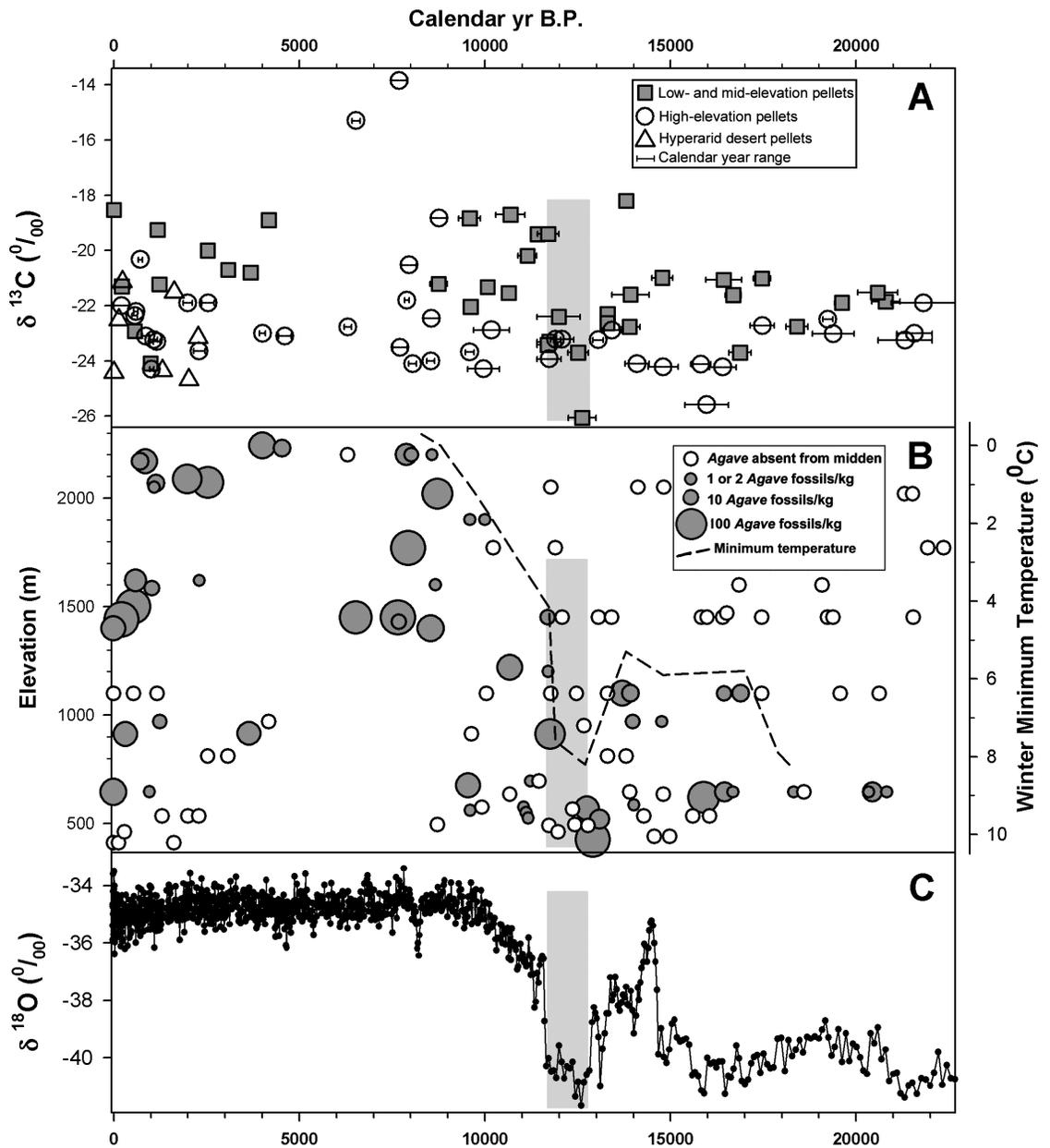
scale are denoted as radiocarbon yr B.P. (yr B.P.). The age estimates of the most critical midden records were improved from previous values using 52 additional radiocarbon determinations, reducing the average uncertainty of 330 yr (at 1σ) for the pre-1985 analyses to <85 yr for the post-1995 analyses. These redeterminations were essential for interpreting the climate fluctuations of the Pleistocene-Holocene transition, such as the Younger Dryas (YD). In detailed chronostratigraphic records (e.g., Grootes and Stuiver, 1997; Barron et al., 2003), the YD period appears to last only ~1300 calendar years, from ca. 12.9 to 11.6 ka, and <900 radiocarbon years, from ca. 10,900 to 10,060 yr B.P.

The results from the δ13C and 14C analyses (Fig. 1A; Table DR1 [see footnote 1]) demonstrate that fossil middens from low to middle elevations (410–1200 m) generally have pellets with higher δ13C values than those from high elevations (1450–2200 m) during most time periods. However, during the late Holocene, samples from below 600 m elevation also had low δ13C values (triangles in Fig. 1A). These hyperarid desert sites are below the current limits of many CAM species, especially Utah agave (see following).

These δ13C results also demonstrate temporal trends. For low- to mid-elevation pellets, the highest Pleistocene value occurred at 14 ka during the Bølling/Allerød Interval (B/A), and then declined sharply to the lowest value ca. 12.7 ka at the beginning of the YD. Isotope values from low- to mid-elevation pellets then increased dramatically ca. 11.7 ka at the end of the YD. There was not a comparable increase at high elevations until sometime between 9.5 and 8.7 ka. High-elevation samples then reached their highest values ca. 7.7 ka and 6.5 ka.

UTAH AGAVE PALEOZONATION METHODS AND RESULTS

In order to examine the source of the past fluctuations in δ13C, we investigated a plant species that might be causing these changes. Utah agave (*Agave utahensis*) is exceptionally abundant within the Grand Canyon. It was found in >50% of 478 plant plots throughout all plant communities and substrates between 1000 and 2000 m elevation (Cole and Cannella, 2005). It is not only one of the primary plant species in packrat diets in the Grand Canyon, but its abundance within packrat middens can be easily quantified using its readily identifiable fossil leaves, spines, fruits, and seeds. It should be an important

source of the variability in fecal pellet $\delta^{13}C$, because its CAM metabolic pathways produce extremely high $\delta^{13}C$ values, averaging $-10.5‰ \pm 1.5‰$ (Table DR1; see footnote 1).

However, the concentration of Utah agave fossils found within middens was only a partial predictor of pellet $\delta^{13}C$ values. While pellets from middens containing Utah agave averaged a marginally higher $\delta^{13}C$ ($-21.7‰$) than middens without agave ($-22.6‰$) and were significantly different using a T-test (P = 0.046), the concentration of Utah agave only explained a modest portion of the variance in the pellet $\delta^{13}C$ values from the same middens ($r^2 = 0.27$).

These results reflect the importance of additional CAM and C4 species within the packrat diet in generating pellet $\delta^{13}C$ values, and possibly a poor correlation between the packrat diet and abundance of identifiable plant parts within a midden. The predominant CAM species in packrat diets and middens are likely species of prickly pear cactus (*Opuntia* spp.), which are more difficult to quantify and identify to species, but have similarly high $\delta^{13}C$ values (averaging $-10.4‰$; Table DR1). This suggests that Utah agave concentration could be an additional indicator of past climate that is somewhat independent from the pellet $\delta^{13}C$ values.

In order to understand the climatic controls on Utah agave, a detailed map of its modern range (Cole and Cannella, 2005) was combined with seasonal precipitation and temperatures of the twentieth century climates of western North America. Monthly values for precipitation and monthly mean maximum and mean minimum temperatures were sorted into five seasons most relevant for the range of Utah agave: winter, spring, early summer, monsoon, and fall. These values were modeled to an ~1 km spatial grid, and the seasonal climate extremes controlling the distribution of Utah agave were ranked in importance using a chi-square statistic (Arundel, 2005, 2002; Cole and Arundel, 2005; detailed description in item DR2; see footnote 1). These analyses indicated that the most important variable spatially limiting Utah agave is winter minimum temperature below $-8\,°C$. This modern limit then provides a paleotemperature proxy that can be applied to the past upper limit of Utah agave. Past cold season temperatures were estimated by applying the A.D. 1971 through A.D. 2000 elevational lapse rate ($6.23\,°C/1000$ m) observed among eight climate stations along the Colorado River in northern Arizona.

The abundances of Utah agave in Grand Canyon middens are shown in Figure 1B. Winter minimum temperatures extrapolated from the upper limit of Utah agave are shown by the dashed line with the scale to the right. During the Last Glacial Maximum, prior to ca. 17 ka, minimum temperatures may have been ~8 °C colder than today, although these few midden records have imprecise radiocarbon ages. Then, between 17 and 14 ka, Utah agave was found higher in elevation, suggesting that temperatures were only 6.5–4.5 °C below modern values. This range of possible temperatures was derived by applying the lapse rate between midden records of presence (maximum difference) and absence (minimum difference). There were almost certainly shorter-term temperature fluctuations within this period that remain beyond the resolution of the record.

After 13.5 ka, the absence of Utah agave from three middens at 1100, 950, and 810 m elevation suggests that a significant decline in temperature occurred. Agave was found in three poorly dated middens, ca. 13 ka (Phillips, 1977), below 600 m elevation. Unfortunately, none of the Utah agave macrofossils of Phillips could be located for redating. Nevertheless, accepting these low-elevation records as accurate, a temperature estimate for the start of the YD period ca. 12.7 ka can be estimated to be between a maximum of 8.7 °C below modern (at the Phillips record of presence) and a minimum of 7.5 °C below modern (at the 950 m record of absence).

Utah agave seems to have quickly moved upslope at the close of the YD. In a series of four middens between 912 and 1450 m elevation,

it is absent from a midden dating to 10,150 yr B.P., and then present in the next three middens dating to 10,135, 10,110, and 10,100 yr B.P. Although the uncertainty surrounding any single radiocarbon analysis during this period is large, these values infer a rapid temperature warming between ca. 11.8 and 11.5 ka. Extrapolating the previous estimate of YD temperatures upward to the highest record at 1450 m elevation yields a minimum temperature increase of 4.0 °C during this post-YD warming.

The presence of Utah agave at higher elevations during the early Holocene suggests that this warming trend continued at a slower rate, increasing an additional 4.1 °C between 11.5 and 8.7 ka, with temperatures exceeding modern by 8.5 ka. After that time, climate became warm enough that the detection of winter minimum temperature using Utah agave was above the range of this chronology. The increase of higher-elevation $\delta^{13}C$ values after 8.7 ka further supports this interpretation. Large amounts of Utah agave in the high-elevation middens and exceptionally high $\delta^{13}C$ values during the middle Holocene are suggestive of much warmer temperatures, as is the scarcity of middle Holocene middens below 1400 m elevation (Webb, 1986).

SUMMARY AND REGIONAL COMPARISONS

Figure 1 contrasts the $\delta^{13}C$ of fossil pellets and upper elevational limits of Utah agave with the $\delta^{18}O$ isotope curve taken from a GISP2 (Greenland Ice Sheet Project 2) ice core (Fig. 1C; Grootes and Stuiver, 1997). The three data sets show a remarkable temporal correlation during the B/A, YD, and early Holocene. Both the $\delta^{13}C$ values and Utah agave distributions hint of a warmer B/A ca. 14 ka, as represented by a high $\delta^{13}C$ value in one midden and a high concentration of Utah agave at 1100 m elevation in a separate midden. Subsequently, a decline in $\delta^{13}C$ values after 13.5 ka marks the onset of the YD, including the lowest value obtained in this series ($-26.06‰$ ca. 12.7 ka) when Utah agave was not found above 570 m. At the end of the YD, low- to mid-elevation pellet isotope values increased dramatically while Utah agave quickly moved to higher elevations. Considering the error inherent in the radiocarbon chronology, the timing of this temperature increase in the Grand Canyon is indistinguishable from the corresponding temperature increase in Greenland.

Recent data from Ocean Drilling Program (ODP) sea core ODP 1019, off the coast of northern California (1200 km northwest of the Grand Canyon), also show a remarkable correlation with these records. Alkenone-based estimates of mean annual sea-surface temperatures from this core during the YD were 3.7–4.4 °C below modern values (Barron et al., 2003). When combined with the winter minimum temperature results from this study (7.5–8.7 °C below modern), these estimates suggest YD climates with much colder winters and only somewhat colder summers than today. Shifts in mean annual temperature were likely intermediate between the two. This higher variability in the annual temperature cycle during the YD should be expected because this period also featured the maximum summer solar insolation and minimum winter insolation over the past 50 k.y. for the Northern Hemisphere (Lorenz and Lohmann, 2004).

The decline in temperature between the B/A and YD from this study can also be compared to other data from western North America. Pollen records from the Rocky Mountains suggest that YD summer temperatures were 0.4–0.9 °C lower than those of the preceding period (the B/A?; Reasoner and Jodry, 2000). Yet marine records of planktonic isotopes from the Santa Barbara Basin suggest that mean annual sea-surface temperatures decreased 4 °C from those of the preceding period (the B/A?; Hendy et al., 2002). The disparities between these summer and mean annual temperature proxies support the increased seasonal contrasts proposed here.

The YD climate fluctuations are apparent in detailed paleoclimatic sequences throughout North America, encircling the American South-

west, from the Caribbean (Hughen et al., 2000), New Mexico (Polyak et al., 2004), the California coast (Hendy et al., 2002; Barron et al., 2003), Utah (Oviatt et al., 2005), and Colorado (Reasoner and Jodry, 2000). It seems unlikely that such an extensive event did not also affect the American Southwest, yet previous summaries of packrat midden records have not recognized this YD chronozone. Instead, the climates of the Pleistocene-Holocene transition have either been simplified into a monotonic warming trend extending from the last glacial into the Holocene, or the few plant records dating within the brief YD period have been grouped with others on either side of an arbitrary boundary set at 11,000 or 10,000 yr B.P. (Phillips, 1977; Van Devender et al., 1987; Betancourt et al., 1990; Cole, 1990; Arundel, 2002). In contrast, Cole (1985) analyzed middens across this transition in a sequential manner and discovered that the species richness within middens declined between 12,000 and 9000 yr B.P. (ca. 13.9 and 10.2 ka), suggesting a severe environmental perturbation and/or a slowed vegetational response following an initial change.

This study may explain ongoing discrepancies in the interpretation of late glacial temperatures of the southwestern United States. Van Devender (1990) reported Late Wisconsin winter temperatures to be 5.0–3.6 °C colder than today for the Sonoran Desert. A geostatistical analysis of the same packrat middens reconstructed paleotemperatures that were ~4.5 °C colder than today in winter but only somewhat cooler during the summer (Arundel, 2002). Because most of the middens in this Late Wisconsin period actually date to the B/A as used in this study, these values are compatible with the range of 6.5–4.5 °C colder winter minimums reported herein, but somewhat farther north on the Colorado Plateau.

Other reconstructions have called for much colder paleotemperatures during the full glacial. Galloway (1983) argued that temperatures could have been as low as 10 °C colder than today, while Brakenridge (1978) suggested a 7–8 °C lowering of temperature to explain the lowest elevation cryogenic deposits. These estimates are not inconsistent with the winter minimum temperatures reported from our study for the full glacial and YD.

As a result, what had been sharp disagreements over the severity of late glacial temperature changes may instead simply be a product of overgeneralization of the temporal, seasonal, and spatial variability of temperature. Recording even the extreme temperature fluctuation of the YD not only required a detailed sampling interval and detailed dating methods, but also fossil proxies sensitive to that variable in that location. Fortunately for this study, both pellet δ^{13}C and Utah agave concentration seem to be appropriate proxies for monitoring late glacial winter minimum temperatures within the Grand Canyon. Neither record is by itself definitive; but taken together, this evidence of the YD cold period is well supported.

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