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Calcium-rich tundra, wildlife, and the "Mammoth Steppe"

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Abstract

Moist calcareous tundra has many ecosystem properties analogous to those of the hypothesized "Mammoth Steppe" or steppe tundra of glacial Beringia, and today it is an important range land for arctic wildlife. Moist calcium-rich tundras are associated with moderately drained fine-grained arctic soils with relatively high soil pH. Compared to tussock tundra, moist calcareous tundra has 10 times the extractable Ca in the active layer, half the organic layer thickness, and 30% deeper active layers. The vegetation is less shrubby than that of tussock tundra, has twice the vascular-plant species richness, greater habitat diversity at multiple scales, and contains plants with fewer antiherbivory chemicals and more nutrients (particularly calcium). It has some properties that are unlike the hypothesized steppe tundras, including abundant sedges and a mossy understory. Moist calcium-rich tundra is common north of the acidic shrubby southern tundras and south of the sparsely vegetated polar deserts. Successionally, this tundra type occurs between the present-day dry calcareous dune vegetation and tussock tundra. Thus, at least conceptually, moist calcareous tundra is intermediate between the steppe tundra and tussock tundra and provides insights regarding the transitions from cold arid Beringian ecosystems to present-day moist acidic tundra.

1. Introduction

> The tundra and boreal landscape is … not simply a product of average annual rainfall and degree days. Vegetation itself affects soil character. The largely toxic insulating plant mat, shielded from high evaporation, promotes permafrost, or at least very cool soils, and limits available nutrients … .This, in turn favors the same plants that created those soil conditions. The cycle propels itself; conservative plants on low-nutrient soils must defend themselves against herbivory by large mammals. This largely toxic vegetation limits the species diversity and biomass of the large mammal community. (Guthrie, 1990, p. 207).

The present-day sedge- and moss-dominated vegetation of Beringia is quite unlike that which must have existed in large regions during the last glacial maximum (LGM). The above quotation from Dale Guthrie's *Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe* describes the detrimental effect that the modern blanket of tussock tundra has on ecosystem properties that are important to large mammals. Guthrie argues that the diverse grazing Late Pleistocene megafauna, which included the Chersky horse, wooly rhinoceros, saiga antelope, steppe bison, and mammoth, could have been supported only by arid, grass- and forb-dominated ecosystems. These so-called Mammoth Steppes probably had the following general properties: (1) more fertile soils that formed as a result of continual input of loess, (2) sparse precipitation and shallow winter snow due to the extreme continentality of much of Beringia, (3) sunnier summer climates with deeper summer thaw, (4) longer growing seasons due to the earlier melting snowpack, (5) arid, sparse, but diverse grass- and forb-dominated vegetation that was richer in nutrients and more poorly defended with antiherbivory compounds, (6) sparse or nonexistent moss carpets and firmer substrates and (7) more patchy landscapes with a wider diversity of habitats (Guthrie, 1982, 1990). This characterization must be placed in the context of a long and vigorous debate regarding the nature and extent of the Beringian vegetation (Hopkins et al., 1982). Some investigators have focused on the affinities with Asian steppes (Giterman and

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Golubeva, 1967; Yurtsev, this volume). Others have focused on the nonanalogue nature of the glacial biomes (Matthews, 1976; Guthrie, 1990); others have emphasized the similarities with modern dry cold tundras (Colinvaux, 1980; Ritchie and Cwynar, 1982); and still others have focused on the possible herbivore-driven changes to the ecosystem (Zimov et al., 1995). Recent plant-macrofossil, pollen, and insect data from northern Alaska argue for a more restricted area of steppe tundra in eastern Beringia and a mosaic of vegetation types, corresponding to a highly varied mix of climates and substrates (Anderson et al., 1994; Elias et al., 1996; Alfimov and Berman, 2001; Goetcheus and Birks, 2001). However, it is clear that a cold, dry, graminoid- and forb-rich vegetation on loess soils was an important component of this mosaic (Young, 1982).

Modern arctic tundra exhibits considerable variation due to climate, substrate, and disturbance regimes. Several small-scale arctic plant communities have been proposed as possible steppe-tundra analogues (e.g., Yurtsev, 1982; Edwards and Armbruster, 1989; Walker, 1985; Walker et al., 1991); however, moist calcium-rich tundra, which has been overlooked in this debate, is the only large-scale ecosystem that has many properties that are analogous to those proposed by Guthrie. It has been overlooked because it has gross physiognomic characteristics similar to those of tussock tundra (i.e., sedges and dwarf-shrubs are the dominant plants), but it has very different ecosystem properties. Moist calcium-rich tundra has also been called moist nonacidic tundra (MNT) in previous publications (Walker et al., 1995, 1998). Here, we retain the MNT nomenclature for the sake of consistency and as a contrast to moist acidic tundra while recognizing that a different name would be highly desirable. In this paper, we examine MNT properties that are relevant to wildlife and suggest that it is an intermediate, possibly transitional, ecosystem between the hypothesized nutrient-rich Pleistocene steppes and present-day acidic tussock tundras.

2. Descriptions of moist acidic and nonacidic tundras

Moist acidic tundra (MAT) occurs on moderately drained Low Arctic acidic soils with pH <5.5[1] (Figs. 1 and 2a; Bockheim et al., 1996; Walker et al., 1994, 1998). MAT includes "tussock tundra", *Sphagno–Eriophoretum vaginati* (Walker et al., 1994) (Fig. 2a), and acidic shrub tundras, and covers vast areas of the Arctic Foothills. The dominant plants in tussock tundra are dwarf-shrubs, tussock sedges, and acidophilous bryophytes (*Betula nana*, *Salix planifolia* ssp. *pulchra, Ledum palustre* ssp. *decumbens, Vaccinium uliginosum, V. vitis-idaea, Empetrum hermaphroditum, Rubus chamaemorus, Eriophorum vaginatum, Carex bigelowii, Sphagnum* spp., *Aulocomnium* spp., *Hylocomium splendens, Dicranum* spp., *Polytrichum* spp., and *Ptilidium ciliare*) (see Table 1 for species composition at comparable MNT and MAT study sites). Most studies of modern processes within moist tundra in Alaska have occurred in tussock tundra (Oechel et al., 1993; Chapin III et al., 1995; Reynolds and Tenhunen, 1996). In warmer, moister southern areas, tussock tundra grades into a more shrubby variant, dominated by dwarf birch and willows.

The most common moist nonacidic plant association in northern Alaska is *Dryado integrifoliae–Caricetum bigelowii* (Walker et al., 1994) (Fig. 1b). The dominant plants are sedges (e.g., *Carex bigelowii, C. membranacea, Eriophorum triste*), prostrate and dwarf shrubs (*Dryas integrifolia, Salix reticulata, S. arctica, S. lanata, S. glauca*), and numerous minerotrophic mosses (e.g., *Tomentypnum nitens, Distichium capillaceum, Ditrichum flexicaule*). It has many forb species (e.g., *Chrysanthemum integrifolia, Astragalus* spp., *Hedysarum* spp., *Senecio atropurpureus, Lupinus arcticus, Oxytropis maydelliana, Papaver macounii, Parrya nudicaulis, Pedicularis lanata, P. arctoeuopea, Senecio hieracifolia*) and horsetails (e.g., *Equisetum arvense, E. variegatum, E. scirpoidea*). This plant association corresponds to the association *Carici arctisibiricae–Hylocomietum alaskani* (Matveyeva, 1994) on the Taimyr Peninsula, Russia. Like tussock tundra, moist nonacidic tundras change composition and structure along the north-to-south climate gradient. For example, near the coast at Prudhoe Bay, Alaska, MNT has relatively few forbs and erect dwarf shrubs. At 100 km inland, forbs, such as *Lupinus arctica* and *Oxytropis maydelliana* are common, and scattered shrubs of *Salix lanata* and *S. glauca* attain heights of about 40 cm. Similar latitudinal vicariants have been described for the *Carici arctisibiricae–Hylocomietum alaskani* on the Taimyr Peninsula (Matveyeva, 1994).

[1] The soil pH strongly affects the availability of essential plant nutrients and biochemical processes. Plants adapted to very low soil pH are commonly found in bogs and areas with low input of base cations. Although there is a continuum of plants that dominate communities along a soil pH gradient, there is a strong difference in the composition of plant communities on soils that are essentially base saturated, and those on soils where the exchange complex is saturated with exchangeable acidity. In northern Alaska, most areas of the so-called "moist acidic tundra" have organic horizons with pH <5.0 and mineral B horizons with pH between 5.0 and 5.5. The pH 5.5 break between "acidic" and "nonacidic" tundras is reasonable based on our data showing the mean pH for the B horizon of MNT and MAT soils to be 7.0 and 5.3, respectively (Bockheim et al., 1996). The break between acidic and nonacidic plant communities corresponds approximately to the designation of acidic and nonacidic soil reaction classes for Entisols and Aquepts in the US Soil Taxonomy (Soil Survey Staff, 1996). To be in nonacidic soil families, the pH of the control section (25–50 cm from the mineral soil surface) should be >5.0 as measured in 0.01 M $CaCl_2$ in 1 : 1 soil : water suspension.

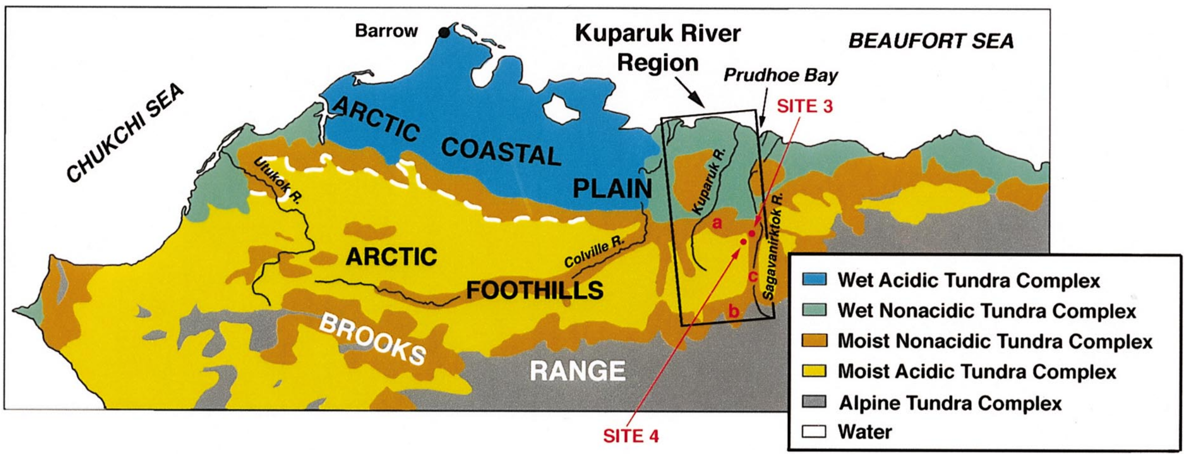

Fig. 1. Distribution of major tundra types in northern Alaska, based on an integration of information from several sources including AVHRR satellite images, soils maps, vegetation maps, and surficial geology maps. Within the Kuparuk River region, calcium-rich moist nonacidic tundra (MNT) occurs in three primary areas: (a) near the northern front of the foothills on loess deposits, (b) near the southern boundary of the foothills on relatively recent Itkillik-age glacial surfaces, and (c) along major floodplains such as the Sagavanirktok River. The location of the pH boundary west of the Colville River (dashed line) is less distinct and unstudied.

Fig. 2. Moist acidic tundra (MAT) and moist nonacidic tundra (MNT). (a) The plant association *Sphagno–Eriophoretum vaginati* (Walker et al., 1994) covers large areas of rolling terrain in the Arctic Foothills of northern Alaska. (b) *Dryado integrifoliae–Caricetum bigelowii* (Walker et al., 1994) is the dominant MNT plant association in northern Alaska.

Within the Arctic Foothills of Alaska, there are two primary regions of MNT. One is near the southern boundary of the foothills on late-Pleistocene glacial surfaces (b in Fig. 1) (Hamilton, 1986; Walker et al., 1995). The other occurs north of a prominent pH boundary near the northern front of the Arctic Foothills (a in Fig. 1). MNT is particularly common east of the Colville River, where all of the major rivers originate in carbonate-rich portions of the Brooks Range (Murray, 1978; Walker and Everett, 1991). Calcium carbonate eroded from limestone and dolomite formations in the Brooks Range is redistributed as till, alluvium and loess over much of the region. West of the Colville, most coastal-plain rivers originate in the Arctic Foothills and do not

Table 1
Comparison of properties of MNT (Site 3) vs. MAT (Site 4) on either side of the pH boundary in Fig. 3. Cover-abundance scores for plant species: + = common but less than 1% cover; 1 = 1–5%; 2 = 5–25%; 3 = 25–50%

MNT	MAT
Landscape	
Broad ridge top with nonsorted circles (36.1 ± 2.0% cover)	Broad ridge top, featureless (1.4 ± 0.7% cover of nonsorted circles)
Soils	
Ruptic Histic Aquaturbel, nonacid (69%) Typic Molliturbel (23%), others (8%)	Typic Aquaturbel (79%), Typic Histoturbel (21%)
Vegetation type	
Dryado integrifoliae–Caricetum bigelowii (Walker et al., 1994)	*Sphagno–Eriophoretum vaginati* (Walker et al., 1994)
Common vascular plant species (cover-abundance scores)	
Arctagrostis latifolia (1), *Arctous rubra* (1), *Astragalus umbellatus* (1), *Polygonum bistorta* (+), *Cardamine hyperborea* (+), *Carex bigelowii* (1), *Carex capillaris* (+), *Carex membranacea* (+), *Cassiope tetragona* (+), *Chrysanthemum integrifolium* (+), *Dryas integrifolia* (2), *Eriophorum triste* (2), *Eriophorum vaginatum* (1), *Juncus biglumis* (+), *Lupinus arcticus* (1), *Luzula arctica* (+), *Minuartia arctica* (+), *Oxytropis maydelliana* (+), *Parrya nudicaulis* (+), *Papaver macounii* (+), *Pedicularis capitata* (+), *Pedicularis lanata* (+), *Polygonum viviparum* (+), *Pyrola grandiflora* (+), *Pyrola secunda* (+), *Rhododendron lapponicum* (+), *Saussurea angustifolia* (+), *Saxifraga oppositifolia* (+), *Salix glauca* (+), *Salix lanata* (+), *Salix reticulata* (2), *Senecio atropurpureus (+)*, *Senecio hieracifolia* (+), *Senecio resedifolius* (+), *Silene acaulis* (+), *Stellaria laeta* (+), *Tofieldia pusilla* (+), *Vaccinium uliginosum* (+)	*Anemone richardsonii* (+), *Betula nana* (2), *Polygonum bistorta* (+), *Eriophorum vaginatum* (3), *Carex bigelowii* (1), *Cassiope tetragona* (+), *Ledum palustre* ssp. *decumbens* (2), *Pedicularis lapponica, Petasites frigidus* (+), *Poa arctica* (+), *Pyrola grandiflora* (+), *Rubus chamaemorus* (+), *Saxifraga nelsoniana* (+), *Salix planifolia* ssp. *pulchra* (2), *Senecio atropurpureus* (+), *Vaccinium uliginosum* (+), *Vaccinium vitis-idaea* (1)
Common bryophytes	
Dicranum elongatum (1), *Distichium capillaceum* (1), *Ditrichum flexicaule* (1), *Drepanocladus uncinatus* (+), *Hylocomium splendens* (2), *Rhytidium rugosum* (2), *Thuidium abietinum* (+), *Tomentypnum nitens* (4)	*Aulacomnium turgidum* (1), *A. palustre* (1), *Blepharostoma trichophyllum* (+), *Dicranum angustum* (1), *Dicranum* spp. (2), *Hylocomium splendens* (3), *Polytrichum strictum* (+), *Ptilidium ciliare* (1), *Sphagnum girgensohnii* (1), *S. lenense* (1), *Sphagnum warnstorfii* (1)
Common lichens	
Cetraria cucullata (+), *Cladonia gracilis* (+), *Cladonia pyxidata* (+), *Lecanora epibryon* (+), *Ochrolechia frigida* (1), *Peltigera aphthosa* (+), *Peltigera canina* (+), *Thamnolia subuliformis* (1)	*Cetraria cucullata* (+), *Cetraria islandica* (+), *Cladina rangiferina* (+), *Cladonia amaurocraea* (+), *Cladonia gracilis*, *Dactylina arctica* (+), *Peltigera aphthosa* (1), *Peltigera canina* (+), *Thamnolia subuliformis* (+)

carry alluvium rich in calcium. Extensive areas of nonacidic soils occur along major floodplains such as the Sagavanirktok River (c in Fig. 1) and in limestone areas of the foothills and mountains. Isolated studies elsewhere along the northern front of the foothills (Ebersole, 1985; Walker et al., 1982), and extrapolation of map information from the Kuparuk River region to the Arctic Slope of Alaska using AVHRR satellite data indicate that MNT occurs along much of the northern front of the foothills (Fig. 1). Many of these areas are beyond the influence of significant modern loess input from the major braided river systems. Some of these areas are part of a late-Pleistocene age upland silt deposit complex (O'Sullivan, 1961; Carter, 1981).

3. System properties relevant to wildlife

In 1995, as part of the Land–Atmosphere–Ice Interactions (LAII) Flux Study, we measured ecosystem properties of MAT and MNT on either side of a relatively sharp pH boundary in the Kuparuk River watershed (Fig. 1, sites 3 and 4) (Walker et al., 1998). The boundary permitted simultaneous monitoring of MNT and MAT ecosystem processes under nearly identical summer weather conditions. Site 3 is an MNT site located north of the boundary, and site 4 is an MAT site about 7 km southwest of site 3. Data from these and other sites in the Kuparuk River watershed are used here to help illustrate key differences between MNT and MAT that are important to present-day wildlife.

3.1. Soils

In addition to offering more for grazers to eat, Mammoth Steppe vegetation may also have provided more minerals and other nutrients for growth than is available today…. The present humic acid-rich soils of Alaska restrict cation cycling. Theoretically, at least, herbivore diets on the Mammoth Steppe would have been richer in minerals. (Guthrie, 1990, p. 215.)

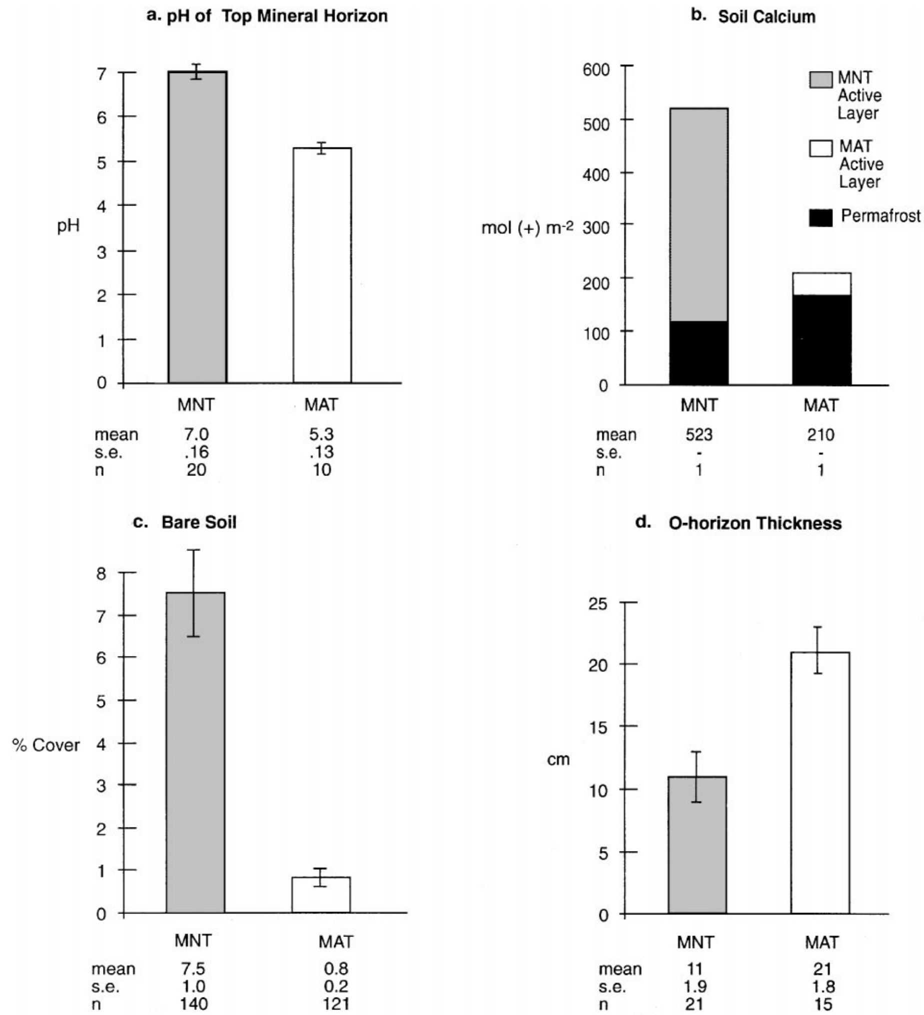

Fig. 3. Key soil properties in MNT and MAT. (a) Soil pH from sites throughout the Kuparuk River Basin (Bockheim et al., 1998). (b) Soil calcium from soil pits at sites 3 (MNT) and 4 (MAT) (Michaelson et al., 1996). (c) Bare soil estimated during aerial surveys of vegetation in the Kuparuk basin. O-horizon thickness within the Kuparuk River basin (Walker et al., 1998).

Two features of MNT soils are of primary importance to plant communities and wildlife: (1) their high soil pH and abundance of cations, particularly calcium, and (2) the high degree of frost stirring which results in the nonsorted circles and thin, discontinuous organic layers (Fig. 3). Soils of MNT are dominantly Ruptic-Histic Aquaturbels (nonacid) with some Typic Molliturbels (soil terminology follows the new Gelisol order of the US Soil Taxonomy; Bockheim and Tarnocai, 1998). These soils have a broken organic layer over a mollic epipedon (dark-colored, base-saturated surface horizon) over a cambic horizon with gleyed features. All horizons are highly cryoturbated (Michaelson et al., 1996; Bockheim et al., 1998).

The average soil pH of the top mineral horizon of MNT soils within the Kuparuk River basin is 7.0, and the average pH of MAT soils is 5.3 (Bockheim et al., 1998) (Fig. 3a). MAT soil pH tends to increase with depth, indicating that these soils are leached; whereas the pH of MNT soils tend to remain the same or decrease with depth, indicative of a continual input of base cations at the surface. Cation enrichment of the soil surface can be achieved through a wide variety of processes, including eolian deposition, cryoturbation, alluvial processes, or other disturbance factors. MNT soils are rich in nutrients, particularly calcium (Bockheim et al., 1998) (Fig. 3b). For example, the MNT soil at site 3 had about 400 mol Ca $(+)\,m^{-2}$ in the active layer compared to only 35 mol Ca $(+)\,m^{-2}$ in MAT at site 4. The MNT soil also contained greater amounts of extractable Mg, P, and total extractable cations, and significantly less total extractable N and Al (Bockheim et al., 1998). The abundance of calcium is also evident in the plant tissues (discussed below).

Nonsorted circles (small partially vegetated patches of frost-stirred soil about 1–2 m in diameter and spaced 1–5 m apart (Washburn, 1980)) play a large role in the nutrient dynamics, active layer thickness (zone of summer-thawed soil above the permafrost), and habitat diversity of MNT (Bockheim et al., 1998). For example, at the site 3 MNT site, nonsorted circles covered 36% of the surface and barren patches covered about 4%, whereas at the site 4 MAT site, nonsorted circles covered less than 2%, and barren areas covered 0.2%. Samples from the entire Kuparuk River basin showed that bare soil averaged 8% for MNT and 0.8% for MAT (Fig. 3d). The high degree of frost churning within MNT soils continually exposes mineral soil, brings calcareous subsoils to the surface, and prevents the buildup of the thick organic horizons (Fig. 3). The average thickness of the organic mat was 11 cm in MNT and 21 cm in MAT. These circles often are bare in the center and promote a great deal of intrasite heterogeneity at small scales (see Section 3.4).

3.2. Energy flux and depth of the active layer

> We have to consider the possibility that the Mammoth Steppe had the unusual combination of relatively deep summer thaws and an accumulation of deeply frozen ground …
>
> Although there are some significant temperature (insolation) differences between those of today and those that prevailed during full glacial (isotope stage 2), I argue that, in the far north, insulation is also a significant force. Today's soils are well insulated all year. Snow limits the amount of heat extracted from the ground in winter, and during summer the vegetation mat decreases the amount of heat gained. These insulators buffer soil temperatures. (Guthrie, 1990, p. 221).

MNT soils are less buffered against temperature changes than MAT soils, due in large part to their thinner organic mats, greater carbon storage, and abundant nonsorted circles (Michaelson et al., 1996; Bockheim et al., 1998). In summer, they are warmer and more deeply thawed than MAT soils, despite being more common at colder, more northerly latitudes (Nelson et al., 1997). The thinner, discontinuous organic layers of MNT allow more summer heat into the soils and create deeper active layers (Fig. 4). During simultaneous 10-d midsummer measurements at sites 3 and 4, the soil heat flux at the MNT site was 1.7 times that of the MAT site, and the average active layer of MNT across the Kuparuk River basin was 59 cm compared to 37 cm in MAT (Nelson et al., 1997; Walker et al., 1998).

There is also a strong association between thin snow cover, cryoturbation, and MNT. In Russia, the plant association *Carici arctisibiricae–Hylocomietum alaskani* (Matveyeva, 1994), described above, occurs on sites with abundant nonsorted circles ("spotty tundra"). Spotty tundras have been described all across northern Russia and are generally found in windy northern areas with shallow snow cover (Perfil'yev, 1934; Tikhomirov, 1948;

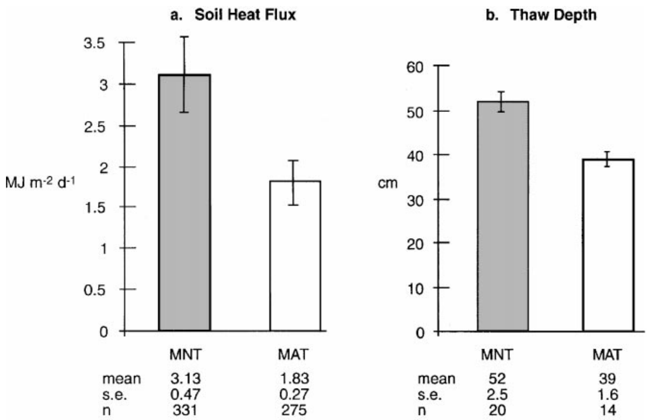

Fig. 4. Energy flux and thaw depth. (a) Soil heat flux, measured at sites 3 and 4 during the period 19–29 July 1995 (Fig. 3) (Eugster et al., 1997). (b) Average thaw depth within the Kuparuk River basin (Walker et al., 1998).

Gorodkov, 1956; cited in Alexandrova, 1980). Snow strongly insulates the soil (Zhang et al., 1996). There are generally thinner snowpacks on the coastal plain than in the foothills (Matthew Sturm, pers. comm.). There are also strong feedbacks between shrubs and snow. The shrubs accumulate more snow in winter, and the increased moisture and winter protection provided by the snow cover promotes more shrub growth.

The generally warmer (in summer) soils of MNT promote a wide variety of biological activity in the soil that is at present poorly studied. We know that there is greater microbial activity and more decomposed organic matter in MNT soils (Dai et al., 1997; Lemme et al., 1997), but we know little about the differences in the microbes, insects, and other organisms. The active layer depth also affects the rooting depth of many plant species and the depths to which small mammals can burrow.

3.3. Vegetation properties

> I wish to propose that these changes we see at the end of the Pleistocene were a cycle or syndrome of events triggered by a seasonal change of moisture in the northern Holarctic which affected soil temperatures, floristic and vegetational composition, antiherbivory compounds, available nutrients in the substrate, litter decomposition, soil insulation, primary productivity, and finally, the kind, quality, and numbers of large herbivores. (Guthrie, 1990, p. 318).

The greater shrub cover of MAT gives it a generally greener appearance that is evident in color aerial photographs and multispectral satellite imagery (Walker et al., 1998). MAT has about 35% more aboveground biomass than MNT, about 40% greater net CO_2 uptake in midsummer, greater leaf area indices (LAI), higher

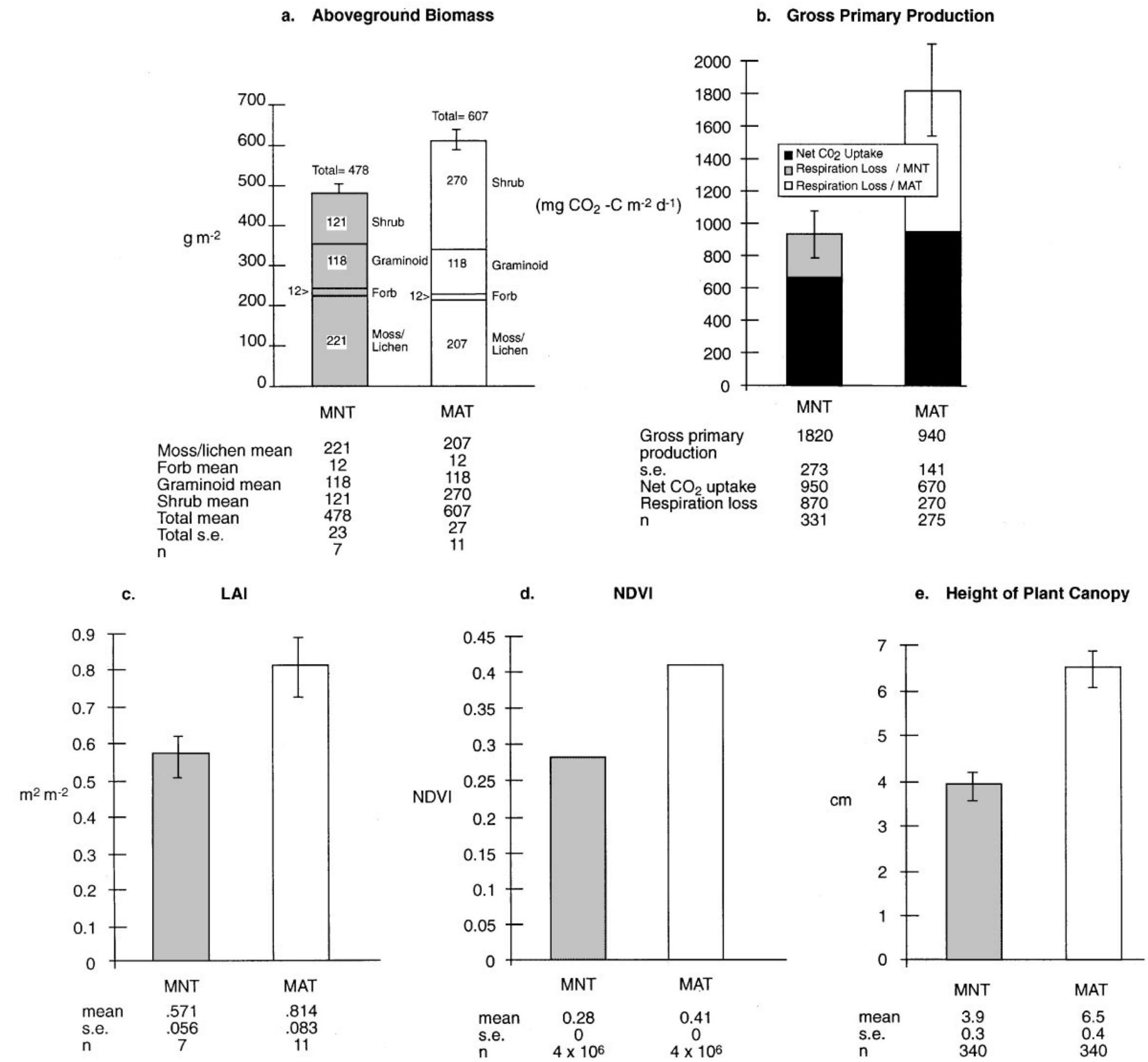

Fig. 5. Vegetation properties. (a) Biomass, measured from clip harvests of MNT and MAT plots in the Toolik Lake area (Shippert et al., 1995). (b) Gross primary production, measured at sites 3 and 4 during the period 19–29 July 1995 (Fig. 3) (Eugster et al., 1997). (c) LAI, measured at MNT and MAT plots in the Toolik Lake area using an LI-COR PCA 2000 Plant Canopy Analyzer (Shippert et al., 1995). (d) NDVI, measured on the same plots using a PS-II portable spectrometer (Shippert et al., 1995). (e) Height of plant canopy, measured at 340 random points at sites 3 and 4.

normalized difference vegetation indices (NDVI),[2] and taller plant canopies (Fig. 5) (Walker et al., 1998). Shrubs, mainly *Betula nana, Ledum decumbens,* and *Salix planifolia* ssp. *pulchra,* account for most of the difference in the biomass (Fig. 5a). In MNT, erect shrubs, if present, are scattered. Although the greater biomass of MAT would seem to translate into more available forage for animals, this is not the case because MAT is dominated by plants that are high in phenols and other secondary protective compounds (e.g., *Ledum palustre, Betula nana, Empetrum nigrum*) (Kuropat and Bryant, 1980; White and Trudell, 1980; Chapin III et al., 1986). Many plants in MAT are unpalatable or even toxic to large mammalian herbivores. The dominant plants on acidic sites tend to be evergreen shrubs and species that retain their nutrients in the foliage and protect themselves from herbivores with a variety of chemical compounds (Chapin III, 1980a).

MNT also has much more leaf-tissue calcium (Bockheim et al., 1998). Calcium is important to mammals for bone development, lactation, and antler growth. For example, the bone in a well-developed set of caribou antlers weighs about 6 kg, of which about 30% is calcium. This has to be replaced every year. Females have even higher calcium needs for calf production and milk. MAT soils are depleted of Ca as discussed earlier.

[2] The normalized difference vegetation index (NDVI) is a measure of landscape greenness that can be monitored from space using multispectral sensors. The NDVI is the ratio of the difference between the reflectance of the red and infrared spectral bands divided by their sum [NDVI = (ir − *r*)/(ir + *r*)].

Table 2
Tissue chemistry of moist nonacidic and moist acidic tundra at sites 3 and 4 near Sagwon Bluffs, Alaska (data from Bockheim et al., 1998)

Species	Tissue	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)
Moist nonacidic tundra							
Arctous rubra	Leaves	1.2	0.1	0.39	1.32	0.13	0.06
Arctous rubra	Branches	0.6	0.06	0.16	1.06	0.14	0.06
Carex bigelowii	Aboveground	0.7	0.07	0.3	0.63	0.06	0.06
Cassiope tetragona	Aboveground	0.6	0.06	0.2	1.02	0.08	0.06
Cetraria cucullata	Aboveground	0.3	0.05	0.2	1.67	0.05	0.02
Dryas integrifolia	Aboveground	0.7	0.07	0.18	2.57	0.13	0.05
Eriophorum triste	Aboveground	1	0.12	0.54	0.64	0.09	0.08
Hylocomium splendens	Aboveground	0.6	0.06	0.21	1.12	0.11	0.05
Lupinus arcticus	Aboveground	1.1	0.08	0.66	5.47	0.44	0.05
Rhododendron lapponicum	Aboveground	0.7	0.07	0.23	0.38	0.05	0.06
Rhytidium rugosum	Aboveground	0.7	0.08	0.26	1.23	0.15	0.06
Salix glauca	Leaves	1.5	0.11	0.58	1.59	0.36	0.13
Salix glauca	Branches	0.5	0.06	0.33	1.17	0.07	0.04
Salix lanata	Leaves	1.6	0.14	0.66	3.14	0.41	0.12
Salix lanata	Branches	0.6	0.06	0.22	0.88	0.07	0.04
Salix reticulata	Leaves	1.1	0.1	0.57	2.46	0.25	0.08
Salix reticulata	Branches	0.5	0.08	0.27	1.27	0.11	0.04
Tomentypnum nitens	Aboveground	0.5	0.05	0.2	1.65	0.14	0.04
	Average	0.8	0.08	0.35	1.62	0.16	0.06
Moist acidic tundra							
Betula nana	Leaves	0.6	0.09	0.22	0.6	0.3	0.04
Betula nana	Branches	0.7	0.09	0.24	0.2	0.07	0.05
Carex bigelowii	Aboveground	1	0.06	0.8	0.38	0.09	0.11
Cassiope tetragona	Aboveground	0.9	0.08	0.19	0.44	0.07	0.05
Eriophorum vaginatum	Aboveground	0.9	0.09	0.36	0.21	0.07	0.07
Hylocomium splendens	Aboveground	0.6	0.07	0.24	0.41	0.07	0.05
Ledum decumbens	Leaves	1.3	0.14	0.44	0.49	0.12	0.08
Ledum decumbens	Branches	0.6	0.08	0.19	0.27	0.06	0.05
Salix pulchra	Leaves	1.1	0.06	0.19	0.84	0.2	0.08
Salix pulchra	Branches	0.7	0.08	0.24	0.75	0.08	0.06
Sphagnum lenense	Aboveground	0.4	0.04	0.26	0.42	0.09	0.03
Sphagnum warnstorfii	Aboveground	0.6	0.07	0.34	0.38	0.09	0.04
Vaccinium vitis-idaea	Aboveground	0.7	0.08	0.27	0.64	0.13	0.05
	Average	0.8	0.08	0.31	0.46	0.11	0.06

Although we presently have data from only one late-season comparison, there is clearly more calcium in the MNT plants (Table 2, Fig. 6). The primary MAT forage shrub species, *Betula nana* and *Salix pulchra,* had 0.6 and 0.8% dry-weight leaf-tissue Ca, respectively, compared to 3.1 and 1.6% for *Salix lanata* and *S. glauca*, the dominant forage shrubs in MNT. The primary graminoid species in MAT, *Eriophorum vaginatum*, had 0.2% tissue Ca compared to 0.7% in the dominant MNT sedge, *Carex bigelowii*. Species growing in both MAT and MNT (*Carex bigelowii, Cassiope tetragona,* and *Hylocomium splendens)* had over twice as much calcium on the MNT site. Forbs in MNT have very high percentages of Ca (e.g., 5.5% Ca in *Lupinus arcticus).* These forb species are strongly selected by several herbivores. There was little difference in late-summer plant-tissue nitrogen or phosphorus. Chapin III (1980b) have shown that evergreen tundra shrubs of MAT have much higher concentrations of Ca than deciduous shrubs, such as willows that are common in nutrient-rich habitats. Zimov et al. (1995) have reviewed the feedbacks between the nutrient-deficient soil environment of MAT and moss growth.

Another vegetation factor that makes the MNT areas more favorable for wildlife is its firmer, smoother footing. Tussock tundra is notoriously difficult to traverse because of the large cottongrass tussocks, which vary in height from less than 15 cm at some sites near the coast to over 30 cm at some inland sites. MNT moss carpets are thinner, and there are far fewer tussocks and pits.

3.4. Diversity of plant species and habitats

> …the mammoth steppe was not characterized by homogeneous communities but a diverse, rather fine- to medium-grained vegetational mosaic. (Guthrie, 1982, p. 315).

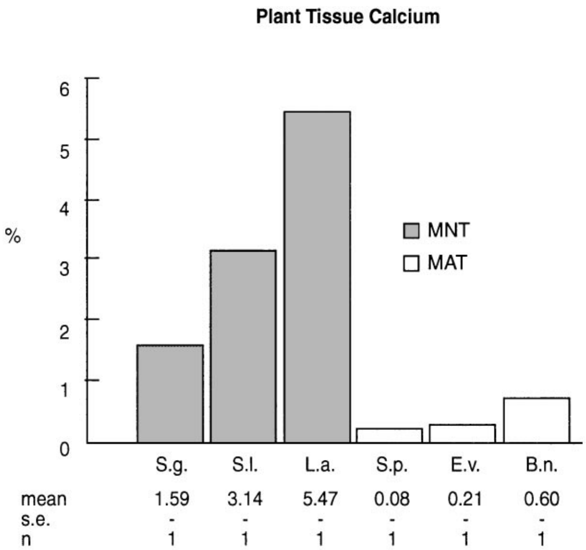

Fig. 6. Plant tissue calcium in common forage plants of caribou collected at sites 3 and 4 in August 1995 (Bockheim et al., 1998).

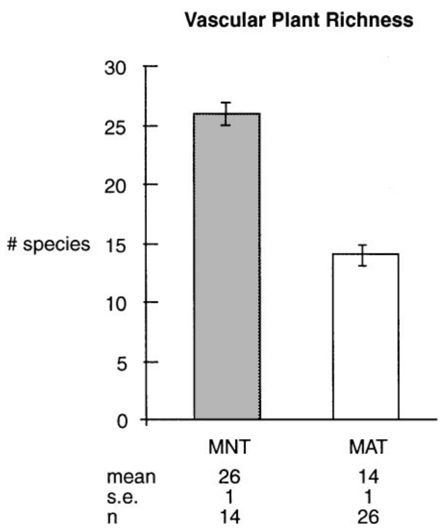

Fig. 7. Vascular plant richness, measured on 40 $10\,m^2$ plots in the Toolik Lake vicinity (Walker et al., 1994).

MNT is rich in both species and habitats. Matveyeva (1994) noted very high plant-species diversity (216 species including mosses and lichens) in the *Carici arctisibiricae–Hylocomietum alaskani* across the Taimyr Peninsula, and commented that such high species diversity is not known for any other vegetation type in the tundra zone. In northern Alaska, MNT has about twice the number of vascular plants per $100\,m^2$ as MAT (Fig. 7). Many of the common MNT forb species, such as *Lupinus arcticus, Hedysarum alpinum,* and *Equisetum arvense* are important constituents of grizzly bear and caribou diets (Hechtel, 1985; White and Trudell, 1980). In the Russian equivalent to MNT on the Taimyr Peninsula, Matveyeva found 130–160 plant species (including mosses and lichens) per $100\,m^2$, and this richness is also reflected in the invertebrate fauna (Chernov and Matveyeva, 1997). The high species diversity of MNT is partially a consequence of greater microscale habitat diversity associated with nonsorted circles, which consist of a suite of regularly spaced fine-scale plant communities that occupy the circle centers, margins, and intercircle areas. The density of nonsorted circles increases from south to north along the climate gradient, and this strongly affects the habitat and species diversity (Chernov and Matveyeva, 1997).

At coarser scales, MAT covers vast areas of subdued monotonous topography resulting from long periods of erosion and mass wasting (Hamilton, 1986); whereas MNT occurs most frequently in regions where disturbance is common at a variety of temporal and spatial scales. A study of plant-community diversity on five major terrain types in a watershed near Toolik Lake, Alaska found that the highest diversity occurred on floodplains where MNT is common, and that the lowest diversity on hillslope deposits, where MAT is dominant (Walker et al., 1989). Bedrock outcrops, glacial till, and basin colluvium had intermediate diversities. Within larger landscapes, which differed in their time since release from glaciation, there was less richness and evenness of vegetation communities on older landscapes where MAT was more abundant and MNT less abundant (Walker, 1995).

Some of the best present-day northern Alaskan analogues of hypothesized arctic Beringian steppe vegetation types are found in small, isolated, disturbed, arid patches within nonacidic regions of the Arctic Slope. For example, south-facing pingo slopes are highly disturbed by arctic ground squirrels, foxes and grizzly bears, and contain diverse graminoid-forb communities (Walker, 1990; Walker et al., 1991) (Fig. 8a). Similar pingo communities are not found on pingos in acidic regions of the western Arctic Coastal Plain.

Previous habitat research in northern Alaska has not recognized calcium-rich tundra as a distinctive vegetation type. Our general observations from years of vegetation surveys suggest that detailed wildlife studies recognizing calcium-rich tundra would be warranted for a wide range of organisms, including invertebrates, fish, birds and mammals. For example, all three of the major Alaskan arctic caribou herds appear to calve and forage in areas where MNT is a major component of the vegetation mosaic (Fig. 9). Caribou utilize tussock tundra mainly during the spring migration, when they feed on the nitrogen-rich flower buds of *Eriophorum vaginatum*, but as the tussock tundra progresses through its phenological stages, the tussocks become less palatable, and the caribou switch to other food sources that are more common in MNT and other vegetation types which are more common further north (Kuropat, 1984; McCabe et al., 1997). In Canada, most of the arctic caribou herds calve

Fig. 8. Steppe analogues. (a) Pingo near Prudhoe Bay, Alaska. Note the wide diversity of habitats. Small barren patches (arrows) are soil piles outside animal burrows of arctic ground squirrels and arctic foxes. (b) Rich grass and forb community on south-facing pingo slope. Plant species include *Potentilla hookeriana, Poa glauca, Bromus pumpellianus, Polemonium acutiflorum, Agropyron boreale* ssp. *hyperarcticum, Draba glabella, Oxytropis maydelliana, Bupleurum triradiatum*, and *Tortula ruralis*. (c) Sand dunes in the Canning River delta. (d) *Artemisia borealis, Trisetum spicatum* community on partially stabilized sand dunes in the delta of the Sagavanirktok River.

in northern tundra areas with nonacidic soils (Reid et al., 1987; Tarnocai, 1997, pers. comm.). On the Taimyr Peninsula, Russia, the large caribou herds calve north of the acidic tundra regions in areas of nonacidic "typical tundra" and "arctic tundra" (Chernov and Matveyeva, 1997).

Other large mammals, such as muskoxen, are also found primarily in areas of calcium-rich tundra. In spring and early summer, grizzly bears feed heavily on common MNT forbs, such as *Hedysarum* (Eskimo potato) and *Equisetum* (horsetails), and later after the soils thaw, they feed on arctic ground squirrels (Hechtel, 1985). Small prey species, such as voles, collared lemmings, and ground squirrels, are more common in the warmer, more deeply thawed MNT soils (Batzli and Sobaski, 1980), and

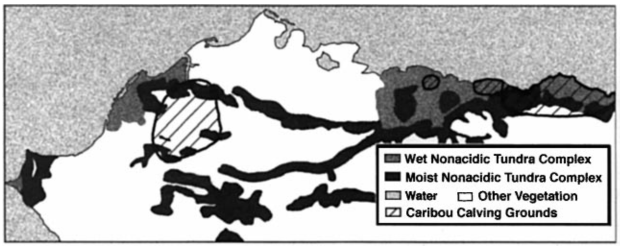

Fig. 9. Major Arctic-Alaska caribou calving grounds in relation to nonacidic tundra regions.

predators, such as the grizzly bear, wolf, and arctic fox, are found where there are abundant prey species and good denning sites.

Disturbance caused by animals could also be a major factor maintaining the presence of MNT. Disturbances that disrupt moss cover promote MNT, and in the absence of these disturbances, the development of complete moss cover results in relatively rapid development of MAT. In the Pleistocene, trampling by megafauna would have contributed to the sparse or absent moss cover (Zimov et al., 1995), allowing abundant cryoturbation (a positive feedback maintaining MNT). Extinction of the megafuana by human hunting and climate change (Martin, 1984; Guthrie, 1990) would have removed this source of disturbance and promoted conversion to moss-dominated MAT (Zimov et al., 1995). Today, the concentration of animals in MNT is an important source of disturbance that reduces the opportunity for moss dominance, thereby promoting cryoturbation. This effect of animal disturbance in changing vegetation is well documented for ground squirrels (Batzli and Sobaski, 1980), grizzly bears (Hechtel, 1985; Walker, 1990), voles (Batzli, 1977; Chernov, 1978), and caribou (Thing, 1984; Zimov et al., 1995). These animals must be a crucial factor in maintaining MNT today.

3.5. Vegetation gradient from dunes to tussock tundra

Pleistocene eolian activity made a dusty landscape: dust in the air, dirty snow, and hazy skies. Sunrises and sunsets must have been spectacular .... (Guthrie, 1982, p. 315).

Soil aridity was a key aspect of Pleistocene northern Alaska, as is evident from the large dune fields west of the Colville River (Black, 1951; Carter, 1981). This aridity was possibly a function of both a drier climate and greater disturbance caused by the continual input of loess, cryoturbation, and abundant wildlife. Today there are small dune fields in the deltas of most of the rivers. The vegetation downwind of calcareous dunes, such as those in the Sagavanirktok River delta, provide small-scale examples of the formerly more extensive eolian ecosystems and insights regarding Pleistocene loess landscapes and successional processes that occurred as the present-day thaw-lake landscape developed during the Holocene (Smith, 1997; Walker and Everett, 1991).

The successional sequence involved with calcareous dunes is quite different from that of acidic dunes west of the Colville River, where ericaceous shrubs and other acidophilous plant species are important (Peterson and Billings, 1978). West of the Sagavanirktok River dunes, soil pH decreases from greater than 8.0 in the dunes to less than 5.5 in areas far downwind outside of the area of loess influence. Soil textures grade from fine sands to clay loams, and soil bulk densities decrease because of higher organic matter concentrations. Water-holding capacities increase, and active layers decrease downwind. Nutrients, particularly calcium and nitrates, increase downwind in areas of nonacidic soils because of higher nutrient-holding capacity of finer-grained soils; but in acidic soils outside of the region of loess, most nutrients, except potassium, decline with lower pH. A conceptual model relating distance from the dunes to soil pH, soil organic matter, carbonates, soil particle size, thaw depth, soil moisture retention, nutrients, community floristics, and productivity has been presented by Walker (Walker, 1985; Walker and Everett, 1991).

The desert-like character of the sand dunes is a striking contrast to the surrounding wet and moist nonacidic tundra (Fig. 8c). The most active dunes are barren or sparsely vegetated with *Elymus arenarius* (1 in Table 3). Semistable areas (2 in Table 3) have a wide diversity of forbs and graminoid species, including *Kobresia myosuroides, Androsace chamaejasme, Draba lactea, D. cinerea, Artemisia borealis, A. glomerata, Festuca rubra, Salix ovalifolia, Polygonum viviparum, Pedicularis capitata, P. arctoeuropaea, Dryas integrifolia, Parrya nudicaulis, Armeria maritima, Oxytropis nigrescens, Potentilla uniflora, Encalypta* spp., *Distichium capillaceum,* and *Ditrichum flexicaule.*

A variety of paleoecological evidence, including pollen data, and macrofossils, stomach contents of Pleistocene grazers recovered from the permafrost, suggest that *Kobresia* and *Artemisia* were important components of the Mammoth Steppe (Livingstone, 1955; Nelson, 1982; Anderson and Brubaker, 1986; Goetcheus and Birks, 2001). Today, sand dunes along some of the rivers in the eastern portion of the Arctic Coastal Plain may have some of the best analogues for the hypothesized Pleistocene *Kobresia*- and *Artemisia*-dominated communities. These areas have many of the same plant species as the *Kobresia*-dominated communities that were covered by tephra 18,000 yr ago on the Seward Peninsula (Goetcheus and Birks, this volume), and other areas within the dunes complexes contain extensive stands of *Artemisia borealis* mixed with numerous grasses, primarily *Deschampsia caespitosa, Poa* spp., and *Trisetum spicatum* (Fig. 8d). *Kobresia* is an important component of many MNT plant communities in northern Alaska today. Mosaics of *Kobresia*- and *Artemisia*–dominated

Table 3
Vegetation sequence on flat moist sites downwind of the Sagavnirktok River dunes (modified from Walker and Everett, 1991)

Landscape, soil pH (distance from active dunes in km)	Common plant species (Stand type numbers, Walker, 1985)
1. Active dunes, pH 7.8–8.5 (0 km)	*Elymus arenarius, Polemonium boreale* (B9)
2. Partially stablilized dunes, pH 7.8–8.5 (< 0.5 km)	*Salix ovalifolia, Dryas integrifolia, Kobresia myosuroides, Artemisia borealis, A. glomerata, Draba* spp., *Armeria maritima, Parrya nudicaulis, Oxytropis nigrescens, Androsace chamaejasme, Pedicularis capitata, Festuca rubra, Chrysanthemum integrifolium, Polygonum viviparum, Pedicularis arctoeuropaea, Ditrichum flexicaule, Distichium capillaceum* (U14).
3. Mesic sites with sandy substrates, pH 7.8–8.0 (1 km)	*Carex aquatilis, Dryas integrifolia, Polygonum viviparum, Distichium capillaceum, Salix ovalifolia, Equisetum variegatum*
4. Mesic sites with silty substrates, pH 7.0–7.5 (1–20 km)	*Eriophorum triste, Carex membranacea, C. bigelowii, Dryas integrifolia, Salix reticulata, S. arctica, S. lanata, Polygonum viviparum, Senecio atropurpureus, Pedicularis lanata, P. capitata, Papaver macounii, Chrysanthemum integrifolium, Tomentypnum nitens, Ditrichum flexicaule, Hypnum bambergeri, Orthothecium chryseum, Meesia uliginosa, Thamnolia subuliformis, Cetraria* spp., *Dactylina arctica, Peltigera* spp. (U3 = *Dryado integrifoliae–Caricetum bigelowii* (Walker et al., 1994))
5. Mesic tussock tundra sites on the coastal plain with silty substrates, pH 6.0–7.0 (20–70 km)	*Eriophorum vaginatum, Cassiope tetragona, Polygonum bistorta, Salix planifolia* ssp. *pulchra, Carex bigelowii, Eriophorum triste, Dryas integrifolia, Salix reticulata, Carex misandra, Tomentypnum nitens, Hylocomium splendens, Ptilidium ciliare, Distichium capillaceum, Ditrichum flexicaule, Orthothecium chryseum, Oncophorus wahlenbergii, Aulocomnium turgidum, A. palustre, Cladonia gracilis, Thamnolia subuliformis* (U1).
6. Mesic sites west of the Colville River with sandy substrates, pH < 5.0 (> 70 km)	*Eriophorum vaginatum, Ledum palustre* ssp. *decumbens, Betula nana, Salix planifolia* ssp. *pulchra, Vaccinium vitis-idaea, V. uliginosum, Arctous rubra, Polygonum bistorta, Rubus chamaemorus, Sphagnum* spp., *Hylocomium splendens, Dicranum* spp., *Aulacomnium turgidum, A. palustre, Ptilidium ciliare, Polytrichum* spp., *Cladonia* spp., *Cladina* spp., *Peltigera aphthosa, Dactylina arctica* (= *Sphagno–Eriophoretum vaginati* (Walker et al., 1994))

communities could have also coexisted in close proximity to each other in unstable eolian landscapes during the last glacial maximum.

Mesic tundra areas just west of the dunes receive substantial dune-derived eolian sands (3 in Table 3). *Carex aquatilis, Dryas integrifolia, Salix ovalifolia* and *Polygonum viviparum* are the dominant vascular species on these sandy and nutrient-poor sites. Mosses are not abundant in mesic microsites near the dunes due to generally dry sandy soils, although thick moss mats form in wet basins of low-centered ice-wedge polygons. Further downwind, the soils become finer, and mosses are abundant on mesic sites. Areas with silty soils (4 in Table 3) have well-developed moss mats and a species-poor type of MNT vegetation typical of cold coastal areas of the Prudhoe Bay region (Walker and Everett, 1991).

Tussock tundra gradually increases in abundance far downwind of the dunes, and is generally associated with older stable surfaces (Walker et al., 1994, 1995; Walker and Walker, 1996) that are outside the influence of modern loess. On the coastal plain east of the Colville River, tussock tundra has small *Eriophorum vaginatum* tussocks, and poorly developed shrub components with several of the MNT species such as *Eriophorum triste, Dryas integrifolia, Salix reticulata, Carex misandra,* and the mosses *Tomentypnum nitens, Distichium capillaceum, Ditrichum flexicaule,* and *Orthothecium chryseum* (5 in Table 3). Acidophilous species, such as *Sphagnum, Dicranum, Ledum, Vaccinium, Betula,* and *Cladina* are uncommon on the coastal plain east of the Colville River, but are important in the tussock tundra of the sandy region west of the Colville (6 in Table 3) (Komárková and Webber, 1980).

4. Conclusion

Modern areas of calcium-rich tundra have many of the ecosystem properties that Guthrie hypothesized would be important to support the diverse Beringian megafauna, including firm, relatively warm, well-drained, nutrient-rich soils, high diversity of plant species and habitats, and plants low in secondary protective compounds. Plant-tissue calcium is much higher in calcium-rich areas and could be a major factor affecting wildlife patterns in the Arctic. Globally, moist calcium-rich tundra is most common north of the relatively moist, warm, acidic, shrubby "southern tundras" and south of the arid, cold, more barren polar deserts (Matveyeva, 1998). Successionally, it lies along a gradient intermediate between drier calcareous dune vegetation and tussock tundra. It has some properties that are unlike the hypothesized steppe tundras including mossy understories, abundant sedges, and few grasses. It is, thus, at least conceptually intermediate between the Beringian calcareous-loess steppe tundras and present-day moist acidic tundra.

Although it is still not clear what the vegetation of northern Alaska was like during the last glacial maximum, the large Pleistocene dune fields west of the Colville River are evidence that eolian processes were a dominant aspect of coastal-plain ecosystems. These processes are still locally important today and affect a large portion of the Arctic Coastal Plain. Moist calcium-rich tundra was likely a minor component of dry Pleistocene landscapes, where it probably occurred in moist microenvironments. It probably increased as humid, mild climates of the Holocene caused paludification (waterlogging of formerly dry substrates), resulting in thaw-lakes and marshy landscapes near the coast (Tomirdiaro, 1982). Today, moist calcareous tundra is the dominant vegetation in nonacidic portions of the coastal plain. In more southern warmer regions, such as the foothills, where loess and cryoturbation did not continually freshen the soil surface with calcareous materials, paludification eventually led to acidification and colonization by *Sphagnum* and other acidophilous plant species, and eventually to the unpalatable tussock tundra of today. The constriction of areas of nutritious forage during the Holocene probably affected the extinction of some of the Pleistocene mammals as well as human use of these landscapes during the past several thousand years (Guthrie, 1982, 1990; Olivier, 1982; Kunz and Mann, 1997; Mann et al., 1997) and vice versa (Zimov et al., 1995). As northern climates become even warmer and wetter, calcareous tundra will continue to decrease as loess sources shrink, cryoturbation becomes less intense, and moist acidic tundra proliferates.

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