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Carbon and oxygen isotopic variability in Neogene paleosol carbonates: constraints on the evolution of the C₄-grasslands of the Great Plains, USA

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Abstract

Understanding the development of grassland ecosystems is critical for understanding the evolution of their associated vertebrate faunas. We focus on the central and southern portions of the Great Plains, which is the largest continuous grassland in North America and has a well-documented mammalian fossil record. Modern biomass in this region is dominated by C₄ grasses, but paleontological evidence indicates the region was forested prior to the middle Miocene, implying the region was formerly dominated by C₃ plants. We examine long- and short-term variations in the abundance of C₄ grasses and climatic conditions in the central and southern Great Plains using the stable carbon and oxygen isotope composition of paleosol carbonates from 28 sections of 11 lithostratigraphic units in the region.

The carbon isotope composition ($\delta^{13}\text{C}$) of paleosol carbonate reflects the proportion of C₃ and C₄ plants that grew in an ancient soil. The long-term pattern of $\delta^{13}\text{C}$ values indicates that the percentage of C₄ grasses in the Great Plains was moderate (ca. 20%) throughout most of the Miocene, increased from 6.4 to 4.0 Ma, and reached modern levels by 2.5 Ma. Based on the range in $\delta^{13}\text{C}$ values within sections and the mean $\delta^{13}\text{C}$ values for different carbonate morphologies that reflect different intervals of carbonate accumulation, the abundance of C₄ biomass did not vary substantially on short time scales. The variability in C₄ biomass on short time scales does not correlate with age of section, latitude, longitude, or the mean percentage of C₄ biomass.

The oxygen isotope composition ($\delta^{18}\text{O}$) of soil carbonate is controlled by soil temperature and the $\delta^{18}\text{O}$ value of soil water. Great Plains paleosol $\delta^{18}\text{O}$ values vary considerably in relation to time and latitude. Removing the variation due to latitude with least squares linear regression reveals a temporal pattern that is consistent with the global pattern of Neogene climate change. Quantitative interpretation of the $\delta^{18}\text{O}$ record is difficult without independent control on temperature or the oxygen isotope composition of soil water, both of which have probably varied with long-term climate change. Comparisons of measured $\delta^{18}\text{O}$ values for each section with predicted values based on modern temperature data and estimated modern meteoric water $\delta^{18}\text{O}$ values suggest that (1) most Miocene sections have $\delta^{18}\text{O}$ values consistent with warmer temperatures and more positively shifted soil water $\delta^{18}\text{O}$ values than today, (2) three Miocene sections in western Nebraska probably had soil water compositions that were more negative than similar-aged localities in the region, and (3) the Plio-Pleistocene sections have $\delta^{18}\text{O}$ values consistent with cooler temperatures and more negative soil water $\delta^{18}\text{O}$ values than today. The paleosol $\delta^{13}\text{C}$ values do not

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correlate strongly with the pattern of climate change recorded by the $\delta^{18}\text{O}$ values, suggesting that long-term change in mean temperature is not the main control on the abundance of $\delta^{13}\text{C}$ biomass in the Great Plains.

We propose two testable hypotheses to account for our data and other published data that bear on the evolution of the Great Plains ecosystem.

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1. Introduction

Grasslands are ecologically and historically important ecosystems, and their origins have had major consequences for the global carbon cycle, mammalian evolution, and the development of complex human societies. Grasslands occupy approximately one-quarter of the Earth's land surface and among modern terrestrial ecosystems only forests have higher primary productivity (Schantz, 1954; Lauenroth, 1979). As a consequence of this high productivity, grasslands and their soils are a major sink for organic carbon (Schlesinger, 1997) and have historically supported highly co-evolved communities of mammalian herbivores with greater biomass than found in any other terrestrial ecosystem (Bell, 1970; MacFadden, 1997; Frank et al., 1998; Olff et al., 2002). The evolution of these mammal communities has long been linked to the development of grasslands (Kowalevsky, 1873; Webb, 1977; Janis et al., 2002, 2004). Grasslands have also been critical to the development of complex human societies as the principal source of domesticated cereal species and a primary environment for intensive food production (Diamond, 1997).

The Great Plains of North America, which extends from central Canada to northern Texas, is the largest continuous area of grassland in North America. Like other expansive grassland ecosystems, the Great Plains is a phenomenon of the late Cenozoic (Jacobs et al., 1999). In the central and southern Great Plains (the region south of about 43°N , referred to hereafter as the Great Plains; Fig. 1), grasses using the C_4 photosynthetic pathway comprise 50–100% of modern, non-agricultural plant productivity (Epstein et al., 1997; Tieszen et al., 1997). Plant macrofossils and mammalian faunas suggest that relatively closed forest or woodland biomes dominated the Great Plains prior to the middle Miocene (ca. 15 Ma; Webb, 1977; Axelrod,

1985; Jacobs et al., 1999; Janis et al., 2002, 2004; but see Strömberg, 2004). As essentially all modern trees and shrubs (and cool-climate grasses) use the C_3 photosynthetic pathway (Sage, 2001), the region would have been dominated by C_3 biomass prior to the development of grasslands.

Fox and Koch (2003) used the carbon isotope composition of 274 samples of pedogenic carbonate from 28 early Miocene to early Pleistocene sections in the Great Plains to reconstruct the development of the modern C_4 -dominated grasslands of the region (Fig. 2; see discussion of isotope systematics below). They found relatively high $\delta^{13}\text{C}$ values throughout the Miocene, implying that C_4 biomass was moderately high (12–34%) throughout most of the Miocene (ca. 23–6.4 Ma). Because the mean offset in $\delta^{13}\text{C}$ values of co-occurring paleosol carbonate and organic matter occluded in the carbonate was statistically indistinguishable from the mean offset for modern soils, Fox and Koch (2003) were able to rule out aridity and low soil productivity as explanations for paleosol carbonates enriched in ^{13}C compared to expected end-member C_3 values. Fox and Koch (2003) did not observe any detrital carbonate or distributed sparry (i.e., diagenetic) calcite in thin sections of 23 samples that are outwardly typical, indicating that neither parent material with high $\delta^{13}\text{C}$ values (such as grains of Paleozoic carbonate) nor diagenesis could account for the high $\delta^{13}\text{C}$ values of Miocene paleosol carbonates. The proportion of C_4 biomass appears to have increased somewhat during the latest Miocene and early Pliocene (ca. 6.4–4.0 Ma) and reached modern levels by the late Pliocene (ca. 2.5 Ma). These results were surprising given prior research showing that mammals with C_4 -dominated diets appeared globally during the late Miocene, implying that C_4 -dominated ecosystems appeared at that time (Cerling et al., 1997).

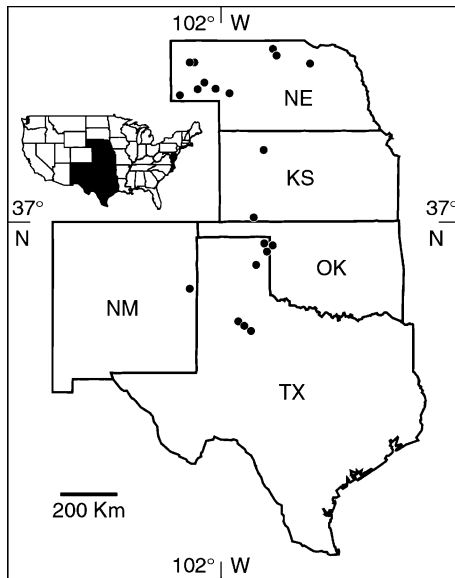


Fig. 1. Map of localities sampled in this study. Some localities are too close together to be distinguished at this scale, hence only 20 symbols are visible.

In this paper, we focus on several aspects of the Great Plains paleosol isotopic record that Fox and Koch (2003) did not address in detail. First, we look at geographic variability in the carbon isotope record. Second, we examine temporal and geographic trends in the range of $\delta^{13}\text{C}$ values within sections. Because the $\delta^{13}\text{C}$ values of C_3 and C_4 plants are sensitive to environmental factors, variation in $\delta^{13}\text{C}$ values within sections might reflect short-term variations in either the C_3/C_4 ratio or factors that affect the $\delta^{13}\text{C}$ of plant organic matter (hence soil carbonate), such as light stress, water stress, or canopy cover (Ehleringer and Monson, 1993; van der Merwe and Medina, 1991). Third, we present the oxygen isotope record from the Great Plains paleosol carbonates and examine temporal and geographic variability in the long-term record and within individual sections. As discussed below, the $\delta^{18}\text{O}$ value of pedogenic carbonate is sensitive to both soil temperature and the isotopic composition of soil water and is a potential source of paleoclimatic information. We do not have independent evidence for either of the variables that control carbonate oxygen isotope composition, so we explore the paleoclimatic significance of the oxygen isotope record by comparing measured values to those predicted based on

modern air temperature and meteoric water composition at each sampling locality.

Finally, we present two hypotheses to explain the history of the Great Plains ecosystem and propose means to test these alternatives. Many, though not all, lines of evidence suggest differences in the timing of grassland development in the Great Plains after the middle Miocene. The plant macrofloral record supports the appearance of grass-dominated habitats in some areas of the Great Plains by 13–10 Ma and the appearance of open grassland habitats by 8 Ma (MacGinitie, 1962; Thomasson, 1990), but the stratigraphic and geographic distribution of diverse and well-sampled plant macrofloras in the Great Plains is not sufficient to reconstruct the development of grasslands in detail (see Strömberg, 2004, for a discussion of the implications of the grass phytolith record for the history of grassland development). Changes in molar tooth morphology of herbivorous mammals from middle Miocene to early Pleistocene localities in and around Nebraska imply that grasslands expanded gradually from the middle Miocene to the end of the Pliocene (Janis et al., 2002). Paleodietary reconstructions for diverse species of equids (horses) using carbon isotope ratios in fossil tooth enamel (Wang et al., 1994; Passey et al., 2002) suggest that C_4

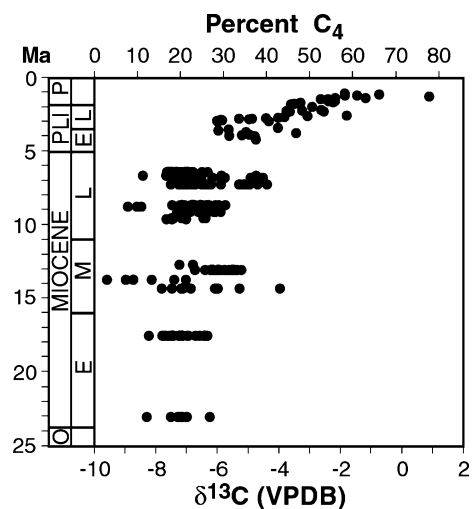


Fig. 2. Variation in $\delta^{13}\text{C}$ values of Great Plains paleosol carbonates. Percent C_4 calculated based on linear mixing of end-member C_3 and C_4 biomass with $\delta^{13}\text{C}$ values of -25.5‰ and -11.5‰ , respectively. After Fox and Koch (2003).

content in the diet of some species increased rapidly in the Great Plains after 6.6 Ma during the latest Miocene. However, changes in the trophic structure and dietary preferences of Miocene to Pleistocene mammalian herbivore communities in the Great Plains do not necessarily reflect changes in the proportions of C₃ and C₄ plants that were present in an ancient ecosystem, as mammal diets reflect the availability of resources, plant–animal interactions, and ecological interactions among animal species competing for those resources. In contrast, the carbon isotope composition of paleosol carbonate directly records the proportions of C₃ and C₄ plants that were growing in an ancient soil over the time period of carbonate formation.

The development of grasslands has traditionally been associated with late Cenozoic climate change, particularly decreasing temperatures, increasing aridity, and increasing seasonality of temperature and/or precipitation (Webb, 1977; Axelrod, 1985). More recently, a decrease in atmospheric CO₂ levels has been hypothesized to play a role in the expansion of C₄ grasses. Plants using the C₄ photosynthetic pathway have anatomical and biochemical adaptations for concentrating CO₂ within leaf cells prior to photosynthesis, which may lead to a selective advantage over C₃ plants under conditions of low atmospheric *p*CO₂ (Cerling et al., 1997; Sage, 2001). However, two studies using proxies for atmospheric *p*CO₂ based on the stable isotope composition of marine algal biomarkers (Pagani et al., 1999) and planktonic foraminifera (Pearson and Palmer, 2000) have not found evidence for a sharp and permanent decrease in atmospheric CO₂ levels during the late Miocene.

Mechanistic hypotheses explaining the pattern of C₄ expansion in the Great Plains recorded by paleosol carbonate must account for the patterns of ecological change identified by previous floral, faunal, and paleodietary studies. However, viable hypotheses must also explicitly address the implications of the paleosol record carbon isotope record: C₄ biomass was relatively abundant in the Great Plains throughout the Miocene and only increased substantially after the Late Miocene, as demonstrated by Fox and Koch (2003), and the C₃/C₄ ratio did not vary much spatially or temporally during the Miocene, as discussed in detail in this paper. In brief, the first hypothesis we propose is that grasslands did in fact

begin expanding at the expense of forest and woodland habitats during the Middle Miocene, but the initial expansion was of C₃-dominated grasslands that were supplanted by C₄ grasses only after the Late Miocene. Our second hypothesis returns the focus of grassland origins in the Great Plains to the well-known pattern of global climatic cooling during the late Cenozoic (Zachos et al., 2001) and suggests that the Pliocene increase in C₄ biomass was driven by the ecological consequences of reduced growing seasons. Both hypotheses and means of testing them are discussed in greater detail after discussion of the variability in the δ¹³C and δ¹⁸O records of the Great Plains paleosol carbonates, which provides important constraints on hypotheses of grasslands origins in the Great Plains.

2. Stable isotopes in paleosols

2.1. Carbon

Because of the anatomical and biochemical differences associated with different photosynthetic pathways, C₃ and C₄ plants fractionate carbon isotopes to different degrees during photosynthesis. Modern C₃ plants have a mean δ¹³C² value of −27‰ (range −35‰ to −22‰; values are relative to VPDB) and C₄ plants have a mean value of −13‰ (range −14‰ to −10‰) (O'Leary, 1988; Tieszen and Boutton, 1989). Plants using a third pathway, crassulacean acid metabolism, have values overlapping those of C₃ and C₄ plants, but they are a minor component of most non-desert ecosystems in temperate and subtropical latitudes and are not considered further.

Authigenic soil carbonate forms in carbon isotopic equilibrium with CO₂ dissolved in soil water (Cerling, 1984; Cerling et al., 1989). At shallow depth, soil CO₂ is a mixture of atmospheric CO₂ and biogenic CO₂

² By convention, stable isotope compositions are expressed in δ notation, which is the permil (‰, parts per thousand) difference between the ratio of rare to abundant isotope in a sample (*R*_{sam}) and the same ratio in a standard material (*R*_{std}). Thus, δ¹³C = ((*R*_{sam}/*R*_{std}) − 1) × 1000. For carbonate δ¹³C values, the standard is Vienna Pee Dee Belemnite (VPDB). Carbonate δ¹⁸O values can also be expressed relative to VPDB, but we have converted our δ¹⁸O values to the Vienna Standard Mean Ocean Water (VSMOW) scale for comparison with meteoric water compositions.

derived from root respiration and microbial oxidation of soil organic matter. At typical soil respiration rates and modern atmospheric composition, soil CO₂ below about 30 cm in a soil is almost entirely biogenic, with a $\delta^{13}\text{C}$ value related to that of overlying biomass (Cerling et al., 1991). Overall, pedogenic carbonate formed at depth reflects the contributions of isotopically distinct C₃ and C₄ biomass to soil CO₂ but is enriched in ¹³C by 14–17‰ relative to soil organic matter due to diffusion of CO₂ from soil to atmosphere and temperature dependent carbon isotope fractionation during carbonate precipitation (Cerling et al., 1989, 1991). Thus, if soil respiration was moderate to high, the $\delta^{13}\text{C}$ values of paleosol carbonate can be used to estimate the proportion of above-ground biomass fixed by plants using the C₃ versus C₄ photosynthetic pathway.

2.2. Oxygen

Pedogenic carbonate forms in oxygen isotope equilibrium with soil water (Cerling and Quade, 1993), and the $\delta^{18}\text{O}$ value of soil carbonate is a function of temperature and soil water composition (Friedman and O'Neil, 1977). Soil temperature at shallow depth in a soil is similar to air temperature (Brady, 1990). Soil water is derived from meteoric recharge, although soil water can differ from local meteoric water due to enrichment through evaporation from the soil surface, mixing with evaporatively enriched infiltrating water, and addition of isotopically distinct water from overland and vadose zone flow (Cerling and Quade, 1993; Hsieh et al., 1998). Nevertheless, $\delta^{18}\text{O}$ values of modern soil carbonates have a strong positive correlation with the composition of local meteoric water ($\delta^{18}\text{O}_{\text{mw}}$; Cerling and Quade, 1993). Because modern $\delta^{18}\text{O}_{\text{mw}}$ values have a strong positive correlation with local air temperatures (Rozanski et al., 1993), the $\delta^{18}\text{O}$ of paleosol carbonate has potential as a paleoclimatic indicator. However, on the time scale of this study, the slope and intercept of the modern relationship between $\delta^{18}\text{O}_{\text{mw}}$ values and air temperature would not necessarily hold due to factors such as long-term secular variations in the oxygen isotope composition of water vapor source areas as a function of global ice volume (Zachos et al., 2001), changes in source water temperature (Boyle, 1997), and changes atmospheric circulation that

would alter the transport trajectories and isotopic evolution of moist air masses (Amundson et al., 1996). As a result of these factors, and those that cause soil water $\delta^{18}\text{O}$ values to deviate from local $\delta^{18}\text{O}_{\text{mw}}$ values, soil temperature and the oxygen isotope composition of soil water may not both be directly linked to air temperature and may record additional aspects of climate change. Thus, to make quantitative paleoclimatic inferences from paleosol oxygen isotope compositions, it is necessary to have independent evidence for either paleotemperature or past soil water composition. Without constraint on paleotemperature or ancient soil water oxygen isotope composition, temporal and geographic variations in paleosol $\delta^{18}\text{O}$ values can only be used to identify qualitative changes in these variables.

3. Materials and methods

3.1. Sampling and age assignment

We collected paleosol carbonates from 10 lithostratigraphic units exposed in 24 outcrops in the central and southern Great Plains (Fig. 1; Table 1). At several outcrops, we sampled superposed lithostratigraphic units, so we sampled a total of 28 distinct lithostratigraphic sections. At each locality, we collected a stratigraphic series of samples, usually collecting several nodules or caliche samples per sampling level. The mammalian biostratigraphy of the Great Plains is well understood, and our sampling targeted sections and lithostratigraphic units that contain biostratigraphically distinct mammalian faunas. In those sections that included a known mammalian fauna, age assignments are based on the midpoint of the age range for the locality based on either the traditional North American Land Mammal Age system (Tedford et al., 1987; Voorhies, 1990; Martin et al., 2000) or a more recent quantitative biostratigraphic approach (Alroy, 2000). In sections that did not contain known mammalian faunas in the specific outcrop sampled, assigned ages are based on the midpoint of the age range for the lithostratigraphic units, which are based on the biostratigraphy of the units across their entire areas of outcrop (Tedford et al.,

Table 1
Geographic coordinates, lithostratigraphic units, and age assignments for sampled sections

Locality (nearby town, state)	Lat. (°N)	Long. (°W)	Lithostratigraphic units sampled	Samples	Meters sampled	Age (Ma)	Reference
(1) Borchers Badlands (Meade, KS)	37.2	100.4	Crooked Creek Fm	17	16.0	1.0–2.3	5
(2) Aries Quarry (Meade, KS)	37.2	100.4	Crooked Creek Fm	4	3.3	1.2–1.6	5
(3) Alien Canyon (Meade, KS)	37.0	100.6	Ballard Fm	23	26.0	2.6–4.2	5
(4) CR E/93 N of Bellview, NM	34.9	103.1	Ogallala Fm	30	20.5	6.4	4
(5) Coffee Ranch (Lora, TX)	35.7	100.5	Ogallala Fm	13	9.0	6.6	1,6,7
(6) FM 211 (Southland, TX)	33.3	101.5	Bridwell Fm	11	9.4	6.8	1,10
(7) Yellowhouse Canyon 1 (Slaton, TX)	33.5	101.6	Bridwell Fm	10	4.5	6.8	1,10
(8) Yellowhouse Canyon 2 (Slaton, TX)	33.5	101.6	Bridwell Fm	4	3.3	6.8	1,10
(9) Lake McConnaughy Dam (Ogallala, NE)	41.2	101.7	Ogallala Group	9	5.5	7.3	8
(10) NE 71/CR 30 (Kimball, NE)	41.2	103.6	Ash Hollow Fm	16	10.0	7.3	8
(11) Breakneck Hill (Broadwater, NE)	41.6	102.8	Ash Hollow Fm	1	–	7.3	8
(12) Wildhorse Canyon (Oshkosh, NE)	41.3	102.4	Ash Hollow Fm	20	6.5	8.7	1,2
(13) Higgins Quarry (Higgins, TX)	36.1	100.0	Ogallala Fm	2	0.5	8.8	1,9
(14) Box T 1 (Higgins, TX)	36.2	100.1	Ogallala Fm	3	3.0	8.8	1,7
(15) Box T 2 (Higgins, TX)	36.2	100.1	Ogallala Fm	5	3.0	8.8	1,7
(16) Greenwood Canyon (Dalton, NE)	41.5	103.1	Ash Hollow Fm	19	21.0	9.1	1,2
(17) Minium Q (Morland, KS)	39.4	100.1	Ogallala Fm	7	13.0	9.6	1,9
(18) Port of Entry Pit (Arnett, OK)	36.1	100.0	Ogallala Fm	3	14.0	9.6	1,7
(19) Ashfall Fossil Beds SHP 1 (Orchard, NE)	42.4	98.2	Cap Rock Mbr	2	0.5	12.7	1
(20) Yellowhouse Canyon 1 (Slaton, TX)	33.5	101.6	Crosbyton Mbr, Couch Fm	16	7.0	13.1	1,10
(21) Yellowhouse Canyon 2 (Slaton, TX)	33.5	101.6	Crosbyton Mbr, Couch Fm	12	3.0	13.1	1,10
(22) Ashfall Fossil Beds SHP 1 (Orchard, NE)	42.4	98.2	Devil's Gulch Mbr, Valentine Fm	4	7.5	13.7	1
(23) Ashfall Fossil Beds SHP 2 (Orchard, NE)	42.4	98.2	Devil's Gulch Mbr, Valentine Fm	3	1.5	13.7	1
(24) Norden Bridge Quarry (Norden, NE)	42.8	100.0	Valentine Fm	8	7.1	14.3	1
(25) Egelhoff Quarry (Norden, NE)	42.8	100.0	Valentine Fm	2	2.5	14.3	1
(26) NE 71/2 (Hemingford, NE)	42.4	103.3	Dawes Clay Mbr, Box Butte Fm	13	4.0	17.5	3,8
(27) Hemingford, NE	42.4	103.1	Dawes Clay Mbr, Box Butte Fm	8	3.0	17.5	3,8
(28) Breakneck Hill (Broadwater, NE)	41.6	102.8	Monroe Creek/ Harrison Fms	9	3.0	23.0	8

Ages are midpoints of age range from references for each locality. References: 1, Alroy, 2000; 2, Breyer, 1981; 3, Galusha, 1975; 4, Gustavson, 1996; 5, Martin et al., 2000; 6, Passey et al., 2002; 7, Schultz, 1990; 8, Tedford et al., 1987; 9, Thomasson et al., 1990; 10, Winkler, 1990.

1987). Samples in the three sections in southwestern Kansas (Fig. 1, Table 1) are assigned ages based on their superpositional relationship to the Huckleberry Ridge (2.1 Ma) and Cerro Toledo B (1.2–1.5 Ma) ashes in the Crooked Creek Formation (Martin et al., 2000) and an assumed linear sedimentation rate. Although different biostratigraphic schemes (Tedford et al., 1987; Voorhies, 1990; Alroy, 2000) yield different

age assignments for some Miocene localities, all are unambiguously Miocene in age based on lithostratigraphy and biostratigraphy.

We sampled multiple localities in the middle and late Miocene and the number of samples per locality in these intervals spans a wide range; the correlation between number of samples and age is weak ($r = -0.24$) and not statistically significant

($p=0.22$) (Fig. 3A). Sampled sections varied in length from less than 1.0 to more than 25.0 m (Table 1) and, not surprisingly, the correlation between number of samples and the length of section sampled is strong, positive, and statistically significant ($r=0.72$, $p<0.01$). The correlation between the number of samples per locality and latitude is weak ($r=-0.20$) and not statistically significant ($p=0.32$), but that with longitude is stronger ($r=0.53$) and is statistically significant ($p<0.01$). However, given the limited longitudinal scope of our sampling, we do not expect significant trends in $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values with longitude.

With the exception of the sections in southwestern Kansas, all samples in a section are given the same age regardless of their superpositional sequence as sedimentation rates and age ranges within these sections are not known. However, the sediments are dominantly fluvial and cut-and-fill features are abundant in the Cenozoic cover of the Great Plains, so local sections probably do not preserve all of the time represented by each lithostratigraphic unit. Although we cannot constrain the amount of time represented in most local sections sampled, we can use the number of samples and the length of sampled sections to examine shorter-term variations in the paleosol $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ records.

We also use the maturity of carbonate development to examine patterns in vegetation on time scales shorter than the duration of each section. Based on the classification of calcareous soil morphologies (Gile et al., 1966; Machette, 1985), we assume that small carbonate nodules (<ca. 5 cm) accumulated in the least amount of time and that the duration of carbonate accumulation increases progressively from large nodules (>ca. 5 cm) to thin caliche horizons (<ca. 25 cm thick) to massive caliche horizons (typically 50–200 cm thick). Machette (1985) suggested that massive caliches in the arid southwestern U.S. take 0.50–0.75 Ma to form. Given the age range of some lithostratigraphic units that include numerous massive caliches (e.g., the Ash Hollow Formation), the durations reported by Machette (1985) are probably longer than is typical for most Great Plains caliches. Overall, small nodules should have the greatest variability, assuming that landscape scale variations in the C_3/C_4 ratio occur on time scales

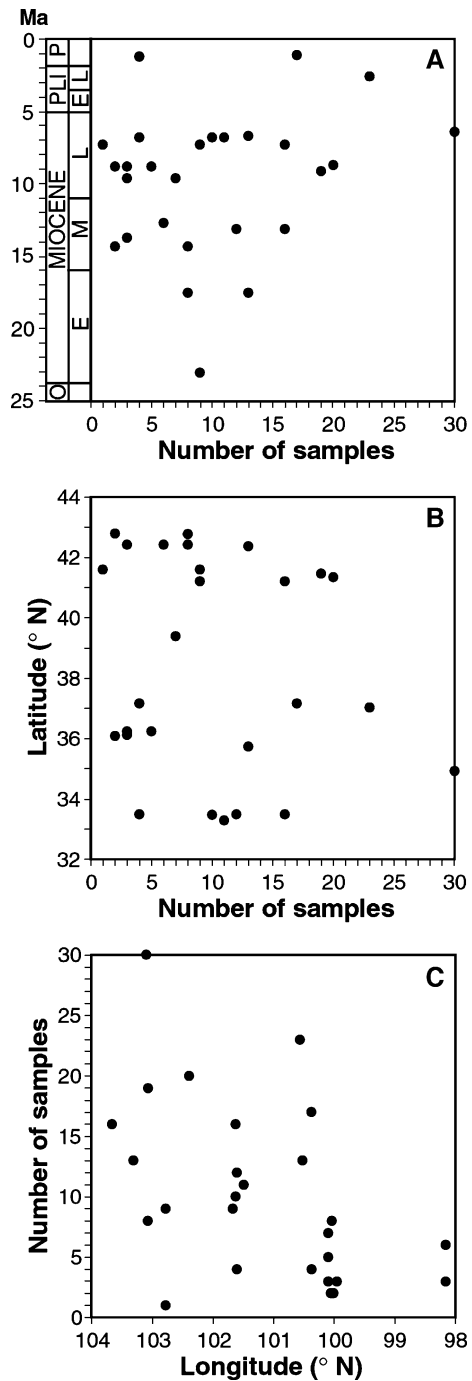


Fig. 3. Temporal and geographic variation in sampling. (A) Number of samples from each locality in relation to the age of the localities. (B) Number of samples from each locality in relation to latitude. (C) Number of samples from each locality in relation to longitude.

similar to the hundreds to thousands of years represented by such nodules. Small nodules could also exhibit some bimodality if ecosystems varied between C_3 -dominated closed canopy forests and more mixed parkland type environments that are consistent with the mean Miocene $\delta^{13}C$ value (see below and Fox and Koch, 2003). Massive caliches should provide the most integrated signal. Two temporal patterns of habitat variation can lead to massive caliches with the same mean value as other carbonate morphologies but lower variability: (1) habitats that varied between distinctive closed forests with little C_4 biomass and more mixed parklands with greater C_4 biomass on time scales short relative to the duration of massive caliche development and (2) stable habitats that do not vary much from the long-term average C_3/C_4 ratio on time scales long relative to the development of massive caliches. Massive caliches should have similar mean $\delta^{13}C$ value and similar variability compared to other carbonate morphologies if habitats varied between closed forests with little C_4 biomass and mixed parklands with more C_4 biomass on time scales long relative to the accumulation of massive caliches, so that each caliche only sampled a single, persistent habitat. We also examine results for 16 carbonate samples that do not fit into one of these four categories. These include distributed carbonate, thin carbonate stringers, and carbonate-cemented sandstone pods within strata. To determine whether differences in mean $\delta^{13}C$ values for different carbonate morphologies are significant, we use one way ANOVA with carbonate morphology as the grouping variable and the post hoc Scheffé test for multiple comparisons to determine which specific differences are significant at $\alpha=0.05$. We focus comparisons of different carbonate morphologies on Miocene samples ($n=230$), which have relatively constant $\delta^{13}C$ values. Including the Plio-Pleistocene values from Kansas would complicate the analysis because of the sharp increase in $\delta^{13}C$ values recorded in those sections independent of carbonate morphology. Also, because $\delta^{18}O$ values of paleosol carbonates vary widely and complexly in both time and space, we do not compare $\delta^{18}O$ values from different carbonate morphologies.

Carbonate-bearing paleosols were recognized in the field based on the following criteria: crumbly texture,

interpreted as an indication of soil ped preservation; absence or disruption of primary sedimentary structures; development of horizonation or mottling; presence of rhizoconcretions, interpreted as root traces; and presence of carbonate nodules or caliche horizons, which varied in thickness from several centimeters to ca. 2 m thick. Samples were collected in situ either from trenches or from caliche beds (following removal of the weathered surface). Carbonate was collected at least 50 cm below pedogenic or sedimentological features marking the uppermost preserved level in a paleosol. Few of the paleosols we sampled had preserved A horizons. Paleosols without horizonation for several vertical meters were interpreted as cumulative soils and sampled opportunistically or at intervals of 50–100 cm. Caliche beds thinner than 50 cm were sampled from the lowermost indurated surface; those thicker than 50 cm were sampled from the lower and upper surfaces.

To examine isotopic variation within individual nodules and caliche field samples, we analyzed two discrete samples from each of 259 sampling levels. We present results of these analyses as sample means and discuss intrasample variability below. For an additional 15 collecting levels, we analyzed only single samples. To examine variation within sampling levels, we analyzed pairs of samples from each of two separate nodules or hand samples of caliche from 70 collecting levels in 12 lithostratigraphic units at 11 outcrops. In total, we report 274 carbon and oxygen isotope values resulting from 533 individual analyses.

3.2. Analytical techniques

Samples for carbonate analysis were roasted in vacuo at 400 °C for 1 h to eliminate water and organic matter and reacted with 100% H_3PO_4 at 90 °C in a Micromass Isocarb automatic carbonate extraction system. The isotope composition of the resulting CO_2 was measured using either the Micromass Prism or Optima isotope-ratio mass spectrometer in the Stable Isotope Lab at the University of California, Santa Cruz. Sample values were normalized to the mean isotope composition of six to eight samples of granular Carrera marble analyzed as a laboratory standard with each set of paleosol samples. The correction factor was checked by applica-

tion to two samples of the carbonate standard NBS-19 (certified $\delta^{13}\text{C}$ value=1.95‰; certified $\delta^{18}\text{O}$ value=-2.20‰) run with each set of samples and Carrera marble standards. The mean normalized $\delta^{13}\text{C}$ of 45 samples of NBS-19 analyzed over 23 sets of analyses during this project was 1.96 ± 0.05 ‰ (1 S.D.). The corresponding $\delta^{18}\text{O}$ value is -2.21 ± 0.19 ‰ (1 S.D.).

3.3. Estimating abundance of C_4 biomass from paleosol carbonate $\delta^{13}\text{C}$ values

We use a simple linear mixing model between end-members with mean C_3 and C_4 carbon isotope compositions to estimate the percentage of C_4 biomass implied by paleosol carbonate $\delta^{13}\text{C}$ values. For simplicity, we assume a pre-industrial atmospheric CO_2 carbon isotope composition of -6.5 ‰ (Friedli et al., 1986). This implies mean $\delta^{13}\text{C}$ values for C_3 and C_4 plant biomass of -25.5 ‰ and -11.5 ‰, respectively. We also assume a fractionation factor between soil CO_2 and soil carbonate of ± 15.5 ‰, which is roughly the midpoint of observed modern values (Cerling and Quade, 1993). Water stress under arid growing conditions would shift organic matter compositions to less negative $\delta^{13}\text{C}$ values and would lead to an overestimate of C_4 biomass (Farquhar et al., 1989). However, the offsets between $\delta^{13}\text{C}$ values of co-occurring Great Plains paleosol carbonate and organic matter do not suggest high aridity (Fox and Koch, 2003). Under closed canopy cover, mixing of atmospheric CO_2 with plant and soil respired CO_2 previously fractionated by photosynthetic processes reduces the $\delta^{13}\text{C}$ value of plant biomass (van der Merwe and Medina, 1991) and could lower soil carbonate $\delta^{13}\text{C}$ values, leading to an underestimate of C_4 biomass. Passey et al. (2002) used time series of $\delta^{13}\text{C}$ values from planktonic foraminifera to estimate the $\delta^{13}\text{C}$ value of atmospheric CO_2 at different intervals during the Miocene, and then used those estimates to calculate expected $\delta^{13}\text{C}$ values for C_3 and C_4 plant tissues. Using their highest estimates of Miocene atmospheric CO_2 would only decrease the percentage of C_4 biomass we calculate from paleosol carbonate $\delta^{13}\text{C}$ values by about 7% (assuming mean C_3 and C_4 $\delta^{13}\text{C}$ values); using their lowest estimates would only increase the estimated C_4 biomass by about 3%.

3.4. Interpreting paleosol carbonate $\delta^{18}\text{O}$ values

Because we lack estimates of soil temperature or water composition, we cannot make explicit quantitative paleoclimatic inferences from the paleosol oxygen isotope record. However, we can compare measured values from paleosols with values expected in the same locations based on present-day temperatures and $\delta^{18}\text{O}_{\text{mw}}$ values using the experimentally determined fractionation between calcite and water:

$$1000 \ln \alpha = ((2.78 \times 10^6) T^{-2}) - 2.89, \quad (1)$$

where α is the fractionation factor and is calculated as

$$\alpha = (1000 + \delta^{18}\text{O}_{\text{CO}_3}) / (1000 + \delta^{18}\text{O}_{\text{H}_2\text{O}}) \quad (2)$$

and T is temperature in Kelvin (Friedman and O'Neil, 1977). For each locality, we use air temperatures from the National Climate Data Center summary of the day database for the closest weather station with a long-term daily temperature record. We predict carbonate $\delta^{18}\text{O}$ values using both the mean annual temperature and the mean maximum temperature from each weather station. For soil water compositions, we use estimates of local meteoric water $\delta^{18}\text{O}$ values based on a recent global meteoric water model (Bowen and Wilkinson, 2002; Bowen and Revenaugh, in press). The model converts latitude, longitude, and elevation into an estimate of $\delta^{18}\text{O}_{\text{mw}}$ using regression equations and long-term mean $\delta^{18}\text{O}_{\text{mw}}$ values from monitoring stations of the Global Network of Isotopes in Precipitation maintained by the International Atomic Energy Agency (IAEA). Geographic coordinates for each sampling locality were measured in the field using a handheld GPS unit. Elevations were taken from USGS 7.5' topographic maps. Although most sections are in relatively shallow (<200 m) valleys cut into the High Plains surface, we used the approximate average elevation of the High Plains surface to predict $\delta^{18}\text{O}_{\text{mw}}$ values. For the Great Plains, differences in elevation of several hundred meters only change estimated $\delta^{18}\text{O}_{\text{mw}}$ values by about 0.1‰. We also use Eqs. (1) and (2) to determine what soil water compositions are implied by paleosol $\delta^{18}\text{O}$ values assuming soil temperature in the past was the same as modern air temperature,

and what temperatures are implied assuming soil waters had the same composition as estimated modern meteoric water.

4. Paleosol carbon isotope variation

4.1. Long-term variation in $\delta^{13}\text{C}$ values and C_4 abundance

Fox and Koch (2003) discussed the long-term pattern of paleosol carbonate $\delta^{13}\text{C}$ values (Fig. 2) in detail; this discussion will only be summarized here. Miocene paleosol carbonate $\delta^{13}\text{C}$ values are generally less negative than expected for end-member C_3 values, even accounting for the effects of aridity. The Miocene samples have a mean $\delta^{13}\text{C}$ value of $-6.8 \pm 0.83\text{‰}$ ($n=230$; all mean values reported ± 1 S.D.). On average, C_4 biomass constituted about 23% of primary productivity during the Miocene and did not vary substantially. We discuss the geographic and shorter-term pattern of variation in the abundance of C_4 biomass during the Miocene in the following sections. The average abundance of C_4 biomass increased somewhat during an unsampled interval from ca. 6.4–4.0 Ma. The Pliocene–Pleistocene samples are all from southwestern Kansas and record a steady increase in the abundance of C_4 biomass to modern levels (Kelly et al., 1991) by ca. 2.5 Ma. The mean $\delta^{13}\text{C}$ value for the Plio-Pleistocene samples is $-3.6 \pm 1.63\text{‰}$ ($n=44$).

4.2. Variation in $\delta^{13}\text{C}$ values within samples and collecting levels

Carbon isotope variation both within individual samples and within collecting levels is similar. The mean difference between pairs of analyses from the same carbonate nodule or caliche sample is $0.2 \pm 0.24\text{‰}$ ($n=253$). The mean difference between pairs of samples from the same collecting level is $0.3 \pm 0.28\text{‰}$ ($n=70$). This variation is much lower than either the variation around the mean Miocene value (1 S.D.= 0.83‰ , range 5.6‰) or the variation in values during the Pliocene transition to a C_4 grassland (1 S.D.= 1.53‰ , range= 10.5‰). Thus, the overall trends discussed above and the variations within individual sections discussed below are

not a function of either intrasample or interlevel variability.

4.3. Geographic variability in $\delta^{13}\text{C}$ values and C_4 abundance

The $\delta^{13}\text{C}$ values from Miocene paleosols have statistically significant weak correlations with both latitude (Fig. 4A, $r=-0.16$, $p=0.02$) and longitude (Fig. 4B, $r=-0.21$, $p=0.001$). The abundance of C_4 biomass for Miocene samples decreases slightly to the north in the southern Great Plains from ca. $33\text{--}36^\circ\text{N}$

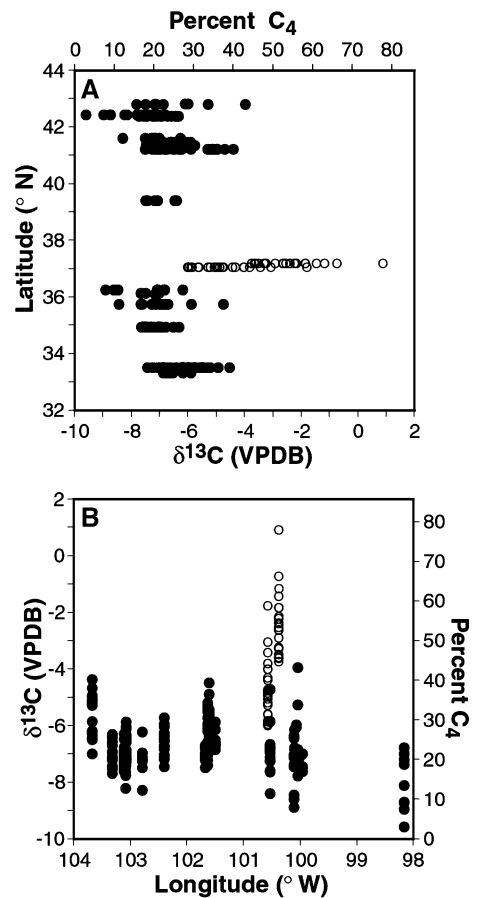


Fig. 4. Geographic variation in Great Plains paleosol carbonate $\delta^{13}\text{C}$ values and estimated percentage of C_4 biomass during the Neogene. ●, Miocene samples. ○, Plio-Pleistocene samples from southwestern Kansas. (A) Latitudinal gradient in $\delta^{13}\text{C}$ values and percent C_4 biomass. (B) Longitudinal gradient in $\delta^{13}\text{C}$ values and percent C_4 biomass.

and is more or less constant through the central Great Plains in northern Kansas and Nebraska. Moving from west to east, the average percentage of C₄ biomass in Miocene sections decreases slightly but is generally close to 20%. The sharp increase in C₄ abundance at ca. 37°N and ca. 100.3°W is a reflection of the Plio-Pleistocene increase in $\delta^{13}\text{C}$ values and C₄ biomass recorded in paleosol carbonates in southwestern Kansas. Including the Plio-Pleistocene values does not alter the correlation with latitude ($r=-0.16$, $p=0.005$), but the correlation with longitude is weaker and is not statistically significant ($r=-0.11$, $p=0.07$).

4.4. Short-term variability in $\delta^{13}\text{C}$ values and C₄ abundance

As discussed above, variation in $\delta^{13}\text{C}$ values within sections should be an indication of variation in the composition of plant biomass on relatively short temporal scales and small geographic scales. We assume that the number of samples and the length of section sampled correlate positively with the amount of time represented, but we cannot quantify these relationships at present. Because we are interested primarily here with the maximum abundance of C₃ and C₄ biomass within sections, we use the range in $\delta^{13}\text{C}$ values within sections of each lithostratigraphic unit (Fig. 5; Table 2), rather

than the standard deviation, to examine variation in the composition of biomass within sections. However, the ranges within sections have a strong positive correlation with the standard deviations that is statistically significant ($r=0.91$, $p<0.01$), so the range gives a reasonable approximation of the statistical behavior of the variation in $\delta^{13}\text{C}$ values within sections.

Most sections exhibit relatively little variability, suggesting relatively little heterogeneity in the composition of local ecosystems on short time scales. The average range within sections is 1.7‰, which corresponds to a range in abundance of C₄ biomass of only 11.4%. No temporal trend in the shorter-term degree of variability in the composition of Great Plains ecosystems is evident over the late Cenozoic (Fig. 5) and the correlation between age and range in $\delta^{13}\text{C}$ values is weak and not statistically significant ($r=-0.20$, $p=0.31$). The most variable sections are two of the three sections in southwestern Kansas that record the sharp increase in the abundance of C₄ biomass. The third section in southwestern Kansas (Aries Quarry) has a high mean $\delta^{13}\text{C}$ value but exhibits little variability, which is probably related to the small number of samples ($n=4$) from that section. Shorter-term variation does not change consistently with either latitude ($r=0.10$, $p=0.63$) or longitude ($r=-0.05$, $p=0.79$). The number of samples and the meters sampled have the strongest correlations with the range in $\delta^{13}\text{C}$ values. Although these correlations are only moderately strong ($r=0.47$ and 0.46 , respectively), they are statistically significant ($p=0.01$ and 0.02 , respectively). The positive correlations with sampling are unsurprising because short-term fluctuations in habitat composition are more likely to be recovered in more densely sampled sections and in samples from longer sections that presumably represent more time. Additionally, the correlations are probably strengthened by sections with few samples and very short sections, which are less likely to vary much than more densely sampled and longer sections.

A second means of examining short-term variability in the composition of local plant biomass, at least for the Miocene samples, is to compare $\delta^{13}\text{C}$ values for carbonate morphologies that represent different durations of carbonate accumulation. The mean $\delta^{13}\text{C}$

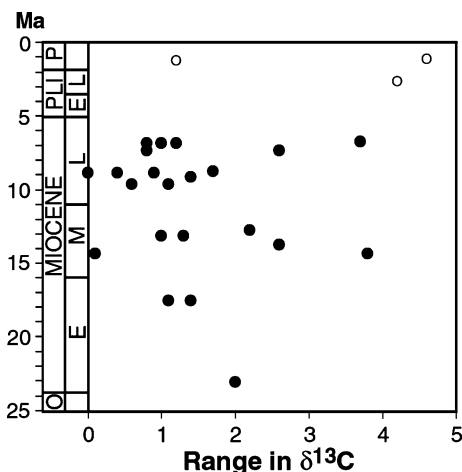


Fig. 5. Temporal variation in the within section range in $\delta^{13}\text{C}$ values of paleosol carbonates. ●, Miocene samples. ○, Plio-Pleistocene samples from southwestern Kansas.

Table 2

Summary statistics for carbon and oxygen isotope values of Great Plains paleosol carbonates

Locality (numbers as in Table 1)	$\delta^{13}\text{C}$ (VPDB)					$\delta^{18}\text{O}$ (VSMOW)				
	Mean	Std. dev.	Max.	Min.	Range	Mean	Std. dev.	Max.	Min.	Range
(1) Borchers Badlands (Meade, KS)	-6.6	1.30	-4.0	-7.8	3.8	21.2	1.51	23.3	19.8	3.5
(2) Aries Quarry (Meade, KS)	-1.9	0.54	-1.2	-2.4	1.2	21.7	0.31	22.0	21.3	0.7
(3) Alien Canyon (Meade, KS)	-4.8	1.06	-1.8	-6.0	4.2	22.4	0.67	23.5	21.2	2.2
(4) CR E/93 N of Bellview, NM	-7.2	0.33	-6.3	-7.6	1.3	25.8	0.23	26.2	25.4	0.8
(5) Coffee Ranch (Lora, TX)	-6.9	0.89	-4.7	-8.4	3.7	26.2	0.19	26.5	25.9	0.6
(6) FM 211 (Southland, TX)	-6.5	0.28	-5.9	-6.9	1.0	26.8	0.38	27.4	26.2	1.2
(7) Yellowhouse Canyon 1, Bridwell Fm (Slaton, TX)	-7.0	0.24	-6.6	-7.4	0.8	26.1	0.24	26.6	25.8	0.8
(8) Yellowhouse Canyon 2, Bridwell Fm (Slaton, TX)	-5.2	0.62	-4.5	-5.8	1.2	25.9	0.20	26.2	25.7	0.5
(9) Lake McConnaughey Dam (Ogallala, NE)	-7.0	0.25	-6.7	-7.5	0.8	19.2	0.87	20.4	17.9	2.5
(10) NE 71/CR 30 (Kimball, NE)	-5.6	0.78	-4.4	-7.0	2.6	21.3	0.42	21.9	20.4	1.5
(11) Breakneck Hill (Broadwater, NE)	-7.2	-	-	-	-	20.7	-	-	-	-
(12) Wildhorse Canyon (Oshkosh, NE)	-6.6	0.44	-5.7	-7.5	1.7	19.3	0.86	21.5	17.8	3.7
(13) Higgins Quarry (Higgins, TX)	-7.1	0.01	-7.1	-7.1	0.0	25.6	0.53	26.0	25.2	0.7
(14) Box T 1 (Higgins, TX)	-8.6	0.22	-8.5	-8.9	0.4	26.3	0.02	26.3	26.3	0.0
(15) Box T 2 (Higgins, TX)	-6.8	0.37	-6.2	-7.1	0.9	25.8	0.39	26.2	25.2	1.0
(16) Greenwood Canyon (Dalton, NE)	-6.8	0.45	-5.9	-7.3	1.4	18.6	1.04	21.4	17.0	4.4
(17) Minimum Q (Morland, KS)	-7.0	0.43	-6.4	-7.5	1.1	23.5	0.56	24.2	22.6	1.6
(18) Port of Entry Pit (Arnett, OK)	-7.4	0.33	-7.0	-7.6	0.6	25.8	0.44	26.2	25.3	0.8
(19) Ashfall Fossil Beds SHP 1, Cap Rock Mbr (Orchard, NE)	-7.0	0.31	-6.8	-7.2	0.4	22.9	0.15	23.0	22.8	0.2
(20) Yellowhouse Canyon 1, Couch Fm (Slaton, TX)	-5.8	0.34	-5.2	-6.2	1.0	26.6	0.25	27.1	26.2	0.9
(21) Yellowhouse Canyon 2, Couch Fm (Slaton, TX)	-6.0	0.37	-5.4	-6.7	1.3	26.6	0.46	26.9	25.2	1.8
(22) Ashfall Fossil Beds SHP 1, Devil's Gulch Mbr (Orchard, NE)	-8.6	0.36	-8.1	-9.0	0.8	24.6	0.25	24.8	24.2	0.6
(23) Ash Fall Fossil Beds SHP 2 (Orchard, NE)	-8.0	1.39	-7.0	-9.6	2.6	25.2	1.48	26.1	23.5	2.6
(24) Norden Bridge Quarry (Norden, NE)	-6.6	1.30	-4.0	-7.8	3.8	21.2	1.51	23.3	19.8	3.5
(25) Egelhoff Quarry (Norden, NE)	-6.0	0.07	-6.0	-6.1	0.1	23.4	0.24	23.6	23.2	0.3
(26) NE 71/2 (Hemingford, NE)	-7.0	0.46	-6.3	-7.7	1.4	22.2	0.98	23.6	20.7	2.8
(27) Hemingford, NE	-7.5	0.34	-7.1	-8.2	1.1	23.1	0.39	23.6	22.6	1.1
(28) Breakneck Hill, Monroe Cr/Harrison Fms (Broadwater, NE)	-7.2	0.54	-6.3	-8.3	2.0	22.2	1.08	24.0	20.7	3.2

Table 3

Sample statistics and *p*-values for one-way ANOVA and post-hoc Scheffé test for significance of differences between mean $\delta^{13}\text{C}$ values of Miocene paleosol carbonates grouped by carbonate morphology

	Mean (‰ VPDB)	S.D.	No.	<i>p</i> -values for differences in means			
				Small nodules	Large nodules	Thin caliche	Massive caliche
Small nodules	-6.8	0.88	109	-	-	-	-
Large nodules	-7.0	0.54	32	0.91	-	-	-
Thin caliche	-6.2	0.97	5	0.56	0.38	-	-
Massive caliche	-6.4	0.82	68	0.02	0.02	0.99	-
Other	-6.8	0.61	16	>0.99	0.98	0.66	0.42
All	-6.8	0.83	230				

Results in bold face are statistically significant at $\alpha=0.05$.

values (Table 3) and distributions (Fig. 6) for the different carbonate morphologies are similar, although the sample size for thin caliches is small. Small and large nodules are slightly depleted in ^{13}C relative to both thin and massive caliches. Based on one-way ANOVA and Scheffé post hoc tests for multiple comparisons, the differences in means are statistically significant between small nodules and massive caliches and between large nodules and massive caliches. Small nodules are the most variable, but if the two most extreme values in the small nodule distribution (Fig. 6A) are ignored the distribution is similar to the others. Massive caliches are less variable than small nodules and thin caliches and more variable than large nodules, although these differences are small. The ecological significance of the slight differences in means and distributions for different carbonate morphologies is not clear as they imply only slight

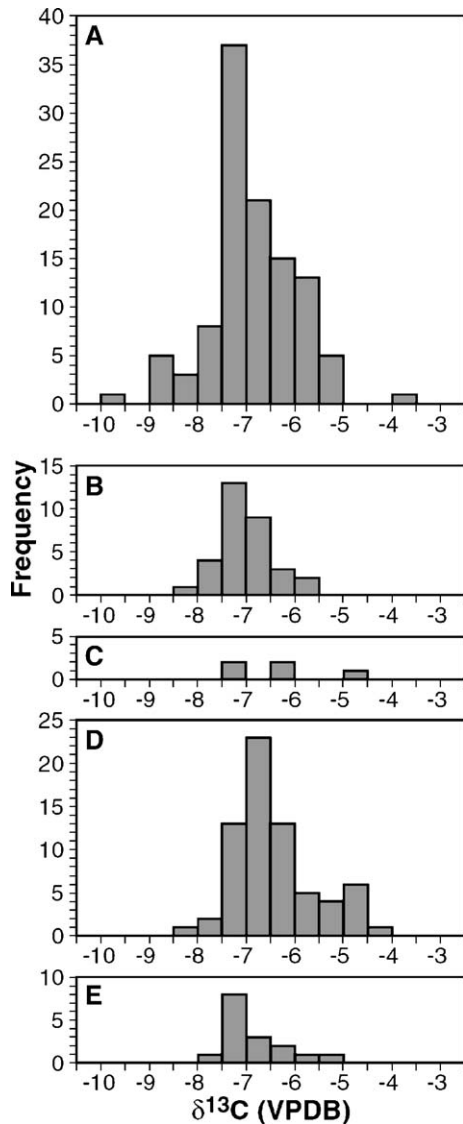


Fig. 6. Histograms of $\delta^{13}\text{C}$ values for Miocene paleosol carbonates by carbonate morphology or stage of development. (A) Small nodules (<ca. 5 cm diameter). (B) Large nodules (>ca. 5 cm diameter). (C) Thin caliches (<ca. 25 cm in thickness). (D) Massive caliches (50–200 cm in thickness). (E) Other morphologies (e.g., disseminated carbonate, thin carbonate stringers).

differences in the abundance of C_4 biomass on different time scales. Throughout the Miocene, the relative abundances of C_3 and C_4 biomass appear to vary about the average composition on time scales shorter than the average amount of time represented by small nodules.

5. Paleosol oxygen isotope variability

5.1. Long-term and geographic variability in $\delta^{18}\text{O}$ values

The long-term oxygen isotope record (Fig. 7) is much more variable temporally and geographically than the carbon isotope record. The mean $\delta^{18}\text{O}$ value for all samples is $23.4 \pm 2.90\text{‰}$, the mean for the Miocene samples is $23.5 \pm 3.00\text{‰}$, and the mean for the Plio-Pleistocene samples is $22.7 \pm 2.26\text{‰}$. Interpreting the long-term temporal (Fig. 7A) and geographic patterns (Fig. 7B and C) is difficult because each of these patterns includes significant variability expressed in the others. After the early Miocene, the $\delta^{18}\text{O}$ values show a wide range of variability that is mostly a product of the greater latitudinal coverage of the sampling after the middle Miocene (Fig. 3). However, as the Plio-Pleistocene samples are all from the same area in southwestern Kansas, the values in that interval more clearly reflect local changes in climate or soil moisture composition (or both) through time. The sharp increase of more than 6‰ in the late Pliocene is recorded in three sampling levels spanning about 1.5 m of section. These nodules and the surrounding sediments are outwardly similar to those at levels higher and lower in the same section. The increase is too extreme to reflect a change in temperature, and we suspect it might represent a short interval of intense aridity or some change in local hydrology that led to increased evaporative loss from soil water.

The primary geographic pattern in the data is latitudinal and probably results from the latitudinal gradient in air temperatures and hence in the $\delta^{18}\text{O}_{\text{mw}}$ values during a given time interval. The modern latitudinal gradient in $\delta^{18}\text{O}_{\text{mw}}$ values in this region is well documented, and if the present is any guide, we would not expect a strong longitudinal gradient (Rozanski et al., 1993; Fricke and O'Neil, 1999; Bowen and Wilkinson, 2002). While it is tempting to interpret the geographic gradient in paleosol carbonate $\delta^{18}\text{O}$ values (Fig. 7B) solely in relation to the modern gradient in meteoric water composition, this is inappropriate because the record may conflate temporal and geographic changes.

The residuals from least squares linear regression provide a way to deconvolve the independent tempo-

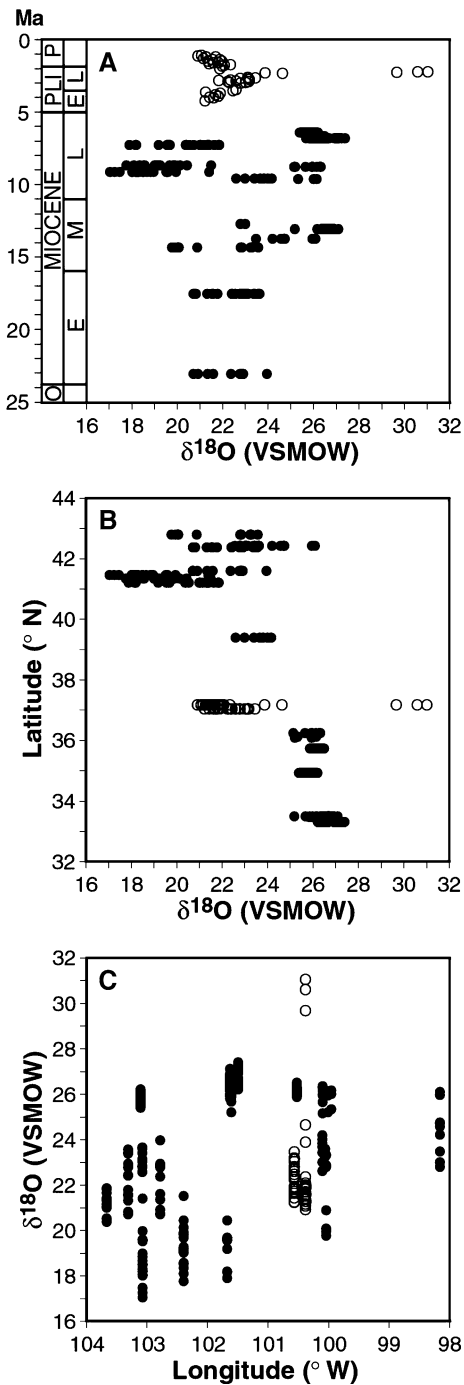


Fig. 7. Variation in $\delta^{18}\text{O}$ values of Great Plains paleosol carbonates. ●, Miocene samples. ○, Plio-Pleistocene samples from southwestern Kansas. (A) Temporal variation in $\delta^{18}\text{O}$ values. (B) Latitudinal gradient in $\delta^{18}\text{O}$ values. (C) Longitudinal gradient in $\delta^{18}\text{O}$ values.

ral and latitudinal changes in the oxygen isotope record. A least squares linear regression with age of sample as the independent variable and $\delta^{18}\text{O}$ value as the dependent variable explains essentially none of the variability in $\delta^{18}\text{O}$ values ($r^2 < 0.001$) and the slope (-0.01) is not significantly different from 0 ($p = 0.70$). This is not surprising given the lack of any clear association between age and $\delta^{18}\text{O}$ values (Fig. 7A, $r = -0.02$, $p = 0.70$). However, a regression with latitude as the independent variable explains a higher percentage of the variability in the $\delta^{18}\text{O}$ values ($r^2 = 0.58$) and the slope (-0.68) is statistically significant ($p < 0.001$). The residuals from this analysis represent the variability not explained by latitude. The residuals have a different pattern in relation to time than do the measured $\delta^{18}\text{O}$ values (Fig. 7A) or than the measured values do in relation to latitude (Fig. 7B).

The residuals exhibit a coherent, albeit noisy, pattern of variation through time that has two features in common with the long-term record of global climate change for the late Cenozoic recorded by benthic foraminifera (Zachos et al., 2001). First, relatively high positive residuals during the middle Miocene, suggesting higher paleosol carbonate $\delta^{18}\text{O}$ values than expected based on latitude, correlate with the Mid-Miocene Climatic Optimum, the warmest interval of the Neogene. It is reasonable to assume that mean annual temperatures in the Great Plains, hence the average soil temperature during paleosol carbonate precipitation, were higher during this interval. However, for a given soil water isotopic composition, warmer soil temperatures alone would lead to lower carbonate $\delta^{18}\text{O}$ values (Eqs. (1) and (2)). Thus, the positive residuals imply positively shifted soil water $\delta^{18}\text{O}$ values, either as a result of enhanced evaporative enrichment or the positive correlation between air temperature and $\delta^{18}\text{O}_{\text{mw}}$ values (Rozanski et al., 1993). Second, the residuals show a strong, and possibly stepped, decrease after the middle Miocene, corresponding to the interval of late Cenozoic cooling. Again, the primary control on this trend is assumed to be a decrease in the $\delta^{18}\text{O}$ value of meteoric water, as the temperature effect alone would lead to higher $\delta^{18}\text{O}$ values for soil carbonate. The increase in ice volume during the Plio-Pleistocene would have led to marine sources of water vapor with positively shifted $\delta^{18}\text{O}$ values, so the decrease in $\delta^{18}\text{O}_{\text{mw}}$ suggested by the

residuals for the Plio-Pleistocene is again probably related to the effect of air temperature on the composition of local meteoric water.

Minimum $\delta^{18}\text{O}$ values from each section might reflect the least evaporatively enriched soil water compositions on shorter time scales than the duration of the whole record, so we performed the same regression analysis on minimum carbonate $\delta^{18}\text{O}$ values from each section (Fig. 8B). Although sampling is not dense in the earliest part of the Miocene, the overall pattern is consistent with the climatic implications discussed above, with the exception of three late Miocene sec-

tions in Nebraska (Lake McConaughy Dam, Wildhorse Canyon, and Greenwood Canyon; localities 9, 12, and 16 in Table 1). Residuals from latitude for the minimum $\delta^{18}\text{O}$ values of these sections are strongly negative. The other localities from this time interval (6–10 Ma) that show positive residuals are located further south, with the exception of one section in western Nebraska represented by a single sample (Ash Hollow Formation at Breakneck Hill; locality 11 in Table 1). This suggests that soil waters at the three anomalous Nebraska localities may have had much lower $\delta^{18}\text{O}$ values than expected based on their latitude and age.

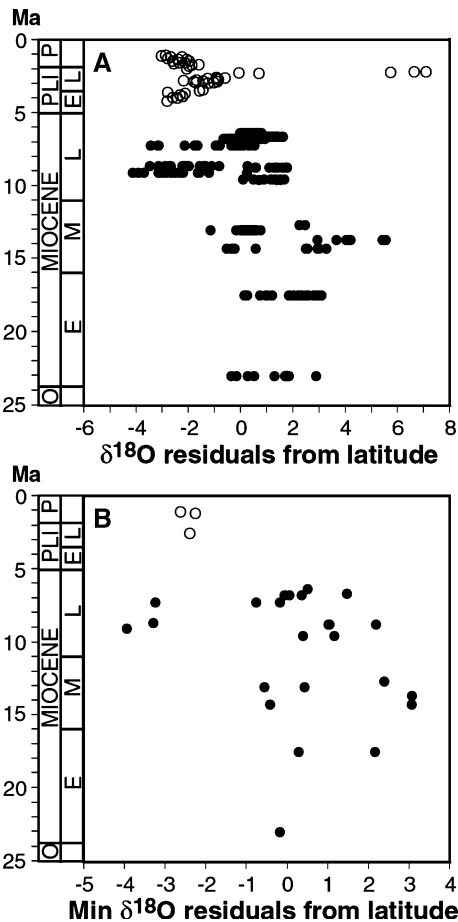


Fig. 8. Residuals from least squares linear regressions with latitude as the independent variable and $\delta^{18}\text{O}$ values as the dependent variable. ●, Miocene samples. ○, Plio-Pleistocene samples from southwestern Kansas. (A) Temporal variation in residuals of individual $\delta^{18}\text{O}$ values from latitude. (B) Temporal variation in residuals of minimum within section $\delta^{18}\text{O}$ values from latitude.

5.2. Variation in $\delta^{18}\text{O}$ values within samples and collecting levels

Oxygen isotope variation within individual samples and collecting levels is lower than the variability in the long-term record by about an order of magnitude and is similar to the within sample and within level variability in $\delta^{13}\text{C}$ values discussed above. The mean difference between pairs of analyses from the same samples is $0.2 \pm 0.30\text{‰}$ and the range is 2.4‰. The mean difference between pairs of samples from the same collecting level is $0.4 \pm 0.49\text{‰}$ and the range is 2.4‰. Given the temporal variability in $\delta^{18}\text{O}$ values (Fig. 7A), we do not treat Miocene samples and younger samples differently.

5.3. Short-term variability in $\delta^{18}\text{O}$ values

As for the carbon isotope compositions, we use the range in $\delta^{18}\text{O}$ values within sections as a measure of variability in paleosol carbonate oxygen isotope composition on time scales shorter than the duration of the entire record (Fig. 9; Table 2). As before, the range in $\delta^{18}\text{O}$ values within sections has a strong, positive correlation with the standard deviation around the mean value within sections ($r=0.89$, $p<0.01$). In general, variability within sections is relatively low and does not change through time (Fig. 9A). The exception to this is the section from southwestern Kansas that includes three unusually high $\delta^{18}\text{O}$ values (Borchers Badlands; locality 1 in Table 1; Fig. 7A). If those three samples (out of 17 total for that section) are not considered, the range for that section is more typical and the mean range for all sections is

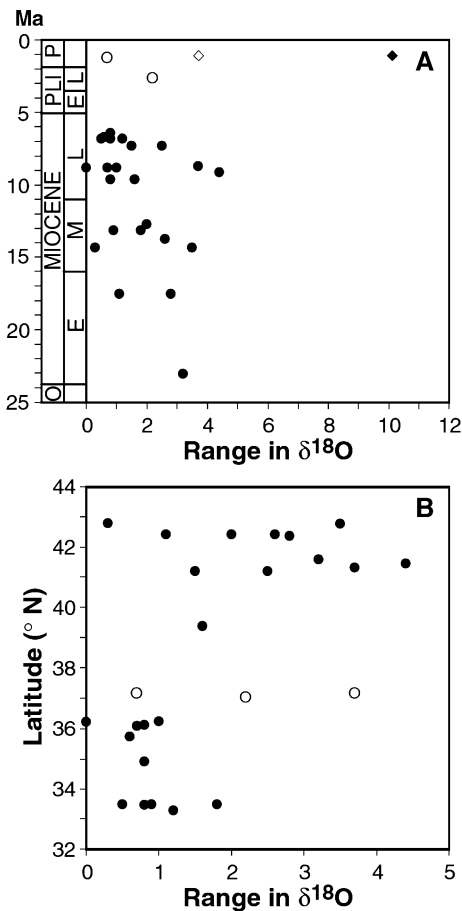


Fig. 9. Within section variation in oxygen isotope compositions of Great Plains paleosol carbonates. ●, Miocene samples. ○, ◇, ◆, Plio-Pleistocene samples from southwestern Kansas. (A) Temporal variation in the within section range in $\delta^{18}\text{O}$ values. F, range for all samples from Borchers Badlands, KS; A, range for Borchers Badlands excluding three samples with unusually high $\delta^{18}\text{O}$ values. (B) Latitudinal gradient in the within section range in $\delta^{18}\text{O}$ values.

$1.7 \pm 1.25\text{‰}$. The range in $\delta^{18}\text{O}$ values (without the outliers in the Borchers Badlands sections) has a very weak correlation with age that is not statistically significant ($r=0.14$, $p=0.50$).

Variability in $\delta^{18}\text{O}$ values seems to be lower on average in the southern Great Plains than in the central Great Plains (Fig. 9B). The exception to the pattern is the same section in southwestern Kansas that contains the three high $\delta^{18}\text{O}$ values (although those three outliers are not included in the range plotted in Fig. 9B for that section). Even including the range for that section, the correlation between the range in $\delta^{18}\text{O}$

values and latitude is moderate and statistically significant ($r=0.52$, $p=0.03$). The apparent contrast between the central and southern Great Plains may reflect greater variability in the sources or transport paths of moisture in the central Great Plains on time scales similar to the duration of soil carbonate accumulation, although an underlying mechanism for such variability is not readily apparent. Variability in $\delta^{18}\text{O}$ values has a relatively weak correlation with longitude that is not statistically significant ($r=0.34$, $p=0.08$). The range in $\delta^{18}\text{O}$ values has moderate, positive correlations with both the number of samples per section ($r=0.43$, $p=0.03$) and the length of section sampled ($r=0.32$, $p=0.10$), as was the case with the ranges in $\delta^{13}\text{C}$ values within sections.

5.4. Modeling paleosol carbonate $\delta^{18}\text{O}$ values

We used Eqs. (1) and (2) to compare measured and predicted soil carbonate $\delta^{18}\text{O}$ values for each sampling locality based on modern air temperatures recorded at nearby weather stations and estimates of meteoric water composition based on interpolation of the IAEA dataset (Bowen and Wilkinson, 2002; Bowen and Revenaugh, in press). We calculate predicted carbonate values assuming both modern mean annual and maximum temperatures, both of which reflect the strong latitudinal gradient in temperature in the mid-continent (Fig. 10A). Estimated $\delta^{18}\text{O}_{\text{mw}}$ values also exhibit a strong latitudinal gradient (Fig. 10B) and the overall latitudinal variation exceeds the 95% confidence intervals for individual localities. Estimated $\delta^{18}\text{O}_{\text{mw}}$ values for the sections near Slaton and Southland, TX (-6.1 ± 0.56 , 95% confidence interval) are in good agreement with published $\delta^{18}\text{O}_{\text{mw}}$ values for Lubbock, TX (-6.6‰ , Nativ and Riggio, 1990), which is about 25 km to the northwest of the sections. Estimated $\delta^{18}\text{O}_{\text{mw}}$ values in western Nebraska, which range from -10.2‰ to -11.7‰ , are somewhat depleted in ^{18}O relative to published $\delta^{18}\text{O}_{\text{mw}}$ values for North Platte, NE (-9.6‰ ; Harvey and Welker, 2000), which is 100–200 km east of those localities. For most of the western Nebraska localities, the North Platte value is within the 95% confidence interval for the estimated $\delta^{18}\text{O}_{\text{mw}}$ value.

The predicted carbonate $\delta^{18}\text{O}$ values based on modern environmental conditions (Fig. 10C) reflect the strong latitudinal gradients in temperature and

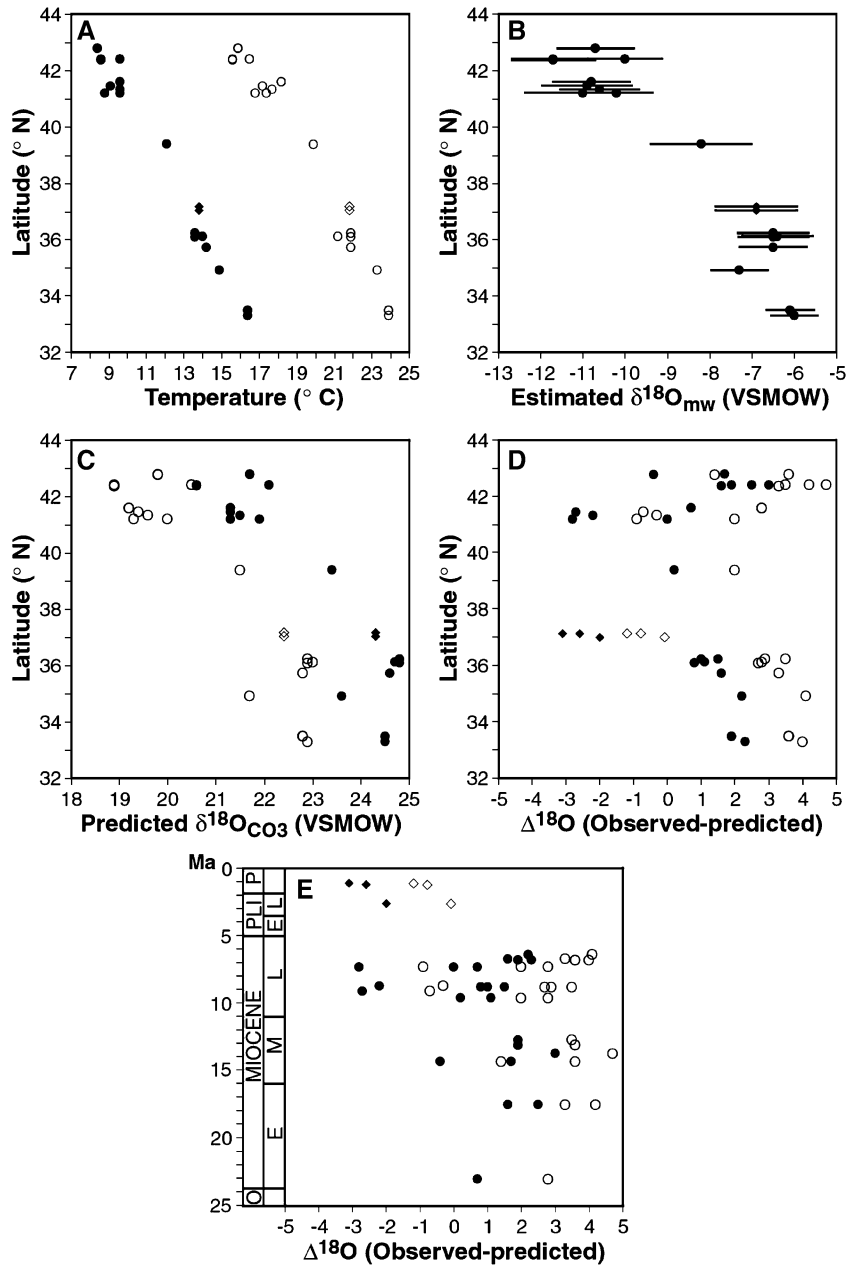


Fig. 10. Predicted soil carbonate $\delta^{18}\text{O}$ values. Filled symbols correspond to mean annual temperature and calculations based on mean annual temperature; open symbols correspond to annual maximum temperature and calculations based on annual maximum temperature. ●, ○, Miocene localities. ◇, ◆, Plio-Pleistocene localities in southwestern Kansas. (A) Latitudinal gradient in mean annual temperature and annual maximum temperature. (B) Latitudinal gradient in estimated $\delta^{18}\text{O}_{\text{mw}}$ values. Error bars indicate 95% confidence intervals around estimates. Estimated $\delta^{18}\text{O}_{\text{mw}}$ values are not based on either mean annual or annual maximum temperatures in A. (C) Predicted carbonate $\delta^{18}\text{O}$ values based on data in A and B and Eqs. (1) and (2). (D) Latitudinal variation in the deviation of the mean of measured values in each section (Table 2) from predicted values in C. (E) Temporal variation in the deviation of the mean of measured values in each section from predicted values in C.

estimated $\delta^{18}\text{O}_{\text{mw}}$ values. Because of the influence of temperature on the fractionation factor between water and calcite (Eq. (1)), the predicted values using mean annual temperature are enriched in ^{18}O by about 1.7‰ relative to the predictions based on annual maximum temperatures. The range in the predicted values (4.1‰) is the same regardless of which temperature is used in Eq. (1) and is half the observed range among mean values from the sections sampled (8.2‰). This implies that the temporal variation since the early Miocene in the factors that control paleosol carbonate $\delta^{18}\text{O}$ values (soil temperature and water composition) was greater than the latitudinal variation in these factors today.

Deviations of observed mean $\delta^{18}\text{O}$ values within sections from the values predicted based on modern conditions exhibit weak, negative correlations that are not statistically significant with latitude ($r=-0.22$ and $p=0.28$ for mean annual temperature, $r=-0.20$ and $p=0.31$ for annual maximum temperature; Fig. 10D). Most deviations are positive, indicating that measured values are greater than values predicted for today. The cluster of negative deviations at about 41°N are the same three late Miocene sections with high, negative residuals from that latitude (Fig. 8), indicating again that the measured values from those sections stand out from data from similar aged sections. The negative deviations around 37°N are the samples from southwestern Kansas and presumably reflect the cooler global climates and lower $\delta^{18}\text{O}_{\text{mw}}$ values of the Plio-Pleistocene relative to today. The deviations in observed and predicted $\delta^{18}\text{O}$ values have a similar pattern in relation to the age of sections (Fig. 10E) in that most sections have similar positive deviations and the same six sections with negative deviations stand out.

The deviations of observed mean $\delta^{18}\text{O}$ values from predicted can be interpreted in one of three ways. One end-member interpretation is that temperatures in the Great Plains were the same as today throughout the late Cenozoic and that deviations result solely from changes in soil water composition that reflect temporal changes in meteoric water composition as a result of factors such as global ice volume, vapor source temperature, and vapor transport history. In this case, measured paleosol carbonate $\delta^{18}\text{O}$ values higher than predicted would imply higher $\delta^{18}\text{O}_{\text{mw}}$ values at a given latitude or in the past than estimated for today.

Conversely, the six sections with negative deviations would have had considerably lower $\delta^{18}\text{O}_{\text{mw}}$ values than in those areas today. If annual maximum temperatures are assumed instead of mean annual temperatures, positive deviations imply even higher $\delta^{18}\text{O}_{\text{mw}}$ values, although the negative deviations are not too different from estimated modern values. However, this case is unrealistic based on the global pattern of climate changes during this interval (Zachos et al., 2001). Miocene temperatures should generally be higher than today and Plio-Pleistocene temperatures should on average be lower than today given that glacial intervals are generally longer than interglacials.

The opposite end-member is that the oxygen isotope composition of meteoric water, hence soil water, was the same across the Great Plains as estimated for today and only temperatures varied. In this case, positive deviations of observed paleosol carbonate $\delta^{18}\text{O}$ values from predicted modern values would imply considerably lower temperatures than observed today in the region, and negative deviations would imply considerably higher temperatures. With the exception of the negative deviations for the three late Miocene localities in western Nebraska, these implications are the opposite of expectations based on the late Cenozoic pattern of climate change.

Thus, reconciling the paleosol carbonate $\delta^{18}\text{O}$ values with the pattern of climate change requires a third option: both temperature and meteoric water composition were different than modern values, which is not a surprising conclusion. Miocene carbonates presumably formed at elevated mean temperatures relative to today. For those Miocene sections with small positive deviations of measured carbonate $\delta^{18}\text{O}$ values from the predicted values, higher temperatures by 1–4 °C would imply higher soil water $\delta^{18}\text{O}$ values in the past by 1.0–1.7‰ relative to the $\delta^{18}\text{O}$ of local meteoric water today. For Miocene sections with large positive deviations, the same range of temperature changes would imply soil waters enriched in ^{18}O by 2.5–3.0‰ relative to local meteoric water today. This implied enrichment of soil waters could indicate higher $\delta^{18}\text{O}_{\text{mw}}$ values in the past relative to today (possibly independent of warmer local air temperatures) or enhanced evaporative enrichment of soil water derived from meteoric water with $\delta^{18}\text{O}$ values similar to today. For the three

Miocene sections with large negative deviations, higher temperatures by 1–4 °C require lower soil water $\delta^{18}\text{O}$ values by 1.2–2.1‰ relative to local meteoric water today, with the smaller changes in soil water $\delta^{18}\text{O}$ values corresponding to the higher temperatures. Evaporative enrichment would counter the effect of lower soil water $\delta^{18}\text{O}$ values for a given temperature, supporting the suggestion above that the Miocene sections with negative residuals from latitude and negative deviations relative to predicted $\delta^{18}\text{O}$ values had isotopically distinct soil water relative to other localities of similar age. The three Plio-Pleistocene sections in southwestern Kansas, which have large negative deviations, would have formed at lower temperatures relative to today. Assuming temperature was lower by 1–4 °C in the Plio-Pleistocene relative to today requires soil water to have been depleted in ^{18}O by 3.2–3.9‰ relative to local meteoric water today to reconcile the measured and predicted $\delta^{18}\text{O}$ values for those sections.

6. Covariation between paleosol carbonate $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values

If the C_3/C_4 ratio of Great Plains ecosystems, as recorded by paleosol carbonate $\delta^{13}\text{C}$ values, is related to long-term patterns of climate change, as recorded by the residuals of the $\delta^{18}\text{O}$ values from latitude, then the two isotopic records should be strongly correlated. However, the two records do not exhibit a coherent pattern overall (Fig. 11A), and the correlation for the entire data set is relatively weak, although statistically significant ($r=-0.31$, $p<0.01$). The $\delta^{18}\text{O}$ residuals for the Miocene samples are more variable than the corresponding $\delta^{13}\text{C}$ values, but the correlation for those samples is lower than that for the overall dataset, but also statistically significant ($r=-0.22$, $p<0.01$). The correlation for the Plio-Pleistocene data is even weaker and not statistically significant ($r=-0.006$, $p=0.97$), but this is strongly influenced by the three outlier residuals for the samples from Borchers Badlands with extremely high values. However, excluding those outliers does not substantially improve the correlation for the Plio-Pleistocene samples ($r=-0.22$, $p=0.17$). The correlation between the within section ranges in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values is stronger and statistically significant ($r=0.51$, $p<0.01$; Fig. 11B), but this relationship is

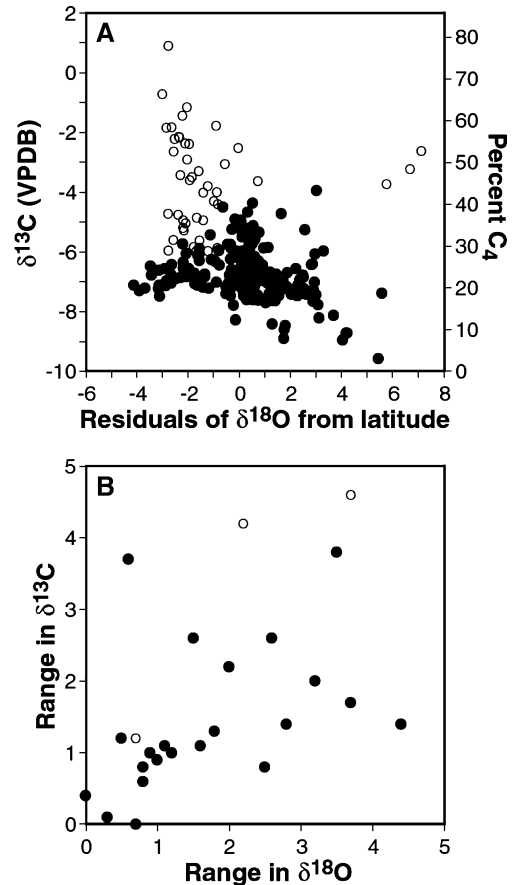


Fig. 11. Covariation in carbon and oxygen isotope compositions of Great Plains paleosol carbonates. J, Miocene samples. E, Plio-Pleistocene samples from southwestern Kansas. (A) Covariation between $\delta^{13}\text{C}$ and residuals of $\delta^{18}\text{O}$ values from latitude for all samples. (B) Covariation between within section range in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values.

strongly influenced by the large cluster of localities with low ranges ($<1.5\text{‰}$) for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. Sections that are more variable in $\delta^{13}\text{C}$ values, $\delta^{18}\text{O}$ values, or both do not show any consistent relationship. Despite the statistical significance of some of these correlations, the lack of consistently strong covariation between the carbon and oxygen isotope compositions suggests that climatic changes on the time scales recorded by paleosol carbonates (ca. 10^3 – 10^6 years; Machette, 1985) cannot be the primary factor controlling the relative abundances of C_3 and C_4 biomass. This is particularly clear for the Plio-Pleistocene sections in which paleosol carbonates record a

strong gradient in the abundance of C₄ biomass (Fig. 2) and numerous records document major changes in global climates (Zachos et al., 2001).

7. Alternative hypotheses for the history of C₄ grassland development in the Great Plains

C₄ grasslands are undeniably a phenomenon of the late Cenozoic (Jacobs et al., 1999), yet paleosol carbonate isotope records from the Great Plains and other regions such as South Asia (Quade and Cerling, 1995; Quade et al., 1995), Argentina (Latorre et al., 1997, Kleinert and Strecker, 2001), and Kenya (Kingston et al., 1994) do not record temporally consistent patterns of C₄ expansion. We suggest that regional ecological and climatic factors, in conjunction with the pattern of global climate change (Zachos et al., 2001), are probably the likeliest factors controlling the development of C₄ grasslands on different continents.

Any model for the development of the modern C₄-dominated grasslands of the Great Plains must account for a number of observations, starting with those described here and by Fox and Koch (2003): (1) Miocene ecosystems included a moderate amount of C₄ biomass (ca. 20%) that did not vary substantially on short time scales or geographically during the Miocene (Fox and Koch, 2003). (2) C₄ biomass increased in abundance over typical Miocene levels after 6.5 Ma and only dominated Great Plains ecosystems during the Pliocene (Fox and Koch, 2003). (3) Paleosol carbonate $\delta^{13}\text{C}$ values do not correlate with the climatic signal recorded by carbonate $\delta^{18}\text{O}$ values, so changes in average climatic conditions on time scales of 10³–10⁶ years are not sufficient to explain the pattern of C₄ expansion in the Great Plains (this study). (4) Species richness of browsers (herbivorous mammals that fed on the leaves and other parts of dicots) in middle Miocene (ca. 15 Ma) mammalian faunas of the Great Plains was greater than that in any known modern mammalian faunas (Janis et al., 2002, 2004). This suggests high productivity biomes dominated by C₃ biomass and C₃ feeders. (5) The relative abundance of browsers declined steadily from the middle Miocene (ca. 15 Ma) to at least the end of the Pliocene (ca. 2 Ma). The decrease in browsers was caused by true extinction and not by lineages of browsers evolving grazing habits (Janis et al., 2002, 2004). (6) Extinction among browsers was

greater for small and medium sized species than for larger species (Janis et al., 2002, this volume). (7) The relative abundance of grazers (species that fed primarily on grasses) and mixed-feeders (species that fed on both dicots and grasses) increased from 18 to 10 Ma (Janis et al., 2002, 2004). This might imply the gradual development of grasslands during this interval. The increase in grazers was a result of both speciation and immigration. (8) Absolute species richness of large herbivorous mammals declined steadily after ca. 13 Ma (Janis et al., 2002, 2004). This might imply a gradual decrease in ecosystem productivity after a high earlier in the middle Miocene. (9) Some equid (horse) lineages in the Great Plains evolved morphological adaptations for grazing or open-habitat feeding (e.g., high-crowned cheek teeth) around 10 Ma (Wang et al., 1994), suggesting grasslands or open-habitats had developed by that time. (10) Carbon isotope compositions of fossil tooth enamel indicates that some equid lineages in the Great Plains evolved mixed C₃–C₄ or pure C₄ diets after 6.6 Ma, although other lineages maintained C₃-dominated diets (Wang et al., 1994; Cerling et al., 1997; Passey et al., 2002). (11) Carbon isotope compositions of serial samples of tusk enamel indicate that *Gomphotherium* (an extinct genus of Proboscidea) had C₃-dominated diets that did not vary seasonally (Fox and Fisher, in press). This implies the presence throughout the year of sufficient C₃ biomass to sustain populations of large-bodied mammalian herbivores until at least 8 Ma.

We propose two hypotheses for the pattern of C₄ expansion recorded by paleosol carbonates in the Great Plains. Both hypotheses start with highly productive middle Miocene (ca. 15 Ma) ecosystems that have either uniformly spread C₃ trees and shrubs over a carpet of C₄ grass, or a spatially complex mosaic of C₃- and C₄-dominated patches that migrate laterally on time scales shorter than the most rapidly accumulated paleosol carbonates (i.e., small nodules). These interpretations of middle Miocene localities are necessary to explain the moderately high and uniform $\delta^{13}\text{C}$ values from Miocene paleosol carbonates (observations 1 and 2 above and Fig. 2), as well as the unusual species richness of browsers during the middle Miocene (observation 4 above; Janis et al., 2002, 2004).

In the first hypothesis, the expansion of open grasslands at the expense of more wooded habitats begins in the middle Miocene after the peak in

browser diversity. However, this initial expansion represents an increase in the abundance of C₃ grasses relative to C₃ trees and shrubs in ecosystems that otherwise maintained a constant abundance of C₄ grasses. This expansion of C₃ grasses would have decreased the forage available for browsers. The replacement of trees and shrubs by C₃ grasses would continue gradually over the course of the middle and late Miocene and C₄ grasses would have only increased in abundance after the end of the Miocene. This hypothesis can account for a number of the relevant observations: the paleosol carbonate $\delta^{13}\text{C}$ record (1, 2), the changes in the species richness, trophic structure, and body size distributions of herbivore communities (4–8), and the morphological and isotopic changes in equid teeth (9, 10). This hypothesis is more descriptive than mechanistic and so has two weaknesses. First, an initial expansion of C₃ grasses, which today are found primarily in cool-climate habitats, is not consistent with the climatic conditions of the middle Miocene (Zachos et al., 2001). Second, it is not clear what could cause a switch from C₃ to C₄ grasses during the late Miocene given that the climate would be cooling and several studies have found no evidence of a decrease in atmospheric $p\text{CO}_2$ during this interval (Pagani et al., 1999; Pearson and Palmer, 2000).

The second hypothesis focuses on reduction in the length of the growing season as a result of global cooling since the middle Miocene as the mechanism ultimately underlying the Plio-Pleistocene expansion of C₄ grasses in the Great Plains. According to this hypothesis, annual minimum temperatures were sufficiently high during the middle Miocene that Great Plains ecosystems maintained high primary productivity throughout the year. This inferred high annual productivity, combined with the paleosol carbon isotope evidence for mostly C₃ biomass, provides a basis for the unusual species richness of browsers during the middle Miocene (observation 4 above). As temperatures decreased during the middle and late Miocene, the annual minimum temperature would have decreased to the point that a winter growing season was no longer possible for either C₃ or C₄ plants. This could have occurred by lowering mean annual temperature and maintaining the same seasonal range in temperature or by also increasing the seasonal range as mean temperatures decreased. The resulting decrease

in the quality of winter forage would have led to the extinction of small and medium browsers (observation 6 above) because of the scaling of metabolic requirements with body size and digestive physiology (Janis et al., 1994). Based on the same scaling argument, larger-bodied browsers (e.g., gomphotheres) would have been able to extract sufficient nutrients from low quality winter C₃ forage (observation 11 above; Fox and Fisher, *in press*). The proportions of C₃ and C₄ biomass during the shortened growing season would not change relative to earlier in the Miocene, hence soil carbonates would not record any change in the average composition of soil biomass (observation 1 above and Fig. 2). The shortened growing season and reduced annual availability of high quality forage would have led to greater competition and resource partitioning among herbivore species. Under this hypothesis, the evolution of mixed C₃–C₄ and C₄ diets among some species of equids during the late Miocene (observation 10 above) is a result of this resource partitioning and not a result of an increase in the absolute abundance of C₄ biomass.

In this hypothesis, the post-Miocene dominance by C₄ grasses is really an indirect ecological consequence of lower minimum temperatures and a shorter, distinct growing season. In essence, this hypothesis suggests a loss of C₃ biomass, not an initial expansion of C₄ biomass. The shortened growing season would have led to increased browsing pressure by the remaining browsers, which would have acted as an increase in disturbance within late Miocene ecosystems of the Great Plains. In modern ecosystems that contain a mixture of woody C₃ dicots and C₄ grasses, regular disturbance is necessary to maintain the dominance of C₄ grasslands (Sage, 2001). The increased browsing pressure would have gradually reduced the abundance of C₃ biomass in favor of C₄ biomass over the course of the Pliocene. Disturbance by proboscideans has been argued to be an important control on the structure and mammalian species richness of some modern African ecosystems (Owen-Smith, 1988), but such top down models of ecosystem control are quite complex. An alternative explanation for the relatively late increase in the abundance of C₄ biomass is continued reduction in the length of the growing season during the Plio-Pleistocene and maintenance of sufficiently warm growing season temperatures to favor C₄ grasses. Assuming the low atmospheric $p\text{CO}_2$ recorded during

the last several glacial intervals in the Vostok ice core (Petit et al., 1999) is a general pattern of all Plio-Pleistocene glacial intervals, C_4 grasses would have an advantage over C_3 plants even for only moderately warm growing season temperatures during the majority of the Plio-Pleistocene.

The second hypothesis also accounts for a number of the relevant observations enumerated above, including the overall pattern of the paleosol carbonate carbon and oxygen isotope records (1–3) and the patterns of faunal change (4–8). The isotopic and morphological evidence for fossil horse (9–10) and gomphothere (11) diets are also plausibly explained by this hypothesis. The hypothesis is also consistent with the climatic preferences of C_3 and C_4 grasses and with the pattern of late Cenozoic climate change. One weakness of this hypothesis is that the proposed control on the Pliocene expansion of C_4 grasses, disturbance by increased browsing pressure, probably operates on relatively short (i.e., “ecological”) time scales and small spatial scales, and not on the longer geological time scale reflected in the carbon isotope record of the Plio-Pleistocene in the Great Plains. A second weakness is that changes in annual minimum temperature in the Great Plains are still unknown and will probably not be easy to reconstruct empirically.

Although neither hypothesis is without flaws, both are testable based on alternative predictions regarding the types of diets expected among large herbivorous mammals as the hypotheses predict distinct combinations of feeding style (browsing, mixed, grazing) and food choice (C_3 , mixed, C_4). Browsers, mixed-feeders, and grazers can be distinguished accurately based on a combination of relative tooth crown height (Janis et al., 2002), mesowear analysis (Fortelius and Solounias, 2000), and differences in craniodental morphology (Mendoza et al., 2002). The carbon isotope composition of tooth enamel from the same species can be used to discriminate C_3 -feeders, mixed feeders, and C_4 -feeders (e.g., Feranec, 2004).

The first hypothesis predicts four types of diets among large bodied mammals. Specialized browsers should have low-crowned teeth, craniodental features of browsers, and C_3 isotopic signatures. Species feeding in open habitats while C_3 grasses are abundant would have high crowned teeth (to counter tooth wear from abrasive grass tissues and grit on forage of any type), craniodental features of grazers, mixed-feeders,

or browsers, and C_3 isotopic signatures. A third category that should begin to appear as C_4 grasses increase in abundance after the late Miocene is species with high-crowned teeth, craniodental features of mixed-feeders and grazers, and intermediate $\delta^{13}C$ values reflecting consumption of both C_3 and C_4 plants. The final category, appearing only in the late Miocene under the first hypothesis, is species with high-crowned teeth, the craniodental features of grazers, and C_4 isotopic signatures. Species with those characteristics should not co-occur with C_3 grazers. The evolution of high-crowned teeth in some equid lineages several million years before isotopic evidence for either mixed C_3 – C_4 or pure C_4 diets (Wang et al., 1994) is consistent with these predictions, but more representative sampling of whole faunas is necessary to see how common this pattern is within other mammalian clades.

The second hypothesis predicts herbivores with three sets of characteristics. Specialized browsers will have the same features noted above: low-crowned teeth, the craniodental characteristics of browsers, and C_3 isotopic signatures. As this hypothesis does not predict a change in the openness of habitats during the middle and late Miocene, the second category is species with high-crowned teeth, the craniodental features of mixed-feeders, and intermediate isotopic signatures reflecting consumption of C_3 browse and C_4 grasses. The final category, which should begin to appear after loss of the winter growing season, is species with high-crowned teeth, the craniodental features of grazers, and C_4 isotopic signatures. Under the second hypothesis, no species should have high-crowned teeth, craniodental features of grazers, and C_3 isotopic signatures.

Testing these hypotheses, and probably developing new hypotheses based on the results of those tests, will be critical to our understanding of the evolution of the flora and fauna of the Great Plains over the last 25 Ma.

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