Tertiary history of C_4 biomass in the Great Plains, USA

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ABSTRACT

We use the carbon isotope composition of paleosols to reconstruct the history of C_4 biomass on the Great Plains from ca. 23 to 1 Ma. The proportion of C_4 biomass was uniform and moderate (12%–34%) throughout the Miocene, increased between 6.4 and 4.0 Ma, and reached modern levels by 2.5 Ma. Ecological changes in Great Plains ungulates preceded the increase in C_4 biomass. The contrasts in the paleosol and ungulate records may indicate initial development of C_3 grasslands after the middle Miocene or a greater role for ecological interactions within communities in structuring ungulate faunas. Contrasts in paleosol records from different continents point to regional rather than global controls on the evolution of C_4 grasslands.

Keywords: Great Plains, Tertiary, grasslands, C_4 grasses, carbon isotopes, paleosol carbonate.

INTRODUCTION

Grasslands are widespread ecosystems with major impacts on the carbon cycle (Schlesinger, 1997), mammalian evolution (Janis et al., 2002), and the origin of human agriculture (Diamond, 1997). Expansive grasslands are late Cenozoic phenomena long linked with climate change, especially decreasing temperatures and increasing aridity and seasonality (Webb, 1977; Jacobs et al., 1999; Retallack, 2001). The increasing dominance of grasses using the C_4 photosynthetic pathway since the late Miocene has been attributed to a drop in atmospheric pCO_2 (Cerling et al., 1997). C_4 plants have CO_2-concentrating mechanisms that, at low pCO_2, may offer a competitive advantage over plants using the C_3 pathway (Sage, 2001). The CO_2 hypothesis is elegant, but proxies for past pCO_2 values do not show a sharp, permanent drop in the late Miocene (Pagani et al., 1999; Pearson and Palmer, 2000). Constraining the timing of grassland development is critical for testing these and other ideas about grassland ecosystems.

We use the stable carbon isotope composition ($\delta^{13}C$) of paleosols to reconstruct the Tertiary history of C_4 biomass on the central and southern Great Plains, the region south of ~43°N (referred to hereafter as the Great Plains). C_4 grasses compose 50%–100% of modern plant biomass in this region (Epstein et al., 1997; Tieszen et al., 1997). Floral and faunal data suggest that forests dominated the Great Plains prior to the middle Miocene (ca. 15 Ma) and that open grasslands gradually increased after this time (Webb, 1977; Jacobs et al., 1999; Janis et al., 2002). As modern trees and shrubs are almost exclusively C_3 (Sage, 2001), the region would have been dominated by C_3 biomass before the middle Miocene. The presence of C_4 grasses in ancient ecosystems has been examined by using $\delta^{13}C$ values from fossil tooth enamel as a proxy for diet and biomass. In the Great Plains, horses with C_4-dominated diets appeared in what is now Texas at 6.6 Ma and are common regionally at younger sites; this has been interpreted as evidence that modern C_4-dominated grasslands developed rapidly in the latest Miocene (Wang et al., 1994; Cerling et al., 1997; Passey et al., 2002). Yet animal diets may offer a biased view of habitat composition because of selective feeding and lags between biome changes and animal ecology. In contrast, paleosols directly record the proportions of C_3 and C_4 plants that were present in an ecosystem.

CARBON ISOTOPES IN PALEOSOLS

Plants using different photosynthetic pathways fractionate carbon isotopes to different degrees during photosynthesis. Modern C_3 plants have a mean $\delta^{13}C$ value of −27‰ (range −35‰ to −22‰; values are relative to Vienna Peedee belemnite [VPDB]), and C_4 plants have a mean value of −13‰ (range −14‰ to −10‰) (O'Leary, 1988; Tieszen and Boutton, 1989). Plants using the CAM pathway have values overlapping those of C_3 and C_4 plants, but they are rare in nondesert ecosystems and are not considered further.

Authigenic soil carbonate forms in isotopic equilibrium with CO_2 dissolved in soil water (Cerling and Quade, 1993). At shallow depths, soil CO_2 is a mix of atmospheric CO_2 and biogenic CO_2 derived from root respiration and oxidation of soil organic matter. At typical soil-respiration rates and modern atmospheric conditions, soil CO_2 below ~30 cm is mostly biogenic and has a $\delta^{13}C$ value similar to plants and soil biomass. Thus, pedogenic carbonate formed at depth reflects the contributions of isotopically distinct C_3 and C_4 biomass to soil CO_2 but is ^{13}C enriched by 14‰–17‰ relative to biomass owing to fractionations associated with diffusion of CO_2 out of the soil and carbonate precipitation.

Aridity and low soil productivity can complicate interpretation of pedogenic carbonate isotopic compositions ($\delta^{13}C_c$). In open and arid habitats, C_3 plants have less negative $\delta^{13}C$ values (Ehleringer and Monson, 1993), which could make carbonates derived from arid-climate C_3 biomass isotopically indistinguishable from those in soils with a low proportion of C_4 biomass. We use published data from 20 Holocene soils in C_3 ecosystems in North America, Russia, and the eastern Mediterranean with mean annual precipitation of <1000 mm to set a threshold for the presence of C_4 biomass. The mean $\delta^{13}C_c$ value for these soils is −8.7‰ ± 1.1‰ (all means reported ± 1 standard deviation, s.d.), and the $\delta^{13}C$ value of organic matter in these soils is −24.6‰ ± 0.76‰; paleosol values significantly greater than these indicate C_4 biomass. Fossil fuel use has increased the $\delta^{13}C$ value of actively cycling Earth surface systems since about A.D. 1850 (Friedli et al., 1986). Holocene soils are unlikely to reflect this change, and we do not adjust our threshold to account for it.

Low soil productivity allows atmospheric CO_2 deeper into a soil. Mixing of atmospheric CO_2 having a preindustrial $\delta^{13}C$ value of ~−6.5‰ (Friedli et al., 1986) and biogenic CO_2 in a typical C_3 soil could increase the $\delta^{13}C_c$ value into the range of a mixed C_3/C_4 soil. We use the $\delta^{13}C$ value of organic matter occluded in paleosol carbonate to assess the influence of atmospheric CO_2 on paleosol $\delta^{13}C_c$ values. A paleosol carbonate-organic matter spacing ($\Delta^{13}C$) similar to that in modern soils would indicate that productivity was not low; $\Delta^{13}C$ values greater than modern ones could indicate the influence of atmospheric CO_2.

METHODS

We analyzed 274 paleosol carbonates from 24 outcrops of 10 lithostratigraphic units. Sample ages are constrained by age assignments for mammal faunas from either the North American Land Mammal Age system (Tedford et al., 1987; Voorhies, 1990; Martin et al., 2000) or a quantitative biostratigraphic approach (Alroy, 2003). Ages in southwestern

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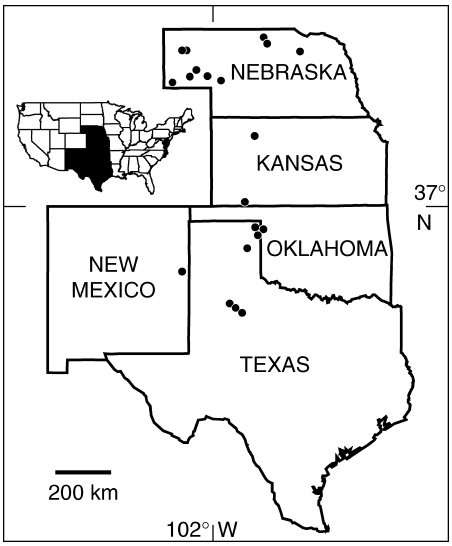

Figure 1. Map of paleosol sampling localities. Several localities are too close for separate symbols. Locality data are available (see footnote 1 in text).

Kansas (Fig. 1) are further constrained by ages for the Huckleberry Ridge and Cerro Toledo B ashes in the Crooked Creek Formation (Martin et al., 2000) and an assumed linear sedimentation rate. Age assignments and isotopic data are available[1].

[1]GSA Data Repository item 2003116, Tables DR1 and DR2, isotopic and locality data for all samples, is available online at www.geosociety.org/pubs/ft2003.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

Suitable paleosols were recognized on the basis of crumbly texture (indicative of soil ped preservation), absence or disruption of primary sedimentary structures, horizonation, presence of rhizoconcretions (interpreted as root traces), and presence of carbonate nodules or caliche beds. Samples were collected in situ from trenches or from fresh surfaces of caliche beds. Carbonate was collected ≥50 cm below pedogenic or sedimentological features marking preserved tops of paleosol. Paleosols without horizonation for several meters vertically were interpreted as cumulative soils and sampled opportunistically or at intervals of 50–100 cm. Caliche beds <50 cm thick were sampled from the lowermost indurated surface; those >50 cm thick were sampled from the lower and upper surfaces.

Carbonate samples were roasted in vacuo at 400 °C for 1 h and then reacted with 100% H_3PO_4 at 90 °C in a Micromass Isocarb automatic carbonate system. The $\delta^{13}C$ value of the resulting CO_2 was measured with either a Prism or Optima isotope ratio mass spectrometer (IRMS). Sample values were normalized to the mean $\delta^{13}C$ value of six to eight samples of Carrara marble analyzed with each set of paleosol samples. The mean normalized $\delta^{13}C$ value of 45 samples of carbonate standard NBS-19 (certified $\delta^{13}C$ value = 1.95‰) analyzed with each set of samples and Carrara marbles over 23 analyses during this project was 1.96‰ ± 0.05‰. The $\delta^{13}C$ of organic matter occluded in carbonate was measured on the HCl insoluble fraction of powdered carbonate samples with a Carlo Erba elemental analyzer coupled to an Optima IRMS. Sample values were normalized to the mean $\delta^{13}C$ value of multiple samples of University of California, Santa Cruz (UCSC), gelatin standard (PUGEL) analyzed with the samples; the analytical precision for these data is ±0.22‰. All analyses were performed in the Stable Isotope Laboratory, UCSC.

PALEOSOL CARBONATE

The mean $\delta^{13}C_c$ value for the Miocene samples is relatively high and invariant (−6.8‰ ± 0.8‰, n = 230) across 7° of latitude and 18 m.y. (Fig. 2A). The means for Miocene localities south (−6.7‰ ± 0.8‰, n = 109) and north of 37°N (−6.8‰ ± 0.9‰, n = 121) are indistinguishable on the basis of an F-test and a two-tailed t-test assuming equal variances (t = 0.96, d.f. = 228, p = 0.34; all p values based on α = 0.05). These values are high if C_4 grasses only appeared in abundance in the region ca. 6.6 Ma, as horse diets suggest (Wang et al., 1994; Cerling et al., 1997; Passey et al., 2002). Our data imply considerable C_4 biomass in the Great Plains throughout the Miocene.

The absence of calcareous paleosols in Miocene sections younger than 6.4 Ma precludes determination of C_4 abundance in the latest Miocene; this gap is also present in the record of horse diets (Passey et al., 2002). The $\delta^{13}C_c$ values (∼−5‰) ca. 4.0 Ma are slightly higher than those for the Miocene, indicating only a small increase in C_4 biomass (Fig. 2A). The main rise in $\delta^{13}C_c$ values is later, and val-

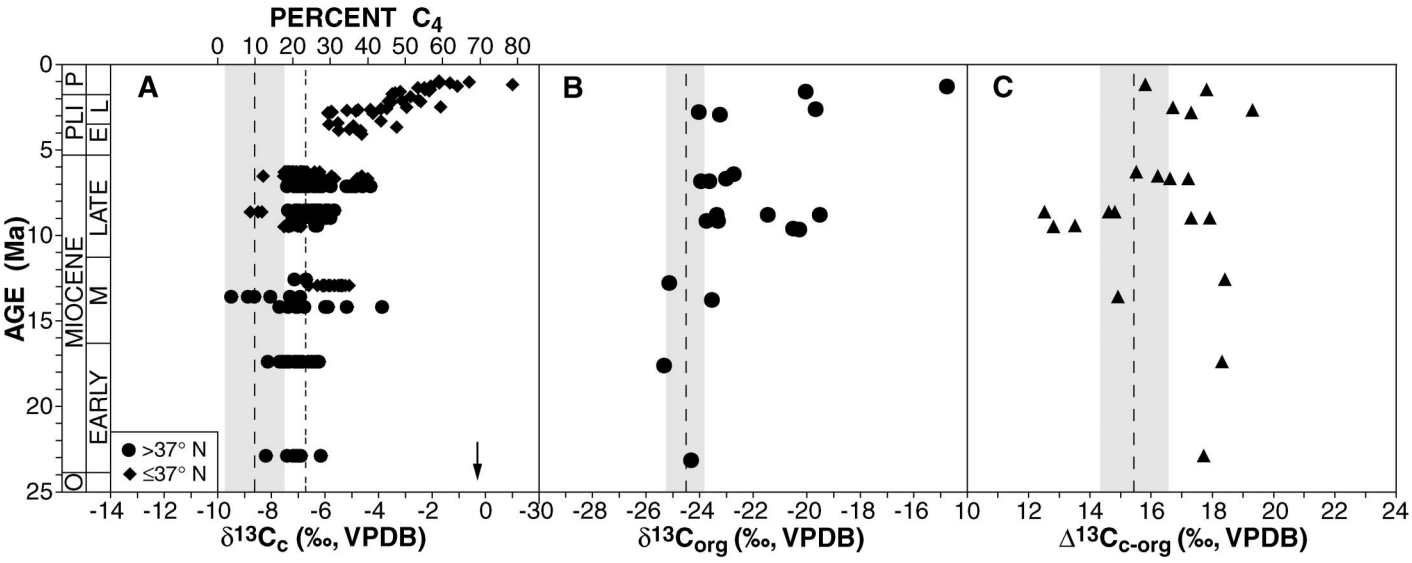

Figure 2. A: $\delta^{13}C_c$ values of paleosols from Great Plains. Single-dash line and gray field indicate mean ±1 standard deviation (s.d., −8.7‰ ± 1.1‰) for 20 Holocene arid-climate C_3 soil carbonates; double-dash line indicates maximum Holocene value (−6.8‰). Arrow indicates mean Holocene C_4 soil carbonate. Percent C_4 assumes linear mixing, $\delta^{13}C_{C3}$ = −25.5‰, $\delta^{13}C_{C4}$ = −11.5‰, and $\Delta^{13}C_{CO_2\text{-}CO_3}$ = +15.5‰. B: $\delta^{13}C$ values of organic matter occluded in paleosol carbonate. Dashed line and gray field indicate mean ±1 s.d. (−24.6‰ ± 0.76‰) for Holocene soils in A. C: $\Delta^{13}C$ values for data in B. Dashed line and gray field indicate mean ±1 s.d. for 41 Holocene soils (15.4‰ ± 1.1‰). Holocene data are from Quade et al. (1989), Cerling and Quade (1993), Wang and Anderson (1998), Monger et al. (1998), and Khokhlova et al. (2001). VPDB—Vienna Peedee belemnite. O—Oligocene; PLI—Pliocene; P—Pleistocene; E—early; M—middle; L—late.

ues typical of the modern C_4 grasslands (~−2.5‰ to +1.5‰; Kelly et al., 1991) do not occur until 2.5 Ma. Three sections in southwestern Kansas record the increase in $\delta^{13}C_c$ values with unequivocal age control provided by ashes (Martin et al., 2000). A section in northern Texas (not shown) also records the increase, but age control is poor; the increase occurs ~26 m above the late Miocene Christian Ranch fauna (Johnston and Savage, 1955). Our Pliocene data from Kansas are similar to values for well-dated paleosols in Arizona and New Mexico (Mack et al., 1993; Wang et al., 1993), indicating that abundant C_4 biomass was a widespread phenomenon during the late Pliocene.

ALTERNATIVES TO ABUNDANT MIOCENE C_4 BIOMASS

Several alternate explanations for the high Miocene $\delta^{13}C_c$ values can be ruled out. Aridity could have shifted the $\delta^{13}C$ of C_3 biomass positively so that paleosol carbonates spuriously appear to include C_4 biomass. However, the mean Miocene $\delta^{13}C_c$ value (−6.8‰) is significantly greater than that of the modern arid climate C_3 soils (−8.7‰ ± 1.1‰; Fig. 2A) (*F*-test and one-tailed *t*-test assuming equal variances; $t = 9.8$, d.f. = 248, $p \ll 0.001$). All Miocene levels sampled but one (13.7 Ma) have some $\delta^{13}C_c$ values greater than the maximum in the modern arid climate C_3 data (−6.8‰, for a soil in Nevada with a mean annual rainfall of 46 mm), and 55% of the Miocene values are >−6.8‰. The mean $\delta^{13}C$ value of the Miocene organic samples (−22.9‰ ± 1.7‰) is also significantly greater than that of the modern arid climate C_3 soils (−24.6‰ ± 0.76‰) (*F*-test and a one-tailed *t*-test assuming unequal variances, $t = -3.6$, d.f. = 18, $p < 0.001$). Moreover, attributing high paleosol $\delta^{13}C_c$ values to aridity is ad hoc, because no compelling geologic evidence supports extreme aridity in the Miocene of the Great Plains.

Low soil productivity or high atmospheric pCO_2 values during all of the Miocene could have allowed atmospheric CO_2 deeper into soils. Under both circumstances, $\delta^{13}C_c$ and organic-matter $\delta^{13}C$ values should diverge, leading to higher $\Delta^{13}C$ values. The $\delta^{13}C$ values of organic matter occluded in paleosol carbonates parallel the trend in $\delta^{13}C_c$ values (Fig. 2B; $r = 0.68$). Organic matter in Miocene samples is not a modern contaminant, because it does not have the C_4 signature of modern biomass in the region. On the basis of an *F*-test and a one-tailed *t*-test assuming unequal variances, the mean $\Delta^{13}C$ values for Miocene (15.8‰ ± 2.0‰; Fig. 2C) and Holocene paleosols from Africa, Australia, the eastern Mediterranean, North America, and Russia (15.4‰ ± 1.1‰, $n = 41$) are indistinguishable ($t = 0.70$, d.f. = 17, $p = 0.24$). Additionally, species richness of ungulate browsers in middle Miocene faunas was greater than in any modern community (Janis et al., 2002), which is inconsistent with low-productivity ecosystems.

Detrital Paleozoic carbonate in soil parent material could increase the $\delta^{13}C$ of paleosol carbonate, and diagenetic recrystallization might contribute to the uniformity of Miocene values. However, we identified neither detrital carbonate nor distributed sparry (i.e., diagenetic) calcite in thin sections of 23 samples that are outwardly typical. Diagenesis should homogenize $\delta^{18}O$ values to a greater degree than $\delta^{13}C_c$ values (Wang and Cerling, 1994), yet Miocene $\delta^{18}O$ values (not shown) are more variable (s.d. = 3.0‰) than the $\delta^{13}C_c$ values (s.d. = 0.83‰) and have a coherent latitudinal gradient not seen in the $\delta^{13}C_c$ values.

Decreased C_3 fractionation under Miocene atmospheric conditions and only C_3 biomass cannot explain high Miocene $\delta^{13}C_c$ values in the Great Plains because coeval paleosols from Pakistan (Quade and Cerling, 1995), Nepal (Quade et al., 1995), and Argentina (Latorre et al., 1997; Kleinert and Strecker, 2001) have low $\delta^{13}C_c$ values typical of modern C_3 ecosystems. For example, the mean $\delta^{13}C_c$ value of Miocene paleosols older than 8 Ma in Pakistan (−10.1‰ ± 0.94‰, Quade and Cerling, 1995) is 3.3‰ lower than the mean for coeval Great Plains samples. Additionally, coeval paleosols in Kenya (Kingston et al., 1994) also record mixed C_3/C_4 ecosystems.

The Great Plains paleosol record may be biased toward atypical environments with high C_4 biomass, but the scope of our sampling makes this explanation implausible.

IMPLICATIONS

The history of C_4 biomass in the Great Plains extends at least to the early Miocene (ca. 23 Ma), but ecosystems with substantially >50% C_4 biomass, like those in the region today, only appeared in the Pliocene. All Miocene sections sampled except one unambiguously record the presence of C_4 biomass. If C_3 and C_4 biomass had average preindustrial $\delta^{13}C$ values (~−25.5‰ and −11.5‰, respectively), the mean Miocene $\delta^{13}C_c$ value and simple linear mixing imply the persistent presence of 12%–34% C_4 biomass, depending on the temperature of carbonate precipitation. Miocene ecosystems of the Great Plains probably do not have a modern analogue. Janis et al. (2002) reached a similar conclusion about middle Miocene ungulate faunas of the Great Plains. The paleosol and faunal data suggest highly productive Miocene habitats with uniformly spread C_3 trees and shrubs over a carpet of C_4 grass. The variability in the $\delta^{13}C_c$ values in individual sections (Fig. 2A) suggests some landscape-scale variation in the C_3:C_4 ratio. By the early Pleistocene, the Great Plains probably looked much as they did historically, with expansive areas of open grassland and riparian wooded habitats.

Our results have several broader implications. First, ecological changes among Miocene ungulates in the Great Plains (relative decrease in browsers after 15 Ma, relative increase in grazers from 18 to 10 Ma, absolute decrease in species richness after 13 Ma; Janis et al., 2002) did not result from an increase in the abundance of C_4 grasses. Grassland expansion may still have influenced ungulate faunas, if C_3 grasses increased relative to C_3 trees and shrubs in ecosystems that retained a constant proportion of C_4 biomass. This possibility is consistent with the appearance of grazing adaptations in some horse species several million years before the earliest isotopic evidence for C_4 diets in horses at 6.6 Ma (Wang et al., 1994). If a decrease in forest areas lowered primary productivity, initial expansion of C_3 grasses could also account for decreasing ungulate species richness after 13 Ma. However, expansion of C_3 grasses would be surprising given the warm global climates of the middle Miocene (Zachos et al., 2001) and the cool climate distribution of C_3 grasses today.

Second, C_4 grazing in some horse species beginning in the late Miocene was not coupled to an increase in C_4 biomass. Horses with mixed and C_4-dominated diets are first known from the Coffee Ranch fauna at 6.6 Ma, although some species maintained C_3 diets (Wang et al., 1994; Cerling et al., 1997; Passey et al., 2002). A stratigraphic sequence of 12 samples through the Coffee Ranch section has a mean $\delta^{13}C_c$ value of −6.8‰ ± 0.9‰, identical to the mean Miocene value. Regardless, horses from other late Miocene and younger localities in the Great Plains had diets that range from pure C_3 to pure C_4. The contrast in the paleosol and horse records indicates that the focus of isotopic paleo–dietary studies on single clades (e.g., horses) may mask more complex ecological interactions within communities, such as changes in resource partitioning. Either such interactions or ecosystem changes that cannot be detected in paleosol compositions caused the increase in C_4 grazing in some horses during the late Miocene.

Finally, mechanistic hypotheses for the spread of C_4 grasslands during the Tertiary will have to focus on local factors, possibly in concert with one or more global factors. Differences in coeval paleosol records from

different continents cast doubt on explanations strongly tied to global causal factors. Quaternary shifts in C_3:C_4 ratios (Huang et al., 2001) indicate that local climate is an important control on C_4 abundance. We suggest that the likeliest global factor in the history of C_4 grasslands is cooling after the middle Miocene climatic optimum (Zachos et al., 2001) and shortened growing seasons. Plausible scenarios for the Tertiary evolution of C_4 grasslands in specific regions will have to combine global cooling with local ecological and perhaps tectonic changes. Such explanations are inevitably less elegant than those that cite only global causal factors, but we suspect they will have greater explanatory power.

ACKNOWLEDGMENTS

This research was supported by the National Science Foundation through an Earth Science Postdoctoral Research Fellowship (to Fox) and grant EAR-0087742 (to Koch). We thank B. Beitler, M. Clementz, R. Diffendal, J. Head, J. Honey, J. Newton, J. Thomasson, and R. Zakrewski for help with field and lab work; M. Voorhies for information on localities in Nebraska; C. Badgley and F. Smith for comments on an earlier version of this paper; and H. Fricke and B. MacFadden for helpful reviews.

REFERENCES CITED

Alroy, J., 2003, North American mammalian paleofaunal database: http://www.nceas.ucsb.edu/~alroy/nampfd.html (May 2003).

Cerling, T.E., and Quade, J., 1993, Stable carbon and oxygen isotopes in soil carbonate, *in* Swart, P.K., et al., eds., Climate change in continental isotopic records: American Geophysical Union Geophysical Monograph 78, p. 217–231.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., and Ehleringer, J.R., 1997, Global vegetation change through the Miocene/Pliocene boundary: Nature, v. 389, p. 153–157.

Diamond, J., 1997, Guns, germs, and steel: New York, W.W. Norton and Co., 480 p.

Ehleringer, J.R., and Monson, R.K., 1993, Evolutionary and ecological aspects of photosynthetic pathway variation: Annual Review of Ecology and Systematics, v. 24, p. 411–439.

Epstein, H.E., Lauenroth, W.K., Burke, I.C., and Coffin, D.P., 1997, Productivity patterns of C_3 and C_4 functional types in the U.S. Great Plains: Ecology, v. 78, p. 722–731.

Friedli, H., Lötshcer, H., Oeschger, H., Siegenthaler, U., and Staufer, B., 1986, $^{13}C/^{12}C$ ratio of atmospheric CO_2 in the past two centuries: Nature, v. 324, p. 237–238.

Huang, Y., Street-Perrott, F.A., Metcalfe, S.E., Brenner, M., Moreland, M., and Freeman, K.H., 2001, Climate change as the dominant control on glacial-interglacial variations in C_3 and C_4 plant abundance: Science, v. 293, p. 1647–1651.

Jacobs, B.F., Kingston, J.D., and Jacobs, L.L., 1999, The origin of grass-dominated ecosystems: Missouri Botanical Garden Annals, v. 86, p. 590–643.

Janis, C.M., Damuth, J., and Theodor, J.M., 2002, The origins and evolution of the North American grassland biome: The story from the hoofed mammals: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 177, p. 183–198.

Johnston, C.S., and Savage, D.E., 1955, A survey of various late Cenozoic vertebrate faunas of the panhandle of Texas, Part I: University of California Publications in Geological Sciences, v. 31, p. 27–50.

Kelly, E.F., Amundson, R.G., Marino, B.D., and DeNiro, M.J., 1991, Stable carbon isotopic composition of carbonate in Holocene grassland soils: Soil Science Society of America Journal, v. 55, p. 1651–1658.

Khokhlova, O.S., Kovalevskaya, I.S., and Oleynik, S.A., 2001, Records of climatic changes in the carbonate profiles of Russian Chernozems: Catena, v. 43, p. 203–215.

Kingston, J.D., Marino, B.D., and Hill, A., 1994, Isotopic evidence for Neogene hominid palaeoenvironments in the Kenya rift valley: Science, v. 264, p. 955–959.

Kleinert, K., and Strecker, M.R., 2001, Climate change in response to orographic barrier uplift: Paleosol and stable isotope evidence from the late Neogene Santa María basin, northwestern Argentina: Geological Society of America Bulletin, v. 113, p. 728–742.

Latorre, C., Quade, J., and McIntosh, W.C., 1997, The expansion of C_4 grasses and global change in the late Miocene: Stable isotope evidence from the Americas: Earth and Planetary Science Letters, v. 146, p. 83–96.

Mack, G.H., Cole, D.R., James, W.C., Giordano, T.H., and Salyards, S.L., 1993, Stable oxygen and carbon isotopes of pedogenic carbonate as indicators of Plio–Pleistocene paleoclimate in the southern Rio Grande rift, south-central New Mexico: American Journal of Science, v. 294, p. 621–640.

Martin, R.A., Honey, J.G., and Paláez-Campomanes, P., 2000, The Meade basin rodent project: A progress report: Paludicola, v. 3, p. 1–32.

Monger, H.C., Cole, D.R., Gish, J.W., and Giordano, T.H., 1998, Stable carbon and oxygen isotopes in Quaternary soil carbonates as indicators of geomorphic changes in the northern Chihuahuan Desert, USA: Geoderma, v. 82, p. 137–172.

O'Leary, M.H., 1988, Carbon isotopes in photosynthesis: BioScience, v. 38, p. 328–336.

Pagani, M., Arthur, M.A., and Freeman, K.H., 1999, Late Miocene atmospheric CO_2 concentrations and the expansion of C_4 grass: Science, v. 285, p. 876–878.

Passey, B.H., Cerling, T.E., Perkins, M.E., Voorhies, M.R., Harris, J.M., and Tucker, S.T., 2002, Environmental change in the Great Plains: An isotopic record from fossil horses: Journal of Geology, v. 110, p. 123–140.

Pearson, P.N., and Palmer, M.R., 2000, Atmospheric carbon dioxide concentrations over the last 60 million years: Nature, v. 406, p. 695–699.

Quade, J., and Cerling, T.E., 1995, Expansion of C_4 grasses in the late Miocene of northern Pakistan: Evidence from stable isotopes in paleosols: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 115, p. 91–116.

Quade, J., Cerling, T.E., and Bowman, J.R., 1989, Systematic variations in the carbon and oxygen isotopic composition of pedogenic carbonate along elevation transects in the southern Great Basin, United States: Geological Society of America Bulletin, v. 101, p. 464–475.

Quade, J., Cater, J.M.L., Ojha, T.P., Adam, J., and Harrison, T.M., 1995, Late Miocene environmental change in Nepal and the northern Indian subcontinent: Stable isotopic evidence from paleosols: Geological Society of America Bulletin, v. 107, p. 1381–1397.

Retallack, G.J., 2001, Cenozoic expansion of grasslands and climatic cooling: Journal of Geology, v. 109, p. 407–426.

Sage, R.F., 2001, Environmental and evolutionary preconditions for the origin and diversification of the C_4 photosynthetic syndrome: Plant Biology, v. 3, p. 202–213.

Schlesinger, W.H., 1997, Biogeochemistry: San Diego, Academic Press, 592 p.

Tedford, R.H., Skinner, M.F., Fields, R.W., Rensberger, J.M., Whistler, D.P., Galusha, T., Taylor, B.E., Macdonald, J.R., and Webb, S.D., 1987, Faunal succession and biochronology of the Arikareean through Hemphillian internal (late Oligocene through earliest Pliocene epochs) in North America, *in* Woodburne, M.O., ed., Cenozoic mammals of North America: Berkeley, University of California Press, p. 153–210.

Tieszen, L.L., and Boutton, T.W., 1989, Stable carbon isotopes in terrestrial ecosystem research, *in* Rundel, P.W., et al., eds., Stable isotopes in ecological research: New York, Springer-Verlag, p. 167–195.

Tieszen, L.L., Reed, B.C., Bliss, N.B., Wylie, B.K., and DeJong, D.D., 1997, NDVI, C_3 and C_4 production, and distributions in Great Plains grassland land cover classes: Ecological Applications, v. 7, p. 59–78.

Voorhies, M.R., 1990, Vertebrate biostratigraphy of the Ogallala Group in Nebraska, *in* Gustavson, T.C., ed., Geologic framework and regional hydrology: Upper Cenozoic Blackwater Draw and Ogallala Formations, Great Plains: Austin, Texas, Bureau of Economic Geology, p. 115–151.

Wang, D., and Anderson, D.W., 1998, Stable carbon isotopes of carbonate pendants from Chernozemic soils of Saskatchewan, Canada: Geoderma, v. 84, p. 309–322.

Wang, Y., and Cerling, T.E., 1994, A model of fossil tooth and bone diagenesis: Implications for paleodiet reconstruction from stable isotopes: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 107, p. 281–289.

Wang, Y., Cerling, T.E., Quade, J., Bowman, J.R., Smith, G.A., and Lindsay, E.H., 1993, Stable isotopes of paleosols and fossil teeth as paleoecology and paleoclimatic indicators: An example from the St. David Formation, Arizona, *in* Swart, P.K., et al., eds., Climate change in continental isotopic records: American Geophysical Union Geophysical Monograph 78, p. 241–248.

Wang, Y., Cerling, T.E., and MacFadden, B.J., 1994, Fossil horses and carbon isotopes: New evidence for Cenozoic dietary, habitat, and ecosystem changes in North America: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 107, p. 269–279.

Webb, S.D., 1977, A history of savanna vertebrates in the New World: Part I. North America: Annual Reviews of Ecology and Systematics, v. 8, p. 355–380.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K., 2001, Trends, rhythms, and aberrations in global climate, 65 Ma to present: Science, v. 292, p. 686–693.

Manuscript received 17 February 2003
Revised manuscript received 15 May 2003
Manuscript accepted 25 May 2003

Printed in USA