Invited Review

Pleistocene graminoid-dominated ecosystems in the Arctic

Mikhail S. Blinnikov [a,*], Benjamin Gaglioti [b], Donald A. Walker [c], Matthew J. Wooller [d], Grant D. Zazula [e]

[a] Department of Geography, St. Cloud State University, St. Cloud, MN 56301, USA
[b] Alaska Stable Isotope Facility, Water and Environmental Research Center, University of Alaska, Fairbanks, AK 99775, USA
[c] Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775, USA
[d] Alaska Stable Isotope Facility, Water and Environmental Research Center and School of Fisheries and Ocean Sciences, University of Alaska, Fairbanks, AK 99775, USA
[e] Yukon Palaeontology Program, POB 2703, Whitehorse, YT Y1A 2C6, Canada

ARTICLE INFO

ABSTRACT

We review evidence obtained from analyses of multiple proxies (floristics, mammal remains, paleo-insects, pollen, macrofossils, plant cuticles, phytoliths, stable isotopes, and modeling) that elucidate the composition and character of the graminoid-dominated ecosystems of the Pleistocene Arctic. The past thirty years have seen a renewed interest in this now-extinct biome, sometimes referred to as "tundra-steppe" (steppe-tundra in North American sources). While many questions remain, converging evidence from many new terrestrial records and proxies coupled with better understanding of paleoclimate dynamics point to the predominance of xeric and cold adapted grassland as the key former vegetation type in the Arctic confirming earlier conjectures completed in the 1960s–1980s. A variety of still existing species of grasses and forbs played key roles in the species assemblages of the time, but their mixtures were not analogous to the tundras of today. Local mosaics based on topography, proximity to the ice sheets and coasts, soil heterogeneity, animal disturbance, and fire regimes were undoubtedly present. However, inadequate coverage of terrestrial proxies exist to resolve this spatial heterogeneity. These past ecosystems were maintained by a combination of dry and cold climate and grazing pressure/disturbance by large (e.g., mammoth and horse) and small (e.g., ground squirrels) mammals. Some recent studies from Eastern Beringia (Alaska) suggest that more progress will be possible when analyses of many proxies are combined at local scales.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

The influence of future climate change on vegetation in the Arctic is likely to be very pronounced (Post et al., 2009), and could potentially see the expansion of graminoid (i.e. grass and sedge) dominated ecosystems at high latitudes (Chapin et al., 2005). Of particular interest for Arctic terrestrial research is the past nature of graminoid-dominated vegetation, which is also thought to have been more extensive during the Pleistocene. This review aims to summarize recent advances in paleovegetation studies of grami-noid vegetation in the Arctic.

"Graminoid-dominated ecosystems" are often broadly defined, but frequently include temperate (prairie, steppe, veld, pampas) and tropical (llanos, *Spinifex* steppe) grass- or sedge-dominated ecosystems, as well as certain tundras, woodlands, and may also include shrub- or forb-rich ecosystems such as semi-deserts or floodplain meadows as long as grasses or sedges remain a major component (Coupland, 1992; Gibson, 2009). White et al. (2000) estimated that non-woody grasslands (excluding savannas) currently occupy 10.74 million km^2 worldwide with additional 7.44 million km^2 covered by tundra. Dominance of the grass family, Poaceae is expected in a 'true' grassland, but some authors also include other graminoids (e.g., members of the order Poales, which in the Northern Hemisphere are also represented by Cyperaceae and Juncaceae families, APG, 2009) and even all "low-growing non-woody plants" (Milner and Hughes, 1968) in the list of expected dominants. Risser (1988) defined a grassland as a type of vegetation with a "canopy dominated by grass and grass-like species, subject to periodic drought, and with fewer than 10–15 trees per ha." However, this definition excludes woodlands and wetlands, which may also be graminoid-dominated. While temperate and tropical grasslands presently occupy 36% of the land area worldwide (White et al., 2000), only about 20% of the present-day Arctic is covered with graminoid tundras (Fig. 1). The four graminoid tundra types in the Circumpolar Arctic Vegetation Map assessment (2003) occupy

* Corresponding author. Tel.: +1 320 308 2263. .
  E-mail addresses: msblinnikov@stcloudstate.edu (M.S. Blinnikov), bvgaglioti@alaska.edu (B. Gaglioti), ffdaw@uaf.edu (D.A. Walker), mjwooller@alaska.edu (M. J. Wooller), Grant.Zazula@gov.yk.ca (G.D. Zazula).
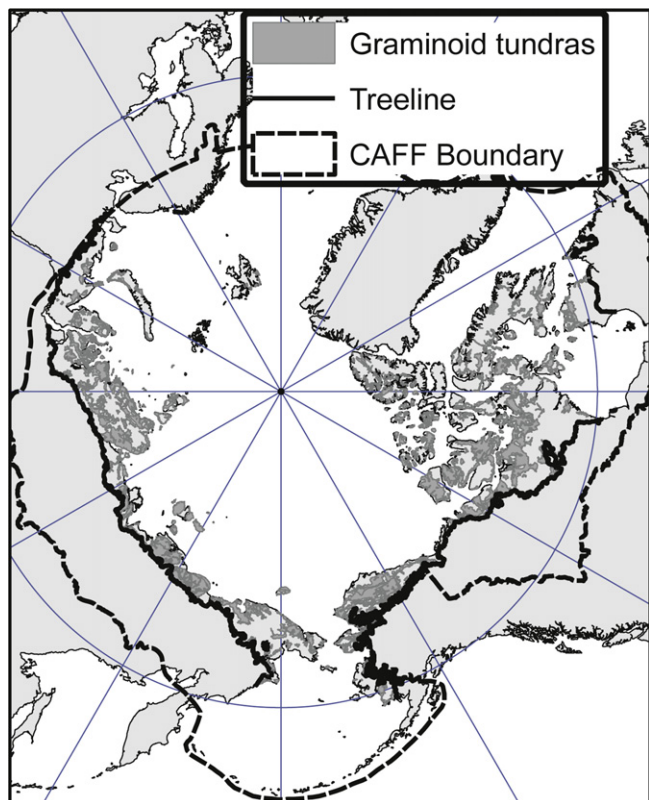
Fig. 1. Circumpolar distribution of graminoid tundras in the Arctic today (CAVM, 2003). The shaded areas north of the treeline include rush/grass-forb-cryptogam (G1), graminoid-prostrate dwarf shrub-forb (G2), non-tussock sedge-dwarf shrub-moss (G3) and tussock sedge − dwarf shrub − moss (G4) vegetation types. Although graminoid, such communities are dominated mostly by sedges, not grasses. They exclude wetlands or shrub-dominated types and cover 1,475,000 km^2 out of the total 7,182,000 km^2 north of the treeline (20.5%).

mesic sites with summer temperatures ranging from very cold (G1) to moderately warm (G4). All graminoid tundras in the Arctic today, even on the driest end of the continuum, are dominated by prostrate shrubs, mosses, and sedges, not grasses. Very few tundra communities are grass-dominated, and those are only found in azonal locations such as south-facing slopes with high insolation and low snow cover (Yurtsev, 1962; Kassler, 1979; Walker, 1990). Although these graminoid-dominated ecosystems were persistent at high latitudes during much of the Quaternary, reviews of the environmental and taxonomic details are lacking for this biome. In this review we focus specifically on the techniques, the species present, and spatial and temporal variability of taxa and environmental controls of high-latitude graminoid-dominated ecosystems during the Pleistocene.

During the Pliocene, most of the Arctic was dominated by forests and shrubby vegetation, extending all the way to the shores of the Arctic Ocean. In the early Pleistocene, the Kap København Formation from North Greenland records trees growing at the Arctic Ocean shore at 2.4 ma BP (million years ago), about 1000 km north of the modern treeline in Canada (Funder et al., 2001). During the middle Pleistocene, high-latitude graminoid-dominated ecosystems are thought to have become much more extensive, when "steppe-tundra" or "tundra-steppe" (Nehring, 1890; Tugarinov, 1929; Hibbert, 1982) is hypothesized to have covered large portions of North America and, especially, Eurasia, particularly during the coldest stages. The Pleistocene epoch started with the Gelasian stage (2588 to 1806 ka, MIS 103), ended with the onset of the Holocene MIS 1, 11.7 ka cal yrs (Martinson et al., 1987; ICS, Gibbard et al., 2007), and is an important time period because frequent high amplitude shifts in past climate led to dramatic effects on ecosystem composition, function and structure, which were especially pronounced in the circumpolar regions. The vast majority of the paleovegetation studies from the Arctic, however, focus only on the Late Pleistocene (MIS 5-2, 130 to 12 ka), given the lack of records with reliable chronology from the Middle and Early Pleistocene (Table 1). Spatially the Arctic can be defined as the zone north of the Arctic Circle at 66°33′N and selected subarctic locations in greater Beringia (an area between the Lena River in Siberia and the Mackenzie River in Canada, including the now submerged Bering and Chukchi continental shelves, Fig. 2), in Taymyr, the lower reaches of the Ob River in Central Siberia, and a few sites in northern Europe for which paleovegetation data are available (Fig. 3a,b). Lack of records from Scandinavia and most of eastern Canada is due to the presence of the large continental ice sheets there for much of the Pleistocene, except during the interglacials and some interstadials. (Brigham-Grette, 2001; Muhs et al., 2001)

Early studies into the nature of high-latitude communities of the Pleistocene were dominated by classical paleontology (Nehring, 1890; Chersky, 1891; Tugarinov, 1929), floristics (Hultén, 1937; Yurtsev, 1962), Quaternary geology and sedimentology (Péwé, 1955; Hopkins, 1967, 1972), and pollen and spore analysis (Grichuk and Zaklinskaya, 1950). These approaches greatly expanded our understanding of high-latitude paleovegetation, most significantly in Beringia, as summarized by Hopkins et al. (1982). More recently, data derived from analyses of macrofossils, plant cuticles, phytoliths, paleoinsect and paleoDNA are making important contributions to our understanding of the composition and variability of these environments over space and time (Elias, 2001; Willerslev et al., 2003; Zazula et al., 2003, 2005, 2006a; Shapiro and Cooper, 2003; Shapiro et al., 2004; Fox-Dobbs et al., 2008; Blinnikov et al., 2010). Additional insights have also stemmed from analyses of loessal stratigraphy (Muhs et al., 2003), stable isotope studies (Wooller et al., 2007) and paleoclimate modeling (Bartlein et al., 1998; Kaplan et al., 2003; Bromwich et al., 2005). Most terrestrial records of vegetation from the Pleistocene Arctic are pollen-derived and are only available for the last glacial−interglacial cycle from 130 ka to present (MIS 5e to MIS 1) with most sites considerably younger, <40 ka BP (MIS 3 or 2).

In terms of global climate, the warmest interval over the past 250 ka is thought to have occurred during the MIS 5e (130−116 ka

Table 1
Correlation of the Pleistocene regional stratigraphic schemes (Anderson and Lozhkin, 1995; Svendsen et al., 2004; Arkhipov et al., 1999; Lozhkin et al., 2007; Velichko et al., 1999).

Ages (ka)	West European	European Russia	Siberian	Alaskan	Laurentide	Marine Isotope Stages
Since 11.7	Holocene	Holocene	Holocene	Holocene	Holocene	MIS 1
c. 30−11.75	Late Weichselian	Late Valdai (Veps)	Sartan	Itkillik/McKinley	Late Wisconsinan	MIS 2 (LGM)
c. 50−30	Mid Weichs.	Middle Valdai (Dunai)	Karginsky[a]		Middle Wisconsinan	MIS 3−MIS 4
c. 115−50	Early Weichs.	EarlyValdai (Kalinin)	Ermakovo, Zyryan		Early Wisconsinan	MIS 4−MIS 5a-d
c. 130−115	Eemian	Mikulino	Kazantsevo[a]		Sangamonan	MIS 5e
c. 200−130	Saalian	Moscow	Tazovsky		Illinoian	MIS 6

[a] Astakhov and Nazarov (2010) suggest that Karginsky is ca. 130 ka and Kazantsevo − mid-Pleistocene in age, based on newest OSL dates.
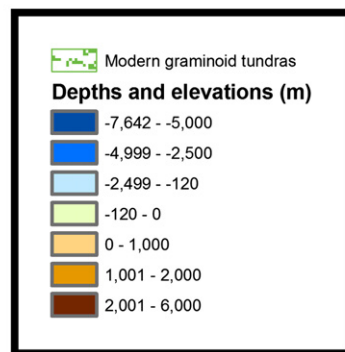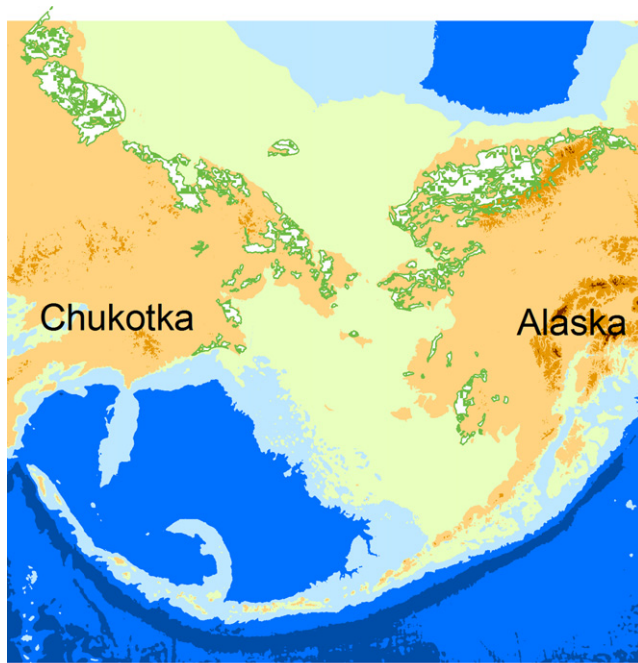
Fig. 2. Elevations above and below sea level in the Bering Land Bridge area and modern distribution of graminoid tundras in Beringia. Tundra distribution is from CAVM 2003, elevations are from ETOPO2 dataset as resampled by Manley (2002).

BP, Kukla et al., 2002; Muller et al., 2010). At that time, global ice volumes were less than today with the Earth's orbital parameters aligned to generate 11% higher insolation values (Fig. 4) as compared to present during the Northern Hemisphere's summer (Huybers, 2007). This caused temperatures over land in the Arctic to be 4–5 °C above present (CAPE, 2006) and the treeline to be 600 km north of its present position (Ritchie and Hare, 1971; Fradkina et al., 1999; Muller et al., 2010). In contrast, MIS 2 (14–29 ka BP) was apparently the coldest period in the last 125 ka, and potentially the last 350 ka since MIS 10 (Muller et al., 2010). The Last Glacial Maximum (LGM) occurred between 25 and 21 ka and was followed by a warming that lead to the onset of the Holocene ~11.7 ka ago. During the LGM, global annual temperatures were 5–6 °C lower than at present (Jansen et al., 2007; Muller et al., 2010). With the exception of parts of Beringia and eastern Siberia, much of the Arctic was under continental ice sheets and/or extensive mountain ice caps, especially in Greenland (as today), Eastern Canada, and Scandinavia, but also in the Polar Urals, Taymyr Peninsula, Chersky Range, and parts of Alaska (Hamilton, 1982, 1994; England et al., 2009). Generally, the continental interiors were much drier than today, as evidenced by the nearly synchronous activation of aeolian deposits across unglaciated terrain in much of Beringia at that time (Carter, 1981; Lea and Waythomas, 1990; Bateman and Murton, 2006). The scarcity of lake sediments dated to the LGM also indicates extreme aridity as discussed by Guthrie (2001) and Mann et al. (2002a, b).

Despite recent progress, past terrestrial environments of substantial areas in the Arctic remain poorly studied due to their remoteness and lack of suitable vegetation records. The following issues stand out as some of the most relevant and interesting:

1. What was the species composition of the graminoid-dominated arctic communities of the Pleistocene? Was the pool of species composing those communities similar to today, albeit of different proportion, or did it include many extraregional species (e.g., species that are currently found in dry steppe or even deserts much further to the south)?
2. What was the vertical and horizontal spatial structure of these communities? How much local variability was there with respect to individual community types as compared to today? What was their average productivity? To what extent were these communities climate-driven as opposed to disturbance-driven (herbivory, fire, loess and sand deposition)? How fast did these communities respond to past environmental changes? How variable was this response across the Arctic?

Due to their abundance during rapid climate changes in the past, understanding the former structure and responses of past graminoid-dominated ecosystems (GDE) is important for predicting and mitigating future responses due to ongoing climate changes (Kaplan and New, 2006). Some today are resilient and even adapted to a variety of climates and disturbance regimes, including herbivory, soil perturbations, and fire (Higuera et al., 2008). However, the environmental changes occurring in the Arctic are likely to alter many existing high-latitude ecosystems, but the degree of vegetation response is poorly understood (Callaghan et al., 1998; Kittel et al., 2000; van Wijk et al., 2003). Overall, it is thought that tree- and other woody-dominated vegetation types will have an advantage over the grass- or moss-dominated ones, under most climate scenarios for the 21st century (Nelson et al., 2008). Alternatively, in some regions, steppe-tundra analogues may undergo expansions in response to future climate scenarios that have modeled multi-year droughts and frequent tundra fires (Chapin and Starfield, 1997; Rupp et al., 2000). Unlike global change forecasts for contemporary biomes, there is no widespread modern analogue of steppe-tundra to model vegetation responses of climate variation in the future. Studying the behavior of past grass-dominated communities during the Pleistocene, especially during the abrupt glacial terminations (e.g., end of MIS 12, 10, 6 and 2), may inform our management choices in dealing with the unprecedented warming in the Arctic during this century (Callaghan et al., 1998; Chapin et al., 2005; Walker et al., 2006). Below we review the information and perspectives that can be gained from analyses of various proxies of past GDE in the Arctic, which is best achieved using multiple lines of evidence (Wooller and Beuning, 2002).

2. Animal paleontology perspectives on the arctic grasslands

2.1. Vertebrate paleontology

Classical vertebrate paleontological studies were among the first to inform us about the nature of the past graminoid-dominated communities of the Pleistocene at high latitudes. Numerous sites across the unglaciated Holarctic contain abundant bones, teeth, or partially preserved carcasses in paleosols and permafrost (Sher, 1971; Harington, 1978; Guthrie, 1990; Ukraintseva, 1990), 1993).

The idea that much of northern Europe had a steppe-like climate and a landscape populated by a diverse fauna dominated by large grazers wasdiscussed in the late 19th century by). The idea that much of northern Europe had a steppe-like climate and a landscape populated by a diverse fauna dominated by large grazers wasdiscussed in the late 19th century by Nehring (1890) and Chersky (1891). Typical grazers of these communities included the musk-ox (*Ovibos moschatus*), mammoth (*Mammuthus primigenius* Blum.), woolly rhinoceros (*Coelodonta antiquitarius* Blum.), horse (*Equus* spp.), Steppe bison (*Bison priscus* Boj.) and saiga antelope (*Saiga tatarica* L.). Tugarinov (1929) noted the imbalanced character of the faunal assemblages from the Pleistocene of Eurasia that contained mixtures of steppe and tundra species with no modern analogs. The fact that grazers, not browsers, were dominant, suggested a different vegetation from that which is typical of the taiga or tundra at present. Guthrie (1982, 1990) proposed the term "mammoth-steppe" to represent the no-analog nature of this grazer-dominated ecosystem, which stretched from Europe to northwest Canada during Pleistocene cold stages. It is important to note that although the faunas from Eurasia and North America included many of the same species, a few were present only on one side of the Bering Land Bridge. For example, western camels (*Camelops hesternus*), badgers (*Taxidae taxus*), and short faced bears (*Arctodus simus*) were present only in Alaska, yet not in Siberia,
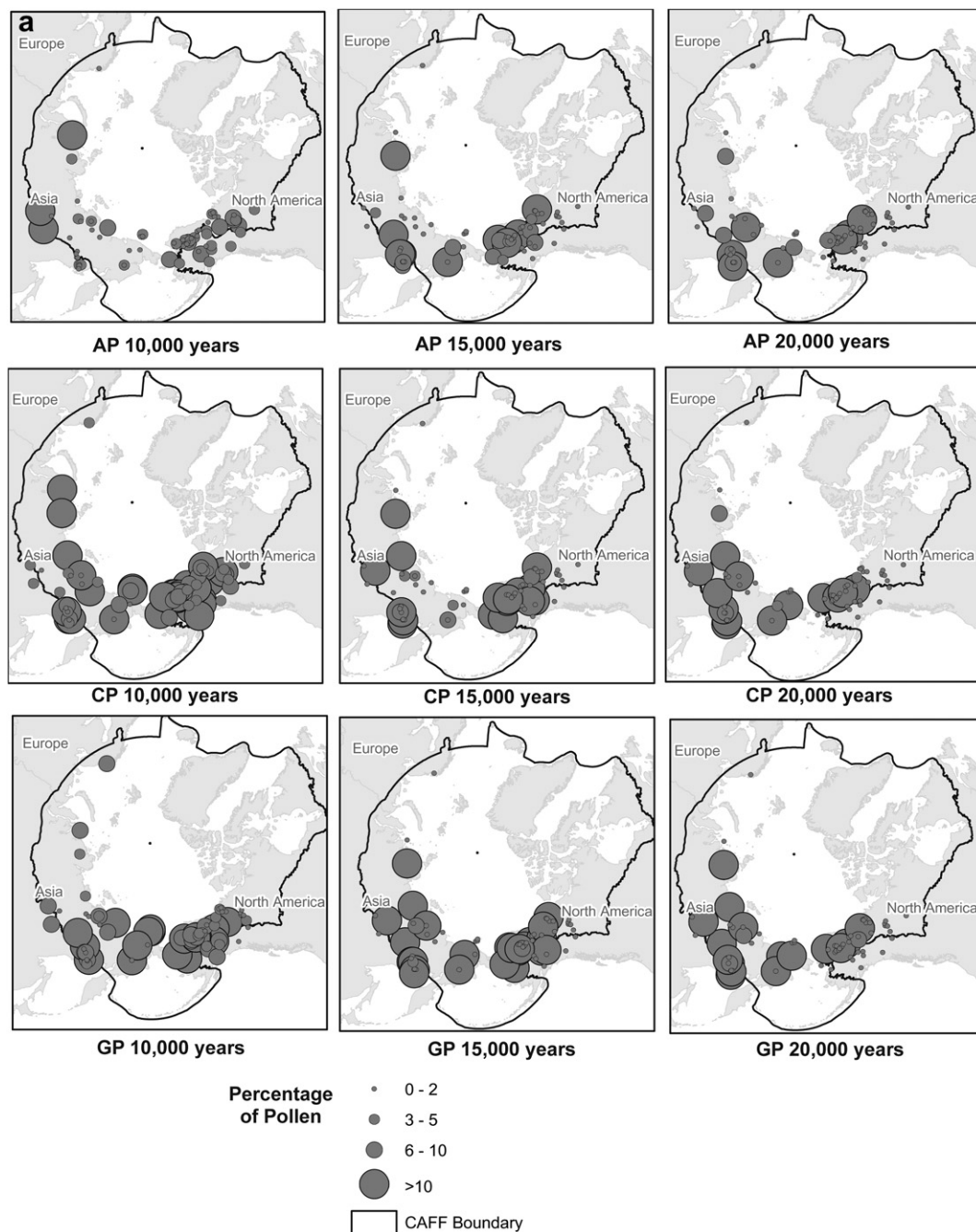

Fig. 3. Distribution of Poaceae, Cyperaceae, and *Artemisia* pollen percentages from selected sites in the Arctic and subarctic N of 60°N at 10, 15 and 20 ka BP. Data are from Global Pollen Database and Andreev et al. (2008), Lozhkin et al. (2007).
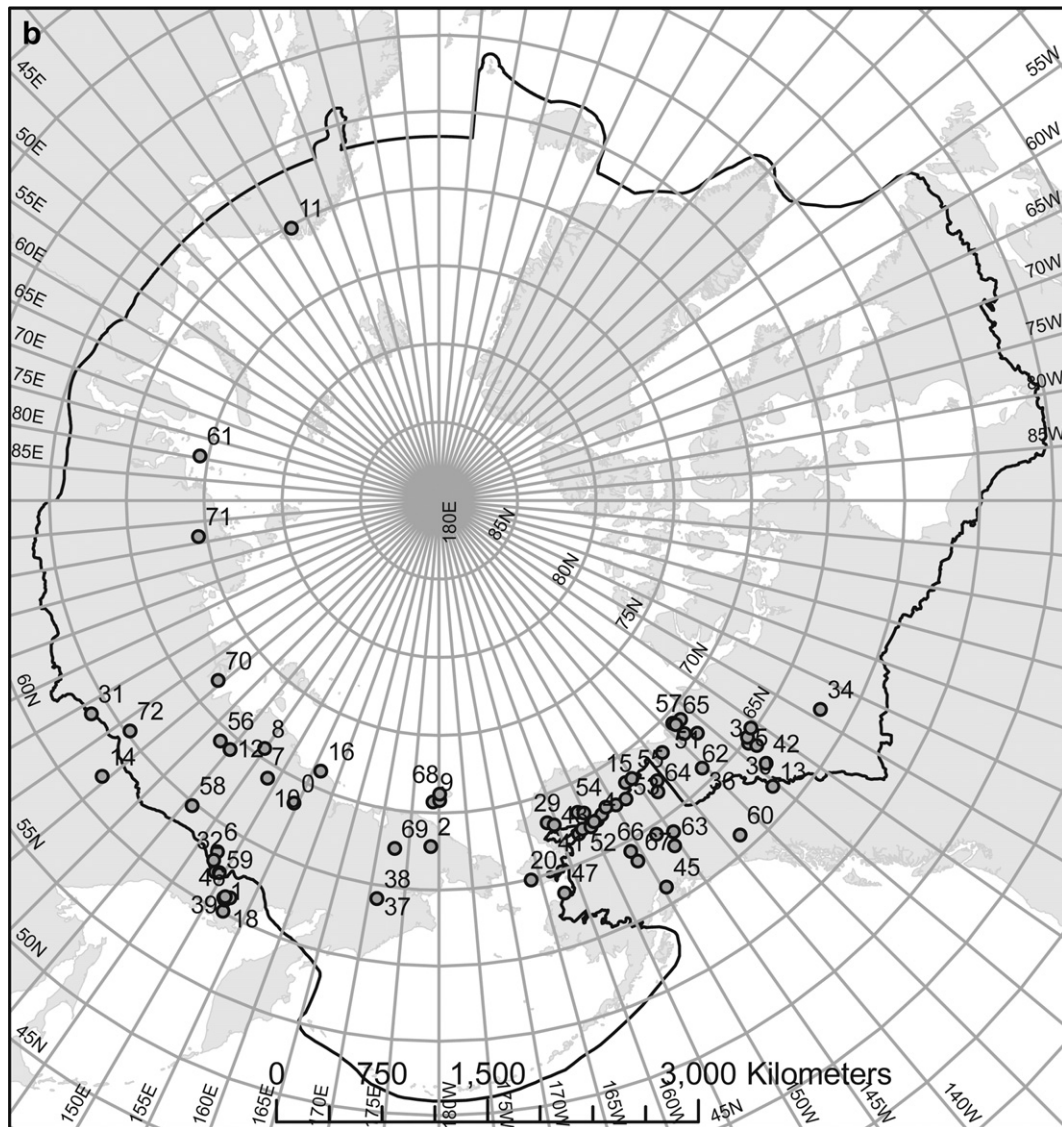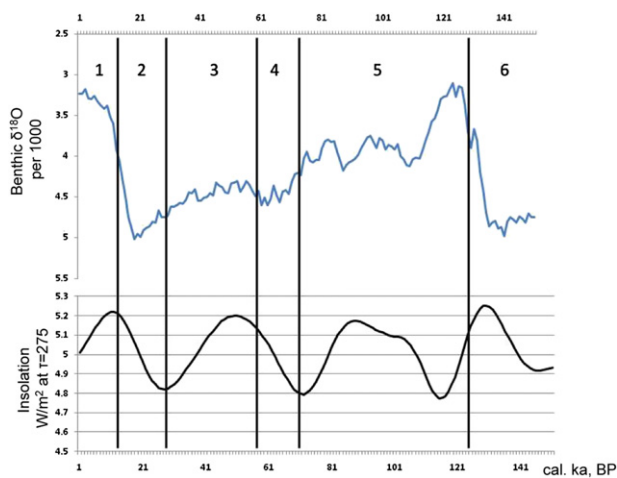
Fig. 3. (*continued*).

Fig. 4. Last glacial−interglacial cycle based on an average of 57 globally distributed benthic d^{18}O records (departures per 1000) which measure global ice volume and deep ocean temperature (Lisiecki and Raymo, 2005) - top curve and insolation values for 65°N (W/m^2 at τ = 275 threshold) (Huybers, 2006) - bottom curve. Horizontal values are ka BP.

while woolly rhinoceros did not occur in North America. These differences in faunal communities between continents led Guthrie (2001) to suggest that a reduction in adequate steppe-tundra habitats in the central Bering Land Bridge served as a biogeographic filter and prevented the transcontinental migration of some species.

It is clear from mammoth-, horse- and bison-dominated fossil assemblages of the Pleistocene that the unglaciated holarctic regions were inhabited by grazing specialists that evolved in close association with the steppe-tundra environment (Stuart et al., 2002; Westgate, 2003). Evidence for Pleistocene mammals being grazers is provided by their high-crowned, hypsodont teeth with complex crown patterns, which evolved in association with dependence on silica-rich diet of grasses. These extreme forms of dentition are best exemplified by the Beringian woolly mammoths (Maglio, 1973; Boeskorov, 2005; Harington, 2005) and horses, which have the most complex teeth of any living or extinct proboscideans or equids, respectively (Guthrie, 1990). Direct evidence for graminiod specialization of this fauna has been recovered through the multi-proxy analysis of permafrost, preserved stomach contents (Ukraintseva, 1993; van Geel et al.,

2008) and of fossil dung (van Geel et al., in press). The replacement of this diverse grazing fauna with a relatively species-poor large mammal fauna dominated by browsers or mixed feeders such as moose (*Alces alces*), elk (*Cervus elaphus*) and caribou (*Rangifer tarandus*) at the end of the Pleistocene is marked by the establishment of present-day woodland and tundra habitats.

Based on paleontological evidence, about 40 species of animals over 40 kg (a megafauna threshold *sensu* Burney and Flannery, 2005), populated Pleistocene high latitude grasslands, which suggests vegetation of high productivity (Guthrie, 1968, 1982; Martin et al., 1982). However, most contemporary tundra types, even with abundant grass or graminoid cover (e.g., G1-G4 in CAVM, 2003) are unpromising analogues for vegetation inhabited by these now-extinct large grazing mammals. Net primary productivity can be an index for large mammal carrying capacity of an ecosystem For example, above-ground net primary productivity (ANPP) of vascular plants in modern-day low-shrub tundra in North America ranges from 125 to 175 g/m^2 and cottongrass-herb tundra from 150 to 200 g/m^2 (Bliss, 2000, p. 25, p. 25). In contrast, in modern-day temperate and tropical grasslands ANPP ranges from 500 to 5000 g/m^2 with the mean of 1021 g/m^2 (Gibson, 2009, p. 134). Thus Guthrie (1968, 1982, 1990, 2001) and Yurtsev (1982, 2001) argued for the extensive Pleistocene "tundra-steppes" with productive vegetation more akin to modern temperate steppes, rather than contemporary graminoid tundras. Steppe-tundra (tundra-steppe in the Russian literature) also reflects geomorphic evidence that the continental interior environment was both dry *and* cold (Yurtsev, 1982; Barber and Finney, 2000), and implies an ecological mixing of typical steppe and tundra taxa in association without modern analogue (Brubaker et al., 1989). Guthrie (1990) also argued that the foot morphology and loading capabilities of the dominant Pleistocene large mammals suggested the steppe-tundra substrates were much firmer, and thus, drier than contemporary arctic tundras (Zimov, 2005).

2.2. Invertebrate paleontology

The remains of beetles (Coleoptera), specifically from the families Curculionidae (weevils) and Carabidae (ground beetles) are common within late Cenozoic sediments and provide important paleoecological information for the origins and history of high latitude graminoid ecosystems (Matthews and Telka, 1997; Elias, 2000, 2007; Elias et al., 2000, 2006, 2007; Zazula et al., 2006a, 2007; Kuzmina et al., 2008, 2010). Beetles, including members of the *Cryobius* group of the ground beetle genus *Pterostichus* from the Early Pliocene Begunov Formation at the Krestovka site in the Kolyma Basin record the earliest appearance of open patches of steppe or steppe-tundra habitats within coniferous woodlands in northeast Siberia (Sher et al., 1977; Kiselyov, 1981). The widespread establishment of steppe-tundra is recorded in the Late Pliocene-Early Pleistocene Olyor Formation at several sites across Siberia with an abundance of *Pterostichus* (*Cryobius*) species, as well as the ground beetle *Amara alpina*, leaf beetles in the genus *Crosita*, the weevil *Coniocleonus ferrugineus* and the pill beetle *Morychus viridis* (Kiselyov, 1981; Elias et al., 2006). In Siberia, there is a significant increase in the abundance of steppe beetles in the Middle and Late Pleistocene faunas in comparison to the more tundra-rich Olyorian Formation beetle faunas, indicating an increasing importance of steppe-tundra throughout the Quaternary (Elias et al., 2006). In Alaska, the earliest appearance of a tundra ecosystem in Eastern Beringia is recorded in the early Pleistocene (1.8 Ma) beetle fauna at Cape Deceit, which includes the grassland ground beetle *Trachypachus holmbergi*, the weevils *Lepidophorus lineaticollis*, *Vitavitus thulius*, and *Ceuthorhynchus subpubescens* (Matthews, 1974; Matthews and Telka, 1997; Elias et al., 2006). Importantly,

L. lineaticollis, one the most important species of Pleistocene beetles in Eastern Beringia, was present in northeastern Siberia during the Miocene, but has not been recovered there in any younger faunas (Elias et al., 2006). Although some differences in Pleistocene beetle assemblages have been identified between Eastern and Western Beringia, Late Pleistocene cold stage faunas from both regions are clearly dominated by taxa indicative of cold, dry, and largely open steppe-tundra habitats. This view is reinforced by detailed entomological studies of present day azonal and zonal steppe communities, which suggest close analogs with the Pleistocene steppe-tundra. Matthews (1982) suggested that Pleistocene faunas dominated by species of *Amara*, *Morychus* (likely an extinct species distinct from those in Siberia) and *L. lineaticollis* provide evidence for widespread steppe-tundra habitats across Eastern Beringia. Additional research in the region (Matthews and Telka, 1997; Kuzmina et al., 2008; Zazula et al., 2006a, b, 2007, 2010) highlights the presence of the weevil *Connaticela artemisiae* in Pleistocene faunas, which at present is restricted to azonal steppe communities in the Yukon Territory where it feeds on plants of prairie sage (*Artemisia frigida*). Although evidence from beetles for steppe-tundra habitats is well documented for much of the interior and northern areas of Eastern Beringia, assemblages from a number of sites in Western Alaska and the central Bering Land Bridge lack steppe-tundra indicator beetles and support the model of increased mesic tundra conditions that interrupted the Holarctic steppe-tundra (Elias et al., 1997, 2000; Elias and Crocker, 2008; Guthrie, 2001). Similar to the central Beringia filtering large mammal species, this proposed "mesic buckle" (Guthrie, 2001; Elias and Crocker, 2008) seems to have served as a biogeographic barrier that also prevented the transcontinental exchange of many steppe beetles between Western and Eastern Beringia during the Pleistocene (Elias et al., 2000). As such, although Pleistocene faunas in Western Beringia are also dominated by steppe-tundra beetles, the composition of these faunas are taxonomically distinct from those in North America and there are few truly amphiberingian steppe species. Western Beringian Pleistocene beetle faunas lack the North American steppe-tundra endemics *L. lineaticollis* and *C. artemisiae*, however are often dominated by *M. viridis* and species of *Stephanoceonus*. The biogeographic relationship between present azonal steppe and Pleistocene steppe-tundra beetle faunas is much better documented for Eurasia, than it is for northwest North America.

Based on the distribution and Mutual Climate Range (MCR) temperature estimates from Late Pleistocene beetles of Western Beringia, Berman et al. (2010) suggested that steppe-tundra ecosystems did not extend eastward completely across the Bering Land Bridge, rather, it fell short by approximately 100 km, terminating near the Anandyr River Basin at about 180° East longitude. This interruption in the Holarctic steppe-tundra by a more mesic tundra barrier may not have been geographically contiguous. Species of *Morychus* along with the cryoxerophilus sedge *Kobresia myosuroides* during the LGM indicate that steppe-tundra extended to the Seward Peninsula of western Alaska (Kuzmina et al., 2008). Together, beetle faunas from across Beringia indicate that steppe or steppe-tundra habitats were much more extensive during the late Pleistocene than they are at present at both local and regional scale.

3. Floristic perspectives

Due to their well-described habitat preferences, and ubiquity in the fossil record, plant identification, indicating both modern (floristic approach) and past (based on pollen, phytoliths, and macrofossils) biogeography is particularly telling approach for past GDEs and their former climates in the Arctic. The present-day arctic flora comprises approximately 1500 species of vascular plants (Abbott and Brochmann, 2003). The checklist of the Panarctic flora

(PAF, Elven, 2007) attempts to reconcile the long-standing discrepancy between Russian and North American floras and presents an emerging consensus between the extensive splitting of taxa by many Russian botanists and the equally extensive lumping of many North American botanists. PAF's definition of the Arctic is "non-forested areas where growth and reproduction is restricted by a short vegetation period (mostly less than 60–90 days) with low temperatures (nearly always <10 °C for the warmest months) and/or low heat sum, and a long winter with stable or nearly stable frost and snow." Their definition is fairly narrow and geographically similar to that of the Conservation of Arctic Flora and Fauna (CAFF) project (Fig. 1). Although CAFF boundary is decided by a political consensus and does not have immediate ecological parameters behind it, we chose to use it here as a convenient commonly accepted boundary used by many interdisciplinary researchers of the modern Arctic.

The current version of PAF (Elven, 2007) lists approximately 300 Poaceae species in 47 genera for the Arctic thus defined. It also lists 100 species of Cyperaceae in nine genera of which *Carex* is the most represented (67) with potentially many contributors to the xeric vegetation of the Pleistocene from among upland sedge species (along with *Kobresia*). Of course, there is a possibility that some components of the Pleistocene GDEs in the Arctic are no longer present in the region today. Nevertheless, most botanists of the Arctic, starting with Hultén (1937), seemed to have embraced the view that the majority of taxa contributing to the Pleistocene communities are still present in the Arctic today albeit in more restricted habitats.

The origins of Poaceae, a major contributor to the flora at high latitudes in the Pleistocene, and the corresponding rise of grass-dominated ecosystems at low-latitudes are relatively well known (GPWG, 2001; Wooller and Beuning, 2002; Strömberg, 2005; Edwards et al., 2010). Grasses originally evolved in the tropics, but have a cosmopolitan distribution today (Watson and Dallwitz, 1994). The origin and relatively early differentiation of grasses into subfamilies in the mid- to late Cenozoic is now well established (Kellogg and Watson, 1993; Prasad et al., 2005); however, it is important to note that the evolution of the C_4 photosynthetic pathway in graminoids happened much more recently (late Miocene to Pliocene, Kellogg and Watson, 1993; Strömberg, 2005; Edwards et al., 2010). C_4 graminoids are virtually absent from the Arctic flora today, although their possible former presence remains poorly studied (see section on phytoliths and stable isotopes).

Other important taxa that may have contributed to the former graminoid communities in the Arctic are xeric steppe lichens (e.g., *Cornicularia steppae*, *Diploschistes steppicus*, *Acarospora schleicheri*, *Parmelia vagans*), rushes (*Luzula*), dwarf-shrubs (*Dryas*, *Empetrum*), and forbs from Polygonaceae, Chenopodiaceae, Caryophyllaceae, Ranunculaceae, Papaveraceae, Brassicaceae, Saxifragaceae, Rosaceae, Fabaceae, Apiaceae, Ericaceae, Primulaceae, Gentianaceae, and Asteraceae families, all well represented in the modern arctic flora and well represented in the alpine zone of the mountains of Eurasia and North America today.

Relatively little is known about the exact origins of the arctic plants, but paleobotanical and now increasingly molecular, research points to the importance of high mountain ranges in plant diversification during the Tertiary (alpine origin). Other arctic species may be descendants of the herbaceous and shrub under-story of the previously extensive arctic forests of the same period (Abbott and Brochmann, 2003) or they may represent autochthonous species of the recent arctic origin. During most of the Tertiary (65-2 Ma), forests grew at high latitudes in the Arctic, including much of Greenland, the Canadian High Arctic, and arctic islands off the northern coast of Siberia (Arkhipov et al., 1999; Fradkina et al., 1999; McIver and Basinger, 1999). Based on both pollen and macrofossil studies, tundra does not appear prominently in the Northern Hemisphere until the mid-to late Pliocene (3.6 Ma) (Matthews and Ovenden, 1990). For example, Arkhipov et al. (1999) reconstructed a progressively cooling climate with subtropical vegetation in Western Siberia (Ob river basin) in the Paleocene and Eocene, drier and cooler deciduous forests (*Carpinus*, *Ulmus*, *Quercus*, *Tiliain*, *Morus*) in the Miocene, and even drier forest-steppe and desert in mid-Pliocene. True steppes do not appear in the region until mid-upper Pliocene, or about 4.3 Ma. In Yakutia, Fradkina et al. (1999) likewise described widespread early Pliocene forests consisting of *Betula*, with some *Pinus*, *Picea*, *Tsuga* and *Larix* and only a minor presence of graminoids. These forests extended all the way to the present-day Arctic Ocean shoreline.

Hultén's (1937) classic paper on the history of arctic and boreal biota during the Quaternary demonstrated similarities of Eurasia and North America floras based on what he termed "progressive areas of present plant species." He challenged the views' of Darwin, Hooker and Agassiz that arctic animals and plants were forced to migrate south of the advancing ice sheets in the Pleistocene and was a proponent of local refugia. He based his paper on an extensive study of floristic literature on the distribution of about 2000 species, augmented by his own extensive field work in Kamchatka, Alaska and northern Europe. He proposed that ice-free refugia sheltered by local topoedaphic and microclimatic conditions in Beringia played a significant role in preserving local diversity of the flora during the coldest phases. In Eurasia, he separated the flora into eight groups based on their biogeographic distribution and hypothesized that for some of these groups ice-free refugia in easternmost Siberia (Beringia) and elsewhere in Asia were the most likely source of origin and differentiation, based on the nested character of their ranges. He also recognized the connections between steppe fauna and flora across the Holarctic during continental glaciations. His model of past vegetation changes in the Arctic points to Beringia, the region he named, as a pivotal region responsible for great biotic exchange during glacial advances. Hultén emphasized that while the floral diversity of modern Beringia is poor, with only about 2000 species, most of these can be easily traced to a common origin in unglaciated portions of northeastern Eurasia and westernmost North America (Hulten, 1968). His views are still supported by more recent research on phytogeography (Nimis et al., 1998) and molecular evolution (Abbott et al., 2000; Stentström et al., 2001) of the arctic flora. Additionally, the North Atlantic has emerged as a likely conduit for species between the Old and New Worlds based on the genetic similarities between Northeastern North America and Scandinavia (Abbott and Brochmann, 2003; Eidesen et al., 2007). Molecular studies indicate a much more complex pattern of multiple refugia in addition to Beringia (e .g., in parts of Northern Europe, Taymyr Peninsula, or on the margins of Greenland) than that envisioned by Hultèn.

Floristic work of Yurtsev (1962, 1972, 2001) stretching over 40 years built on Hultén's work and demonstrated many more floristic affinities between Asia and North America across the Bering Land Bridge (Table 2). Yurtsev was an early champion of the Pleistocene tundra-steppe hypothesis and pointed out dozens of modern analog sites scattered over western Beringia in Chukotka, Magadan, eastern Yakutia, and Wrangel Island that in his view represented true relics of the once extensive cryoxeric steppes of the Pleistocene. He listed 142 species of xerophytes, mesoxerophytes and petroxerophytes (some classified as "microthermous," i.e. cold-adapted category and some as "hemicryophilous," i.e., cool-adapted) in the Yakutia flora that he believed were likely candidates of the more extensive Pleistocene tundra-steppes (Yurtsev, 1982). Of these species, about a quarter are also found across the Bering Strait in North America, and another quarter have taxonomically close, vicariant species in North America. Among

Table 2
Presence of Poaceae species in the modern Beringia that were probable constituents of the upland graminoid-dominated ecosystems of the Arctic during the Pleistocene based on ecological and floristic analyses of Swenson for Eastern Beringia (2006) and Yurtsev for Western Beringia (2001).

Species	Western Beringia	Eastern Beringia
Alopecurus alpinus Sm.	X	X
Arctagrostis latifolia (R. Br.) Griseb.	X	X
Bromus pumpellianus Scribn.	X	X
Calamagrostis canadensis (Michx.) P. Beauv.		X
C. stricta (Timm) Koeler	X	X
C. lapponica (Wahlenb.) Hartman	X	X
C. purpurascens R. Br.	X	X
Deschampsia cespitosa (L.) Beauv.	X	X
Elymus alaskanus (Scribn. & Merr.) A. Löve		X
E. macrourus (Turcz.) Tzvelev	X	X
E. trachycaulis (Link) Gould ex Shinners		X
Elymus yukonensis (Scribn. & Merr.) A. Löve		X
Elymus villosus Muhl ex Willd.	X	
Festuca altaica Trin.	X	X
F. auriculata	X	
F. brachyphylla J.A. Schultes	X	X
F. lenensis Drobow	X	X
F. rubra L.	X	X
F. kolymensis	X	
Helictotrichon krylovii	X	
Hierochloë alpine (Sw.) Roemer and J.A. Schultes	X	X
H. hirta (Schrank) Borbas		X
Hordeum jubatum L.	X	X
Koeleria asiatica Domin.	X	X
Poa artica R. Br.	X	X
P. glauca Vahl (other *Stenopoa*)	X	X
P. pratensis L.	X	X
P. paucispicula Scribn. & Merr.	X	X
Pseudoroegneria spicata (Pursch) A. Löve		X
Puccinelia hauptiana (Krecz.) Kitagawa	X	X
Trisetum spicatum (L.) Richter	X	X

graminoids, he listed bunchgrasses *Festuca lenensis*, *Poa botryoides*, *Helictotrichon krylovii*, and *Agropyron jacutorii*, as well as the *Carex duriuscula* s.l. (narrow-leaved upland sedge) as the most important. For Chukotka, he listed 85 species of which 21% are endemic to western Beringia and 51% are shared with North America, with an additional 18% represented in North America by vicariants. In addition to the same species as in Yakutia, he listed *Calamagrostis purpurascens*, *Carex pediformis, C. obtusata, C. supina* and some forbs (e.g., *Potentilla arenosa, Anemone patens*) as probably important components of the former Pleistocene tundra-steppe. Modern analogs for such communities are described as belonging to the classes Cleistogenetea squarrosae and Carici-Kobresieta in accordance with floristic classification (Kucherov and Daniels, 2005).

More recently, Swanson (2006) compiled a list of the 25 most likely tundra-steppe candidates among lowland grass species from 11 genera based on their geographic distribution (both sides of the Bering Land Bridge), growth form (mostly bunchgrasses with large biomass) and preferred habitat (mesic to dry, fine-grained lowland soils). Many of the species are identical to Yurtsev's steppe-tundra flora (e.g., *C. purpurascens, F. lenensis*) proposed for western Beringia (Table 2) and are supported by the presence of macrofossils (see section below). All of the species are C_3 grasses from the subfamily Pooideae (Triticodae and Poodae supertribes *sensu* Watson and Dallwitz (1994)). According to both Yurtsev and Swanson, Beringian grasslands could have been composed entirely of the local taxa that are still present in the region today. This is important because, if true, it provides evidence for the resilience of the local flora. Also, it is a testable hypothesis that can be refuted should representatives of more southern affinities be found in Pleistocene paleosamples (e.g., members of Panicoideae,

Chloridoideae, or Arundinoideae subfamilies). This is of course also testable using phytoliths or stable carbon isotope analyses of plant remains (see below).

Ukraintseva (1993) and Kozhevnikov and Ukraintseva (1999) presented a dissenting view from Yurtsev. First, they argued that floristic studies of the Eurasian steppes and tundras indicate a few disparate sources of origin of key flora elements, some affiliated with steppes and semi-deserts, but others affiliated with modern tundras, alpine areas, and even forests. Second, they argued against widespread zonal tundra-steppe of the Pleistocene and interpreted the presence of some steppe-affiliated species in the Arctic today as more recent, accidental arrivals. They also critiqued pollen interpretations (e.g, *Artemisia* pollen may come from shrubby *A. frigida* and other sagebrushes which are steppe indicators, but also from tundra-affiliated forbs *A. arctica, A. glomerata* or *A. borealis*) and downplayed the importance of Beringia-wide species by pointing out that the majority of the flora on either side of the Bering Strait today are in fact affiliated with Asia and North America respectively and rarely cross over, especially when non-graminoids are taken into account. They observed that many forbs common to both eastern and western Beringia are cushion plants (*Draba stenopetala, Stellaria dicronoides*), which would suggest their affinity with polar deserts rather than steppes. Finally, they argued that proposed "tundra-steppe" grasses have ecological niches too broad to be of much interpretive value (e.g. *Festuca rubra* that is found in a great variety of habitats today from steppe to forest to meadows and even tundra). Krestov et al. (2009) pointed out that while many components of the Pleistocene tundra-steppe were recruited from the floras of continental Eurasian steppes, even more were probably forest or alpine species from the communities of the Pacific Eurasia, including the Russian Far East and Japan, as well as from coastal western North America. Clearly, a floristic approach alone cannot adequately detect the past vegetation of the Arctic and paleobotanical approaches, such as pollen, macrofossils, and phytoliths are needed.

4. Pollen perspectives

Analysis of pollen and spores in lakes, bogs, and similar contexts provided the earliest, and most extensive, evidence for the composition of the Pleistocene vegetation at high latitudes (Grichuk and Zaklinskaya, 1950; Colinvaux, 1964; Ravski, 1972; Ritchie, 1977, 1982; Cwynar and Ritchie, 1980; Ritchie and Cwynar, 1982; Hu et al., 1993; Anderson and Brubaker, 1994; Anderson et al., 1994; Edwards et al., 2000; Bigelow and Edwards, 2001; Andreev et al., 2003; Müller et al., 2010). Original interpretations of the Pleistocene pollen assemblages from Eastern Beringia reconstructed the Arctic as a polar desert similar to the high arctic islands today (Cwynar and Ritchie, 1980; Cwynar, 1982). However, reinterpretations of pollen records have since acknowledged the presence of both steppe and tundra pollen types (i.e. Chenopods and *Juniperus* for steppe and Cyperaceae for tundra) during the full glacial period (MIS 2), and open spruce (*Picea* sp.) woodlands with tundra and steppe mosaics during portions of MIS 3 (Matthews, 1974; Young, 1982; Elias et al., 1997; Ager, 2003). The main limitation of pollen analysis is the low taxonomic resolution for graminoid taxa. Pollen can reliably identify most of the common boreal tree taxa to the genus level (e.g., *Picea, Alnus, Betula, Quercus* and *Ulmus*) and some to subgenus level (*Pinus*), but graminoid vegetation can only be resolved into Cyperaceae (sedges) and Poaceae (grasses) families. Steppe tundra pollen interpretations have been supplemented from indicator taxa such as *Artemisia* (sagebrush shrubs and forb forms), *Ephedra*, other Asteraceae pollen, Chenopodiaceae, Rosaceae and a few other taxa (Faegri and Iversen, 1989). However, pollen analysis lacks the taxonomic resolution to identify

graminoids into subfamilies, tribes, or genera, making the detailed nature and variability of the steppe tundra an unresolved issue in palynology.

A few dozen long pollen records exist for Eastern Beringia (Edwards et al., 2000). An increasing number of well-dated sequences is also available from Siberia (Andreev et al., 2003; Lozhkin et al., 2007; Anderson et al., 2010). Continent-wide pollen-based biome reconstructions allow quick synthesis of pollen information (Whitmore et al., 2005; Tarasov et al., 1998, 2000), however, a major limitation of pollen analysis remains its lack of sensitivity to more subtle, local variation in plant cover and/ or productivity. Even small lakes of a few ha in size catch airborne pollen from hundreds of km away (Wright, 1967; Minckley et al., 2008). Although pollen can sometimes be also extracted from bogs, cave deposits, or peat cushions on the forest floor, most of the published well-dated sequences come from lakes (Andreev et al., 2003; Viau et al., 2008; Anderson et al., 2010). Interpreting pollen percentages in a sample in the form of vegetation types requires an extensive understanding of the local vegetation's composition, pollen production and dispersal as well as the lake's source area for pollen (Birks and Birks, 1980). For example, Holocene pollen records from the arctic tundra have indicated that within a given region local vegetation can have varying responses to past climate change depending on soil types (Oswald et al., 2003a). However, this conclusion required a judicious survey of modern pollen representation in the region, and the statistical separation of rare pollen types (Oswald et al., 2003c). Such studies have not been conducted for the steppe-tundra vegetation (Oswald et al., 2003b).

With GDEs, no satisfactory threshold of pollen percentages can distinguish between grasslands from grassy tundra, nor wet sedge meadows from sedge-dominated dry upland communities. For example, the *Paleoatlas of Beringia* (www.ncdc.noaa.gov/paleo/parcs/atlas/beringia) uses <5% of *Picea*, 20–40% *Betula* + *Alnus* and >20% Cyperaceae + Poaceae pollen values as the rule to infer grass-shrub tundra, while <20% *Betula* + *Alnus*, >20% Cyperaceae + Poaceae and <10% "other herbs" to infer grass tundra. In the temperate regions, however, the former could be matched to birch woodland and the latter to a mesic prairie. Oswald et al. (2003b) found Poaceae values particularly high on the Arctic Coastal plain in Alaska (>25%) in the prostrate shrub tundras. In some of the same communities, Cyperaceae values reach over 45% reflecting the importance of *Carex bigelowii* and *Eriophorum vaginatum* in these communities. Given the presence of shrubs and a continuous peatland as well as very low values for pollen of *Artemisia* in these same sites, they are clearly not analogous to the postulated Pleistocene tundra-steppes (Fig. 3a,b & Tables 3, 4).

As an alternative approach to rule-based matching, direct matching of paleosamples to modern datasets by pollen dissimilarity techniques can be used, but this frequently results in poor matches due to lack of true modern analogs (Overpeck et al., 1992; Williams et al., 2001). Poaceae are a cosmopolitan pollen type and are present in virtually all pollen samples. In western North America, for example, average values of grass pollen were 11% in grassland, 7% in pinyon/juniper woodland and in desert, 6% in sagebrush steppe and 2% in alpine tundra, based on 1884 modern pollen samples (Minckley et al., 2008). True grasslands can be more reliably differentiated from savannas, tundras, and deserts when *Pinus* and *Betula* pollen from surrounding vegetation types are taken into account (Minckley, pers. comm.). Thus, the very nature of pollen analysis precludes its application to answer more localized questions concerning graminoid-dominated environments.

An additional pervasive limitation of pollen analysis is the lack of suitable lake records spanning more than the last 12–15 ka over much of the Arctic, especially where glaciations was recent and/or extensive. For example in the open-access Global Pollen Database (GPD http://www.ncdc.noaa.gov/paleo/gpd.html), only 98 records are available for areas north of 60°N and only 23 of them have dates older than 15 ka (Fig. 3b). Edwards et al. (2000) used 11 sites with oldest dates around 18 ka ^{14}C, of which 3 were in Western and 8 in Eastern Beringia, to reconstruct pollen-based biomes for Beringia at 18, 6 and 0 ka. Additional records from Chukotka, Magadan Oblast, and Yakutia represent pollen-reconstructed vegetation from MIS 3 (Lozhkin and Anderson, 2011). The new >250 ka record from the El'gygytgyn impact crater in northeastern Russia (Brigham-Grette et al., 2007; Lozhkin et al., 2007) yielded important new vegetation data from pollen spanning at least two full glacial cycles, however, even this truly exceptional record will only represent a point sample in space, and is unlikely to shed light on the exact nature of graminoid-dominated vegetation based solely on pollen.

Despite some of the limitations associated with the application of pollen analyses at high latitudes, Eastern Beringia is perhaps the most studied region within the high latitudes with respect to pollen. Since the earliest pollen studies in Europe and Russia, the combined presence of high *Artemisia* and Poaceae pollen was thought to indicate dry grasslands similar to modern-day steppe (Grichuk and Zaklinskaya, 1950). Vangengeim and Ravski (1965) recognized that the vast expanses of eastern Siberia must have been covered by a rather homogenous cold and xeric steppe, and that taiga vegetation was either not present at all, or very rare, during much of the Pleistocene. A comparison of pollen profiles from modern-day shortgrass steppe and Pleistocene Beringia reveals a grass-dominated ecosystem with over 50% of all pollen being grass or sedge derived (Guthrie, 1990). Other indicators of steppe-like vegetation include *Juniperus*, *Artemesia*, *Chenopodium* and *Plantago* pollen. These taxa are all represented in modern-day temperate grasslands (discussed by Young, 1982). Ritchie and

Table 3

Vegetation reconstructionsà for the Pleistocene of the northern latitudes in Eurasia and eastern Beringia based on pollen evidence. Tundra-steppe is implied when Poaceae >40% and *Artemisia* > 10% of the total pollen. Shrub-tundras have 20–40% *Alnus* + *Betula* pollen, but <20% Poaceae pollen, almost no *Artemisia* and about 20% Cyperaceae pollen.

Age (ka BP)		Northern Scandinavia	NE European Russia	Western Siberia	Eastern Siberia	Western Beringia	Eastern Beringia
Since 11.7	MIS 1	Shrub tundra to forest-tundra	Boreal forest to forest-tundra	Shrub tundra to forest-tundra	Shrub tundra	Shrub tundra	Shrub tundra to herb tundra
c. 30–11.75	MIS 2(LGM)	Ice sheet	Tundra-steppe	Herb tundra to tundra-steppe	Herb tundra to tundra-steppe	Tundra-steppe	Herb tundra to tundra-steppe
c. 50–30	MIS 3/MIS 4	Ice sheet	Forest-tundra	Forest-tundra to boreal forest	Tundra-steppe to forest-tundra	Tundra-steppe	
c. 115–50	MIS 4/MIS5a-d	Ice sheet	Forest-tundra	Shrub-tundra to forest-tundra	Forest-tundra	Shrub tundra	
c. 130–115	MIS 5e		Boreal forest to forest-tundra (*Betula, Picea*)	Forest-tundra to boreal forest (*Abies, Picea*)	Boreal forest (*Pinus*)	Shrub tundra	
c. 200–130	MIS 6					Tundra-steppe	

Table 4
Pollen records longer than 10 kyr available from the Global Pollen Database (GPD, http://www.ncdc.noaa.gov/paleo/gpd.html) and selected literature for the areas north of 60°N.

ID	Site	Latitude (dec. deg. N)	Longitude (dec. deg. E (+) or W (−))	Elevation (m a.s.l.)	Reference
0	Alazeya_River_	68.50	154.50	40	Lozhkin (GPD)
1	Alut_Lake	60.10	152.30	480	Lozhkin (GPD)
2	Amguema_River_Valley_	67.80	178.70	175	Kotov (GPD)
3	Andy_Lake	64.70	−128.10	1360	Szeicz (GPD)
4	Angal_Lake	67.10	−153.90	820	Brubaker (GPD)
5	Bell's_Lake	65.00	−127.50	580	Szeicz (GPD)
6	Berelekh_River	63.30	147.80	800	Lozhkin (GPD)
7	Berelyekh_River,_Indigirka_Lowland	70.60	145.00	20	Lozhkin (GPD)
8	Berelyekh_River,_Indigirka_Lowland	70.60	145.00	20	Lozhkin (GPD)
9	Blossom_Cape	70.70	178.90	6	Lozhkin (GPD)
10	Bludlivaya_River	69.10	148.40	100	Lozhkin (GPD)
11	Bruvatnet	70.20	28.40	119	Hyvarinen (GPD)
12	Byllatskoye_Exposure	69.20	140.10	316	Grinenko (GPD)
13	Candelabra_Lake	61.70	−130.60	1040	Cwynar (GPD)
14	Chabada_(central_Yakutia)	62.00	129.40	290	Andreev (GPD)
15	Crowsnest_Lake	68.30	−146.50	881	Anderson (GPD)
16	East_Siberian_Sea_Coast_10730	71.10	156.50	33	Lozhkin (GPD)
17	Elgennya_Lake	62.10	149.00	1040	Anderson (GPD)
18	Elikchan_4_Lake	60.80	151.90	810	Anderson (GPD)
19	Etivlik_Lane	68.10	−156.00	631	Anderson (GPD)
20	Glacial_Lake	64.90	−166.30	120	Eisner (GPD)
21	Goluboye_Lake	61.10	152.30	810	Lozhkin (GPD)
22	Hanging_Lake	68.40	−138.40	500	Cwynar (GPD)
23	Harding_Lake	64.40	−146.90	0	Ager (GPD)
24	Headwaters_Lake	67.90	−155.10	820	Brubaker (GPD)
25	Hidden_Lake	63.90	−144.70	0	Ager (GPD)
26	Jack_London_Lake	62.20	149.50	820	Anderson (GPD)
27	Jack_London_Lake_(Wrangle_Island)	70.80	−179.80	7	Lozhkin (GPD)
28	Joe_Lake	66.80	−157.20	183	Anderson (GPD)
29	Kaiyak_Lake	68.20	−161.40	190	Anderson (GPD)
30	Keele_Lake	64.20	−127.60	1150	Szeicz (GPD)
31	Khomustakh_Lake	63.80	121.60	120	Andreev (GPD)
32	Kirgirlakh_Stream,_Berelyekh_River_Basin	62.70	148.00	700	Lozhkin (GPD)
33	Kollioksak	67.00	−156.40	213	Anderson (GPD)
34	Lac_Demain	62.00	−118.70	745	MacDonald (GPD)
35	Lac_Meleze	65.20	−126.10	650	MacDonald (GPD)
36	Lateral_Pond	65.90	−135.50	470	Ritchie (GPD)
37	Ledovyi_Obryu_Exposure,_Southern_Section	64.10	171.20	44	Lozhkin (GPD)
38	Ledovyi_Obryu_Exposure,_Northern_Section	64.10	171.20	57	Lozhkin (GPD)
39	Maltan_River_Exposure	60.90	151.60	735	Lozhkin (GPD)
40	Maria_Lake	68.30	−133.50	105	Ritchie (GPD)
41	Minakokosa_Lake	66.90	−155.00	122	Anderson (GPD)
42	Natla_Bog	63.00	−128.80	1380	MacDonald (GPD)
43	Niliq_Lake	67.90	−160.40	274	Anderson (GPD)
44	Ped_Pond	67.20	−142.10	211	Brubaker (GPD)
45	Point_Woronzof_Peat_Section	61.10	−149.50	0	Ager (GPD)
46	Priyatnoye_Lake	61.00	151.70	980	Lozhkin (GPD)
47	Puyuk_Lake	63.50	−162.20	15	Ager (GPD)
48	Ranger_Lake	67.10	−153.60	820	Brubaker (GPD)
49	Rebel_Lake	67.40	−149.80	914	Anderson (GPD)
50	Redstone_Lake	67.30	−152.60	914	Brubaker (GPD)
51	Reindeer_Lake	69.10	−132.20	0	Spear (GPD)
52	Ruppert_Lake	67.10	−154.20	210	Brubaker (GPD)
53	Sakana_Lake	67.40	−147.90	640	Brubaker (GPD)
54	Screaming_Yellowlegs_Pond	67.60	−151.40	650	Brubaker (GPD)
55	Seagull_Lake	68.30	−145.20	637	Brubaker (GPD)
56	Selennyakhskaya-1_Exposure	69.20	137.80	354	Grinenko (GPD)
57	Sleet_Lake	69.30	−133.60	0	Spear (GPD)
58	Smorodinovoye_Lake	64.80	141.10	800	Lozhkin (GPD)
59	Sosednee_Lake	62.20	149.50	822	Anderson (GPD)
60	Sulphur_Lake	61.00	−138.00	847	Lacourse (GPD)
61	Sverdrup	74.50	79.50	7	Tarasov (GPD)
62	Sweet_Little_Lake	67.70	−132.00	0	Ritchie (GPD)
63	Ten_Mile_Lake	63.10	−145.70	1000	Anderson (GPD)
64	Tiinkdhul_Lake	66.60	−143.10	189	Anderson (GPD)
65	Tuktoyaktuk_5	69.10	−133.40	60	Ritchie (GPD)
66	Wien_Lake	64.30	−151.30	305	Hu (GPD)
67	Wonder_Lake	63.50	−151.10	610	Anderson (GPD)
68	Wrangel_Island_Exposire_12	71.20	−179.80	200	Lozhkin (GPD)
69	Elgygytgyn	67.50	172.80	489	Lozhkin et al. (2007)
70	Mamontovy_Khayata	71.80	129.30	0	Schirrmeister et al. (2002)
71	Levinson-Lessing	74.50	98.60	47	Andreev et al. (2003)
72	Billyakh	65.28	126.78	340	Müller et al. (2010)

Cwynar (1982) postulated a "herb pollen zone" as the most characteristic of the full glacial conditions at Hanging Lake and Lateral Pond in northeastern Yukon. The oldest dates for Hanging Lake are around 20 ka ^{14}C (Kurek et al., 2009) and for Lateral Pond around 15 ka ^{14}C. The low pollen influx values (100/cm^2/yr) were indicative of low productivity of these communities and true steppe would have produced influx values of an order of magnitude higher. The evidence from high values of Poaceae + Cyperaceae + *Artemisia* combined percentages they interpreted as compatible with "herb tundra", rather than "tundra-steppe". Colinvaux (1996) argued that very low presence of *Artemisia* pollen (<5%) during Wisconsin glaciations in most coastal plain samples from Eastern Beringia (e.g., Imuruk Lake on central Seward Peninsula, zone J) implied a herb tundra, rather than a tundra-steppe. The steppe-like view of the late Pleistocene Beringia has nevertheless been supported by a wide variety of evidence (Hopkins et al., 1982, Guthrie, 2001; Zazula et al., 2003, 2007) that came since the 1980s from the use of alternative proxies to pollen, especially vertebrate and invertebrate paleontology and plant macrofossils (see section 5), and revised statistical approaches.

Edwards et al. (2000) reconstructed pollen-based "biomes" of Beringia based on pollen-to-plant functional type assignment. Their proposed map for the last glacial maximum (LGM, around 21 ka cal.) in Beringia is dominated by "tundra", not true steppe. Nevertheless, steppe and xeric forbs are prominently represented in many of the sites (Kaiyak Lake and Sands of Time Lake respectively) in Eastern Beringia, especially away from the coast, while in Western Beringia shrubs and heath are prominent, suggesting that steppe-shrubland may have been actually present there instead of shrubless tundra. Thus, according to Edwards et al. (2000), "tundra" at the LGM is a broad generalization with the actual community at that time being non-analog to any modern tundra. The name for that "biome" can be a matter of semantics and could just as well be called "tundra-steppe."

Müller et al. (2010) provided compelling evidence for the presence of tundra-steppe in the Verkhoyansk Mountains of NE Siberia based on pollen analyses of a core from Lake Billyakh from 50.7 to 13.5 ka BP, just 140 km south of the Arctic Circle. As in other studies, they based their reconstruction on high values of Poaceae, Cyperaceae and *Artemisia* pollen and noted that pollen concentrations were low, which implies a reduced vegetation cover. They postulated that the coldest period was between 31 and 13 ka, more or less coincident with the LGM/MIS 2. They also noted that some mesophytic shrubs were present during this period, precluding interpretation of a polar desert at that time.

Andreev et al. (2008) reconstructed a 115 ka vegetation record on Bol'shoy Lyakhovsky Island, which is the southernmost one in the New Siberian Archipelago group NE of the Lena River delta at 73°20′ N, based on a multi-proxy study of a permafrost sequence involving pollen, beetles, macrofossils, diatoms, and soil data. They recorded vegetation similar to today's subarctic tundra for the earliest part of the record (Eemian/early Weichselian), with colder and dryer tundra during the early Weichselian, later transitioning into "tundra and steppe" vegetation during the more moderate Mid-Weichselian. The island is famous for large deposits of mammal bones from the grazing guild described earlier, which was noted as early as 1887 (Bunge). The presence of sufficient graminoid cover to support these grazers in the late Pleistocene is therefore expected.

Further west, Andreev et al. (2003) detailed vegetation change in the late Pleistocene as recorded in Levinson-Lessing Lake (LLL) at 74°28" N and other lakes of the Taymyr Peninsula. The LLL record spans about 30 ka. Its MIS 2 samples are heavily dominated by Poaceae (20–40%) and Artemisia (35-20%) pollen with strong presence of Cyperaceae (10%) and Caryophyllaceae. Their interpretation of these spectra was that of "open steppe-like and tundra-like herb communities" developing under very cold and dry conditions. Samples from southern Taymyr suggested much less severe environments, which included communities with small presence of trees (forest-tundra).

While pollen studies have yielded many important insights about the regional distribution of plant communities, macrofossils and cuticle analysis can provide much higher taxonomic resolution and more localized signal of ancient plant communities.

5. Macrofossils and cuticle analysis

Plant macrofossils, including seeds, fruits, leaves and stems, from ice rich Pleistocene sediments and soils have provided direct evidence derived from local sources of the past species composition across the high latitudes (Matthews, 1982; Kienast et al., 2001; Goetcheus and Birks, 2001; Kienast et al., 2005; Sher et al., 2005; Zazula et al., 2003, 2006a, 2007). In comparison to fossil pollen, macrofossils of grassland plants such as Poaceae and Cyperaceae and herbs species can often be reliably identified to the species level and better represent local scale plant community cover. In addition, the exceptional preservation of plant materials in permafrost enables detailed reconstructions of plant community composition and structure across the high latitudes.

Some of the first plant macrofossil data demonstrating the existence of late Pleistocene steppe vegetation were from the periglacial regions of Western Europe (Godwin, 1975; West, 2000). British records of the Devensian and earlier cold stages indicated that regional vegetation was dominated by plant taxa and communities that were significantly different from the modern vegetation with much greater coverage of grasses (*Festuca*), and cryoxerophilus herbs (*Corispermum* sp., *Onobrychis viccifolia*, *Centaurea scabiosa*) with arctic, alpine and continental affinities (Godwin, 1975; West, 2000). Amongst the most important records from Siberia that document steppe-tundra vegetation are macrofossils recovered from Late Pleistocene sediments in the Lena River delta (Kienast et al., 2005). Well preserved macrofossils of the grasses *Koeleria cristata*, *Festuca* sp., *Poa* sp., sedges *K. myosuroides* and *C. duriuscula*, and forbs *Alyssum obovatum*, *Androsace septentrionalis*, *Silene repens* and *Linum perenne* indicate that local presence of productive steppe-tundra and meadow habitats, with close modern analogs to relict azonal steppe communities in central and northeast Yakutia.

Analyses of a Central Beringian vegetation surface dated to 21,500 cal ka from the Seward Peninsula, Alaska showed that *K. myosuroides*, a dry-adapted sedge, found on calcareous substrates, was the dominant graminoid on local upland surfaces (Goetcheus and Birks, 2001). This upland record contrasted with plant macrofossil data from lowland sites in central Beringia, which have indicated a greater coverage by mesic graminoid-birch tundra (Elias et al., 1997). Thus, there is evidence for local variability of the past communities based on their topographic position, just as there is today.

The most informative plant macrofossil assemblages from interior Eastern Beringia are derived from permafrost preserved nests and caches (middens) of Late Pleistocene arctic ground squirrels (*Urocitellus parryii*; Zazula et al., 2006b, 2007; 2010; Gaglioti et al., submitted). Hundreds of analyzed nests from the Klondike region of central Yukon demonstrate that Late Pleistocene ground squirrels inhabited diverse steppe-tundra communities rich in grasses (*Poa*, *Elymus trachycaulus*), sedges, (*K. myosuroides*, *Carex* spp.), prairie sage *A. frigida*, and forbs (*Polygonum bistorta*, *Phlox hoodii*, *Draba* spp., *Plantago canescens*) (Fig. 5). Importantly, arctic ground squirrels are known to forage for nest material and cache food in a limited range from their burrow entrances, indicating
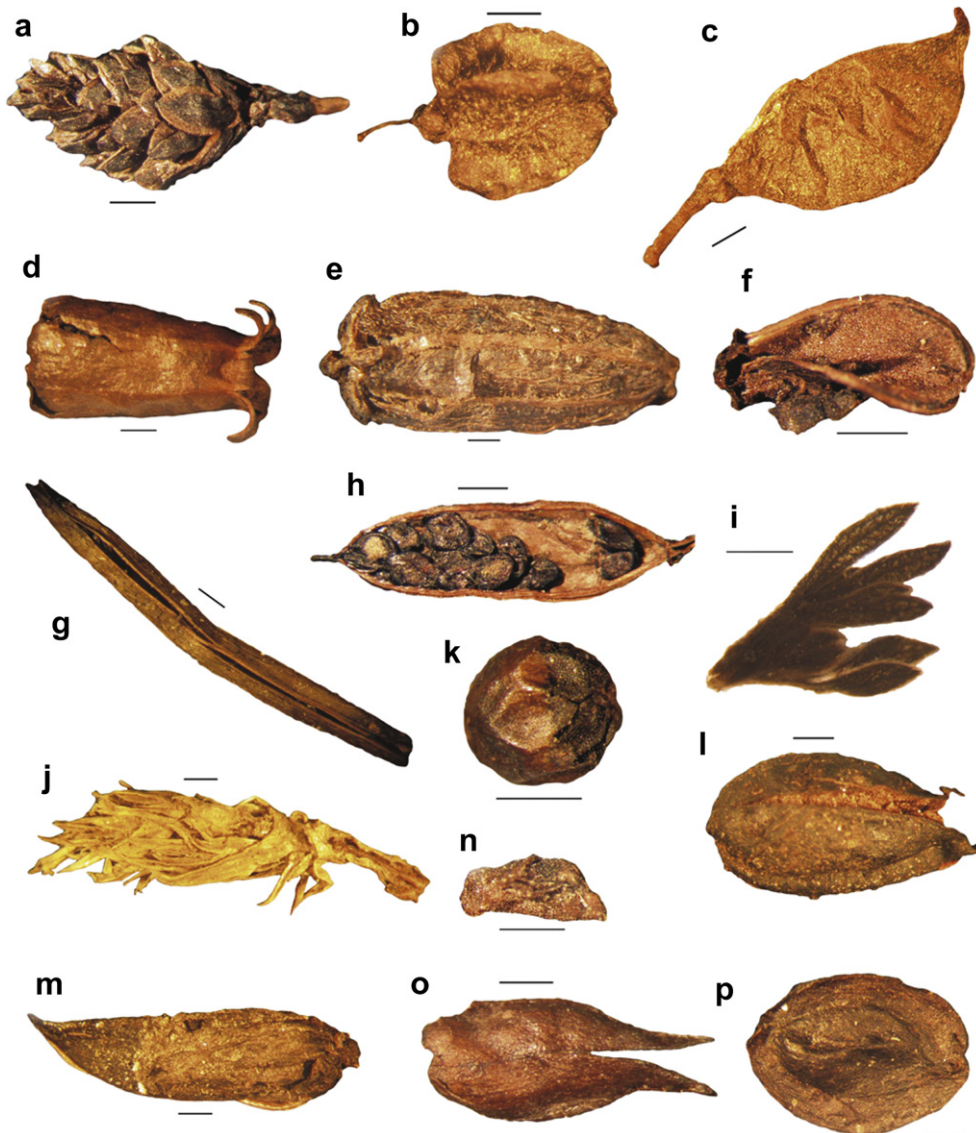
Fig. 5. Selected plant macrofossils from arctic ground squirrel middens. Scale bar = 1 mm. (a) *Carex albo-nigra* spike; (b) *Rumex acetosa* calyx; (c) *Astragalus eucosmus* legume; (d) *Silene taimyrensis* capsule; (e) *Papaver* cf. *mcconnellii* capsule; (f) cf. *Spiraea beauverdiana* follicle; (g) *Erysimum* cf. *cheiranthoides* silique; (h) *Draba* silique; (i) *Artemisia frigida* leaves; (j) *Phlox hoodii* leaves; (k) *Androsace septentrionalis* capsule; (l) *Castilleja* capsule; (m) *Pedicularis* cf. *lapponica* capsule; (n) *Penstemon gormanii* seed; (o) *P. gormanii* capsule half; (p) *Anemone narcissiflora* achene. Redrawn from Zazula et al. (2007).

these records document a great floristic diversity at a local scale (Batzli, 1980). Similar to Siberian macrofossil records, Late Pleistocene plants documented in the Yukon squirrel middens have close floristic analogs with present day azonal steppe and steppe-tundra communities dominated by bunchgrasses in northwest North America (Young, 1982; Lloyd et al., 1994; Laxton et al., 1996; Vetter, 2000). Macrofossil evidence for steppe and tundra vegetation co-existing in local habitats are not limited to the eastern extreme of Beringia (the Yukon), but have also been confirmed with the analysis of fossil ground squirrel middens from interior Alaska (Gaglioti et al., submitted). In western Beringia, Gubin et al. (2001, 2003) demonstrated the utility of using the same approach, and have developed taxonomically similar fossil ground squirrel midden records that have documented the presence of steppe-tundra vegetation. Binney et al. (2009) presented a new Eurasia-wide database of macrofossils that mainly focuses on woody taxa. An extension of this database to include graminoid taxa would be most welcome.

In addition to the traditionally identified reproductive parts found in plant macrofossil assemblages, graminoid leaves are also a common constituent of the fossil remains in fossil ground squirrel middens and soil surfaces. Graminoid leaf material exhibits taxonomically distinct, micro-morphological features on the leaf epidermis (cuticle) that are preserved on fossil specimens and available for paleoecological reconstructions based on the taxa's habitat preferences (Wooller, 2002) and the presence of features that reduce transpiration (Wooller et al., 2007). Gaglioti et al. (2010) surveyed SEM images of modern graminoid leaves and distinguished 38 Beringian steppe-tundra species based on the nature, abundance and distribution of 50 cuticle features. A cuticle identification guide was subsequently applied to fossil leaf material from interior Alaska (Wooller et al., 2011; Gaglioti et al., submitted), and indicated that mesic tundra species such as *Puccinellia* sp., and *Calamagrostis stricta* occurred with relatively dry-adapted sedges such as *Carex albonigra* in Alaska's steppe tundra (Figs. 6 and 7). Dry-adapted sedges (i.e. *C. albonigra* and *Kobresia* sp.) were common in
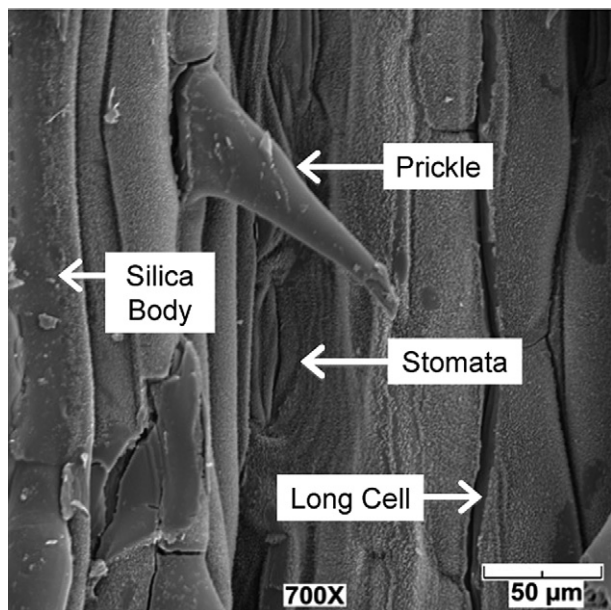
Fig. 6. Close-up image of abaxial (back) side of *Calamagrostis stricta* leaf sampled from University of Alaska Museum of the North (ALA # V135709). The nature, distribution abundance of the features shown can be taxonomically distinct and used for identifying graminoid cuticles from the Pleistocene. (Redrawn from Gaglioti et al., 2010).

steppe tundra, indicating that interpretations of fossil sedge pollen from steppe tundra should not be used to infer exclusively wet habitats. These findings have confirmed the widespread presence of steppe-tundra that was originally debated and only inferred by palynological and paleontological evidence, however the more precise question of how these communities were maintained over a widespread region and millennia has yet to be resolved, and the significance of these controls is not exclusive to the past.

Ongoing plant macrofossil analysis lends support to the argument that steppe-tundra vegetation was present in a widespread form at high latitudes during the late Pleistocene. Macrofossil analysis in Eastern Beringia has shown evidence for the co-occurrence of steppe and tundra vegetation on a local (ground squirrel foraging area), extra-local (several ground squirrel middens and soil surfaces around Fairbanks, AK and Dawson City, YT), and regional scale (across Eastern Beringia) persisting between ~75 ka and ~16 ka (Goetcheus and Birks, 2001; Zazula et al., 2005, 2006a, 2007, 2010; Gaglioti et al., submitted). Notably, the spatial and temporal variability of vegetation in Beringia has, so far, been relatively homogenous compared with other regions and times (i.e. Late-Pleistocene southwestern North America, Coats et al., 2008; Nunez et al., 2010; Zazula et al., 2010). The perceived minor variability of steppe-tundra could be a product of limited macrofossil data, however this apparent stability is also supported by the re-occurring predominance of bison, horse and mammoth bones regardless of location or age. The persistence of steppe-tundra can partially be explained by the reduced number of high latitude species that are collectively adapted to cold, dry and disturbed habitats that were perennial during the tenure of steppe-tundra. These conditions may have left a limited number of plant species to persist in the region (Fig. 8), and allowed the large mammal community to evolve specialized foraging niches within this widespread habitat (Guthrie, 1982). This reduction in adaptable plant species and the concept of a relatively homogenous steppe-tundra is an emerging hypothesis that needs to be tested with ongoing macrofossil data over former climatic gradients. The responsiveness of the steppe-tundra vegetation to the climatic variability, including Heinrich events and Milankovitch cycles, must be tested further to assess the future adaptability and migration potential of high latitude vegetation.

6. Phytolith perspectives

Phytoliths are microscopic non-crystalline hydrogenated silica bodies typically 5–200 μm in size. They form in specialized cells in some plants and in cell walls and intercellular spaces in others. Phytoliths from specialized short grass cells are shaped actively under genetic control and can be highly diagnostic of subfamily, tribe and even genus level of the Poaceae (Piperno, 2006). They are a valuable proxy for reconstructing past graminoid-dominated ecosystems. Although their taxonomic resolution is lower than macrofossils, they have better resolution than pollen for graminoid taxa. They also accumulate over more local areas and are remarkably durable in dry acidic conditions (e.g., in paleosols) (Blinnikov et al., 2002; Strömberg, 2005; Piperno, 2006). Phytolith research of terrestrial paleoenvironments to date has focused primarily on tropical or temperate regions outside of the Arctic. Assemblages of silica phytoliths from these settings are dominated by morphotypes from Panicoid, Chloridoid or Bambusoid grasses and tropical taxa (e.g., palms, bananas, and dicot trees) (e.g., Piperno, 2006; Bremond et al., 2008). In temperate regions, ratios of C_3/C_4 grass morphotypes have been used to document regional or subcontinental trends in paleovegetation in mid-latitudes (e.g., in China or North American Great Plains) (Fredlund and Tieszen, 1994; Lu et al., 2006). The high-latitude/high-altitude areas have received considerably less attention, with limited research conducted in the Caucasus and the Alps, where the main phytolith producers are C_3 grasses (Festucoids) and sedges (Cyperaceae) with limited diversity of morphotypes (Blinnikov, 1994; Carnelli et al., 2004). A study utilizing phytoliths in Eastern Beringia (Bombin, 1984) provided limited insight into the nature of glacial communities there, because the evidence was limited to a few phytolith records from lakes spanning only the last 15 ka or so, the usual limitation in pollen analysis. Bombin (1984) analyzed phytoliths from Harding Lake in Central Alaska's Tanana valley. The two samples that were tentatively assigned to MIS 2 were dominated by crenate trapezoids and rondels, consistent with the overall C_3 grassland. The proportion of sedge phytoliths was very low, but higher than that found for the Holocene. He also analyzed Eightmile Lake from the northern foothills of the Alaska Range. That record was dated back to >13.6 ka and the older samples were again dominated by crenate and rondel forms. There was no evidence for any C_4 type grasses (e.g, no bilobate forms). He also undertook analysis of squirrel coprolites from 18.2 ka BP and found evidence for 8 species of grass, two of sedge and *Equisetum*.

Phytoliths can augment other proxies and shed light on the composition of full-glacial non-analog xeric graminoid communities, because there is a better understanding of the taxonomic and spatial resolution and limitations of the method (Piperno, 2006; Yost and Blinnikov, 2011). A limited modern analog collection of samples from grassland sites in central Alaska was assembled by Blinnikov et al. (2010). Modern soil samples from south-facing dry bluffs along the Tanana river valley in central Alaska are dominated by phytoliths from only five genera of C_3 grasses, many of which produce primarily rondels and trapezoid forms (*Calamagrostis*, *Bromus*, *Helictotrichon*, *Poa*, *Festuca*). Because there are correlations between phytolith morphology at the genus level in Festucoid grasses (Blinnikov, 2005), broad reconstructions of paleovegetation may be accomplished, even with limited modern collections, based on botanical match. Using Swanson's (2006) plant list (Table 3), all 13 genera of grasses are C_3 Festucoid grasses (Pooideae subfamily of grasses) expected to produce primarily trapezoid rondels and trapezoid creanate/wavy forms (Fredlund and Tieszen, 1994;
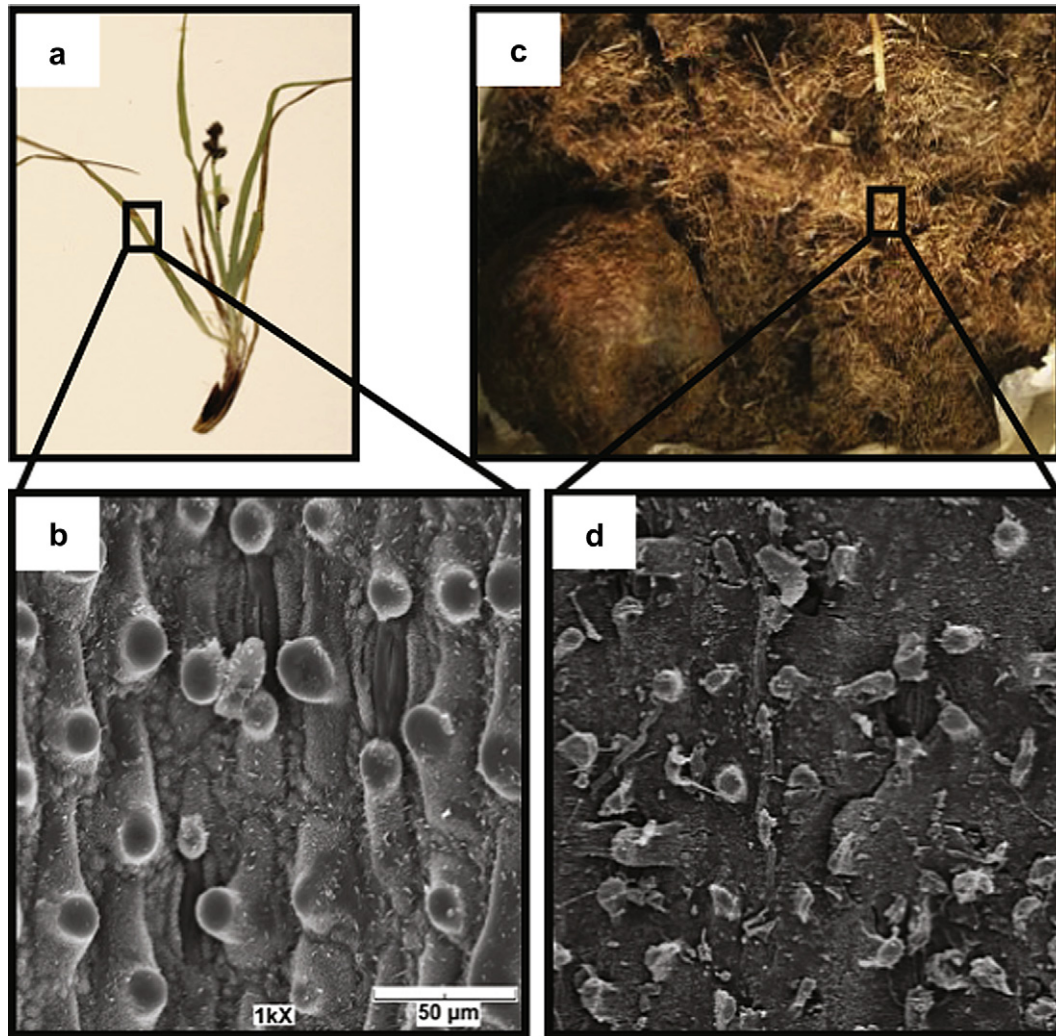
Fig. 7. Herbarium specimen of a) *Carex albonigra* with b) close-up SEM image of leaf sample. c) Ancient arctic ground squirrel nest with squirrel mummy (bottom left) along with d) close-up SEM image of fossil graminoid cuticle identified as *Carex albonigra*. Note the four papillae surrounding stomata with triangular-shaped subsidiary cells on both SEM images.

Fig. 8. Conceptual model of multiple causes for tundra-steppe relates several different processes that lead to selection of dry and disturbance adapted taxa from the pool of available boreal species.

Piperno, 2006). Seven of these genera are in the tribe Aveneae, three in Poeae, one in Bromeae, and two in Triticeae. Fortunately, phytolith production in these groups has been well studied elsewhere, especially in Mongolia (Kiseleva, 1989), western North America (Kerns, 2001; Blinnikov et al., 2002; Blinnikov, 2005; Morris et al., 2009), and North American Great Plains (Blackman, 1971; Mulholland, 1989; Fredlund and Tieszen, 1994) (Table 5).

In the summer of 2009 we obtained samples from 12 modern sites in Central Alaska from dry south-facing bluffs along the Tanana and Delta Rivers and the central portion of the Alaska Range along the Denali Highway. Vegetation at the bluff sites was previously described by Kassler (1979). Most samples come from grasslands dominated by *C. purpurascens*, *Poa glauca*, *Bromus ciliatus*, *Carex* spp., *A. frigida* and arcto-alpine forbs. We also obtained samples from forb- and sedge-rich alpine tundra and a low elevation black spruce-cottongrass bog. All have been processed for silica phytoliths using standard wet oxidation and flotation technique of Blinnikov (2005). All samples, except the bog, yielded abundant silica phytoliths. As expected, Alaskan assemblages are dominated by wavy crenate forms (long and short) with some presence of rondels (Fig. 9 & Table 5).

Phytoliths were also extracted from a paleo-turf fragment removed from the ceiling of the Fox Permafrost Tunnel (www.crrel.usace.army.mil/permafrosttunnel/) located 10 km NE of Fairbanks (Wooller et al., 2011). All of the samples analyzed from the paleo-turf yielded abundant, well-preserved phytoliths. The three most common forms were rectangular plates (5–22%), short wavy or lobed trapezoids (13–38%) and smooth long cells (10–39%). Ninety to ninety-five percent of the phytoliths recovered were from grasses and no sedge or unequivocal tree-phytoliths were observed. All of the grass phytoliths were consistent with those from Festucoid grasses. According to the phytolith data, the grass-dominated habitat included *Poa* and *Agropyron/Elymus* species. Within the

samples there was little variability and the *Stipa*-type bilobate forms were present in small numbers. *Stipa*-type bilobates are most commonly produced by needlegrass or its relatives (*Oryzopsis*). There is no known *Stipa* in modern-day interior Alaska, but it is a common taxon in both Eurasian and Western North American steppe today, much further to the south. The wavy trapezoidal forms, especially short ones, are very common in *Poa* spp. and *Agropyron/Elymus* complex. *Poa* species tend to have trapezoids with more pronounced lobes, while the other group has less pronounced lobes on their phytoliths. Both types were found in all of the samples. Rondels of various shapes may be contributed by the same species, especially long oval and keeled forms, although they can also come from many other Festucoid grasses, especially *Festuca*. *Stipa*-type bilobates could come most likely from *Stipa* or *Oryzopsis*, however, Alaskan grass flora has not been sufficiently studied to consider those locally diagnostic. The grass phytolith reference collection does not have enough taxonomic resolution to distinguish *Agropyron* from *Elymus*. All would contribute short wavy trapezoids in high numbers. Some lobate forms of trapezoids (merged with wavy for the modern analog matching) are likely to be contributed by *Poa*. The application of phytolith analysis at other sites in Beringia and across the Arctic will undoubtedly expand our understanding of the nature of graminoid-dominated vegetation of the Pleistocene.

7. Stable isotopes

Stable carbon isotope analyses of plant remains have been used as a proxy for examining changes in past grassland composition and physiology and have been usefully applied where the vegetation is composed (or was composed) of graminoids using either the C_3 or C_4 photosynthetic pathways. C_3 or C_4 plants have distinctive carbon isotopic values (expressed as $\delta^{13}C$ values) (O'Leary, 1988), which can be used to calculate the proportional contribution of mixed C_3 and C_4 plant taxa to lake sediments, the total organic carbon pool in paleosols (Quade et al., 1994), past faunal diets (Cerling et al., 1993) and even grass pollen grains (Nelson et al., 2008), the carbon occluded in grass phytoliths (Smith and White, 2004; Hodson et al., 2008; Carter, 2009) and graminoid cuticles (Wooller et al., 2000). The modern high latitudes, unlike the tropics and lower latitudes, are dominated by C_3 vegetation and the graminoids are also dominated by C_3 representatives (Wooller et al., 2007; Sage et al., 1999; Welsh, 1974). On first inspection this might seem to limit the applicability of stable carbon isotope analysis in the Arctic. However, a positive outcome of dealing with the Arctic "C_3 world" means that interpretations of fossil $\delta^{13}C$ values can be considered within the environmental and physiological framework that drives isotopic variability in C_3 plants alone, which amongst a number of environmental conditions includes the amount of moisture available to plants (e.g. Kohn, 2010). By focusing on reconstructing past C_3 vegetation, this simplifies explanations needed for 'mixed' (C_3 and C_4) type bulk isotopic values from terrestrial total organic matter in soils, lake sediments and fossil nests (Hughen et al., 2004). Graminoid fossils can be exceptionally well preserved in permafrost at high latitudes (Wooller et al., 2007, 2011; Gaglioti et al., submitted) and $\delta^{13}C$ data from analyses of these specimens can be used to examine changes in the isotopic composition of C_3 graminoids over time (Fig. 10), can be used to reconstruct past environmental conditions (e.g. mean annual precipitation), and can be supplemented using the $\delta^{13}C$ values from past grazers (Kohn, 2010) (Fig. 10). In addition to $\delta^{13}C$ data, stable isotope analyses of fossil plant remains can also simultaneously provide stable nitrogen isotope data, which can used to reconstruct the past feeding ecology of fauna in Beringia (Fox-Dobbs et al., 2008; Veltre et al., 2008; Szpak et al., 2010) and past environmental conditions. By coupling stable isotopes analyses with cuticle analysis, species-specific stable isotope analyses can be

Table 5
Expected phytolith production in selected genera of Poaceae based on anatomical studies Metcalfe, 1960; Blackman, 1971; Blinnikov, 1994; Blinnikov, 2005; Bombin, 1984; Fredlund and Tieszen, 1994; Kiseleva, 1989; Mulholland, 1989; Watson and Dallwitz, 1994).

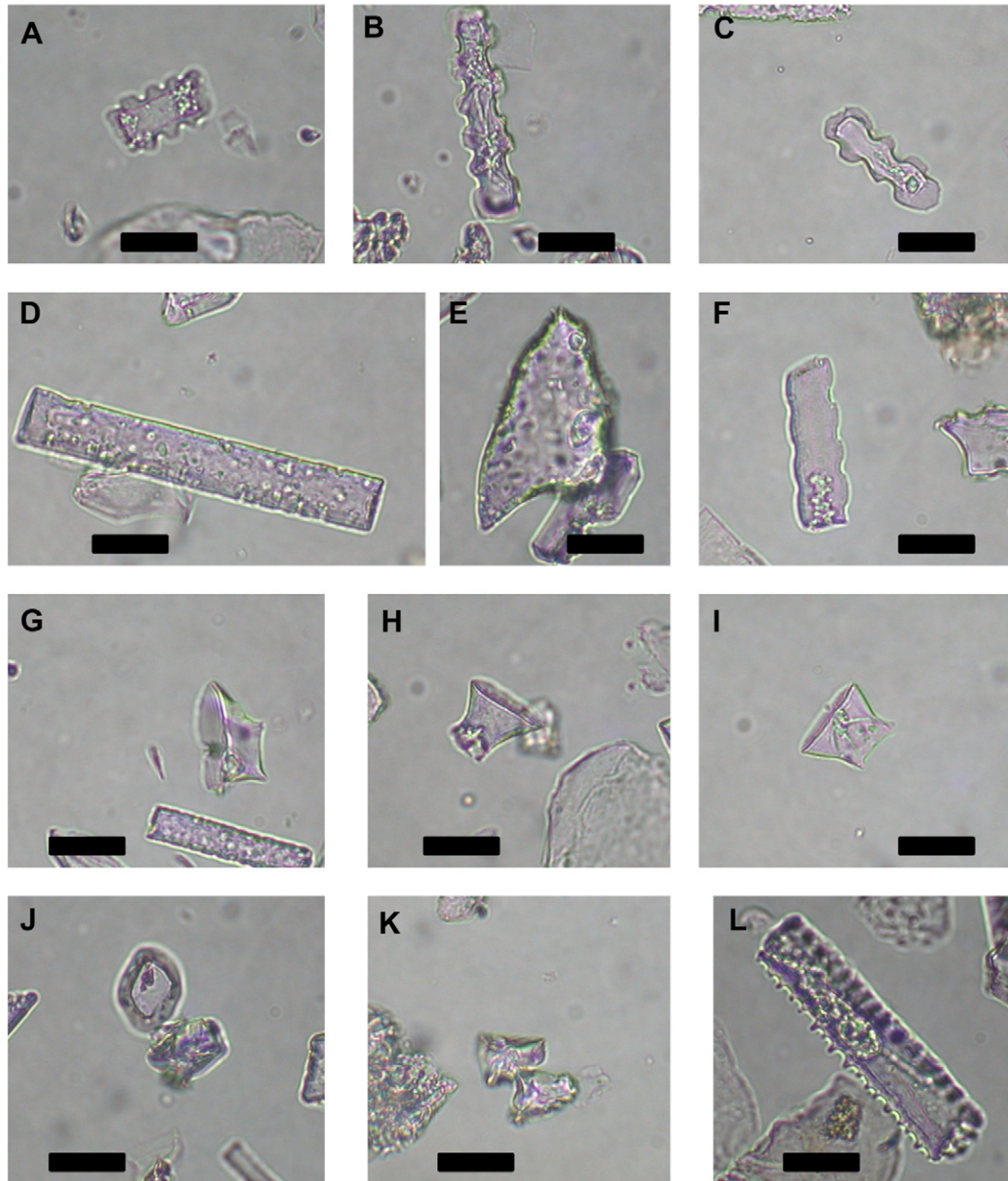| Genus (species in the Arctic flora)	Tribe	Typical phytolith morphotypes
Alopecurus (5)	Avenae	long crenate/sinuous to smooth short trapezoids, narrow in top view
Arctagrostis (2)	Avenae	no to little silica, needs additional study
Calamagrostis (12)	Avenae	long crenate trapezoidal phytoliths (>5 undulations), narrow in top view
Deschampsia (5)	Avenae	crenate/sinuous or smooth trapezoids and small proportion of pointed rondels
Hierochloë (4)	Avenae	crenate/sinuous trapezoids, needs additional study
Koeleria (3)	Avenae	elongated crenate/sinuous to smooth trapezoids (2/3), many with slanted ends, rounded rondels are also common
Trisetum (3)	Avenae	short crenate/sinuous, or trapezoids; apparently no rondels; overall low production
Festuca (16)	Poeae	high proportion of keeled and pointed rondels (over 90% common)
Poa (27)	Poeae	pyramidal, rounded and keeled rondels (2/3); lobate trapezoid forms (1/3)
Puccinellia (28)	Poeae	rondels, including crescentic forms; needs additional study
Bromopsis (3)	Bromeae	elongated crenate/sinuous and some smooth – broad in top view; crown cells present
Elymus (8)	Triticeae	elongated crenate/sinuous and some smooth – broad in top view; small presence of rondels; crown cells present crown cells present
Hordeum (3)	Triticeae	crown cells present

Fig. 9. Typical phytoliths of the graminoid-rich paleocommunity (Fox tunnel photos). Bar is 10 μm. A − short wavy/crenate trapezoid; B − long wavy/crenate trapezoid (cf. *Calamagrostis*); C − short wavy/crenate trapezoid with pronounced lobes (cf. *Poa*); D − long cell smooth; E − trichome; F − short wavy/creante trapezoid with very slight crenulations; G − *Stipa*-type bilobate; H − keeled rondel; I − keeled rondel; J − pyramidal rondel; K − two crown cells cf. Triticeae; L − long cell with slight indentations.

achieved. In some instances fossil graminoids are so well preserved (Fig. 11a) that isotopic analyses along the lengths of consecutive leaves attached to individual culms can be used to examine changes in water-use-efficiency over a single growing season (Wooller et al., 2011), in essence in a similar manner to isotopic analyses of tree rings (Helliker and Ehleringer, 2002). Subsequently these data can be used to quantify precipitation (Kohn, 2010) and at a sub-annual (seasonal) resolution (Fig. 11c) the data can be compared with modern patterns of precipitation during the growing season (Fig. 11d). The interpretation of ancient variation in δ^{13}C in plants will continue to benefit from further geospatial analyses of isotope variability in modern plants at high latitudes (e.g. Wooller et al., 2007; Day et al., 2008; Kohn, 2010; Zhu et al., 2010).

Applications of stable carbon isotope analyses of past plants at high latitudes during the Quaternary will almost certainly continue to center around interpreting data typical of C_3 photosynthesis. However, although the occurrence of C_4 graminoids is relatively rare ($\leq 2\%$) in the modern Arctic and sub-Arctic (Welsh, 1974; Sage et al., 1999) there are a number of reasons for considering whether C_4 graminoids were more extensive at high latitudes at previous periods during the Quaternary. Not least of these reasons is the fact that climatic and environmental changes have occurred in the past and some of these changes, which for example included lower atmospheric CO_2 concentrations and altered disturbance regimes (Sage et al., 1999), could have favored a relative increase in the proportion of C_4 graminoids relative to C_3 graminoids. Certainly δ^{13}C data from fossil graminoid remains are a key and definitive way to classify the C_3 and C_4 identity of plants. This can also be achieved using the taxonomic identity of fossil graminoid remains and cuticle analysis (discussed above), where C_4 graminoids are
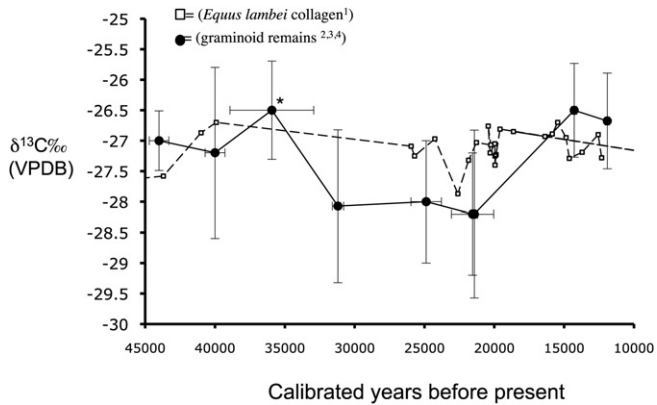
Fig. 10. Carbon isotope values for graminoids (filled circles, Wooller, et al., 2007, Wooller et al., 2011 and Gaglioti et al., submitted) and horses (open squares = *Equus lambei* collagen − Fox-Dobbs et al., 2008) from interior Alaska plotted versus time. Both plant and horse values are corrected for the difference in $\delta^{13}C$ of CO_2 from modern and past atmospheres (Wooller al., 2007) and horse values are corrected for the difference between diet and collagen (Kohn, 2010). * = the turf sample used in Fig. 10 (Wooller et al., 2011).

pooled within relative discrete portions of the Poaceae (Watson and Dallwitz, 1994).

8. Climate and vegetation modeling, role of animals and spatial scale

Global and regional climate and vegetation models provide an opportunity to test the theoretical framework of vegetation change against empirical datasets derived from terrestrial proxies (Bartlein et al., 1998; Jolly et al., 1998). Despite tremendous progress with improving general circulation models (GCMs) and the appearance of coupled dynamic climate-vegetation models (Harrison et al., 1995; Kaplan et al., 2003) in the past decade, the average spatial resolution of these is too coarse to resolve local spatial mosaics of either climate or vegetation (Kutzbach et al., 1998; Moorcroft, 2003). Likewise, most biome derivations based on pollen data utilize the plant functional type approach, which is taxonomically crude and is subject to the low taxonomic resolution of pollen with respect to graminoids as discussed above (Haxeltine and Prentice, 1996; Webb and Prentice, 1998; Kittel et al., 2000; Tarasov et al., 2000). Finally, most of the paleosites lack temporal resolution necessary to address questions related to the speed of change, especially at submillenial time scales (Jiménez-Moreno et al., 2010). Nevertheless, with the expansion of macrofossil, paleoinsect, cuticle, and phytolith analyses discussed above, it may be possible to begin to discern more local variability in terrestrial ecosystems, especially with adequate temporal constraints (e.g., Wooller et al., 2011).

Overall, paleoclimate (COHMAP, 1988; Bartlein et al., 1998; Alfimov and Berman, 2001; Kaplan et al., 2003) and paleo-vegetation (Tarasov et al., 1998, 2000; Edwards et al., 2000, 2001) modeling for the unglaciated parts of North America and Eurasia during the colder stages of the Pleistocene suggest the presence of widespread arid and windy conditions and correspondingly xeric-adapted treeless communities in the continental interiors at the time of glacial maxima. Globally, biome distributions were radically different from present. Although some trees may have been present in local refugia, even near the Arctic circle (Brubaker et al., 2005; Anderson et al., 2010), the prevalent character of vegetation is thought to have been a grassland (Allen et al., 2010). Allen et al.
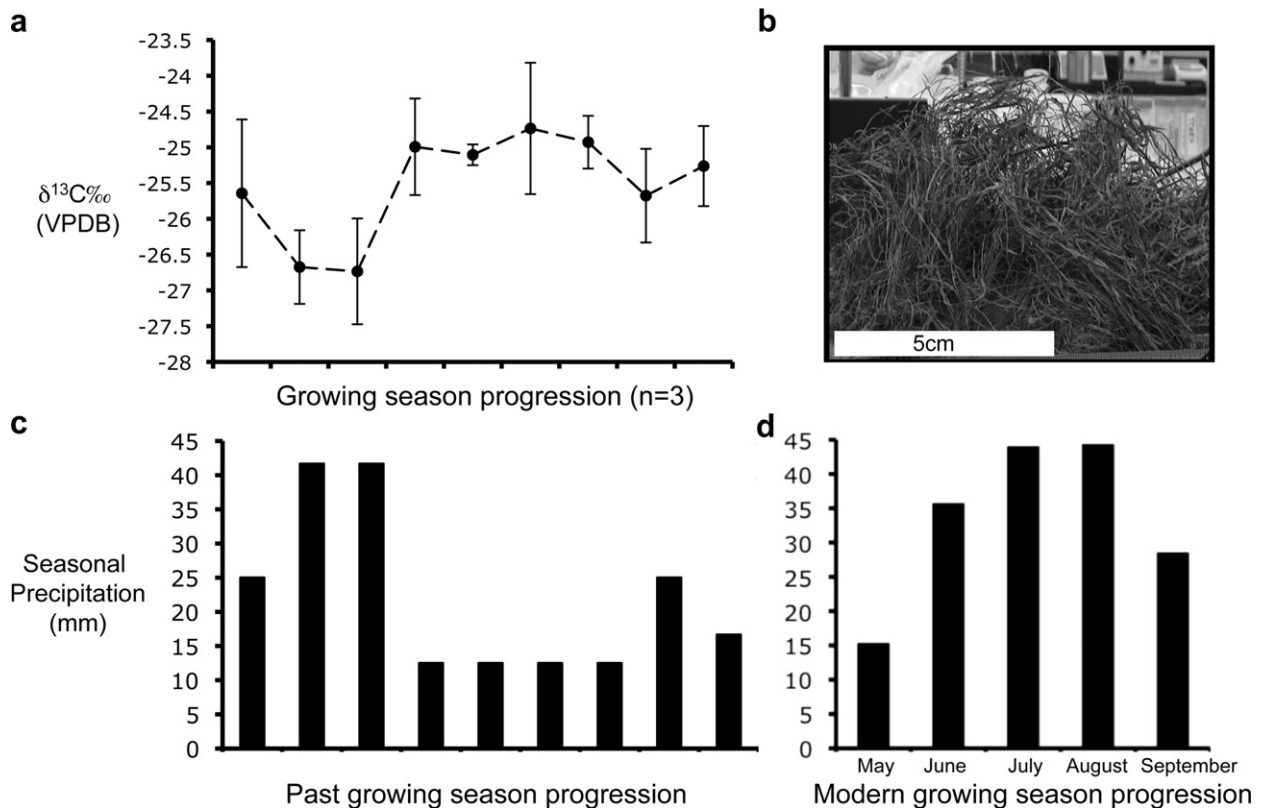

Fig. 11. a) Sequential (sub-annual) $\delta^{13}C$ values from along the leaves of three graminoid specimens attached to the Fox Tunnel paleo-turf b), interior Alaska (redrawn from Wooller et al., 2011), converted to seasonal (growing season) precipitation values c) (Kohn, 2010) and compared with modern seasonal distribution of precipitation in Fairbanks, Alaska d) (Alaska Climate Research Center, 2009).

(2010) simulated vegetation dynamics across northern Eurasia and Alaska, including all of the Arctic, between 42 and 10 ka BP, using a geographically explicit LPj-GUESS dynamic vegetation model. The paleoclimate driving data came from the Hadley Centre Unified Model in 22 time slices. They represented modeled communities as probabilities of occurrence of 11 aggregate plant functional types, including steppe herbs (e.g., *Artemisia* and *Ephedra*) and mesophilous herbs (e.g., Cyperaceae, and Graminoid/forb C$_3$). It is significant that their simulation for 21 ka BP (LGM) showed a pronounced decrease in all arboreal PFTs, while showing a marked increase in mesophilous herbs coverage and higher annual productivity for much of the region, as compared to the late glacial (14 ka BP). Their results are consistent with expectations for the existence of steppe-tundra over large areas of northern Eurasia and North America during the coldest part of the last glacial cycle (Shakun and Carlson, 2010).

Besides climate, the role of abundant grazing mammals that would have trampled snow and vegetation and eventually upturned soils, has been much discussed by several workers. Most notably, Zimov et al. (1995) created a computer model that shows animal disturbance would have perpetuated a steppe-tundra system, even in the absence of particularly dry conditions, that was ultimately interrupted at the end of the Pleistocene by human overhunting of the large mammals (Martin et al., 1982). Modern research in grazing ecology corroborates the model assumptions that animal disturbance promotes grasses (Mckendrick et al., 1980; Mcnaughton, 1984). However, the megafauna in the arctic grasslands would also have been directly feeding on grasses, which produces varying results that suggest grass promotion in some systems and species and grass discouragement in others (Guthrie, 2001). For instance, in sub-Saharan savannah ecosystems wildebeest densities are correlated with shrub-cover because grazing limits grass-fueled fires, which inhibit shrubs (Holdo et al., 2009). This process relies on fire to control woody species, which has not been observed in steppe-tundra.

The herbivore disturbance argument heavily relies on the degree of animal density in the arctic paleograsslands, an estimation that remains elusive for paleontologists. Small mammals, specifically ground squirrels (*Spermophilus/Urocitellus*), may have also contributed to maintaining the paleograsslands. The arctic ground squirrel was apparently more widespread and possibly more common during the late Pleistocene, as documented by the presence of numerous fossil nests and food caches within permafrost sediments at sites in central Alaska and the Yukon (Guthrie, 1968; Eddingaas et al., 2004; Gaglioti et al., submitted; Zazula et al., 2006a, b, 2007, 2010) and over much of NE Eurasia. Today, arctic ground squirrel populations are sustained at stable numbers relative to the snowshoe hare probably due to their avoidance of the winter season bottleneck (hibernation; McLean, 1985). Their overall population is often limited by intraspecific competition for burrows that can be at low availability due to shallow active layers. In arid glacial times, burrow limitations would be eased because seasonal permafrost active layers were much deeper than they are at present due to low soil moisture and thin organic layers across much of this region. Therefore, the colonies may have been more continuous on the landscape (Zazula et al., 2007). This would have proliferated any top-down ecosystem effects from squirrel disturbance that are well documented in modern colonies. The positive effects on Pleistocene grassland productivity and floristic diversity by ground squirrel activity, and their maintenance of habitats used by larger herbivores, may be analogous to the concentrated foraging by plains bison (*Bison bison*) on habitats which include prairie dog colonies (Fahnestock and Detling, 2004).

Squirrel disturbance in the modern arctic tundra favors an increase in grass cover nearby burrow systems (Mckendrick et al., 1980). This is likely due to the annual transport of new, mineral-rich soils from the a and b horizons above ground (Smith and Gardner, 1985). As stated before, grasses thrive in this habitat and are prolific around burrow entrances, even in the most waterlogged landscapes such as the coastal plain of Alaska (Walker et al., 1991). Many squirrel "colonies" on the North Slope of Alaska today are confined to sand and loess−derived riparian zones that allow

Fig. 12. South-facing slope of a bluff in the Tanana valley, Alaska shows a sagebrush (*Artemisia*) − *Poa-Calamagrostis* community with heavy graminoid presence and overall xeric, steppe-like character (Photo by M. Blinnikov).

continuous burrow sites. The expansion of loessal soils on the landscape during the Pleistocene would have made a more continuous habitat for squirrels and perpetuated a disturbance regime needed for a richer grass-dominate ecosystem to sustain the grazing guild (Walker and Everett, 1991).

Although animal disturbance certainly played a role in the ecosystem processes of Pleistocene Beringia, they likely were not the sole driver for a landscape transformation necessary to maintain steppe-tundra. People may have also played a role, especially in Eurasia, where humans have lived for over 100,000 years. Present-day reindeer herder camps on Yamal Peninsula were found to create local disturbance conducive to an increase in grass cover (Walker et al., 2001, 2009, 2011).

Local periglacial geomorphology may also have played a role in maintaining arctic grasslands. Today, pingos in the Arctic frequently have their south-facing slopes occupied by steppe-like vegetation. The existence of steppe forbs and abundant grasses associated with Arcto- alpine species (Fig. 12) prompted researchers to compare these microhabitats to steppe-tundra analogues (Kassler, 1979; Yurtsev, 1982; Walker et al., 1991). Therefore, the processes that maintain these communities can be a natural experiment for the causes of high latitude steppe-tundra. Walker et al. (1991) found that animal disturbances from fox, squirrel and caribou were focused here because of preferred plant selection for nutritional quality, extended snow-free periods and basking. Moreover, insolation is 60% higher on south-facing slopes than on north-facing slopes at high latitudes, and an effective moisture gradient also creates a micro-community that promotes higher soil temperatures, increased mineralization, and fosters the growth of dry-adapted grasses and herbs (Armbruster et al., 2007). As discussed above, these are the wildlife attractors that positively feedback to promote these communities. More research on the community effects of animal exclosures around steppe-tundra analogs will be useful to study these ecosystems.

9. Conclusions

Recent studies involving new proxies such as plant and insect macrofossils, grass and sedge cuticle and phytolith analysis, and stable isotopes, demonstrate great potential to improve our understanding of the taxonomic composition, spatial structure, physiology, and temporal character of the graminoid communities of the Arctic during the Pleistocene. PaleoDNA studies will undoubtedly make further improvements in our ability to detect past plant taxa.

This review demonstrates convincing evidence from multiple proxies that during much of the late Pleistocene (the last glacial–interglacial cycle or 128-12 ka BP), Arctic upland communities were heavily dominated by C_3 Poaceae of the Pooid group, upland sedges, and diverse xeric and cold adapted forbs largely from families typical of the Arctic today, but in different proportions. There is little evidence that a substantial proportion of these communities were elements found much further to the south in either Asia (e.g., Mongolia, Tibet) or North American (e.g., western high deserts of Nevada or Oregon, or the Great Plains) today. Rather, these communities formed primarily from local floral elements in response to the global climate shifts driven by Milankovitch cycles. Communities were further attenuated and maintained in locally shifting mosaics by large mammalian grazers (mammoth, bison, horse, etc.), small mammals (particularly ground squirrels), fire, and changing periglacial landforms (solifluction lobes, pingos). These Pleistocene communities were consistent with what was envisioned by Hultén, Yurtsev, and other proponents of the "tundra-steppe" hypothesis, based on floristic, pollen, and paleontological analysis of mammal remains done earlier in the 20th

century. Such communities were spatially extensive. Away from the ocean, they occupied a majority of upland sites, but were not as spatially homogenous, as reconstructed based on pollen data alone. More mesic communities of sedge and mesophylous grasses formed in the floodplains and close to the open shorelines along the Bering Land Bridge. The most pronounced dry upland communities survived in western Beringia, specifically, in eastern Yakutia, Magadan, and inland Chukotka. Interior Eastern Beringia had similar communities, but developed under less pronounced aridity.

Although we now have more confidence in the taxonomic character of such communities, much remains to be learned about their spatial organization, physiology, and dependence on animal disturbance and other factors. One of the persisting limitations remains sparse data from most of northern Eurasia, especially with respect to macrofossil sites that do not include trees or shrubs, as well as paleoinsect and paleo-phytolith data. Undoubtedly, expansion of the network of well-dated upland sites (e.g., nests, loessal paleosol sequences) will improve our understanding of these ecosystems that occupied large portions of the northern hemisphere of our planet for much of the past 2 million years.

References

Abbott, R.J., Brochmann, C., 2003. History and evolution of the arctic flora: in the footsteps of Eric Hultén. Molecular Ecology 12, 299–313.

Abbott, R.J., Smith, L.C., Milne, R.I., Crawford, R.M.M., Wolff, K., Balfour, J., 2000. Molecular analysis of plant migration and refugia in the Arctic. Science 289, 1343–1346.

Ager, T.A., 2003. Late Quaternary vegetation and climate history of the central Bering land bridge from St. Michael Island, western Alaska. Quaternary Research 60, 19–32.

Alaska Climate Research Center, 2009. A century of climate change for fairbanks. Alaska, Arctic, September 2009. Online at. http://climate.gi.alaska.edu/.

Alfimov, A.V., Berman, D.I., 2001. Beringian climate during the Late Pleistocene and Holocene. Quaternary Science Reviews 20, 127–134.

Allen, J.R.M., Hickler, T., Singarayer, J.S., Sykes, M.T., Valdes, P.J., Huntley, B., 2010. Last glacial vegetation of northern Eurasia. Quaternary Science Reviews 29, 2604–2618.

Anderson, P.M., Brubaker, L.B., 1994. Vegetation history of north-central Alaska: mapped summary of late-Quaternary pollen data. Quaternary Science Reviews 13, 71–92.

Anderson, P.M., Bartlein, P.J., Brubaker, L.B., 1994. Late Quaternary history of tundra vegetation In Northwestern Alaska. Quaternary Research 41, 306–315.

Anderson, P.M., Lozhkin, A.V., 1995. Late Quaternary lacustrine pollen records from northwestern Beringia: new results and paleoenvironmental implications. Geology of the Pacific Ocean 14, 8–17.

Anderson, P.M., Lozhkin, A.V., Solomatkina, T.B., Brown, T.A., 2010. Paleoclimatic implications of glacial and postglacial refugia for *Pinus pumila* in western Beringia. Quaternary Research 73, 269–276.

Andreev, A.A., Tarasov, P.E., Siegert, C., Ebel, T., Klimanov, V.A., Melles, M., Bobrov, A.A., Dereviagin, A.Yu., Lubinski, D.J., Hubberten, H.-W., 2003. Late Pleistocene and Holocene vegetation and climate of the northern Taymyr Peninsula, Arctic Russia. Boreas 32, 484–505.

Anderson, P., Bennike, O., Bigelow, N., Brigham-Grette, J., Duvall, M., Edwards, M., Frechette, B., Funder, S., Johnsen, S., Knies, J., Koerner, R., Lozhkin, A., Marshall, S., Matthiessen, J., Macdonald, G., Miller, G., Montoya, M., Muhs, D., Otto-Bliesner, B., Overpeck, J., Reeh, N., Sejrup, H.P., Spielhagen, R., Turner, C., Velichko, A., CircumArctic PaleoEnvironments (CAPE) – Last Interglacial Project Members, 2006. Last Interglacial Arctic warmth confirms polar amplification of climate change. Quaternary Science Reviews 25, 1383–1400.

Andreev, A.A., Grosee, G., Schirrmeister, L., Kuznetsova, T.V., Kuzmina, S.A., Bobrov, A.A., Tarasov, P.E., Novenko, E.Y., Meyer, H., Derevyagin, A.Y., Kienast, F., Bryantseva, A., Kunitsky, V., 2008. Weichselian and Holocene paleoenvironmental history of the Bol'shoy Lyakhovsky Island, New Siberian Archipelago, Arctic Siberia. Boreas. doi:10.1111/j.1502–3885.2008.00039.x.

Angiosperm Phylogeny Group (APG), 2009. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161, 105–121.

Arkhipov, S.A., Volkova, V.S., Zolnikov, I.D., Zykina, V.S., Krukover, A.A., Kulkova, I.A., 1999. In: Velichko, A.A. (Ed.), Zapadnaja Sibir. Pp. 84–109 in Climate and environment changes during the last 65 million years (Cenozoic: from Paleocene to Holocene). GEOS, Moscow (In Russian).

Armbruster, W.S., Rae, D., Edwards, M.E., 2007. Topographic complexity and biotic response to high-latitude climate change: variance is as important as the mean. In: Orbaek, J.B., Kallenborn, R., Tombre, I., Hegseth, E.N., Falk-Petersen, S., Hoel, A.H. (Eds.), Arctic-Alpine Ecosystems and People in a Changing Environment. Springer.

Astakhov, V., Nazarov, D., 2010. Correlation of Upper Pleistocene sediments in northern West Siberia. Quaternary Science Reviews 29, 3615–3629.

Barber, V.A., Finney, B.P., 2000. Late Quaternary paleoclimatic reconstructions for interior Alaska based on paleolake-level data and hydrologic models. Journal of Paleolimnology 24, 29–41.

Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M., 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparison with paleoenvironmental data. Quaternary Science Reviews 17, 549–585.

Bateman, M.D., Murton, J.B., 2006. Late Pleistocene glacial and periglacial aeolian activity in the Tuktoyaktuk Coastlands, NWT, Canada. Quaternary Science Reviews 25, 2552–2568.

Batzli, G.O.S., 1980. Distribution, abundance, and foraging patterns of ground squirrels near Atkasook, Alaska. Arctic Antarctic and Alpine Research 12, 501–510.

Berman, D., Alfimov, A., Kuzmina, S., 2010. Invertebrates of the relict steppe ecosystems of Beringia, and the reconstruction of Pleistocene landscapes. Quaternary Science Reviews. doi:10.1016/j.quascirev.2010.09.016.

Bigelow, N.H., Edwards, M.E., 2001. A 14,000 yr paleoenvironmental record from Windmill Lake, Central Alaska: Late Glacial and Holocene vegetation in the Alaska Range. Quaternary Science Reviews 20, 203–215.

Binney, H.A., Willis, K.J., Edwards, M.E., Bhagwat, S.A., Anderson, P.M., Andreev, A.A., Blaauw, M., Damblon, F., Haesaerts, P., Kienast, F., Kremenetski, K.V., Krivonogov, S.K., Lozhkin, A.V., MacDonald, G.M., Novenko, E.Y., Oksanen, P., Sapelko, T.V., Valiranta, M., Vazhenina, L., 2009. The distribution of late-Quaternary woody taxa in northern Eurasia: evidence from a new macro-fossil database,. Quaternary Science Reviews 28, 2445–2464.

Birks, H.J.B., Birks, H.H., 1980. Quaternary Palaeoecology. Edward Arnold, London, UK.

Blackman, E., 1971. Opaline silica bodies in the range grasses of southern Alberta. Canadian Journal of Botany 49, 769–781.

Blinnikov, M.S., 1994. Phytolith analysis and Holocene dynamics of alpine vegetation. Veroffentlichungen des Geobotanischen Inst. Stiftung Rübel, Zurich, H. 115, pp. 23–42.

Blinnikov, M.S., 2005. Phytoliths in plants and soils of the interior Pacific Northwest, USA. Review of Palaeobotany and Palynology 135, 71–98.

Blinnikov, M., Busacca, A., Whitlock, C., 2002. Reconstruction of the late Pleistocene grassland of the Columbia basin, Washington, USA, based on phytolith records in loess. Palaeogeography Palaeoclimatology Palaeoecology 177, 77–101.

Blinnikov, M., Wooller, M., Zazula, G., 2010. Grass phytoliths as proxies of tundra-steppe vegetation of eastern Beringia in the late Pleistocene. In: Abstracts of the 40th Arctic Workshop, INSTAAR, Winter Park, CO.

Bliss, L.C., 2000. Arctic tundra and polar desert biome. In: Barbour, M.G., Billings, W.D. (Eds.), Terrestrial Vegetation of the United States. Cambridge University Press, New York, NY, pp. 1–41.

Boeskorov, G.G., 2005. Arctic Siberia: refuge of the Mammoth fauna in the Holocene. Quaternary International 142-143, 119–123.

Bombin, M., 1984. On phytoliths, late Quaternary ecology of Beringia, and information evolutionary theory. Unpublished PhD dissertation, Department of Anthropology, University of Alberta, Edmonton, Alberta, Canada.

Bremond, L., Alexandre, A., Wooller, M.J., Hely, C., Williamson, D., Schafer, P.A., 2008. Phytolith indices as proxies of grass subfamilies on East African tropical mountains. Global and Planetary Change 61, 209–224. doi:10.1016/j.gloplacha.2007.08.016.

Brigham-Grette, J., 2001. New perspectives on Beringian Quaternary paleogeography, stratigraphy, and glacial history. Quaternary Science Reviews 20, 15–24.

Brigham-Grette, J., Melles, M., Minyuk, P., 2007. Overview and significance of a new 250 ka paleoclimate record from El'gygytgyn Crater Lake, NE Russia. Journal of Paleolimnology 37, 1–16.

Bromwich, D., Toracinta, E., Oglesby, R., Fastook, J., Hughes, T., 2005. LGM Summer Climate on the southern margin of the Laurentide ice sheet: wet or dry? Journal of Climate 18, 3317–3338.

Brubaker, L.B., Gajewski, K., Ritchie, J.C., 1989. Modern analogues of late-Quaternary pollen spectra from the western interior of North America. Journal of Biogeography 16, 537–596.

Brubaker, L.B., Anderson, P.M., Edwards, M.E., Lozhkin, A.V., 2005. Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data.

Burney, D.A., Flannery, T.F., 2005. Fifty millennia of catastrophic extinctions after human contact. Trends in Ecology and Evolution 20, 395–401.

Callaghan, T.V., Körner, C., Heal, O.W., Lee, S.E., Cornelissen, J.H.C., 1998. Scenarios for ecosystem responses to global change. In: Heal, O.W., Callaghan, T.V., Cornelissen, J.H.C., Körner, C., Lee, S.E. (Eds.), Global Change in Europe's Cold

Regions. Part 1, 27. European Commission. Ecosystem Research Report, pp. 11–63.

Carnelli, A.L., Theurillat, J.-P., Madella, M., 2004. Phytolith types and type-frequencies in subalpine-alpine plant species of the European Alps. Review of Palaeobotany and Palynology 129, 39–65.

CAVM Team, 2003. Circumpolar Arctic Vegetation Map. (1:7,500,000 scale), Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Carter, L.D., 1981. A Pleistocene sand sea on the Alaskan Arctic coastal plain. Science 211, 381–383.

Carter, J.A., 2009. Atmospheric carbon isotope signatures in phytolith-occluded carbon. Quaternary International 193, 20–29.

Cerling, T.E., Wang, Y., Quade, J., 1993. Expansion of C$_4$ ecosystems as an indicator of global ecological change in the late Miocene. Nature 361, 344–345.

Chapin, F.S., Starfield, A.M., 1997. Time lags and novel ecosystems in response to transient climatic change in Arctic Alaska. Climatic Change 35, 449–461.

Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.L., Tape, K.D., Thompson, C.D.C., Walker, D.A., Welker, J.M., 2005. Role of land-surface changes in Arctic summer warming. Science 310, 657–660.

Chersky, I.D., 1891. Description of the post-Tertiary mammal collection found by New Siberian expedition 1885-1886. Notes of Russian Academy of Science 65, 706.

Coats, L, Cole, K., Mead, J., 2008. 50,000 years of vegetation and climate history on the Colorado Plateau, Utah and Arizona. USA. Quaternary Research 70, 322–338.

COHMAP Members, 1988. Climatic changes of the last 18,000 years: observations and model simulations. Science 241, 1043–1053.

Colinvaux, P., 1964. The environment of the Bering Land Bridge. Ecological Monographs 34, 297–325.

Colinvaux, P., 1996. Pollen records: point Barrow, Pribilof Archipelago, and Imuruk Lake. In: West, F.H. (Ed.), American Beginnings: The Prehistory and Paleoecology of Beringia. University of Chicago Press, Chicago, IL, pp. 83–96.

Coupland, R.T., 1992. Overview of the grassland of North America. In: Natural Grasslands: Introduction and Western Hemisphere. Ecosystems of the World, 8A. Elsevier, Amsterdam, the Netherlands, pp. 147–149.

Cwynar, L.C., 1982. A Late-Quaternary history from Hanging Lake, Northern Yukon. Ecological Monographs 52, 1–24.

Cwynar, L.C., Ritchie, J.C., 1980. Arctic steppe tundra – a Yukon perspective. Science 208, 1375–1377.

Day, T.A., Ruhland, C.T., Xiong, F.S., 2008. Warming increases aboveground plant biomass and C stocks in vascular-plant-dominated Antarctic tundra. Global Change 14, 1827–1843.

Eddingaas, A.A., Jacobsen, B.K., Lessa, E.P., Cook, J.A., 2004. Evolutionary history of the arctic ground squirrel (Spermophilus parryii) in nearctic Beringia. Journal of Mammalogy 85, 601–610.

Edwards, M.E., Anderson, P.M., Brubaker, L.B., Ager, T., Andreev, A.A., Bigelow, N.H., Cwynar, L.C., Eisner, W.R., Harrison, S.P., Hu, F.-S., Jolly, D., Lozhkin, A.V., MacDonald, G.M., Mock, C.J., Ritchie, J.C., Sher, A.V., Spear, R.W., Williams, J., Yu, G., 2000. Pollen-based biomes for Beringia 18,000, 6000 and 0 ^{14}C yr. B.P. Journal of Biogeography 27, 521–554.

Edwards, M.E., Mock, C.J., Finney, B.P., Barber, V.A., Bartlein, P.J., 2001. Modern-climate analogues for paleoclimatic variations in eastern interior Alaska during the past 14,000 years: atmospheric-circulation controls of regional temperature and moisture responses. Quaternary Science Reviews 20, 189–202.

Edwards, E.J., Osborne, C.P., Strömberg, C.A.E., Smith, S.A., 2010. The origins of C$_4$ grasslands: integrating evolution and ecosystem science. Science 328, 587–591.

Eidesen, P.B., Carlsen, T., Molau, U., Brochmann, C., 2007. Repeatedly out of Beringia: Cassiope tetragona embraces the Arctic. Journal of Biogeography 34, 1559–1574.

Elias, S.A., 2000. Late Pleistocene climates of Beringia, based on fossil beetle analysis. Quaternary Research 53, 229–235.

Elias, S.A., 2001. Mutual climatic range reconstructions of seasonal temperatures based on Late-Pleistocene fossil beetle assemblages in Eastern Beringia. Quaternary Science Reviews 20, 77–91.

Elias, S.A., 2007. Beetle records in the Late Pleistocene North America. In: Elias, S.A. (Ed.), Encyclopedia of Quaternary Science. Elsevier, Amsterdam, pp. 222–236.

Elias, S.A., Crocker, B., 2008. The Bering Land Bridge: a moisture barrier to the dispersal of steppe-tundra biota? Quaternary Science Reviews 27, 2473–2483.

Elias, S.A., Short, S.K., Birks, H.H., 1997. Late Wisconsinan environments of the Bering land bridge. Palaeogeography, Palaeoclimatology, Palaeoecology 136, 293–308.

Elias, S.A., Berman, D., Alfimov, A., 2000. Late Pleistocene beetle faunas of Beringia: where east met west. Journal of Biogeography 27, 1349–1363.

Elias, S.A., Kuzmina, S., Kiselyov, S., 2006. Late Tertiary origins of the Arctic beetle fauna. Palaeogeography, Palaeoclimatology, Palaeoecology 241, 373–392.

Elven, R. (Ed.), 2007. Checklist of the Panarctic Flora Vascular Plants. http://www.binran.ru/infsys/paflist/index.htm.

England, J.H., Furze, M.F.A., Doupe, J.P., 2009. Revision of the NW Laurentide Ice Sheet: implications for paleoclimate, the northeast extremity of Beringia, and Arctic Ocean sedimentation. Quaternary Science Reviews 28, 1573–1596.

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analysis. John Wiley & Sons, Chichester, UK.

Fahnestock, J.T., Detling, J.K., 2004. Plant-animal Interactions. Bison-prairie dog-plant interactions in a North American mixed-grass prairie. Oecologia 132, 86–95.

Fox-Dobbs, K., Leonard, J.A., Koch, P.L., 2008. Pleistocene megafauna from eastern Beringia: Paleoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records. Palaeogeography, Palaeoclimatology, Palaeoecology 261, 30–46.

Fradkina, A.F., Alekseev, M.N., Andreev, A.A., Klimanov, V.A., 1999. Vostochanya Sibir (na primere tsentralnoy Yakutii). In: Velichko, A.A. (Ed.), Climate and environment changes during the last 65 million years (Cenozoic: from Paleocene to Holocene). GEOS, Moscow (in Russian), Pp. 110–127.

Fredlund, G.G., Tieszen, L.T., 1994. Modern phytolith assemblages from the North American Great Plains. Journal of Biogeography 21, 321–335.

Funder, S., Bennike, O., Böcher, J., Israelson, C., Petersen, K.S., Simonarson, L.A., 2001. Late Pliocene Greenland – the Kap København formation in North Greenland. Bulletin of the Geological Society of Denmark 48, 177–184.

Gaglioti, B.V., Severin, K., Wooller, M.J., 2010. Developing graminoid cuticle analysis for application to Beringian palaeoecology. Review of Palaeobotany and Palynology 162, 95–110.

Gaglioti, B.V., Barnes, B. M., Zazula, G. D., Beaudoin, A. B., Wooller, M. J. Submitted Late Pleistocene paleoecology of arctic ground squirrel caches and nests from Interior Alaska's mammoth-steppe ecosystem. Quaternary Research.

Gibbard, P.L., Boreham, S., Cohen, K.M., Moscariello, A., 2007. Global chronostratigraphical correlation table for the last 2.7 million years v. 2007b. Subcommission on Quaternary Stratigraphy. Department of Geography, University of Cambridge, Cambridge, England.

Gibson, D.J., 2009. Grasses and grassland ecology. Oxford University Press, New York, NY.

Godwin, H., 1975. The History of the British Flora, second ed.. Cambridge University Press.

Goetcheus, V.G., Birks, H.H., 2001. Full-glacial upland tundra vegetation preserved under tephra in the Beringia National Park, Seward Peninsula, Alaska. Quaternary Science Reviews 20, 135–147.

Grass Phlogeny Working Group (GPWG), 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). Annals of the Missouri Botanical Garden 88, 373–457.

Grichuk, V.P., Zaklinskaya, 1950. Pyltsevoj analiz (In Russian) Moscow.

Gubin, S.V., Maksimovich, S.V., Zanina, O.G., 2001. Analiz sostava semyan rastenij iz iskopaemykh nor suslikov lessovo-ledovykh otlozhenij obnazhenija Zelenyj mys kak pokazatel mestnykh uslovij obitania. (Composition of seeds from fossil gopher burrows in the ice-loess deposits of Zelony Mys as environmental indicator. Kriosfera Zemli 2, 76–82 (in Russian).

Gubin, S.V., Zanina, O.G., Maximovich, S.V., Kuzmina, S.A., Zazhigin, V.S., 2003. Reconstruction of ice complex sediment formation conditions based on study of Late Pleistocene rodent burrows. Kriosfera Zemli 3, 13–22 (in Russian).

Guthrie, R.D., 1968a. Paleoecology of the large-mammal community in interior Alaska during the late Pleistocene. American Midland Naturalist 79, 346–363.

Guthrie, R.D., 1968b. Paleoecology of a late Pleistocene small mammal community from interior Alaska. Arctic 21, 223–244.

Guthrie, R.D., 1982. Mammals of the Mammoth Steppe as paleoenvironmental indicators. In: Hopkins, D.M., MatthewsJr., J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia, pp. 307–326.

Guthrie, R.D., 1990. Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe. University of Chicago Press, Chicago, IL.

Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. Quaternary Science Reviews 20, 549–574.

Hamilton, T.D., 1982. A Late Pleistocene glacial chronology for the southern Brooks range - Stratigraphic record and regional significance. Geological Society of America Bulletin 93, 700–716.

Hamilton, T.D., 1994. Late Cenozoic glaciation of Alaska. In: Plafker, G., Berg, H.C. (Eds.), The Geology of North America, G-1, The Geology of Alaska. Geological Society of America, Boulder, Colorado, pp. 813–844.

Harington, C.R., 1978. Quaternary vertebrate faunas of Canada and Alaska and their suggested chronological sequence. Syllogeus 15, 1–105.

Harington, C.R., 2005. The eastern limit of Beringia: mammoth remains from Banks and Melville islands, Northwest Territories. Arctic 58, 361–369.

Harrison, S.P., Kutzbach, J.E., Prentice, I.C., Behling, P., Sykes, M.T., 1995. The reponse of northern hemisphere extratropical climate and vegetation to orbitally-induced changes in insolation during the last interglacial: results of atmospheric general circulation model and biome simulations. Quaternary Research 43, 174–184.

Haxeltine, A., Prentice, I.C., 1996. BIOME3: an equilibrium biosphere model based on ecophysiological constraints, resource availability and competition among plant functional types. Global Biogeochemical Cycles 10, 693–709.

Helliker, B.R., Ehleringer, J.R., 2002. Grass blades as tree rings: environmentally induced changes in the oxygen isotope ratio of cellulose along the length of grass blades. New Phytologist 155, 417–424.

Hibbert, D., 1982. History of the steppe-tundra concept. In: Hopkins, D.M., MatthewsJr., J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 153–156.

Higuera, P., Brubaker, L., Anderson, P., Brown, T., Kennedy, A., Hu, F., Chave, J., 2008. Frequent fires in ancient shrub tundra: implications of paleorecords for Arctic environmental change. PLoS ONE 3, e0001744.

Hodson, M.J., Parker, A.G., Leng, M.J., et al., 2008. Silicon, oxygen and carbon isotope composition of wheat (*Triticum aestivum* L.) phytoliths: implications for palaeoecology and archaeology. Journal of Quaternary Science 23, 331–339.

Holdo, R.M., Holt, R.D., Fryxell, J.M., 2009. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. Ecological Applications 19, 95–109.

Hopkins, D.M., 1967. The Bering land bridge. Stanford University Press, Palo Alto, CA.

Hopkins, D.M., 1972. The paleogeography and climatic history of Beringia during late Cenozoic time. Internord. International Journal of Nordic Studies 12, 121–150.

Hopkins, D.M., MatthewsJr., J.V., Schweger, C.E., Young, S.B. (Eds.), 1982. Paleoecology of Beringia. Academic Press, New York, NY.

Hu, F.S., Brubaker, L.B., Anderson, P.M., 1993. A 12000-year record of vegetation change and soil development from Wien Lake, Central Alaska. Canadian Journal of Botany 71, 1133–1142.

Hughen, K., Lehman, S., Southon, J., Overpeck, J., Marchal, O., Herring, C., Turnbull, J., 2004. 14C activity and global carbon cycle changes over the past 50,000 years. Science 303, 202–270.

Hultén, E., 1937. Outline of the History of Arctic and Boreal Biota During the Quaternary Period. Bokforlagsaktiebolaget, Stockholm, Sweden.

Hultén, E., 1968. Flora of Alaska and Neighbouring Territories: A Manual of the Vascular Plants. Stanford University Press, Palo Alto, CA.

Huybers, P., 2007. Glacial variability over the last two million years: an extended depth-derived age model, continuous obliquity pacing, and the Pleistocene glaciations. Quaternary Science Reviews 26, 37–55.

Jansen, E., Overpeck, J., Briffa, K.R., Duplessy, J.-C., Joos, F., Masson-Delmotte, V., Olago, D., Otto-Bliesner, B., Peltier, W.R., Rahmstorf, S., Ramesh, R., Raynaud, D., Rind, D., Solomina, O., Villalba, R., Zhang, D., 2007. Palaeoclimate. Contribution of working group I to the Fourth assessment Report of the Intergovernmental Panel on climate change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007 – The Physical Science Basis. Cambridge University Press, Cambridge, United Kingdom and New York, pp. 434–497.

Jiménez-Moreno, G., Anderson, R.S., Desprat, S., Grigg, L.D., Grimm, E.C., Heusser, L.E., Jacobs, B.F., López-Martínez, C., Whitlock, C.L., Willard, D.A., 2010. Millennial-scale variability during the last glacial in vegetation records from North America. Quaternary Science Reviews 29, 2865–2881.

Jolly, D., Harrison, S.P., Damnati, B., Bonnefille, R., 1998. Simulated climate and biomes of Africa during the Late Quaternary: comparison with pollen and lake status data. Quaternary Science Reviews 17, 629–657.

Kaplan, J., New, M., 2006. Arctic climate change with a 2°C global warming: timing, climate patterns and vegetation change. Climatic Change 79, 213–241.

Kaplan, J.O., Bigelow, N.H., Bartlein, P.J., Christiansen, T.R., Cramer, W., Harrison, S.P., Matveyeva, N.V., McGuire, A.D., Murray, D.F., Prentice, I.C., Razzhivin, V.Y., Smith, B., Walker, D.A., Anderson, P.M., Andreev, A.A., Brubaker, L.B., Edwards, M.E., Lozhkin, A.V., Ritchie, J.C., 2003. Climate change and arctic ecosystems II: modeling paleodata-model comparisons, and future projections. Journal of Geophysical Research 108 (D19), 8171. doi:10.1029/2002JD002559.

Kassler, K. C., 1979. Relics of the Late Pleistocene Arctic-Steppe: Investigations of Certain South-Facing Slopes in Interior Alaska. BA Thesis, Middlebury College, VT.

Kellogg, E.A., Watson, L., 1993. Phylogenetic studies of a large data set. 1. Bambusoideae, Andropogonodae, and Pooideae (Gramineae). Botanical Review 59, 273–343.

Kerns, B., 2001. Diagnostic phytoliths for a ponderosa pine-bunchgrass community near Flagstaff, Arizona. Southwestern Naturalist 46, 282–294.

Kienast, F., Siegert, C., Dereviagin, A., Mai, D.H., 2001. Climatic implications of Late Quaternary plant macrofossil assemblages from the Taymyr Peninsula, Siberia. Global and Planetary Change 31, 265–281.

Kienast, F., Schirrmeister, L., Siegert, C., Tarasov, P., 2005. Palaeobotanical evidence for warm summers in the East Siberian Arctic during the last cold stage. Quaternary Research 63, 283–300.

Kiseleva, N.K., 1989. Phytolith analysis of zoogenic deposits and buried soils. In: Dinesman, L.G., Kiseleva, N.K., Kmnyazev, A.V. (Eds.), Istoriya stepnykh ekosistem Mongolskoj narodnoj respubliki. Nauka, Moscow (In Russian).

Kiselyov, S.V., 1981. Late Cenozoic Coleoptera of Northeastern Siberia. U.S.S.R. Academy of Sciences, Paleontological Institute, Nauka, Moscow (in Russian).

Kittel, T.G.F., Steffen, W.L., Chapin III, F.S., 2000. Global and regional modelling of Arctic-boreal vegetation distribution and its sensitivity to altered forcing. Global Change Biology 6 (Suppl. 1), 1–18.

Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. PNAS 107, 19691–19695.

Kozhevnikov, J.P., Ukraintseva, V.V., 1999. . Pleistocene tundra-steppe: arguments pro and con. In: Haynes, G., Klimowicz, J., Reumer, J.W.F. (Eds.), Mammoths and the Mammoth Fauna: Studies of an Extinct Ecosystem, Proceedings of the First International Mammoth Conference, St. Petersburg, Russia, October 16-21, 1995, pp. 199–210.

Krestov, P.A., Barkalov, V.Yu., Omelko, A.M., Yakubov, V.V., Nakamura, Yu., Sato, K., 2009. Relic vegetation complexes in the modern refugia of Northeast Asia. Komarovskie Chteniya 56, 5–63 (in Russian).

Kucherov, I.B., Daniels, F.J.A., 2005. Vegetation of the classes Carici-Kobresietea and Cleistogenetea squarrosae in central Chukotka. Phytocoenologia 35, 1019–1066.

Kukla, G.J., Bender, M.L., de Beaulieu, J.-L., Bon, G., Broecker, W.S., Cleveringa, P., Gavin, J.E., Herbert, T.D., Imbrie, J., Jouzel, J., Keigwin, L.D., Knudsen, K.-L., Mcmanus, J.F., Merkt, J., Muhs, D.R., Müller, H., Poore, R.Z., Porter, S.C., Seret, G., Shackleton, N.J., Turner, C., Tzedakis, P.C., Winograd, I.J., 2002. Last interglacial climates. Quaternary Research 58, 2–13.

Kurek, J., Cwynar, L.C., Vermaire, J.C., 2009. A Late Quaternary paleotemperature record from Hanging Lake, Northern Yukon territory, Eastern Beringia. Quaternary Research 72, 246–257.

Kutzbach, J.E., Gallimore, R., Harrison, S.P., Behling, P., Selin, R., Laarif, F., 1998. Climate and biome simulations for the past 21,000 years. Quaternary Science Reviews 17, 473–506.

Kuzmina, S., Elias, S., Matheus, P., Storer, J.E., Sher, A., 2008. Paleoenvironmental reconstruction of the last glacial maximum, inferred from insect fossils from a tephra buried soil at Tempest Lake, Seward Peninsula, Alaska. Palaeogeography Palaeoclimatology Palaeoecology 267, 245–255.

Kuzmina, S.A., Sher, A.V., Edwards, M.E., Haile, J., Yan, E.V., Kotov, A.V., Willerslev, E., 2010. The late Pleistocene environment of the eastern west beringia based on the principal section at the Main River, Chukotka. Quaternary Science Reviews. doi:10.1016/j.quascirev.2010.03.019.

Laxton, N.F., Burn, C.R., Smith, C.A.S., 1996. Productivity of Loessal grasslands in the Kluane lake region, Yukon territory, and the Beringian 'production paradox'. Arctic 49, 129–140.

Lea, P.D., Waythomas, C.F., 1990. Late-Pleistocene eolian sand sheets in Alaska. Quaternary Research 34, 269–281.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic δ^{18}O records. Paleoceanography 20, PA1003. doi:10.1029/2004PA001071.

Lloyd, A.H., Armbruster, W.S., Edwards, M.E., 1994. Ecology of a steppe-tundra gradient in interior Alaska. Journal of Vegetation Science 5, 897–912.

Lozhkin, A.V., Anderson, P.M., 2011. Forest or no forest: implications of the vegetation record for climatic stability in Western Beringia during Oxygen Isotope Stage 3. Quaternary Science Reviews. doi:10.1016/j.quascirev.2010.12.022.

Lozhkin, A.V., Anderson, P.M., Matrosova, T.V., Minyuk, P.S., 2007. The pollen record from El'gygytgyn Lake: implications for vegetation and climate histories of northern Chukotka since the Late Middle Pleistocene. Journal of Paleolimnology 37, 135–153.

Lu, H.-Y., Wu, N.-Q., Yang, X.-D., Jiang, H., Liu, K.-B., Liu, T.S., 2006. Phytoliths as quantitative indicators for the reconstruction of past environmental conditions in China I: phytolith-based transfer functions. Quaternary Science Reviews 25, 945–959.

Maglio, V., 1973. Origin and evolution of the Elephantidae. Transactions of the American Philosophical Society 63, 1–149.

Manley, W.F., 2002. Digital Elevation Model (DEM) for the Bering Land Bridge: INSTAAR, vol. 1. University of Colorado. http://instaar.colorado.edu/QGISL/bering_land_bridge.

Mann, D.H., Heiser, P.A., Finney, B.P., 2002a. Holocene history of the great Kobuk Sand Dunes, Northwestern Alaska. Quaternary Science Reviews 21, 709–731.

Mann, D.H., Peteet, D.M., Reanier, R.E., Kunz, M.L., 2002b. Responses of an arctic landscape to Lateglacial and early Holocene climatic changes: the importance of moisture. Quaternary Science Reviews 21, 997–1021.

Martin, P.J., 1982. In: Hopkins, D., et al. (Eds.), Digestive and grazing strategies of animals in the Arctic steppe. Paleoecology of Beringia, pp. 259–266.

Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore Jr., T.C., Shackleton, N.J., 1987. Age dating and the orbital theory of the ice ages: development of a long resolution 0 to 300,000-year chronostratigraphy. Quaternary Research 27, 1–29.

Matthews Jr., J.V., 1974. Quaternary environments at Cape Deceit (Seward Peninsula, Alaska): evolution of a tundra ecosystem. Geological Society of America Bulletin 85, 1353–1384.

Matthews, J.V., 1982. East Beringia during Late Wisconsin time: a review of the biotic evidence. In: Hopkins, D.M., Matthews, J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 127–150.

Matthews Jr., J.V., Ovenden, L.E., 1990. Late Tertiary plant macrofossils from localities in arctic, subarctic North America — a review of the data. Arctic 43, 364–392.

Matthews Jr., J.V., Telka, A., 1997. Insect fossils from the Yukon. In: Danks, H.V., Downes, J.A. (Eds.), Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Canada, pp. 911–962.

McIver, E.E., Basinger, J.F., 1999. Early Tertiary floral evolution in the Arctic. Annals of the Missouri Botanical Garden 86, 523–545.

McLean, I.G., 1985. Seasonal patterns and sexual differences in the feeding ecology of arctic ground squirrels. Canadian Journal of Zoology 63, 1298–1301.

Mckendrick, J.D., Batzli, G.O., Everett, K.R., Swanson, J.C., 1980. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. Arctic and Alpine Research 12, 565–578.

Mcnaughton, S.J., 1984. Grazing lawns - animals in herds, plant form, and coevolution. American Naturalist 124, 863–886.

Metcalfe, C.R., 1960. Anatomy of the monocotyledons. Volume I. Gramineae. Clarendon Press, Oxford.

Milner, C., Hughes, R.E., 1968. Methods for the measurement of the primary production of grassland. Blackwell Scientific, Oxford, UK.

Minckley, T.A., Bartlein, P.J., Whitlock, C., Shuman, B.N., Williams, J.W., Davis, O.K., 2008. Associations among modern pollen, vegetation, and climate in western North America. Quaternary Science Reviews 27, 1962–1991.

Moorcroft, P.R., 2003. Recent advances in ecosystem-atmosphere interactions: an ecological perspective. In: Proceedings of the Royal Society B: Biological Sciences, 270, pp. 1215–1227.

Morris, L.R., Baker, F.A., Morris, C., Ryel, R.J., 2009. Phytolith types and type-frequencies in native and introduced species of the sagebrush steppe and pinyon–juniper woodlands of the Great Basin, USA. Review of Palaeobotany and Palynology 157, 339–357.

Muhs, D.R., Ager, T.A., Beget, J.E., 2001. Vegetation and paleoclimate of the Last Interglacial period, Central Alaska. Quaternary Science Reviews 20, 41–61.

Muhs, D.R., Ager, T.A., Bettis, E.A., McGeehin, J., Been, J.M., Beget, J.E., Pavich, M.J., Stafford, T.W., Stevens, D.S.P., 2003. Stratigraphy and palaeoclimatic significance of Late Quaternary loess-palaeosol sequences of the Last Interglacial-Glacial cycle in central Alaska. Quaternary Science Reviews 22, 1947–1986.

Mulholland, S.C., 1989. Phytolith shape frequencies in North Dakota grasses: a comparison to general patterns. Journal of Archaeological Science 16, 489–511.

Müller, S., Tarasov, P., Andreev, A., Tütken, T., Gartz, S., Diekmann, B., 2010. Late Quaternary vegetation and environments in the Verkhoyansk Mountains region (NE Asia) reconstructed from a 50-kyr fossil pollen record from Lake Billyakh. Quaternary Science Reviews 29, 2071–2086.

Nehring, A., 1890. Über Tundren und Steppen der Jetzt- und Vorzeit, mit besonderer Berüchsichtigung ihrer Fauna. Berlin.

Nelson, D.M., Hu, F.S., Scholes, D.R., 2008. Using SPIRAL (Single pollen isotope ratio AnaLysis) to estimate C-3- and C-4-grass abundance in the paleorecord. Earth and Planetary Science Letters 269, 11–16.

Nimis, P.L., Malyshev, L.I., Bolognini, G., Friesen, N., 1998. A multivariate phytogeographic analysis of plant diversity in the Putorana Plateau (N. Siberia). Opera Botanica 136, 1–72.

Nunez, E., MacFadden, B., Mead, J., Baez, A., 2010. Ancient forests and grasslands in the desert: diet and habitat of Late Pleistocene mammals from Northcentral Sonora, Mexico. Palaeogeography, Palaeoclimatology, Palaeoecology 297, 391–400.

O'Leary, M.H., 1988. Carbon isotopes in photosynthesis. Bioscience 38, 328–336.

Oswald, W.W., Brubaker, L.B., Hu, F.S., Gavin, D.G., 2003a. Pollen-vegetation calibration for tundra communities in the Arctic Foothills, Northern Alaska. Journal of Ecology 91, 1022–1033.

Oswald, W.W., Brubaker, L.B., Hu, F.S., Kling, G.W., 2003b. Holocene pollen records from the central Arctic Foothills, northern Alaska: the role of substrate in the response of Tundra to climate change. Journal of Ecology 91, 1034–1048.

Oswald, W.W., Anderson, P.M., Brubaker, L.B., Hu, F.S., Engstrom, D.R., 2003c. Representation of tundra vegetation by pollen in lake sediments of northern Alaska. Journal of Biogeography 30, 521–535.

Overpeck, J.T., Webb, R.S., Webb III, T., 1992. Mapping eastern North American vegetation change of the past 18 000 yr BP: no-analogues and the future. Geology 20, 1071–1074.

Péwé, T.L., 1955. Origin of the upland silt near Fairbanks, Alaska. Geological Society of America Bulletin 66, 699–724.

Piperno, D.R., 2006. Phytoliths: a Comprehensive Guide for Archaeologists and Paleoencologists. AltaMira Press, Lanham, MD.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Hoye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., Aastrup, P., 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325, 1355–1358.

Prasad, V., Strömberg, C.A.E., Alimohammadian, H., Sahni, A., 2005. Dinosaur coprolites and the early evolution of grasses and grazers. Science 310, 1177–1180.

Prentice, I.C., Webb III, T., 1998. BIOME 6000: reconstructing global mid-Holocene vegetation patterns from palaeoecological records. Journal of Biogeography 25, 997–1005.

Quade, J., Solounias, N., Cerling, T., 1994. Stable isotopic evidence from paleosol carbonates and fossil teeth in Greece for forest or woodlands over the past 11 Ma. Palaeogeography, Palaeoclimatology, Palaeoecology 108, 41–53.

Ravski, E.I., 1972. Osadkonakoplenie i klimaty Vnutrennej Azii v antropogene In Russian) (Nauka, Moscow).

Risser, P.G., 1988. Diversity in and among grasslands. In: Wilson, E.O. (Ed.), Biodiversity. National Academy Press, Washington, DC, pp. 176–180.

Ritchie, J.C., 1977. The modern and Late Quaternary vegetation of the Campbell-Dolomite Uplands, near Inuvik, N.W.T. Canada. Ecological Monographs 47, 401–423.

Ritchie, J.C., 1982. The modern and Late-Quaternary vegetation of the Doll Creek Area, North Yukon, Canada. New Phytologist 90, 563–603.

Ritchie, J.C., Cwynar, L.C., 1982. The Late Quaternary vegetation of the North Yukon. In: Hopkins, D.M., MatthewsJr., J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, USA, pp. 113–126.

Ritchie, J.C., Hare, F.K., 1971. Late-Quaternary vegetation and climate near the arctic tree line of northwestern North America. Quaternary Research 1, 331–342.

Rupp, T.S., Chapin, F.S., Starfield, A.M., 2000. Response of subarctic vegetation to transient climatic change on the Seward Peninsula in North-West Alaska. Global Change Biology 6, 541–555.

Sage, R., Wedin, D., Li, M., 1999. The biogeography of C4 photosynthesis: patters and controlling factors. In: Sage, R., Monson, R. (Eds.), C$_4$ Plant Biology. Academic Press, New York, NY, pp. 313–356.

Schirrmeister, L., Siegert, C., Kuznetsova, T., Kuzmina, S., Andreev, A., Kienast, F., Meyer, H., Bobrov, A., 2002. Paleoenvironmental and paleoclimatic records from permafrost deposits in the Arctic region of Northern Siberia. Quaternary International 89, 97–118.

Shakun, J.D., Carlson, A.E., 2010. A global perspective on Last Glacial Maximum to Holocene climate change. Quaternary Science Reviews 29, 1801–1816.

Shapiro, B., Cooper, A., 2003. Beringia as an Ice Age genetic museum. Quaternary Research 60, 94–100.

Shapiro, B., Drummond, A.J., Rambaut, A., Wilson, M.C., Matheus, P.E., Sher, A.V., Pybus, O.G., Gilbert, M.T.P., Barnes, I., Binladen, J., Willerslev, E., Hansen, A.J., Baryshnikov, G.F., Burns, J.A., Davydov, S., Driver, J.C., Froese, D.G., Harington, C.R., Keddie, G., Kosintsev, P., Kunz, M.L., Martin, L.D., Stephenson, R.O., Storer, J., Tedford, R., Zimov, S., Cooper, A., 2004. Rise and fall of the Beringian steppe bison. Science 306, 1561–1565.

Sher, A.V., 1971. Pleistocene mammals and stratigraphy of the far northeast USSR and North America. International Geological Review 16.

Sher, A.V., Virina, E.I., Zazhigin, V.S., 1977. Stratigraphy, paleomagnetism, and mammalian fauna of the Pliocene–Early Quaternary sequence in the lower reaches of the Kolyma River. Doklady Academii Nauk SSSR 234, 1171–1174 (Report of the Academy of Sciences, USSR) (in Russian).

Sher, A.V., Kuzmina, S.A., Kuznetsova, T.V., Sulerzhitsky, L.D., 2005. New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals. Quaternary Science Reviews 24, 533–569.

Smith, D.J., Gardner, J.S., 1985. Geomorphic effects of ground squirrels in the Mount Rae area, Canadian Rocky Mountains. Arctic and Alpine Research 17, 205–210.

Smith, F.A., White, J.W.C., 2004. Modem calibration of phytolith carbon isotope signatures for C-3/C-4 paleograssland reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 277–304.

Stentström, A., Jonsson, B.O., Jónsdóttir, I.S., Fagerström, T., Augner, M., 2001. Genetic variation and clonal diversity in four clonal sedges (Carex) along the arctic coast of Eurasia. Molecular Ecology 10, 497–513.

Strömberg, C.A.E., 2005. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. Proceedings of the National Academy of Sciences 102, 11980–11984.

Stuart, A.J., Sulerzhitsky, L.D., Orlova, L.A., Kuzmin, Ya.V., Lister, A.M., 2002. The latest woolly mammoths (Mammuthus primigenius Blumenbach) in Europe and Asia: a review of the current evidence. Quaternary Science Reviews 21, 1559–1569.

Svendsen, J., Alexanderson, H., Astakhov, V.I., Demidov, I., Dowdeswell, J.A., Funder, S., Matiouchkov, A., 2004. Late Quaternary ice sheet history of northern Eurasia. Quaternary Science Reviews 23, 1229–1271.

Swanson, D.K., 2006. Biogeographical evidence for the grass (Poaceae) species of Pleistocene Beringian lowlands. Arctic 59, 191–200.

Szpak, P., Gröcke, D.R., Debruyne, R., MacPhee, R.D.E., Guthrie, R.D., Froese, D., Zazula, G.D., Patterson, W.P., Poinar, H.N., 2010. Regional differences in bone collagen δ^{13}C and δ^{15}N of Pleistocene mammoths: implications for paleoecology of the mammoth steppe. Palaeogeography, Palaeoclimatology, Palaeoecology 286, 88–97.

Tarasov, P.E., Webb III, T., Andreev, A.A., Afanas'eva, N.B., Berezina, N.A., Bezusko, L.G., Blyakharchuk, I.A., Bolikhovskaya, N.S., Cheddadi, R., Chernavskaya, M.H., Chernova, G.M., Dorofeyuk, N.I., Dirksen, V.G., Eliny, G.A., Filimonova, L.V., Glebov, F.Z., Guiot, I., Gunova, V.S., Harrison, S.P., Jolly, D., Khomutova, V.I., Kvavadze, E.V., Osipova, I.R., Panova, N.K., Prentice, I.C., Saarse, L., Sevastyanov, D.V., Volkova, V.S., Zernitskaya, V.P., 1998. Present-day and mid-Holocene biomes reconstructed from pollen and plant macrofossil data from the Former Soviet Union and Mongolia. I. Journal of Biogeography 25, 1029–1053.

Tarasov, P.E., Volkova, V.S., Webb III, T., Guiot, I., Andreev, A.A., Bezusko, L.G., Bezusko, T.V., Bykova, G.V., Dorofeyuk, N.I., Kvavadze, E.V., Osipova, I.R., Panova, N.K., Sevastyanov, D.V., 2000. Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia. Journal of Biogeography 27, 609–620.

Tugarinov, A.Y., 1929. O proiskhozhdenii arkticheskoy fauny Evrazii. Priroda 7-8, 17–39.

Ukraintseva, V.V., 1993. Vegetation cover and environment of the "Mammoth Epoch" in Siberia. The Mammoth Site of Hot Springs South Dakota, Hot Springs, SD.

van Geel, B., Aptroot, A., Baittinger, C., Birks, H.H., Bull, I.S., Cross, H.B., Evershed, R.P., Gravendeel, B., Kompanje, E.J.O., Kuperus, P., Mol, D., Nierop, K.G.J., Pals, J.P., Tikhonov, A.N., van Reenen, G., van Tienderen, P.H., 2008. The ecological implications of a Yakutian mammoth's last meal. Quaternary Research 69, 361–376.

van Geel, B., Guthrie, R.D., Altmann, J.G., Broekens, P., Bull, I.D., Gill, F.L., Jansen, B., Niemen, A.M., Gravendeel, B., in press. Mycological evidence of coprophagy from the feces of an Alaskan Late Glacial mammoth. Quaternary Science Reviews.

van Wijk, M.T., Clemmensen, K.E., Shaver, G.R., Williams, M., Callaghan, T.V., Chapin III, F.S., Cornelissen, J.H.C., Gough, L., Hobbie, S.E., Jonasson, S., Lee, J.A., Michelsen, A., Press, M.C., Richardson, S.J., Rueth, H., 2003. Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. Global Change Biology 10, 105–123.

Vangengeim, E.A., Ravski, E.I., 1965. About trans-continental type of natural zonation in the Quaternary period. Problemy stratifikatsii kaynozoya (in Russian) Nedra, Moscow. In: О внутри-континентальном тиЦе Природной зональности в четвертичном Церıode (антроЦоЦене) Проблемы страtiГрафии кайнозоя. М.: Недра.

Velichko, A.A., Nechaev, V.P., Arkhipov, S.A., Fradkina, A.F., Lavrushin, Yu.A., 1999. Izmeninie klimatov I landshaftov za poslednie 65 millionov let. Geos, Moscow (in Russian).

Veltre, D.W., Yesner, D.R., Crossen, K.J., 2008. Patterns of faunal extinction and paleoclimatic change from mid-Holocene mammoth and polar bear remains, Pribilof Islands, Alaska. Quaternary Research 70, 40–50.

Vetter, M.A., 2000. Grasslands of the Aishihik-Sekulmun Lakes area, Yukon territory, Canada. Arctic 53, 165.

Viau, A.E., Gajewski, K., Sawada, M.C., Bunbury, J., 2008. Low- and high-frequency climate variability in Eastern Beringia during the past 25 000 years. Canadian Journal of Earth Science 45, 1435–1453.

Walker, M.D., 1990. Vegetation and floristics of pingos, Central Arctic Coastal Plain, Alaska. Cramer-Junk, Dissertationes Botanicae. 283.

Walker, D.A., Everett, K.R., 1991. Loess ecosystems of Northern Alaska - Regional gradient and Toposequence at Prudhoe Bay. Ecological Monographs 61, 437–464.

Walker, M.D., Walker, D.A., Everett, K.R., Short, S.K., 1991. Steppe vegetation on South-facing slopes of Pingos, Central Arctic Coastal-Plain, Alaska, USA. Arctic and Alpine Research 23, 170–188.

Walker, D.A., Bockheim, J.G., Chapin, F.S., Eugster, W., Nelson, F.E., Ping, C.L., 2001. Calcium-rich tundra, wildlife, and the "Mammoth Steppe. Quaternary Science Reviews 20, 149–163.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., Epstein, H.E., Jónsdóttir, I.S., Klein, J.A., Magnússon, B., Molau, U., Oberbauer, S.F., Rewa, S.R., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, Ø., Turner, P.L., Tweedie, C.E., Webber, P.J., Wookey, P.A., 2006. Plant community responses to experimental warming across the tundra biome. In: Proceedings of the National Academy of Science, 103, pp. 1342–1346.

Walker, D.A., Leibman, M.O., Epstein, H.E., Forbes, B.C., Bhatt, U.S., Raynolds, M.K., Comiso, J., Gubarkov, A.A., Khomutov, A.V., Jia, G.J., Kaarlejaärvi, E., Kaplan, J.O., Kumpula, T., Kuss, H.P., Matyshak, G., Moskalenko, N.G., Orechov, P., Romanovsky, V.E., Ukraintseva, N.K., Yu, Q., 2009. Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and social factors affecting the Arctic normalized difference vegetation index. Environmental Research Letters 4, 16.

Walker, D.A., Forbes, B.C., Leibman, M.O., Epstein, H.E., Bhatt, U.S., Comiso, J.C., Drozdov, D.S., Gubarkov, A.A., Jia, G.J., Karlejaärvi, E., Kaplan, J.O., Khumutov, V., Kofinas, G.P., Kumpula, T., Kuss, P., Moskalenko, N.G., Raynolds, M.K., Romanovsky, V.E., Stammler, F., Yu, Q., 2011. Cumulative effects of rapid land-cover and land-use changes on the Yamal Peninsula, Russia. In: Gutman, G., Reissel, A. (Eds.), Eurasian Arctic Land Cover and Land Use in a Changing Climate, vol. VI. Springer, New York, pp. 206–236.

Watson, L., Dallwitz, M.J., 1994. Grass genera of the world. CAB International, Cambridge, UK. http://delta-intkey.com/grass/.

Welsh, S.L., 1974. Anderson's Flora of Alaska and adjacent parts of Canada. Brigham Young University Press, Provo, UT.

West, R.G., 2000. Plant Life of the Quaternary Cold Stages: Evidence from the British Isles. Cambridge University Press.

Westgate, J.A., 2003. Ice age steppe vegetation in east Beringia. Nature 423, 603.

White, R., Murray, S., Rohweder, M., 2000. Pilot analysis of global ecosystems: grassland ecosystems technical report. World Resources Institute, Washington, DC.

Whitmore, J., Gajewski, K., Sawada, M., Williams, J.W., Shuman, B., Bartlein, P.J., Minckley, T., Viau, A.E., Webb III, T., Anderson, P.M., Brubaker, L.B., 2005. North American and Greenland modern pollen data for multi-scale paleoecological and paleoclimatic applications. Quaternary Science Reviews 24, 1828–1848.

Willerslev, E., Hansen, A.J., Binladen, J., Brand, T.B., Gilbert, M.T.P., Shapiro, B., Bunce, M., Wiuf, C., Gilichinsky, D.A., Cooper, A., 2003. Diverse plant and animal genetic records from Holocene and Pleistocene sediments. Science 5620, 791–795.

Williams, J.W., Shuman, B.N., Webb III, T., 2001. Dissimilarity analyses of Late-Quaternary vegetation and climate in eastern North America. Ecology 82, 3346–3362.

Wooller, M.J., 2002. Fossil grass cuticles from lacustrine sediments: a review of methods applicable to the analysis of tropical African lake cores. Holocene 12, 97–105.

Wooller, M.J., Beuning, K.R., 2002. Introduction to the reconstruction and modeling of grass-dominated ecosystems - Preface. Palaeogeography Palaeoclimatology Palaeoecology 177, 1–3.

Wooller, M.J., Street-Perrott, F.A., Agnew, A.D.Q., 2000. Late Quaternary fires and grassland palaeoecology of Mount Kenya, East Africa: evidence from charred grass cuticles in lake sediments. Palaeogeography Palaeoclimatology Palaeoecology 164, 207–230.

Wooller, M.J., Zazula, G.D., Edwards, M., Froese, D.G., Boone, R.D., Parker, C., Bennett, B., 2007. Stable carbon isotope compositions of Eastern Beringian grasses and sedges: investigating their potential as paleoenvironmental indicators. Arctic. Antarctic and Alpine Research 39, 318–331.

Wooller, M.J., Zazula, G.D., Blinnikov, M., Gaglioti, B.V., Bigelow, N.H., Sanborn, P., Kuzmina, S., La Farge, C., 2011. The detailed paleoecology of a mid-Wisconsinan interstadial (~31,000 ^{14}C years) paleo-turf from interior Alaska. Journal of Quaternary Science.

Wright Jr., H.E., 1967. The use of surface samples in quaternary pollen analysis. Review of Palaeobotany and Palynology 2, 321–330.

Yost, C.L., Blinnikov, M.S., 2011. Locally diagnostic phytoliths of wild rice (Zizania palustris L.) from Minnesota, USA: comparison to other wetland grasses and usefulness for archaeobotany and paleoecological reconstructions. Journal of Archaeological Science 38, 1977–1991.

Young, S.B., 1982. The vegetation of the bering land bridge. In: Hopkins, D.M., MatthewsJr., J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 179–194.

Yurtsev, B.A., 1962. O floristicheskih otnosheniyah mezhdu stepyami i preriyami. Botanicheskiy Zhurnal 47, 317—336 (In Russian).

Yurtsev, B.A., 1972. Phytogeography of Northeastern Asia and the problem of trans-Beringian floristic interrelations. In: Graham, A. (Ed.), Floristics and paleo-floristics of Asia and eastern North America. Elsevier, Amsterdam, The Netherlands, pp. 19—54.

Yurtsev, B.A., 1982. Relics of the xerophyte vegetation of Beringia in Northeastern Asia. In: Hopkins, D.M., MatthewsJr., J.V., Schweger, C.E., Young, S.B. (Eds.), Paleoecology of Beringia. Academic Press, New York, pp. 157—177.

Yurtsev, B.A., 2001. The Pleistocene "Tundra-Steppe" and the productivity paradox: the landscape approach. Quaternary Science Reviews 20, 165—174.

Zazula, G.D., Froese, D.G., Schweger, C.E., Mathewes, R.W., Beaudoin, A.B., Telka, A.M., Harington, C.R., Westgate, J.A., 2003. Ice-age steppe vegetation in east Beringia. Nature 423, 603.

Zazula, G.D., Froese, D.G., Westgate, J.A., La Farge, C., Mathewes, R.W., 2005. Paleoecology of Beringian "packrat" middens from central Yukon Territory, Canada. Quaternary Research 63, 189—198.

Zazula, G.D., Froese, D.G., Elias, S.A., Kuzmina, S., La Farge, C., Reyes, A.V., Sanborn, P.T., Schweger, C.E., Scott Smith, C.A., Mathewes, R.W., 2006a. Vegetation buried under Dawson tephra (25,300 ^{14}C years BP) and locally diverse late Pleistocene paleoenvironments of Goldbottom Creek, Yukon, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 242, 253—286.

Zazula, G., Schweger, C., Beaudoin, A., McCourt, G., 2006b. Macrofossil and pollen evidence for full-glacial steppe within an ecological mosaic along the Bluefish River, eastern Beringia. Quaternary International 142, 2—19.

Zazula, G.D., Froese, D.G., Elias, S.A., Kuzmina, S., Mathewes, R.W., 2007. Arctic ground squirrels of the mammoth-steppe: paleoecology of Late Pleistocene middens (similar to 24000—29450 C^{14} yr BP), Yukon Territory, Canada. Quaternary Science Reviews 26, 979—1003.

Zazula, G.D., Froese, D.G., Elias, S.A., Kuzmina, S., Mathewes, R.W., 2010. Early Wisconsinan (MIS 4) Arctic ground squirrel middens and a squirrel-eye-view of the mammoth-steppe. Quaternary Science Reviews 0.1016/j.quascirev.2010.04.019.

Zhu, Y., Siegwolf, R.T.W., Durka, W., Körner, C., 2010. Phylogenetically balanced evidence for structural and carbon isotope responses in plants along elevational gradients. Oecologia 162, 853—864.

Zimov, S.A., 2005. Pleistocene park: return of the mammoth's ecosystem. Science 308, 796—798.

Zimov, S.A., Chuprynin, V.I., Oreshko, A.P., Chapin III, F.S., Reynolds, J.F., Chapin, M.C., 1995. Steppe-tundra transition - a herbivore-driven biome shift at the end of the Pleistocene. American Naturalist 146, 765—794.