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Stable Carbon Isotope Compositions of Eastern Beringian Grasses and Sedges: Investigating Their Potential as Paleoenvironmental Indicators

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Abstract

The nature of vegetation cover present in Beringia during the last glaciation remains unclear. Uncertainty rests partly with the limitations of conventional paleoecological methods. A lack of sufficient taxonomic resolution most notably associated with the grasses and sedges restricts the paleoecological inferences that can be made. Stable isotope measurements of subfossil plants are frequently used to enhance paleoenvironmental reconstructions. We present an investigation of the stable carbon isotope composition ($\delta^{13}C$) of modern and subfossil grasses and sedges (graminoids) from Eastern Beringia. Modern grasses from wet habitats had a mean $\delta^{13}C$ of −29.1‰ (standard deviation [SD] = 2.1‰, *n* = 75), while those from dry habitats had a mean of −26.9‰ (SD = 1.19, *n* = 27). Sedges (*n* = ~50) from dry, wet, marsh, and sand dune habitats had specific habitat ranges. Four modern C_4 grasses had $\delta^{13}C$ values typical of C_4 plants. Analyses were also conducted using subfossil graminoid remains from several sedimentary paleoecological contexts (e.g., arctic ground squirrel nests, loess, permafrost, and paleosols) in Eastern Beringia. Results from these subfossil samples, ranging in age from >40,000 to ca. 11,000 cal. yr BP, illustrate that the $\delta^{13}C$ of graminoid remains has altered during the past. The range of variation in the subfossil samples is within the range from modern graminoid specimens from dry and wet habitats. The results indicate that stable isotopes could contribute to a comprehensive and multiproxy reconstruction of Beringian paleoenvironments.

Introduction

An accurate reconstruction of the glacial-age vegetation of Beringia (the largely unglaciated region lying between the Lena River in the west and the Mackenzie River in the east) (for a recent discussion of the extent and definitions of Beringia, see Harington, 2005) (Fig. 1) is a key element in several areas of scientific investigation. This region was a subcontinental Pleistocene refugium for northern biota (Hultén, 1937) and the exposed Bering land bridge allowed migrations between northeastern Asia and North America. The structure, composition, and productivity of the vegetation of the region would have influenced animal population dynamics, species distributions, and the timing and routes of continental biotic exchange (Hopkins et al., 1982). In addition, land-atmosphere interactions likely contributed (via feedbacks) to the climate changes of the late Quaternary. The challenge of modeling land-cover feedbacks in the context of potential future climate change is partly addressed by testing the capacity of climate models to simulate past conditions that differ markedly from those at present (Paleoclimate Modelling Intercomparison Project, http://www-lsce.cea.fr/pmip/; Kaplan et al., 2003). A critical time for such tests is the height of the Last Glacial Maximum (LGM), ca. 21,000 cal. yr BP, referred to as Marine Isotope Stage (MIS) 2 (Kageyama et al., 2001). However, the nature of the vegetation across Beringia during the last glaciation is unclear, both in terms of large-scale gradients related to temperature and moisture and in the range of variability associated with the topographic and topoclimatic mosaic. The continuing uncertainty rests partly with the logistical challenges of studying this remote region. The uncertainty also stems from the limitations of conventional paleoecological methods to resolve the vegetation taxonomically to the degree necessary to infer its bioclimatic requirements and ecological characteristics.

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During Pleistocene glaciations, Eastern Beringia (unglaciated Yukon Territory and Alaska) was isolated from North America by continental ice sheets and became biogeographically continuous with northeast Asia (Hopkins et al., 1982; Shapiro et al., 2004). However, there exists a long-running and incompletely resolved dilemma: the so-called "steppe-tundra debate," or "productivity paradox," which is by now well rehearsed in the literature (e.g., Cwynar and Ritchie, 1980; Hopkins et al., 1982; Guthrie, 1990; Colinvaux, 1996a; Kozhevnikov and Ukraintseva, 1999; Zazula et al., 2003). Logic suggests that a region spanning ~60–75°N, when LGM global temperatures were colder than today, was most probably covered by some form of tundra (i.e., vegetation occurring where low-growing season temperatures do not permit tree growth; Ritchie, 1984; Viereck et al., 1992). However, numerous dated faunal remains (Guthrie, 1968, 1990; Harington, 2003), and even ancient DNA (e.g., Shapiro and Cooper, 2003; Willerslev et al., 2003), attest to the presence of a diversity of herbivorous and carnivorous mammals throughout the last glaciation. While tundra can take many forms, most contemporary tundra types are unpromising analogs for vegetation that could have supported populations of large grazers, including mammoths, horses, and bison. Thus, Guthrie (1968, 1990, 2001) argued that the ancient Beringian vegetation was more akin to a modern northern steppe (i.e., grassland vegetation where it is too dry for trees) such as that found today in portions of northern and central Asia. Hence there arose the concept of steppe-tundra (tundra-steppe in the Russian literature), which importantly indicates that the environment was both dry and cold (e.g., Yurtsev, 1982). However, steppe-tundra is a flexible enough concept to allow the continuance of a range of interpretations (Colinvaux, 1980a, 1980b, 1996a, 1996b; Colinvaux and West, 1984; Guthrie, 1990). Regional pollen records from the height of the last glaciation show that grasses (Poaceae) and sedges (Cyperaceae) were dominant components of the vegetation that was almost entirely herbaceous (e.g., Anderson and Brubaker, 1994; Edwards et al., 2000). However, the taxonomic resolution for these taxa achievable via pollen analysis is less than that needed to characterize the paleovegetation. This deficiency has resulted in a range of conflicting vegetation reconstructions.

There are a number of sedimentary contexts (in addition to lake sediments) and paleoecological resources (in addition to pollen) found in Eastern Beringia that have considerable potential for enhancing paleoecological reconstructions. Plant macrofossils are somewhat rare, but previous studies demonstrate that they can provide detailed paleoenvironmental information where they have been found (Elias, 1992; Elias et al., 1996, 1997; Goetcheus and Birks, 2001; Zazula et al., 2003, 2005). Sites with *in situ* fossil vegetation and paleosols during the last glaciation are even more rare (Goetcheus and Birks, 2001; Froese et al., 2006; Zazula et al., 2006), though they provide direct information about Pleistocene plant community composition and structure. More recently, subfossil middens (e.g., nests and seed caches) within burrows of arctic ground squirrels (*Spermophilus parryii*) and other rodents from ice-rich silt deposits of interior Yukon Territory provide archives of local Pleistocene flora (Zazula et al., 2003, 2005).

Much of the graminoid macro-remains (leaves and stems) from fossil peat, buried vegetation, and arctic ground squirrel nests cannot be identified reliably based on macro-morphological characteristics. However, these samples could serve as ideal material to conduct stable carbon isotope analyses. The stable carbon isotope composition (δ^{13}C) of plants is influenced by a number of environmental conditions including soil moisture, salinity, humidity, and the stable isotope composition of atmospheric CO_2 (O'Leary, 1988; Ehleringer et al., 1991; Lin and Sternberg, 1992; Arens et al., 2000). The modern vegetation of Eastern Beringia is almost exclusively dominated by plants using the C_3 photosynthetic pathway (e.g., Hultén, 1968; Welsh, 1974; Sage et al., 1999). C_4 plants are rare in modern Eastern Beringia (e.g., Welsh, 1974; Sage et al., 1999) and have distinctive δ^{13}C values between −10 and −14‰ (Ehleringer et al., 1991). By comparison, the total range of δ^{13}C values exhibited by C_3 plants is approximately −35‰ (plants living in moist habitats) to −21‰ (plants living in dry habitats), with an average value of −27‰ (Ehleringer et al., 1991). Under drier conditions, plants using the C_3 photosynthetic pathway tend to become more water-use-efficient (e.g., Ehleringer and Monson, 1993). In an attempt to reduce water losses through transpiration, these plants discriminate less against the heavier stable isotope of carbon (^{13}C) in CO_2. Plant biomass subsequently becomes enriched in the heavier stable isotope of carbon, and the resulting δ^{13}C derived from an analysis of the biomass is higher compared with C_3 plant biomass from a wet environment (O'Leary, 1988). Biomass generated under different environmental conditions tends to retain a unique stable isotopic signature that is subsequently retained in subfossil material of a plant (e.g., Wooller et al., 2003a, 2004). In some instances these signatures can be generated from plants dating from millions of years in the past (Schweizer et al., 2006).

Based on this relationship, we began our research on the stable isotope composition of graminoids from Eastern Beringia by addressing several research questions. Do the stable isotope compositions of modern grasses and sedges reflect the environmental conditions (i.e., wet or dry) of the habitat in which the plants grew? Can we measure the δ^{13}C values of subfossil graminoid material from sites in Eastern Beringia, and how do these values compare with the modern range of data for plants growing in the same region today? In our initial study, we examined the stable isotopic composition of a collection of modern and subfossil graminoids taken from several sites and sedimentary contexts in Eastern Beringia.

Study Sites

Samples of modern grasses and sedges collected in Alaska and Yukon Territory were selected from the collection of plants archived in the Herbarium at the University of Alaska Museum of the North (ALA) in Fairbanks, Alaska. Exact locations of the samples, related to the sample codes in Table 1 and 2, are recorded in the database of specimens at the Herbarium (http://arctos.database.museum).

Subfossil graminoid material was taken from three separate locations with differing sedimentary contexts (Table 1). The first location is the Fox Permafrost Tunnel (http://www.crrel.usace.army.mil/permafrosttunnel/) located roughly 10 km northeast of Fairbanks, off the Steese Highway (Fig. 1). The tunnel, excavated by the U.S. Army from 1963 to 1969, passes through loess deposits that span 10,000 to >40,000 ^{14}C yr BP and contain the remains of subfossil plants (in many instances attached to paleosols—e.g., Figs. 2a and 2b) and animals (Hamilton et al., 1988). The second site is the Quartz Creek locality, a large north-facing placer-mining exposure in the Klondike goldfields of west-central Yukon Territory (Fig. 1). Three rodent nests (e.g., Fig. 2c) directly associated with the late Pleistocene Dawson tephra were excavated in the summer of 2002 from an exposure of ice-rich silt (Zazula et al., 2005). Two of the nests (GZ.02.07.01.31, GZ.02.07.01.33) are those of Pleistocene arctic ground squirrels, while the third (GZ.27.08 #8) is likely that of a microtine rodent. The age of the nests is similar to the age of the Dawson tephra, ca. 25,300 ^{14}C

TABLE 1

The locations and descriptions of sites used in this investigation.

Location	Sample code	Sample type	Age range (^{14}C yr BP)	References
Eastern Beringia	See Table 2 and 3	Leaves from herbarium specimens of modern grasses and sedges	Modern	Collections at the University of Alaska Museum of the North Herbarium
Fox Permafrost Tunnel	NA	Graminoid leaves	10,000 to >40,000	Hamilton et al. (1988)
Quartz Creek, Dawson	GZ02.07.01.31	Graminoid leaves from arctic ground squirrel nest	~25,300	Zazula et al. (2005)
	GZ02.07.01.33	Graminoid leaves from arctic ground squirrel nest	~25,300	Zazula et al. (2005)
	GZ27.08 #8	Graminoid leaves microtine from rodent nest	~25,300	Zazula et al. (2005)
Goldbottom Creek, Dawson		Graminoid leaves from paleo turf	~25,300	Zazula et al. (2005)

yr BP (Froese et al., 2002; Zazula et al., 2006). Nearly 12 m of ice-rich silt composed of both primary and colluviated loess overlies the Dawson tephra (for site details see Site 4 in Froese et al., 2002). The final paleoecological site is an *in situ* vegetated surface, or paleoturf (Fig. 2d), buried by Dawson tephra at Goldbottom Creek, approximately 30 km away from the Quartz Creek locality in the Klondike goldfields (Fig. 1). The buried fossil vegetation is a riparian plant community consisting of dwarf willow (*Salix* cf. *arctica*), abundant tufted hair grass (*Deschampsia caespitosa*), sedges (*Carex* spp.) with interspersed horsetail (*Equisetum* cf. *palustre*), mosses, and limited forbs or other grasses (Zazula et al., 2006; Froese et al., 2006).

Methods

MODERN AND SUBFOSSIL GRAMINOID ANALYSES

Leaf samples of modern sedges and grasses (~200 taxa) from Alaska and Yukon Territory were collected from specimens held at the University of Alaska Museum of the North Herbarium. Caution was taken to avoid any incorporation of material with herbarium glue attached. Four grass specimens from genera known to be C_4 (*Muhlenbergia* and *Setaria*; Watson and Dallwitz, 1994) that were from sites within Eastern Beringia were also analyzed to test whether they were indeed C_4. Species were grouped (using information in Hultén, 1968, and habitat information taken from specimen herbarium labels) according to their habitat (wet or dry). An aliquot (~300 to 500 µg) of each freeze-dried sample of leaf fragments was weighed into a tin capsule, which was sealed and introduced into the autosampler (A2100) of a CE Instruments, NA 2500 series, Elemental Analyzer (EA) at the Alaska Stable Isotope Facility, University of Alaska Fairbanks (UAF). The stable carbon isotope ratio of the combustion gas (CO_2) from each sample was analyzed using continuous-flow, stable isotope ratio mass spectrometry (IRMS, Finnigan MAT, Delta plus XP). The results are presented in standard delta (δ) notation. CO_2 samples were analyzed relative to internal, working gas standards. Carbon isotope compositions ($\delta^{13}C$) are expressed relative to Vienna Pee Dee Belemnite (V-PDB). Peptone was analyzed as a check on the analytical precision associated with the EA-IRMS. Analytical precision (SD) for $\delta^{13}C$ was <0.1‰ (%C = 1.8 and %N = 0.5). Precisions were typically lower than this for replicate ($n = \geq 3$) analyses of subfossil and modern graminoid specimens.

In situ graminoid samples were removed from the loess composing the walls of the Fox Permafrost Tunnel in December 2003. Samples were taken in proximity to a series of radiocarbon-dated points along the tunnel, which are the results of previous investigations and are marked in the tunnel (Hamilton et al., 1988). The radiocarbon years before present for each of five points in the tunnel were reported in Hamilton et al. (1988) and are 11,300 ± 160, 11,910 ± 180, 14,280 ± 230, 31,200 ± 3000, and >40,000 ^{14}C yr BP. Between four and seven separate plants were removed at each of the five locations. Loess was removed from the surface of the samples with a fine-haired brush. The samples were then freeze dried, weighed, and analyzed for their $\delta^{13}C$ (as described above). A scanning electron microscope image of the surface of a graminoid leaf from the Fox Permafrost Tunnel was taken using an Electroscan E2020 environmental scanning electron microscope (ESEM) (Department of Geology and Geophysics, UAF) to examine the preservation state of the samples (e.g., Fig. 2e). Between 5 and 9 samples of separate graminoid remains were removed from each of the Quartz Creek middens and were freeze dried, weighed, and analyzed (as above) for their $\delta^{13}C$. Ten samples of separate graminoid remains were removed from the Goldbottom Creek paleoturf. The surfaces of these samples were brushed with a fine-haired brush to remove dirt. Subsamples of these samples were freeze dried, weighed, and analyzed for their $\delta^{13}C$ (as described above).

DATA ANALYSES

Each of our modern graminoid specimens was classified as representing a wet or dry environment based on herbarium sheet data and ecological information in Hultén (1968). Student's *t*-test was used to examine whether there were statistical differences between different groups of graminoid samples (e.g., plant specimens listed on their herbarium labels as having come from either a dry or wet habitat).

The $\delta^{13}C$ of a plant is influenced by the $\delta^{13}C$ of the surrounding atmospheric CO_2 (e.g., Arens et al., 2000), and the $\delta^{13}C$ of atmospheric CO_2 has changed in the past (Friedli et al., 1986; Leuenberger et al., 1992). To be able to compare the $\delta^{13}C$ of subfossil plant samples and modern plant samples we took into account the difference (~1 ± 0.2‰) in $\delta^{13}C$ of atmospheric CO_2 of modern (Friedli et al., 1986) and paleo (late Quaternary) (Leuenberger et al., 1992) atmospheres. Given that the $\delta^{13}C$ of past atmospheric CO_2 for the date range of our subfossil samples was ~1‰ higher than that of today's atmospheric CO_2 (Friedli et al., 1986; Leuenberger et al., 1992), we added 1‰ to the $\delta^{13}C$ of the modern plants (only when comparing modern and subfossil samples, i.e., Figs. 4 and 5). The $\delta^{13}C$ values reported in the tables herein are unaltered $\delta^{13}C$ values to allow their use in future studies.

TABLE 2

The stable carbon isotope composition and percent C of modern sedge (*Carex*) species from Alaska and the Yukon Territory.

Species	ALA accession	Ecology*	%C	$\delta^{13}C$
Dry sites				
C. albo-nigra	43466	Dry mountain sides	45.9	−25.6
C. bigelowii	10939	Dry places/solifluction soil/mountains	43.5	−26.9
C. crawfordii	V131128	Dry grasslands/roadsides	46.0	−28.7
C. eburnea	86872	Dry sand or rocky places/calcareous soils	43.5	−29.2
C. filifolia	43450	Dry ridges	45.0	−26.4
C. foenea	94961	Woods/river banks/sandy soils	43.1	−26.9
C. glacialis	V1302292	Dry calcareous soils	46.1	−25.3
Mean			44.7	−27.0
Standard deviation			1.3	1.5
Bogs and marshes				
C. capitata	V132883	Bogs/marshes	42.5	−29.4
C. chordorrhiza	44161	Bogs/lake margins/quagmires	45.9	−26.8
C. diandra	38521	Bogs/swamps/mires/borders of ponds	43.2	−28.1
C. diandra	V103152	Bogs/swamps/mires/borders of ponds	41.1	−26.8
C. gynocrates	60125	Wet meadows/marshes	44.6	−24.2
C. heleonastes	n.d.	Peat bogs/swamps	45.6	−28.4
C. holostoma	V134376	Marshes and mountain slopes	45.4	−27.2
C. lasiocarpa	V85249	Bogs/shallow water	46.0	−25.9
C. leptalea	V141806	Bogs/meadows and shores	46.6	−24.2
C. limosa	V143375	Bogs/quagmires/shallow water	47.7	−25.8
C. loliacea	V138710	Moist places/peat soil/muskeg	47.9	−26.2
Mean			45.1	−26.6
Standard deviation			2.1	1.6
Coastal/saline				
C. glareosa	V134815	Brackish marshes	45.3	−27.1
C. gmelinii	V144041	Sandy saline shores	45.9	−29.0
C. lyngbyei	V143833	Coastal salt marshes	46.6	−28.0
C. mackenziei	V143215	Wet places along seashores	42.3	−26.9
C. maritima	80996	shores/sandy soils	46.3	−28.1
C. maritima	90630	shores/sandy soils	42.8	−27.4
C. macrocephala	V04023	Sandy seashores	45.9	−27.4
Mean			45.2	−27.6
Standard deviation			1.7	0.8
Wet/moist places				
C. adelostoma	55014	Wet places	40.4	−28.3
C. aquatilis	V79576	Shallow water/marshes/along rivers	42.8	−28.3
C. arcta	V131115	Wet places	42.4	−28.1
C. atherodes	V117447	Wet meadows	36.1	−29.7
C. atratiformis	V13117	Moist places	42.5	−29.9
C. aurea	V131119	Meadows/moist places	37.3	−29.0
C. bicolor	V134906	Wet gravely places in mountains	40.1	−30.6
C. capillaris	V145250	Moist (or dry) places	43.8	−32.3
C. disperma	V143683	Moist places	44.0	−30.3
C. eleusinoides	24985	Wet places/gravel bars	29.3	−27.6
C. flava	V94575	Moist places/calcareous soils	45.4	−29.1
C. flava	V94575	Moist places/calcareous soils	47.3	−29.2
C. garberi	V080696	Wet places	45.9	−29.1
C. interior	V141199	Wet meadows	46.6	−29.7
C. kelloggii	V117726	Wet places	41.9	−28.1
C. krausei	V139461	Moist places	38.6	−29.9
C. lachenalii	V143687	Alpine tundra/snow beds/above treeline	50.7	−28.9
C. laeviculmis	V135797	Wet meadows	46.2	−27.7
C. lapponica	V141611	Wet grassy places	46.7	−27.7
C. laxa	V141915	Wet places/mostly in woods	40.5	−27.1
C. livida	V143369	Wet places	44.6	−27.9
C. macloviana	96553	Meadows/gravely shores	45.2	−28.2
C. media	V143394	Moist places in lowlands	44.9	−29.8
C. membranacea	V139569	Wet places	47.0	−27.8
C. mertensii	V143693	Wet rocky slopes	46.0	−29.3
Mean			43.0	−28.9
Standard deviation			4.5	1.2

* Taken from the ecological descriptions given on the herbarium sheets.

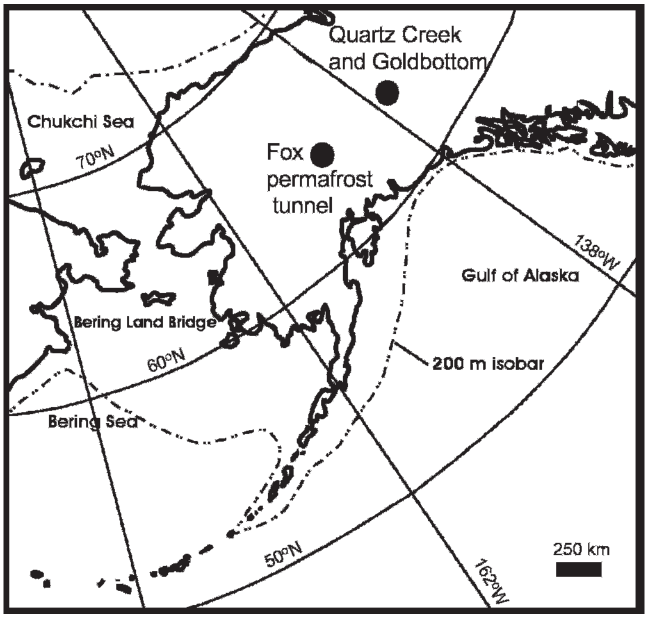

FIGURE 1. The location of study sites used in this investigation. Fox tunnel provided subfossil graminoid specimens from paleosols in permafrost/loess. Goldbottom Creek and Quartz Creek provided subfossil graminoid remains preserved in a paleoturf and paleoarctic ground squirrel nests, respectively.

Results

MODERN GRASSES AND SEDGES

The total analyzed δ^{13}C range for the sedges by habitat from Alaska and the Yukon is −32.3‰ (listed as from wet habitats) to −24.2‰ (listed as from bogs and marshes—permanently inundated with water) (Fig. 3, Table 2). The δ^{13}C range for sedges from dry habitats was −29.2‰ to −25.3‰ with a mean of −27.0‰ (SD = 1.5‰), while the mean δ^{13}C for sedges from bogs and marshes is −26.63‰ (SD = 1.6‰). Sedges from coastal and saline habitats have δ^{13}C with a mean of −27.58‰ (SD = 0.8‰). The sedges from wet places have the most negative δ^{13}C values with a mean of −28.91‰ (SD = 1.2‰). The δ^{13}C values of sedges from wet habitats are significantly lower ($p < 0.005$) than those of a dry habitat. However, there is no significant difference ($p > 0.5$) in the mean %C composition of the sedges from the different habitat types, and the mean %C for sedges was ~45%.

Table 3 presents the δ^{13}C, %C, %N, and C:N data by habitat for modern grasses from Alaska and the Yukon. There is a significant difference ($p < 0.001$) in δ^{13}C by grass habitat (dry vs. wet) (Fig. 3). The grasses from wet habitats have a lower mean δ^{13}C value (−29.1‰, SD = 2.1) compared with those from dry habitats (−26.4‰, SD = 1.2‰). No grasses from dry habitats have a δ^{13}C value below approximately −29‰. Our preliminary analyses show that sedges and grasses from dry habitats have significantly less negative δ^{13}C values compared with those from wet habitats, which is consistent with theory (O'Leary, 1988; Ehleringer et al., 1991). All four of the grasses suspected to be C_4 have δ^{13}C values within the range expected for C_4 plants (−10 to −14‰) (Table 4).

PLEISTOCENE GRASSES AND SEDGES

A number of features, including stomata, prickles, and long cells, showing a high degree of leaf preservation, are evident from the ESEM image (Fig. 2e) taken of a subfossil graminoid leaf surface. In some instances, as in Figures 2a, 2b, and 2c, the graminoid remains are well preserved as whole plants attached to a paleosol. In the case of arctic ground squirrel nests, the collection of plant remains, including grasses, are tangled together. The δ^{13}C and %C values of the graminoid samples taken from the Fox Permafrost Tunnel are presented in Table 5. The %C values of the samples range from 52 to 32 and are not significantly different compared with modern grasses and sedges ($p > 0.2$). The δ^{13}C values of these subfossil specimens range from −28.9 to −24.3‰ and vary significantly ($p < 0.05$) among time points (Fig. 4), with the lowest mean δ^{13}C value (−28‰) seen from an area of the tunnel dated as ca. 11,300 ± 160 ^{14}C yr BP and the highest mean δ^{13}C value (approximately −25.5‰) evident in a portion of the tunnel dated as between 11,910 ± 180 and 14,280 ± 230 ^{14}C yr BP.

The mean %N of the samples was 1.3 ± 0.5, which is significantly smaller than that of the modern grasses (mean = 2.7, SD = 1.0) ($p < 0.001$) but within the range of values by species (Table 5). The %C values (mean = 37, SD = 9) are also significantly lower compared with the modern grasses ($p < 0.001$). The Goldbottom Creek subfossils had the lowest δ^{13}C values (mean = −27‰) compared with the subfossil plants from Quartz Creek. The mean C:N values from Quartz Creek nests 1 and 2 (Table 4) were noticeably smaller (18 and 23) compared with the other Quartz Creek nest (46) and the Goldbottom Creek paleoturf (49).

Discussion

STABLE ISOTOPE AND ELEMENTAL COMPOSITIONS OF MODERN GRAMINOIDS

The δ^{13}C values from analyses of grasses from Alaska and Yukon Territory (Fig. 3) illustrate that, as expected from theory (O'Leary, 1988), grasses from wet habitats had δ^{13}C values that were more negative than those from dry habitats. Although there was considerable overlap among the data from these two habitats, the mean of samples from each habitat were found to be statistically different. Grasses from supposedly wet habitats were found to have δ^{13}C values up to the maximum extent of the range shown by dry grasses. However, no grasses from dry habitats were found with δ^{13}C values below approximately −29‰. The δ^{13}C values of grasses from wet habitats ranged down to approximately −34‰. It seems, therefore, that δ^{13}C values from an unknown grass would be better at typing the specimen as having come from a wet environment when δ^{13}C are less than −29‰.

Whereas the δ^{13}C patterns for wet and dry grasses seem relatively clear, this is not the case for modern sedges (Fig. 3). Like the grasses, sedges from moist habitats had significantly more negative δ^{13}C values compared with those from dry habitats. However, sedges listed as from bogs or marshes had relatively high δ^{13}C values, not significantly different from those for sedges in dry habitats ($p > 0.1$). In fact, the highest δ^{13}C, which is supposedly a marker of dry habitats, was found in a sedge from a bog/marsh (*Carex gynocrates*; Table 2). However, the photosynthetic physiology of plants can be influenced by additional environmental stressors (e.g., Lin and Sternberg, 1992; Dawson and Bliss, 1989). This is why we grouped sedges found in coastal or marine habitats to examine whether sedges potentially exposed to more saline conditions had relatively less negative δ^{13}C values, a trend that has been demonstrated for other plants (Lin and Sternberg, 1992). In fact, the δ^{13}C values of sedges found in coastal and saline conditions were significantly different compared with sedges from moist habitats ($p < 0.005$). Salinity is unlikely to be the driving

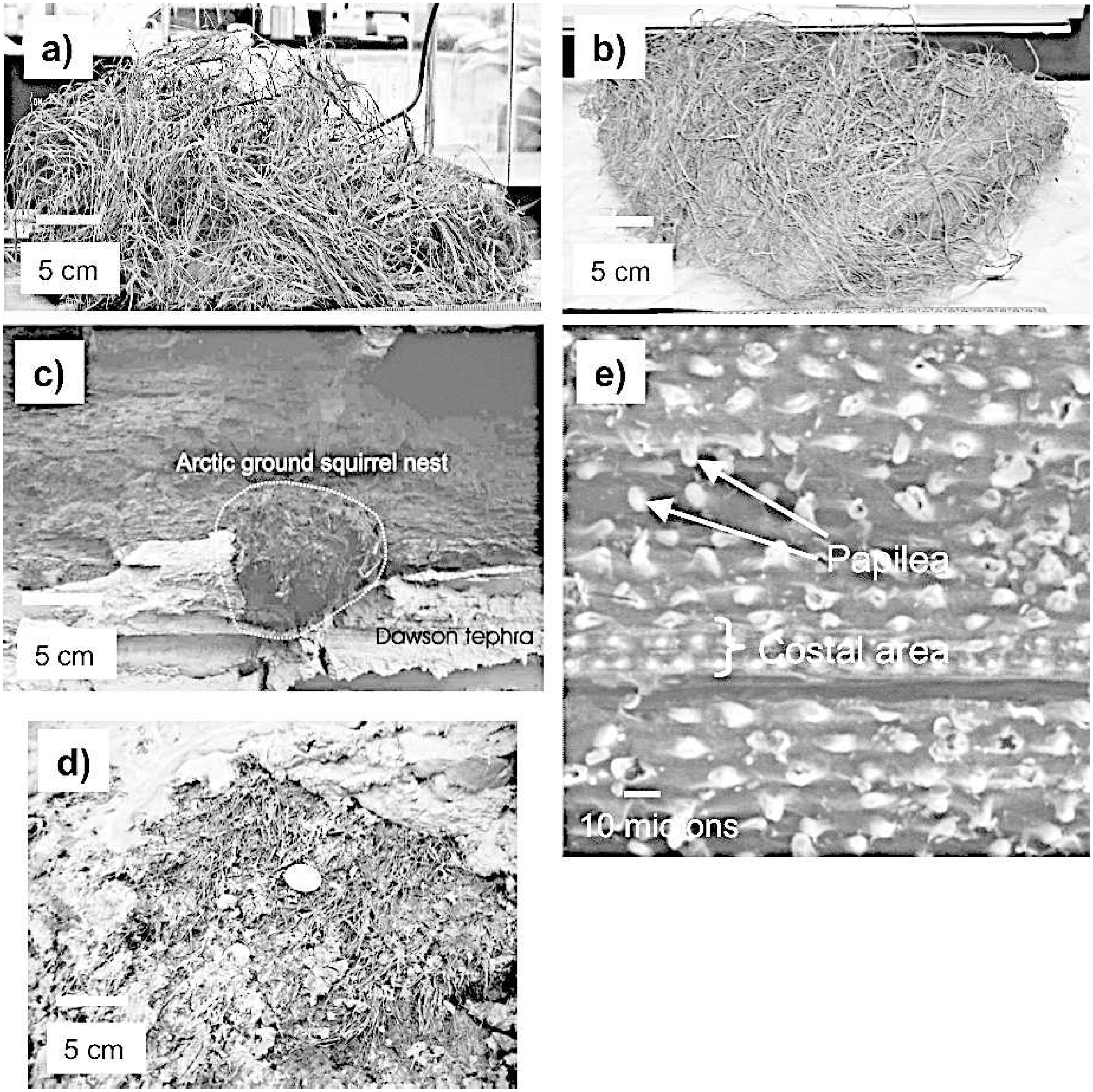

FIGURE 2. (a and b) Plan and side view (respectively) of a paleosol removed from the Fox Permafrost Tunnel with well-preserved grasses and sedges still attached. (c) A subfossil arctic ground squirrel nest above the Dawson tephra (redrawn from Froese et al., 2002). (d) A coin (for scale) lying on the paleoturf at Goldbottom Creek. (e) An environmental scanning electron microscope image of a fossil graminoid cuticle (ca. 31,000 ^{14}C yr BP) from the Fox Permafrost Tunnel, Alaska.

factor of the relatively high δ^{13}C values of sedges found in marshes and bogs (Fig. 3, Table 2). Although we cannot explain the relatively high δ^{13}C values for sedges listed as from bogs and marshes, other researchers (Keeley and Sandquist, 1992) have reported similar results for some C_3 plants growing in waterlogged conditions.

In terms of interpreting the paleoenvironmental record, the modern sedge data suggest a difficulty in separating dry sedges from marsh or bog sedges using their δ^{13}C values. The answer might lie in additional lines of paleoenvironmental evidence, such as the sedimentary context of the sample, i.e., whether from a nest, paleosol, or paleoturf. This would assume that the paleograminoid sample was local to the lithology. This might be a safer assumption when considering an *in situ* paleosol or paleoturf (e.g., Goetcheus and Birks, 2001; Froese et al., 2006; Zazula et al., 2006) compared with a loess sequence in which some material may be detrital. Moreover, when interpreting δ^{13}C from subfossil remains, it is necessary to consider the role diagenesis might have played in altering the isotopic composition of a sample. Some processes associated with the decomposition of organic matter can slightly alter the stable isotopic composition of plant material (e.g., Macko et al., 1993; Fogel and Tuross, 1999; Wooller et al., 2003a), but this would generally be insufficient to shift the signature from one indicating high water-use efficiency (e.g.,

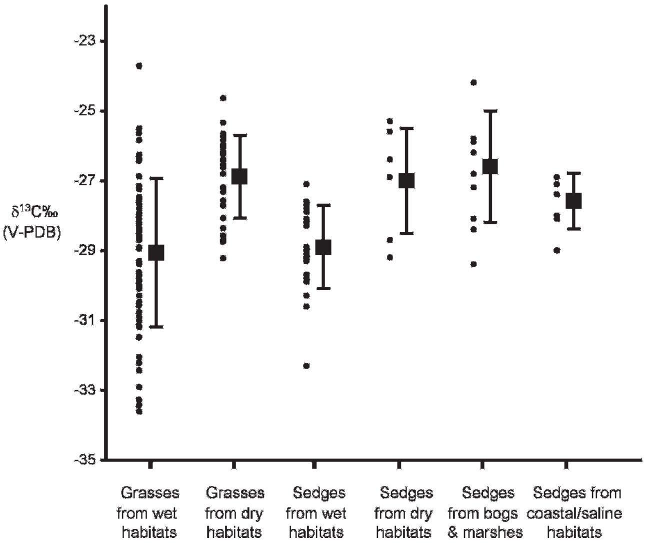

FIGURE 3. The stable carbon isotope composition of modern grasses and sedges from different habitats types in Alaska and Yukon Territory. The square symbols represent the mean of these groups with 1 standard deviation of the means shown. V-PDB = Vienna Pee Dee Belemnite.

$\delta^{13}C = -22‰$) to one of low water-use efficiency (e.g., $\delta^{13}C = -32‰$).

C_4 GRASSES WITHIN THE EXTENT OF MODERN EASTERN BERINGIA

Stable carbon isotopes provide a clear way of identifying grasses as either C_3 or C_4 (Tables 3 and 4). Four modern specimens of C_4 grasses representing two species were identified from sites within Alaska and Yukon Territory (Table 4). This implies that C_4 grasses are able to grow under modern subarctic environmental and atmospheric conditions (e.g., temperature, precipitation, and atmospheric CO_2 concentrations). Some of these conditions are atypical of the wider "natural" environment. For instance, the areas where they grow were glaciated during the late Pleistocene (Duk-Rodkin, 1999). *Setaria viridis* is a Eurasian plant that has only been found as a nonpersistent casual introduction in Yukon, and *Muhlenbergia glomerata* is a plant sometimes associated with hot springs. Nevertheless, these C_4 grasses were growing at relatively high latitudes for C_4 plants (Sage et al., 1999).

The presence of these modern grasses at relatively high latitudes in the modern Eastern Beringia begs the question of whether C_4 grasses could have been present during Pleistocene glacials. There is some literature to suggest that some C_4 plant species existed in glacial refugia during the LGM (StreetPerrott et al., 1997; Boom et al., 2001; Wooller et al., 2001, 2003b). For instance, remains of the C_4 grass genus *Bouteloua* based on phytolith morphology were reported from a Pleistocene fossil arctic ground squirrel nest in Alaska (Guthrie, 1982), though, unfortunately, this report was not confirmed with carbon isotope data.

Environmental change and variation (e.g., in atmospheric CO_2 concentrations, salinity, disturbance or fire frequency, temperature, precipitation amounts, and seasonality) have been found to drive modern (e.g., Hattersley, 1992; Wooller et al., 2005) and past (e.g., Ehleringer et al., 1991; Ehleringer and Monson, 1993; StreetPerrott et al., 1997) proportions of C_4 plants in vegetation. Are there any environmental factors of the LGM that might have favored C_4 plants in Eastern Beringia? Previous research indicates that some areas of Beringia, notably the interior, experienced relatively drier conditions in the past (Hopkins et al., 1982; Barnosky et al., 1987; Kutzbach, 1987; Anderson and Brubaker, 1994). Atmospheric CO_2 concentrations were also lower during the LGM and could have favored C_4 plants in some other locations (StreetPerrott et al., 1997). Although temperature, which is suggested to have been lower during the LGM (although there is limited information on seasonality and data are not quantitative or geographically widespread), favors C_3 photosynthesis over C_4 photosynthesis (Sage et al., 1999), there are some C_4 plants that can survive at relatively lower temperatures (Ehleringer et al., 1991; Ehleringer and Monson, 1993). Our point here is not to suggest that C_4 plants expanded during the past in Eastern Beringia, but rather, stating that conditions for C_4 plant occurrence *may have* been present within the Beringian glacial refugium; and if they were, the presence of C_4 plants in samples such as subfossil ground squirrel nests, loess, or paleoturfs would be obvious if the stable carbon isotopic composition of the graminoid material were analyzed.

STABLE CARBON ISOTOPE MEASUREMENTS OF PALEOSAMPLES

None of the $\delta^{13}C$ values of subfossil graminoids taken from the Fox Permafrost Tunnel, Quartz Creek, or Goldbottom Creek sites were within the range of C_4 grasses. The $\delta^{13}C$ values were all within the range of C_3 plants and within the total range of the modern graminoids analyzed in this study. There were significant differences between ages (Fig. 4) and between sites (Fig. 5), which implies that the past graminoids grew under different environmental conditions. Once the difference (~1‰) in the $\delta^{13}C$ of CO_2 in the modern and past atmospheres has been taken into account, the $\delta^{13}C$ of modern and subfossil graminoids can be compared (Figs. 4 and 5). This approach is consistent with the procedure described by Arens et al. (2000) and allows $\delta^{13}C$ values from plants of different ages to be compared. Having taken this into account, Figure 4 shows that the graminoid specimens from the oldest part of Fox Permafrost Tunnel likely grew in relatively mesic habitats. The ages of these samples suggest these graminoids inhabited wetter, pre-LGM environmental conditions that are characteristic of the Middle Wisconsinan interstadial (Anderson and Lozhkin, 2001). However, the means of the two sample sets from an area of the tunnel dated as between 11,910 ± 180 and 14,280 ± 230 ^{14}C yr BP lay within the range of the modern graminoids from dry habitats. In this respect the $\delta^{13}C$ data imply that the graminoids grew in a relatively dry habitat that characterizes full glacial conditions during the LGM (Anderson and Brubaker, 1994; Kaplan et al., 2003). Analyses of the graminoids from the youngest portion of the tunnel (11,300 ± 160 ^{14}C yr BP) imply a marked change toward wetter conditions, where the $\delta^{13}C$ of the subfossils are within the 1 SD of the mean of wet graminoids and outside the 1 SD of the mean of dry graminoids (Fig. 4). This marked shift toward wetter conditions at this time would be consistent with multiple lines of other evidence from Eastern Beringia that document the rise of the mesic-hydric taiga and tundra vegetation (Guthrie, 2006). Figure 4 does not include the $\delta^{13}C$ range of coastal sedges, given the sedimentary context of the samples (paleosols in loess). Figure 4 also assumes that the subfossil plant remains were not derived from sedges that were once living in bogs and marshes, which were inundated with water. This is also a relatively safe assumption given the sedimentary context of the subfossils.

TABLE 3

The stable carbon isotope and elemental (C and N) composition of modern grasses (all C_3) by habitat from Alaska and the Yukon Territory.

Species	University of Alaska Museum of the North Herbarium accession number	Habitat source*	%N	%C	$\delta^{13}C$	C:N
		Wet sites				
Agrostis alaskana	V130401	2	2.6	47.1	−33.5	18.1
Agrostis mertensii	V104130	2	1.8	45.3	−31.1	24.6
Agrostis clavata	V133576	2	3.3	39.3	−32.9	12.1
Agrostis exarata	87242	3	3.8	47.3	−32.2	12.6
Agrostis geminata	V101618	1	1.3	39.6	−28.5	30.7
Agrostis scabra	V136251	1	1.6	43.5	−30.6	27.1
Agrostis stolonifera	87184	1	1.9	50.1	−32.1	25.8
Agrostis trinii	32710	2	2.6	48.9	−26.3	18.9
Alopecurus aequalis	V145495	1,2	3.4	40.2	−29.0	11.9
Alopecurus alpinus	V08050	2	5.0	52.3	−27.2	10.5
Alopecurus alpinus	V145923	2	4.8	49.9	−26.4	10.3
Alopecurus geniculatus	V90444	1,2	3.9	42.9	−30.0	11.0
Alopecurus pratensis	V084708	1	2.4	43.1	−27.7	17.6
Arctagrostis latifolia	V150486	1,2	4.2	50.2	−27.8	11.8
Arctophila fulva	V124235	1	1.7	44.4	−29.3	25.4
Bromus ciliatus	V98021	1	2.6	49.1	−28.7	18.6
Bromus inermis	V132817	3	1.9	44.0	−28.7	23.3
Bromus pacificus	87314	1	3.3	47.3	−30.5	14.5
Bromus sitchensis	V130430	1	2.4	44.7	−29.4	18.4
Calamagrostis canadensis	37341	1	3.6	45.8	−28.4	12.7
Calamagrostis deschampsioides	V150221	1,2	2.1	42.5	−28.6	20.1
Calamagrostis inexpansa	V98652	1,2	1.4	41.7	−27.9	29.6
Calamagrostis lapponica	V148854	1	1.8	40.0	−27.8	22.6
Calamagrostis nutkaënsis	V135176	2	2.4	51.0	−28.9	21.2
Calamagrostis stricta	V148979	3	2.6	44.9	−29.6	17.6
Catabrosa aquatica	V126356	1,2	2.8	42.7	−30.0	15.5
Colpodium sp.	V126356	1	2.3	49.9	−28.3	21.4
Colpodium wrightii	V134571	1	2.5	47.9	−28.4	19.4
Deschampsia beringensis	V144794	1,2	1.5	51.3	−27.2	33.1
Deschampsia brevifolia	VC73070	2	3.1	52.6	−28.0	17.2
Elytriga repens	79377	1	2.5	45.2	−30.8	17.8
Elymus glaucus	V120708	1	2.8	50.6	−28.2	18.3
Elymus glaucus	V134801	1	3.4	47.2	−27.6	13.8
Elymus hirsutus	10446	1	3.0	45.4	−23.7	15.0
Elymus macrourus	V145983	1	4.8	53.0	−27.3	11.0
Elymus subsecundus	V134753	1	2.9	49.9	−33.3	17.4
Elymus trachycaulus	V134563	1	3.2	45.8	−29.4	14.2
Festuca vahlianum	V150495	1	2.8	57.0	−28.4	20.5
Glyceria borealis	V147874	1	3.5	47.8	−28.7	13.6
Glyceria maxima	3901	1	3.2	44.5	−25.5	13.9
Glyceria pulchella	3929	1	3.4	45.0	−26.9	13.1
Hierochloë odorata	V144344	1,2	2.6	48.8	−27.5	18.5
Hierochloë pauciflora	V120083	1,2	3.7	49.8	−26.4	13.5
Hordeum brachyantherum	V134804	1,2	2.2	45.5	−31.0	20.7
Hordeum caespitosum (jubatum)	V102342	1	4.6	47.5	−33.4	10.4
Koeleria gracilis	V105345	1	2.6	48.4	−28.1	18.8
Leymus mollis	V109145	1	0.4	51.9	−25.7	126.5
Leymus mollis	V112482	1	1.6	45.4	−25.8	28.4
Lolium multiflorum	V120558	1	1.4	39.6	−30.9	27.4
Lolium perenne	V136111	3	3.5	41.5	−31.2	11.7
Melica subulata	V118033	1	5.5	50.9	−33.6	9.3
Phalaris arundinacea	V145470	1,2	3.1	50.4	−28.6	16.2
Phippsia algida	79368	2	2.1	41.9	−26.3	19.9
Pleuropogon sabinei	V90734	1,2	4.2	46.8	−29.4	11.1
Poa annua	V78642	1	2.1	47.7	−31.5	23.0
Poa cusickii	V133885	1	4.0	50.1	−27.5	12.4
Poa eminens	95349	1	1.4	38.1	−30.1	26.7
Poa laxiflora	V1491689	1	3.0	42.9	−29.8	14.3
Poa macrocalyx	V111930	1	2.6	42.3	−32.4	16.5
Poa palustris	V141408	1	2.0	43.5	−29.7	21.3
Podagrostis aequivalis	V146059	2	1.8	48.0	−30.3	26.5

TABLE 3

Continued.

Species	University of Alaska Museum of the North Herbarium accession number	Habitat source*	%N	%C	δ^{13}C	C:N
Podagrostis thurberiana	V146064	2	3.2	49.4	−29.7	15.5
Puccinellia arctica	V95031	1	1.6	51.2	−29.9	31.3
Puccinellia deschampsioides	V125157	1	4.2	52.5	−27.2	12.4
Mean			2.8	46.6	−29.1	19.9
Standard deviation			1.0	4.0	2.1	14.8
		Dry sites				
Avena hookeri	V13072	2	2.2	45.2	−28.0	20.5
Bromus carinatus	V084995	1	1.4	44.9	−27.7	32.0
Calamagrostis purpurascens	V70363	1,2	3.1	50.9	−27.2	16.4
Calamagrostis purpurascens	V114008	1,2	2.5	45.8	−26.0	18.0
Dactylis glomerata	V112039	2	2.6	41.8	−28.6	16.1
Danthonia intermedia	V147827	1	1.4	46.8	−26.6	33.0
Danthonia spicata	V140898	1	1.9	47.6	−25.7	25.5
Elymus alaskanum	85269	1	1.4	45.6	−26.3	33.5
Elymus spicata	n.d.	1	3.2	52.3	−26.8	16.4
Festuca baffinensis	V143087	1	2.4	47.1	−24.6	20.0
Festuca minutiflora	80824	1	2.3	47.8	−25.7	20.9
Festuca pratensis (Lolium pretense)	10307	1	3.2	46.3	−28.8	14.4
Festuca saximontana	44197	1	3.7	44.3	−26.5	12.0
Glyceria striata	V70055	1	2.3	44.3	−25.8	19.4
Hordeum vulgare	V103674	1	0.4	34.1	–29.2	88.5
Poa abbreviata	44209	1	2.7	48.8	−26.2	18.3
Poa alpina	V144897	2	3.2	50.6	−28.7	15.7
Poa arctostepporum	V145360	1	1.0	48.8	−25.7	49.6
Poa glauca	280	2	2.3	49.9	−28.4	21.2
Poa interior	V136512	1	2.0	44.8	−28.1	22.8
Poa pratensis	289	1	3.3	44.8	−26.4	13.7
Psathyrostachys juncea	44311	3	3.2	47.9	−27.2	15.1
Puccunellia pumila	V116375	1	2.4	49.0	−26.0	20.0
Schizachne purpurascens	V137957	1	2.4	51.5	−27.3	21.2
Secale cereale	48653	1	2.1	51.1	−25.4	24.4
Stipa comata	V133110	2	3.8	51.5	−27.6	13.4
Trisetum sibiricum	V083666	1	3.3	51.2	−26.1	15.4
Trisetum spicatum	34532	1	2.6	49.1	−26.4	18.5
Mean			2.4	47.3	−26.9	23.4
Standard deviation			0.8	3.8	1.2	15.0

* Taken from the ecological descriptions from (1) the herbarium sheets; (2) Hultén (1968); and (3) the Internet (http://www.mun.ca/biology/delta/arcticf/_ca/www/pocast.htm, http://www.hort.purdue.edu/newcrop/duke_energy/Bromus_inermis.html#Ecology, http://www.hort.purdue.edu/newcrop/duke_energy/Lolium_perenne.html#Ecology, http://www.fs.fed.us/database/feis/plants/graminoid/psajun/index.html).

TABLE 4

The stable carbon isotope and elemental (C and N) composition of modern C_4 grasses from Eastern Beringia. n.d. = not determined.

Species	University of Alaska Museum of the North Herbarium accession number	Location	Habitat	%N	%C	δ^{13}C	C:N
Muhlenbergia glomerata	20481	Liard River, Yukon Territory, 60°02′N, 128°35′W	n.d.	1.7	47.4	−12.0	28.5
Muhlenbergia glomerata	V128443	Beaver River Hot Springs, 60°22′N, 125°34′W	Growing on gravel bar	1.3	42.0	−13.2	32.9
Muhlenbergia glomerata	41089	Canada, NW Territories, 64°58′N, 123°40′W	Sandy cutbanks along river	1.9	40.5	−13.6	21.2
Setaria viridis	V128403*	Whitehorse, Yukon Territory	Growing in cracks in pavement	2.4	44.0	−14.0	18.0

* Duplicates at University of Alaska Museum of the North Herbarium and B.A. Bennett Herbarium.

TABLE 5

The stable carbon isotope and elemental (C and N) composition of subfossil graminoid from Eastern Beringia. n.d. = not determined.

Age in ^{14}C years BP	%N	%C	δ^{13}C	C:N
Fox Permafrost Tunnel				
11,300	n.d.	32.4	−27.4	n.d.
11,300	n.d.	35.5	−28.9	n.d.
11,300	n.d.	46.3	−27.6	n.d.
11,300	n.d.	46.1	−27.4	n.d.
11,300	n.d.	40.5	−28.9	n.d.
11,910	n.d.	41.1	−24.6	n.d.
11,910	n.d.	47.9	−26.8	n.d.
11,910	n.d.	54.8	−25.7	n.d.
11,910	n.d.	55.2	−25.6	n.d.
11,910	n.d.	31.7	−25.7	n.d.
14,280	n.d.	47.1	−25.0	n.d.
14,280	n.d.	51.2	−24.7	n.d.
14,280	n.d.	47.4	−28.0	n.d.
14,280	n.d.	43.9	−26.8	n.d.
14,280	n.d.	52.2	−24.3	n.d.
14,280	n.d.	48.2	−25.0	n.d.
14,280	n.d.	39.3	−24.7	n.d.
31,200	n.d.	52.2	−26.3	n.d.
31,200	n.d.	48.2	−27.2	n.d.
31,200	n.d.	39.3	−27.4	n.d.
31,200	n.d.	47.4	−28.2	n.d.
31,200	n.d.	46.4	−26.3	n.d.
≥40,000	n.d.	41.1	−26.7	n.d.
≥40,000	n.d.	48.8	−25.9	n.d.
≥40,000	n.d.	52.3	−25.7	n.d.
≥40,000	n.d.	50.3	−26.6	n.d.
Quartz Creek (nest GZ27.08 #8)				
~25,300	0.6	42.6	−25.4	74.6
~25,300	1.2	37.7	−25.5	30.6
~25,300	1.3	26.8	−27.3	20.7
~25,300	0.7	29.7	−24.7	45.0
~25,300	0.8	29.7	−25.1	35.8
~25,300	0.5	34.0	−25.7	69.4
Mean	0.9	33.4	−25.6	46.0
Standard deviation	0.3	5.9	0.9	21.7
Quartz Creek (nest GZ02.07.01.31)				
~25,300	2.4	45.1	−26.3	18.5
~25,300	1.9	30.8	−24.5	16.2
~25,300	1.8	37.2	−26.6	20.8
~25,300	1.6	28.0	−27.2	17.1
~25,300	2.1	32.7	−26.7	15.8
Mean	2.0	34.8	−26.3	17.7
Standard deviation	0.3	6.7	1.02	2.0
Quartz Creek (nest GZ02.07.01.33)				
~25,300	1.5	39.5	−26.8	26.3
~25,300	1.0	33.7	−24.6	34.6
~25,300	1.4	37.4	−24.8	27.1
~25,300	1.2	40.1	−25.9	33.0
~25,300	1.6	26.1	−27.3	16.2
~25,300	1.5	23.9	−27.3	16.5
~25,300	1.6	25.7	−27.3	15.9
~25,300	1.6	26.4	−27.2	16.9
~25,300	1.5	24.6	−27.5	16.1
Mean	1.4	30.8	−26.5	22.5
Standard deviation	0.2	6.8	1.2	7.8
Goldbottom Creek				
~25,300	0.9	48.8	−26.9	53.0
~25,300	0.9	47.2	−28.0	51.3
~25,300	0.9	34.4	−27.0	38.3
~25,300	1.0	45.9	−27.4	45.9
~25,300	0.7	47.3	−26.5	69.5
~25,300	1.0	48.1	−27.1	47.6
~25,300	1.1	47.7	−27.0	45.4
~25,300	1.2	46.4	−28.1	40.3
~25,300	0.8	47.0	−26.8	59.5
~25,300	1.1	43.7	−26.5	40.4
Mean	1.0	45.6	−27.1	49.1
Standard deviation	0.1	4.2	0.5	9.7

Unlike Fox Permafrost Tunnel, the sedimentary context of the graminoids from the arctic ground squirrel nests (Fig. 5) does not allow us to simply rule out the possibility that the graminoids originated from sedge-dominated bogs or marshes. The plants' remains in the nests may have been removed from a nearby habitat by arctic ground squirrels. In fact, the paleoecological reconstruction implies that the nest material likely came from a tundra/steppe upland plant community (Zazula et al., 2005, 2006). In this respect the paleoecological reconstruction is largely consistent with the δ^{13}C analyses of the graminoids from Quartz Creek nest #8, where the mean δ^{13}C value of the subfossil graminoids is within the 1 SD of the mean δ^{13}C of modern grasses and sedges from dry habitats. There is some overlap in the 1 SD of the mean of the δ^{13}C from subfossil graminoids from Quartz Creek nests 1 and 2 with the 1 SD of the δ^{13}C of grasses and sedges from wet and dry habitats. Many paleoenvironmental data point to aridity in glacial Beringia, e.g., widespread sand dunes and sand sheets, loess, and sand wedges (Hopkins et al., 1982; Mann et al., 2002), and greatly lowered lake levels (Barber and Finney, 2000; Abbott et al., 2000; Edwards et al., 2000). GCM simulations of past conditions (e.g., Kaplan et al., 2003) also tend to indicate drier conditions but underestimate the degree of aridity compared with paleoecological data. In Kaplan et al. (2003), only the "driest" of four GCM simulations closely matched the proxy reconstructions for 21,000 cal. yr BP. Hultén (1937) hypothesized mesic environments for the Bering land bridge to explain the present distribution of Beringian plants. Mesic environments may have been more common on the central Bering land bridge than in continental areas of Eastern Beringia, as suggested by plant and insect macrofossils (Elias et al., 1996, 1997), mammalian faunal data (Guthrie, 2001), synthesis of regional pollen data (Anderson and Brubaker, 1994), and macrofossil data (Goetcheus and Birks, 2001). Furthermore, topography and landscape position greatly influence the distribution of arid and mesic habitats in local settings, such as constrained valleys with pronounced changes in relief over short distances. Evidence to support local-scale moisture variability is found in the diversity of vascular and bryophyte macrofossils within subfossil ground squirrel nests, with evidence for hydric, mesic, and xeric habitats all within a short distance (Zazula et al., 2005, 2006). In general, zonal habitats in the interior of Eastern Beringia were probably more arid, due perhaps to enhanced continentality and the influence of the nearby Laurentide ice sheet. A number of proxy- and model-based paleoclimatic reconstructions for glacial Eastern Beringia stress the role of cold, aridity, and clear conditions in the interior (Hopkins et al., 1982; Barnosky et al., 1987; Kutzbach, 1987; Anderson and Brubaker, 1994; Guthrie, 2001). Arid interior climates may have led to a topographically controlled vegetation mosaic with strong steppe-like elements. Modern examples of steppe habitats in Eastern Beringia are restricted to soils with insufficient moisture to support tree growth within the forest zone and are often associated with south-facing slopes with high net insolation and high evaporation (e.g., Edwards and Armbruster,

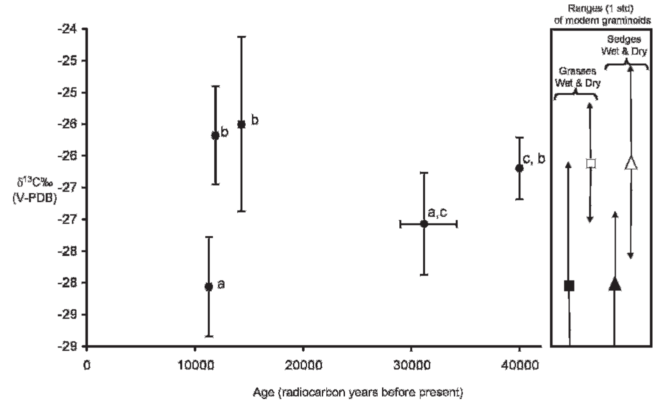

FIGURE 4. The stable carbon isotope composition of subfossil graminoid samples from the Fox Permafrost Tunnel along a timeline. Where a sample set has the same letter as another sample set, then this denotes no significant statistical difference between the data sets ($p \geq 0.05$). Where sample sets have different letters, this denotes there is a significant statistical difference ($p \leq 0.05$). The mean $\delta^{13}C$ (and 1 standard deviation [std] shown) of the modern grasses from wet habitats (filled square) and dry habitats (square), and sedges from wet habitats (filled triangle) and dry habitats (triangle) have been corrected to account for the less negative $\delta^{13}C$ of the atmosphere under which the subfossil plants grew. Given that the $\delta^{13}C$ of past atmospheric CO_2 for the date range of our subfossil samples was ~1‰ higher than that of today's atmospheric CO_2 (Friedli et al., 1986; Leuenberger et al., 1992), we added 1‰ to the $\delta^{13}C$ of the modern plants.

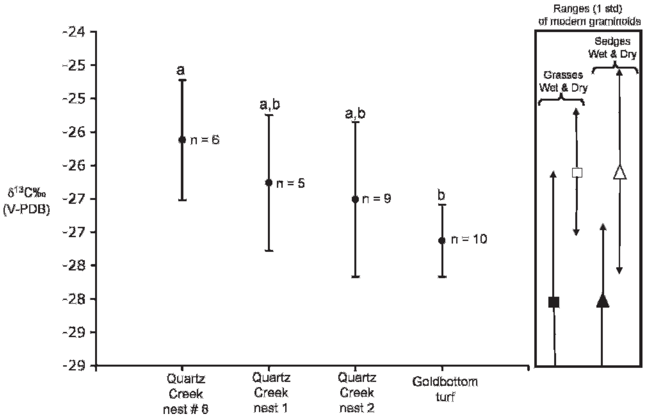

FIGURE 5. The stable carbon isotope composition of subfossil graminoid samples taken from paleoarctic ground squirrel nests from Goldbottom Creek and Quartz Creek sites in Yukon Territory. Where a sample set has the same letter as another sample set, then this denotes no significant statistical difference between the data sets ($p \geq 0.05$). Where sample sets have different letters, this denotes there is a significant statistical difference ($p \leq 0.05$). The mean $\delta^{13}C$ (and 1 standard deviation shown) of the modern grasses from wet habitats (filled square) and dry habitats (open square) and sedges from wet habitats (filled triangle) and dry habitats (open triangle) have been corrected to account for the less negative $\delta^{13}C$ of the atmosphere under which the subfossil plants grew. Given that the $\delta^{13}C$ of past atmospheric CO_2 for the date range of our subfossil samples was ~1‰ higher than that of today's atmospheric CO_2 (Friedli et al., 1986; Leuenberger et al., 1992), we added 1‰ to the $\delta^{13}C$ of the modern plants.

1989; Lloyd et al., 1994; Vetter, 2000). Guthrie (2001) suggested that the effect of clear skies, exposed ground, and resultant increased absorption of solar radiation created warmer and better-drained soils than present. Plant remains and subfossil arctic ground squirrel nests from some sites from the Yukon (Zazula et al., 2003, 2005) also provide supporting evidence for this reconstruction.

The $\delta^{13}C$ values of graminoids from the Goldbottom paleoturf yielded the lowest $\delta^{13}C$ values, which were within the 1 SD of the mean of modern grasses and sedges from wet habitats. In this respect these data imply that the plants from the paleoturf were growing in a relatively wet habitat. This is consistent with the paleoecological reconstruction based on plant remains from the Goldbottom Creek paleoturf, which implies a riparian margin meadow (Froese et al., 2006; Zazula et al., 2006). Although the $\delta^{13}C$ of plants from graminoids from the paleoturf imply a relatively wet habitat, the paleosol that these plant remains were attached to indicates that it was a fairly well-drained site and was not permanently inundated with water (Froese et al., 2006).

FUTURE DIRECTIONS: STABLE CARBON ISOTOPE MEASUREMENTS OF SUBFOSSIL GRAMINOID REMAINS AS A NOVEL PROXY WITHIN AN INTEGRATED MULTIPROXY APPROACH TO RECONSTRUCTING PAST BERINGIAN VEGETATION

Perhaps a better future classification of modern wet vs. dry grasses could be achieved if the classification of the habitat moisture status was based on quantitative (i.e., soil moisture content) rather than qualitative data (i.e., habitat descriptions on herbarium labels). This could subsequently be tested by taking specimens from a series of habitats where the percent soil moisture has been measured.

Our current analysis of modern sedges was restricted to *Carex* specimens, and it would be interesting to analyze the $\delta^{13}C$ values of other genera, e.g., *Eleocharis*, a taxon of which grows in Alaska (Hultén, 1968). Some species of this genus (e.g., *E. baldwinii*) are able to exist as either C_3 or C_4 according to habitat type (wet and dry, respectively; Uchino et al., 1995).

In the case of graminoids, the cuticle micromorphology of preserved leaves can potentially provide independent evidence to support or test a paleoecological reconstruction (Wooller et al., 2000, 2003b; Wooller, 2002; Wooller and Beuning, 2002). Figure 3 shows the well-preserved cuticular micromorphological features of a specimen dated at ca. 31,200 ^{14}C yr BP. The cuticle approach would be especially valuable where subfossil seeds and florets of graminoids are not preserved. The stable isotope data from a paleograminoid specimen could also be compared with a paleoecological reconstruction based on the ecological tolerances of macroscopically identifiable graminoid specimens recovered from the same sample.

We have presented an initial study investigating the application of $\delta^{13}C$ analyses of subfossil graminoids in Eastern Beringian paleoecological research. Previous applications of $\delta^{13}C$ analyses of subfossil plant material has largely been reserved to examine changes in the past proportions of C_3 and C_4 plants in the tropics and subtropics (e.g., Wooller et al. 2003b, 2005). Our data illustrate that $\delta^{13}C$ of subfossil plant remains could also be used to reconstruct the environments of ecosystems dominated by C_3 plants, such as the Arctic and subarctic.

Conclusions

The $\delta^{13}C$ of modern grasses species from Alaska and the Yukon Territory listed as from dry habitats on their herbarium labels is significantly higher than modern grasses from wet habitats. This difference was also seen between modern sedges listed as from dry habitats compared with those from wet habitats. However, sedges listed as specifically from bogs or marshes were found to have a similar isotopic composition compared with dry sedges. To interpret $\delta^{13}C$ from subfossil sedges it would be necessary to consider other lines of paleoenvironmental information, including the sedimentary context of a sample and plant macrofossil data.

Our analyses of subfossil graminoid remains from three separate sites (Fox Permafrost Tunnel, Quartz Creek, and Goldbottom Creek) show considerable variations in $\delta^{13}C$. Our investigation indicates that stable isotope analyses can be used to study past vegetation in Eastern Beringia during the late Quaternary. Information about plant growth conditions, particularly the occurrence of moisture stress, would aid in our understanding of arctic plant responses to climate change. Complementary ecological information can be derived from cuticle and macrofossil analyses of the same samples, and together these methods promise new insights into the paleoenvironments and paleoecology of Beringia.

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