Review of Lectures 2-3

Lecture 2: Climate and macrotopography

1. What is the vegetation ecological definition of the Arctic?
2. What criteria are used for dividing it into bioclimatic subzones?
3. Why is the Arctic considered a maritime biome?
4. What parts of the Arctic have the least maritime influence in summer?
   How might this change with a warming Arctic?
5. What is the primary ocean current exporting cold water (and ice) out of the Arctic? What is the primary current introducing warm water into the Arctic Basin?
6. What is the primary sources of fresh water to the Arctic Basin? What are some of the consequences of increased fresh water in the Arctic?
7. Who was Fridtjof Nansen? What did he demonstrate about the nature of the ocean circulation in the Arctic? How did the Tara Expedition update our knowledge about the Arctic ice circulation?
8. What are some key climate and vegetation characteristics of each of the bioclimatic subzones?
9. How do summer mean temperatures, plant biomass, and biodiversity of plants vary along the Arctic bioclimatic gradient?
10. How does climate and vegetation vary along elevation gradients in mountainous areas of the Arctic?
Review (cont’)

Lecture 3: Permafrost and microtopography

1. What is the technical definition of permafrost?
2. What is the active layer?
3. Why is the water content of permafrost so important?
4. What is the depth of zero amplitude in frozen ground?
5. What causes frost heave in soils?
6. What is differential frost heave? What are some patterned-ground features that are a result of differential frost heave?
7. How are ice-wedge polygons formed?
8. What are some consequences to vegetation of differential frost heave? And ice-wedge polygon formation?
9. How do thaw lakes form?
10. How do pingos form? What are some of the important micro-habitats associated with pingos?
**Field Trip: 8-11 Mar, Cantwell Cabin**

**Focus:**
- Snow and winter ecology

**Place:**
- Parks Highway, Cantwell cabin, Denali Highway vicinity

**Cantwell cabin:**
- No electricity. Bring headlamps. We will bring a couple of lanterns.
- No water, Bring 3-4 quarts for drinking. We will bring more for cooking and cleaning.
- Wood stove for heat. Door needs repair so only a couple of people will be responsible for loading it with wood.
- Will bring Coleman stoves for cooking.
- Outhouse.
- Either qinzhees or Western Shelter yurt for additional space for sleeping

**Attendance:**
- Mandatory unless you have already made other commitments you cannot break.

**Dates:**
- Tentatively planned for 8-11 Mar
  - **Maybe better to move it to either weekend and not screw up the whole break? 10-12 Mar or 16-18 Mar?**

**Transportation:**
- University vehicle, probably a van and a pick up, (need to reserve these ASAP).

**Equipment:**
- I will send checklist of required and desired equipment.
- Bring good winter outdoor gear.
- Sleeping bag and pad for sleeping on the floor.
- Skis preferred, If you are a skier and have back country skis, great!
- If you have never skied or are an avid snow-shoer, snow shoes are preferred.
- Equipment, including sleeping bags, pads, skis, boots, poles, and snowshoes, can be rented at reasonable cost from the Alaska Outdoor Adventures [http://www.uaf.edu/woodcenter/outdoor/rates/](http://www.uaf.edu/woodcenter/outdoor/rates/). (Weekend rates: Sleeping pad and bag, $20, Ski, boots, poles, $20, Snowshoes $10). Probably should reserve soon because it will be Spring Break.)

**Food:**
- We will buy food for the group and ask for reimbursement for the cost. Figure about $45 for the 3 days.
- Let me know if you are vegetarian or have food allergies.
- Breakfasts: Oatmeal or granola, bread, tea.
- Lunches: Sandwiches or wraps, fruit, granola bars (bring your own extras, candy etc.)
- Dinners: Big batch of stew or spaghetti for dinners, salad, bread, hot drink

**Other:**
- Be prepared to pitch in help organize, cook, and clean up after the meals, and thoroughly clean cabin before we leave.
- I'll send more information as plans develop.
Lecture 4
The role of substrate in Arctic vegetation and the Mammoth Steppe: Focus on soil pH

D.A. (Skip) Walker

Biol 488 Arctic Vegetation Ecology, University of Alaska Fairbanks

Rich nonacidic tundra plant community with many forbs and grasses, Sagwon Upland, Northern Alaska, Photo: D.A. Walker
Role of soil pH in vegetation is well studied in Europe...but still not fully understood

- Ellenberg et al. indicator values (1992) are widely applied in Central Europe and elsewhere.
- But pH seems to be one of the most problematic indicators.
- For example: Shaffers et al. conclude: “It is therefore suggested that reaction values are better referred to as ‘calcium values’.”
Not so well studied in the Arctic

- Long tradition in the Central European mountains

- But not so well studied in the Arctic. Examples include:
  
  ➢ Arve Elvebakk (1994) on Svalbard.
  
  ➢ Dave Cooper (1986) differences in communities on limestone and granite in the Arrigetch Mtns., Brooks Range, AK.
  
  ➢ Sylvia Edlund (1982) importance of soil pH in her mapping studies in the Queen Elizabeth Islands, Canada.

---

International Biological Programme Tundra Biome (1969-1973)

• IBP: An international effort to examine the Earth’s major biomes.
• Tundra biome had study sites in 10 countries.
Barrow is located on acidic marine sands and gravels.

Limited access to tundra elsewhere, so most of the studies were focused in the acidic tundra at Barrow.
Terrain at Barrow: Wet coastal plain tundra

Manley, W. F., L. R. Lestak, C. E. Tweedie, and J. A. Maslanik. 2006. High-resolution QuickBird imagery and related GIS layers for Barrow, Alaska, USA. Boulder, CO: National Snow and Ice Data Center. DVD. Courtesy Barrow Area Information Database: http://baid.utep.edu/Map%20Gallery
Main IBP Tundra Biome Study Area at Barrow

- Drained thaw lake basins
- Ice-wedge polygons
Master’s thesis involved multiple-scale mapping of tundra at Barrow

Acidic Tundra at Barrow: pH 3.8-5.0

Photos: D.A. Walker
Discovery of oil at Prudhoe Bay, AK

- Changed everything for Alaska, including Arctic science.
- New airport and road system at Prudhoe Bay provided access to tundra types that were previously unknown.
- I went to Prudhoe Bay mainly to examine the impacts of oil development.
- But became more interested in the tundra contrasts between Barrow and Prudhoe Bay.
Nonacidic Tundra at Prudhoe Bay: pH 6.5-8.0

- Physiognomically similar to Barrow.
- Zonal vegetation is sedge, prostrate dwarf-shrub, moss tundra.
- Species composition is very different.
- Other investigators had noticed different animal populations at Barrow and Prudhoe Bay:
  - Brown lemmings at Barrow and many snowy owls. Mostly collared lemmings at Prudhoe.
  - Large caribou herd at Prudhoe that was not known at the time. Very few caribou at Barrow.
Surface deposits on the Arctic Coastal Plain

- Pleistocene glacial history of the coastal plain still not well understood.
- New work by Jorgenson et al (2010) indicates that the coastal plain was glaciated from the North by glaciers flowing out of Canada along the coast.
- Colville River divides the Arctic Slope.

Fig. 1. Extent of minerotrophic and acidic tundras on the Alaskan North Slope based on Carter (1988) and AVHRR satellite-derived imagery. Upland loess occurs in the Arctic Foethills. Lowland loess occurs on the Arctic Coastal Plain.
Surface deposits on the Arctic Coastal Plain

- **East of Colville R.:**
  - Mainly calcareous gravel and loess deposits derived from Brooks Range.
  - Prudhoe Bay area is mainly shallow loess deposits over braided river gravel deposits.

- **West of Colville R.:**
  - Mainly acidic sands in ancient dunes. Acidic gravels toward the coast.
  - Calcareous loess in uplands downwind of dunes.
  - Nonacidic soils north of Teshekpuk Lake and along major rivers.

Fig. 1. Extent of minerotrophic and acidic tundras on the Alaskan North Slope based on Carter (1988) and AVHRR satellite-derived imagery. Upland loess occurs in the Arctic Foothills. Lowland loess occurs on the Arctic Coastal Plain.
AVHRR image of the North Slope

Numbered points:
1. Wet nonacidic tundra.
2. Moist nonacidic tundra.
4. Moist acidic tundra on old glaciated surfaces in the Arctic Foothills.
5. Nonacidic tundra associated with Itkillik-age (late Pleistocene) glacial and glaciofluvial surfaces at Toolik Lake.

Image courtesy of United States Geological Survey and NASA.
Distribution of nonacidic substrates in Arctic Alaska

From Raynolds et al. 2005.
Braided rivers flowing out of the Brooks Range: source of modern loess

Sagavanirktok River, northern Alaska
Photo: D.A. Walker
Loess: a sediment composed of wind-blown silt, often of glacial origin. Loess deposits are often very thick, more than 100 m in areas of China and the Midwest of the U.S. The soils are often calcareous. Some of the richest grassland soils in the world are formed in loess deposits.
Nonglacial loess deposits

Loess Hills National Landmark, Iowa


Nonglacial loess deposits

Loess Hills National Landmark, Iowa


Yellow River Loess, Bingling Grottos, China

Yedoma deposits

Yedoma: Pleistocene-age loess deposit in permafrost with high ice content (50-90% by volume) and high organic content (about 2% carbon by mass) caused mostly by entrapped steppe tundra roots.

[a] Thermokarst depressions filled with ice-wedge polygon patterns in the Yana-Indigirka Lowland, NE Siberia; [b] Coastal section on Bol’shoy Lyakhovsky Island, New Siberian Archipelago, showing the ice-rich Yedoma deposits (20-30 m) mantling ice-poor deposits of various origin (Photo: V. Tumskoy); [c] The Oygossky Yar coastal section at the Dimitrii Laptev Strait, NE Siberia, exposes about 2-60 m thick Yedoma mantle deposits consisting of up to 80 vol-% of ground ice (both segregated and wedge ice) (Photo: H. Meyer, Alfred Wegner Institute, Potsdam, http://www.diss.fu-berlin.de/diss/servlets/MCRFileNodeServlet/FUDISS_derivate_000000003198/16_ColdClimateLandforms-13-utopia.pdf?hosts=)
Yedoma-like deposits on Mars!

- Examples of landforms in western Utopia Planitia.
- Craters partly filled with layered material about 80 m thick that has polygons, presumably caused by thermal contraction cracking.
- Features are new because no new craters are visible in the deposits.

| 1. Acidic tundra at Barrow (Walker, MS thesis 1977, not shown) |
| 2. Nonacidic tundra at Prudhoe Bay in relationship to loess (Walker & Everett 1991) |
| 3. Classification of acidic and nonacidic tundra (MD Walker et al. 1994) |
| 4. Nonacidic tundra at Toolik Lake in relationship to glaciated substrates (Walker et al. 1995) |
| 5. Biophysical properties of acidic and nonacidic tundra (Walker et al. 1998) |
| 6. Relevance of nonacidic tundra to paleoecology and wildlife (Walker et al. 2002) |
Thesis research on gradient analysis of vegetation of Baffin Island, Canada.


Tundra Biome vegetation research in Colorado Alpine and at Barrow.

Program Director for NSF.

President of International Arctic Research Committee.

Recently retired from Michigan State U.

Strong proponent of interdisciplinary and international Arctic research.
Kaye Everett

- Ohio State University soil scientist.
- Probably had the biggest influence on my field work.
- Worked together mapping soils and vegetation, and examining the linkages between arctic soils and vegetation patterns.
- I spent 15 summers in the field with Kaye.
- Kaye spent over 30 field seasons in the Arctic and Antarctic.
Vera Komárková
Czechloslovakia-U.S., (1942-2005)

- Plant ecologist educated at Charles U.
- Student of Pat Webber’s but she was a mature scientist before coming to the University of Colorado.
- Introduced me to European methods of phytosociology.
- Led first Women’s Expedition to Annapurna, and climbed several peaks in the Himalayas over 8000 m.
- Mostly she influenced me by her example of extremely hard work in the field and her European training in a wide range of disciplines that are needed to do plant ecological research.
Soil pH gradient downwind of the Sagavanirktok River

Effects of calcareous loess on soils and vegetation at Prudhoe Bay

Dominance of silt in nonacidic soils in all moisture classes.

Effect of mineral addition on soil properties on acidic and nonacidic soils either side of the loess boundary

- Dilution of organic material in peaty soils (decreased soil organic matter and increased soil bulk density)
- Decreases the insulative properties of the organic soil horizons, increasing the depth of the Active Layer.

Soil nutrients in nonacidic and acidic tundra

Soil properties vs. distance from the Sagavanirktok River

% Organic matter vs. distance from Sag R. (km)

\[ y = 1.31x + 14.2 \quad r^2 = 0.58 \]

% Soil texture classes vs. distance from Sag R. (km)

- Sand (%): \[ y = 33.9 - 1.48x \quad r^2 = 0.73 \]
- Silt (%): \[ y = 54.4 + 0.96x \quad r^2 = 0.58 \]
- Clay (%): \[ y = 11.7 + 0.52x \quad r^2 = 0.85 \]

Effects of mineral matter on thaw depth and soil moisture

Thaw depth vs. bulk density

Gravimetric soil moisture vs. subjective moisture class

Other gradients downwind of the Sagavanirktok River

Soil properties vs. distance from the Sagavanirktok River (cont’)

Soil pH

\[ y = 0.3x + 7.8 \]
\[ r^2 = 0.77 \]

Soil nutrients

\[ y = 5.5 + 0.66x \]
\[ r^2 = 0.94 \]

\[ y = 8.7 + 0.29x \]
\[ r^2 = 0.75 \]

\[ y = 9.4 + 2.12x \]
\[ r^2 = 0.82 \]

Ordination of relevés from Barrow and Barter Island (similar to Prudhoe Bay)

- Barrow: coastal acidic tundra.
- Barter Island: coastal nonacidic tundra.
- pH and floristic separation decreases with increasing site moisture.

Classification of moist acidic and nonacidic tundra associations according to Braun-Blanquet approach (MD Walker et al. 1994)

MAT
MNT

Sphagno-Eriophoretum vaginatii

Dryado-Carici bigelowii

Photos: D.A. Walker
Landsat-derived land-cover mapping of northern Alaska in 1980s and 1990s revealed large areas of MNT with several origins.

Landsat-derived Landcover Map of the Beechey Point Quadrangle
Walker and Acevedo 1985

Landsat-derived Landcover Map of the Arctic Slope, Alaska
Muller, Racoviteanu, and Walker 1999
Dominant plants in MAT

- Sedges: *Eriophorum vaginatum*
- Dwarf evergreen shrubs: *Vaccinium vitis-idaea*, *Ledum decumbens*
- Dwarf deciduous shrubs: *Betula nana*, *Salix pulchra*
- Forbs: *Bistorta plumosa*
- Mosses: *Sphagnum* spp., *Dicranum* spp., *Hylocomium splendens*,
- Lichens: *Cladonia* spp., *Cetraria* spp., *Dactylina arctica*
Dominant plants in MNT

- Sedges: *Carex bigelowii*, *Eriophorum triste*
- Prostrate evergreen shrubs: *Dryas integrifolia*
- Dwarf deciduous shrubs: *Salix reticulata*, *S. arctica*, *S. lanata*
- Forbs: *Pedicularis lanata*, *Senecio atropurpureus*, *Lupinus arcticus*
- Mosses: *Tomentypnum nitens*, *Hylocomium splendens*
- Lichens: *Thamnolia* spp., *Cetraria* spp., *Dactylina arctica*

Photos: D.A. Walker
Dominant bryophytes in MAT and MNT

**MAT**

- Sphagnum spp.
- Hylocomium splendens
- Dicranum spp.
- Aulacomnium turgidum
- Ptilidium ciliare

**MNT**

- Tomentypnum nitens
- Ditrichum flexicaule
- Distichium capillaceum
- Hylocomium splendens
- Timmia austriaca
- Hypnum bambergeri
- Drepanocladus brevifolius

Photos: D.A. Walker
VI, biomass, and landscape evolution of glaciated terrain in northern Alaska

Walker, N.A. Auerbach, and M.M. Shipper

Machine with aid of Arctic and Alpine Research, Campus Box 450, University of Colorado, Boulder, 80265-4500, USA.

Introduction


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</table>

This paper explores the trends in NDVI in relation to the age of the landscape in the vicinity of Toolik Lake, Alaska. Recent research suggests that the spectral reflectance patterns are related to differences in vegetation composition and biomass associated with landscape evolution occurring during very long time intervals (> 100,000 years) (Walker and Walker, in press). Study site, geology, and vegetation:

The study area was located in the vicinity of Toolik Lake in the foothills of the Brooks Range, North Slope, Alaska, USA (65°20'N, 147°30'W, Fig. 1). This area was selected because of accessibility to glacial deposits of different ages within a few kilometers of the Toolik Lake field site, and because the geology of the region is relatively well known. The region contains primary study sites for the Arctic System Science (AASS) Land-Atmosphere-Lake Interaction Study (LALI) project (Carlson et al., 1991; Melton and others 1991). Details of maps of glacial deposits and vegetation are available for most of the region (Hamilton 1978, 1980; Johnson 1964a; Walker and others 1988).

Landscape age, soil pH, biomass, NDVI relationships at Toolik Lake, AK

Photo: D.A. Walker

Landscape age, soil pH, biomass, NDVI relationships at Toolik Lake, Alaska

Walker, N.A. Auerbach, and M.M. Shipper

Cited in Arctic and Alpine Research, Campus Box 450, University of Colorado, Boulder, 80265-4500, USA.

Introduction

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Toolik Lake

- Arctic field station of the University of Colorado.
- Long-term Ecological Research Site.
- Located in the northern foothills of the Brooks Range in northern Alaska.
Research questions

• How does glacial history, surficial geomorphology, and elevation affect patterns of vegetation?

• How is the pattern of vegetation greenness affected by terrain variables?

• How have the patterns changed during the satellite record?
Simplified Glacial Geology Map
Based on Hamilton (2003)

- **Sagavanirktok age**
  (middle Pleistocene
  Deglaciated by 125,000 y BP)
- **Itkillik I age**
  (late Pleistocene
  Deglaciated by 53,000 y BP)
- **Itkillik II age**
  (late Pleistocene
  Deglaciated by 11,500 y BP)
- **Other surfaces**
  Bedrock, colluvium, alluvium, thermokarst
- **Water**
Characteristics of the glacial surfaces

Sagavanirktok (older) surfaces:
- Few glacial lakes
- Gentle slopes
- Few glacial erratics
- Continuous loess cover
- Broad solifluction slopes
- Abundant watertracks
- Predominantly acidic tussock tundra and well-developed colluvial basins with acidic mires

Itkillik (newer) surfaces:
- More lakes but fewer wetlands
- Stony blockfields
- Abundant sorted and nonsorted stripes and circles
- Few watertracks
- Covered predominantly in nonacidic tundra vegetation

Photos: D.A. Walker
Vegetation

Based on: D.A. Walker and H.A. Maier. 2008. *Geobotanical maps in the vicinity of the Toolik Lake Field Station, Alaska*. Institute of Arctic Biology, Biological Papers of the University of Alaska, No. 27. ISSN: 0568-8604. No. 28.
Characteristic vegetation types

- Lichens barrens
- Rich fen wetland
- Moist nonacidic graminoid tundra
- Dry acidic tundra
- Shrub tundra
Acidic tussock tundra (dark yellow) covers less of the younger landscapes. (61% cover of tussock tundra on the oldest surfaces, 38% on the intermediate-age surfaces, and 24% on the youngest surfaces).

Nonacidic tundra (tan color) is more abundant on the younger surfaces (39% cover on the youngest surfaces, 17% on the intermediate-age surfaces, and 2% on the oldest surfaces).

Younger surfaces also had more lakes, more area of dry tundra, fewer wetlands, and fewer shrublands.
Relationship of biomass and NDVI to acidic and nonacidic tundra

Younger surfaces have lower pH and are less green.

The causes of this relationship are much more complicated than simple vegetation succession however because the whole landscape was much more barren 10,000 years ago.

Effects of soil pH on ecosystem properties

- Part of a large NSF project to examine Arctic transition in the land-atmosphere system (ATLAS).
- Examined the biophysical properties of MAT and MNT (energy and trace gas fluxes, spectral properties, primary production, respiration, etc.)

Energy and trace-gas fluxes across a soil pH boundary in the Arctic


1 Jina Imbume Analytical and Mapping Laboratory, Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80309-0430, USA
2 Soil Dynamics, University of Wisconsin, 522 Observatory Drive, Madison, Wisconsin 53706, USA
3 Department of Integrative Biology, University of California Berkeley, Berkeley, California 94720-3260, USA
4 Department of Earth System Science, University of California Irvine, 205 Physical Sciences Irvine, California 92697-3000, USA
5 Department of Agricultural and Forestry Exploration, University of Alaska Fairbanks, P.O. 91300, Fairbanks, Alaska 99701, USA
6 Department of Geography, University of Delaware, Newark, Delaware 19716, USA
7 Global Change Research Group, Department of Biology, San Diego State University, San Diego, California 92182, USA

Studies and models of trace-gas flux in the Arctic consider temperature and moisture to be the dominant controls over land-atmosphere exchange10, with little attention having been paid to the effects of different substrates. Likewise, current Arctic vegetation maps for models of vegetation change recognize one or two tundra types11 and do not portray the extensive ranges of shrub species within the Arctic. Here we show that rapid changes to ecosystem processes (such as photosynthesis and respiration) that are related to changes in climate and land usage will be un appreciated if not modulated by differences in substrate pH. A sharp soil pH boundary along the northern front of the Arctic Tundra in Alaska separates non-acidic (pH > 6.5) ecosystems to the north from predominantly acidic (pH < 5.5) ecosystems to the south. Most non-acidic tundra has greater heat flux, deeper summer thaw (active layer), is less of a carbon sink, and is a smaller source of methane than most acidic tundra.

In 1999 and 1996, we studied the ecosystem properties on either side of a prominent pH boundary within the tundra biome (KRB in Alaska, the primary study area of the Arctic System Science Lab-Arctic-Alpine-Landscapes interactions [ASCAL]), i.e., Flux Scan (ASCAL) (Fig. 1). We characterized most non-acidic tundra (MNT) and acidic tundra (MAT) ecosystems at two intensive study sites about 7 km apart on either side of the boundary (Fig. 1b, sites 1 and 4). We also collected soil and vegetation data from numerous other MNT and MAT sites within the KRB during an accuracy assessment of the landcover map in Fig. 1b (ref. 6). This adds to earlier information from Toolik Lake, Happy Valley and Prudhoe Bay, Alaska12,13.

The vegetation and soil properties on either side of the boundary are similar to those described for MNT and MAT in other studies12. Site 3 has MAT 10% cover of non-covered circles12. The non-covered circles are partly vegetated patches of high frost-active soils that are 1–2 m in diameter and spaced at intervals of 2–3 m. The base soils contain 0.5% of the vegetation community between the circles is Dryas integrifolia-Curicea tetralifolia, which is dominated by non-tussock sedges (Carex bigelowii, C. meadii, and Eriophorum intermedium) and some species of Vaccinium uliginosum, Salix arctica, S. reticulata, and Arctous rubra) and nitrogen-rich mosses (Hylocomium splendens and Dicranum quercus). Soils of MNT have a broken organic layer over a dark-colored horizon (3 mssol horizon containing organic matter accumulation) with high base saturation, over a gray G horizon (a subsoil mineral horizon relatively unaffected by soil formation except for the presence of gray colors resulting from poor drainage and redoxion)15. All soil horizons have consistently high pH (>6.3) and are highly frost-stressed (crystalline).

Site 4 is covered by tussock tundra (Sphagnum-Eriophorum) with low (<1%) cover of non-covered circles. This vegetation type is dominated by eutrophic shrubs (Kotula nana, Ledum palustre sp., saccobrach, Salix planifolia polonica), tussock sedges (Eriophorum vaginatum) and adokhiophytes (Sphagnum spp., Alopecurus powriei, Poleytrum and Dynnema spp). Soils of MAT have a thick continuous organic horizon over gray minerotrophic material and contain crystalized organic material in the lower part. Both sites 3 and 4 are on highly frost-stressed16. Soil pH of MAT sites tends to increase with depth from 4.0 up to 6.5 at the surface in the frozen C horizons.

The pH boundary extends at least 300 km to the east and west of the study area17. Loess blankets much of the Arctic Coastal Plains and Arctic Tundra, and both MAT and MNT occur on these extensive deposits, so it is difficult to explain the sharp vegetation boundary solely by differences in substrate soils. The boundary may be partly due to a stronger winter Arctic climate north of the topographic barrier of the Arctic Tundra18. A cooler, windier climate with shallower snowpack would promote the formation of non-vegetated circles19 and cause the continual string of non-acidic tussocks to the surface.20.

The abundance of non-vegetated circles and relatively low shrub biomass (to 25% at site 4)21 north of the boundary results in the greener times on the false-color infrared image (Fig. 1a). Lower shrub biomass, lower leaf area index (LAI) and lower normalized difference vegetation index (NDV) of MAT at site 3 is consistent with previous studies22 (Table 1).

South of the boundary, MNT is found only in relatively small areas on limnic terrain and in naturally disturbed systems, such as river floodplains, convex hill crests and stony glacialated areas. In most of the Arctic Tundra, vegetation succession and past formation (paludification) during the Holocene have converted formerly dry tundra to mire, bog and the deposits to MAT. Paludification is enhanced toward the south as a result of increased temperature and precipitation. Moose, particularly Sphagnum, are important to this conversion process. It is all subalpine MAT but not MNT and has numerous unique properties that strongly promote wetland legacy and cold acid soils.

The vegetation and soil differences between MNT and MAT have important consequences for land-atmosphere exchanges. Site 3 (MNT) had 28% more soil heat flux during 10 days of observation and 25% more end-of-summer than site 4 (MAT). Summer fluxes of MAT are consistently deeper than those of MNT, and heat flux decreases as you move south (Fig. 1). At the same time, heat fluxes in MAT are 10% lower than those of MNT (Fig. 1). At the same time, heat fluxes in MAT are 10% lower than those of MNT (Fig. 1).
Broader pattern of acidic and nonacidic tundras in northern Alaska
### Table 1: Comparison of ecosystem properties of MNT and MAT at sites in the Kuparuk River Basin

<table>
<thead>
<tr>
<th>Ecosystem property</th>
<th>Sites 3 and 4</th>
<th>Other sites</th>
<th>Significance</th>
<th>Reference</th>
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<tr>
<td>Soil</td>
<td>MNT</td>
<td>MAT</td>
<td>Significance</td>
<td>MNT</td>
</tr>
<tr>
<td>pH of top mineral horizon</td>
<td>7.6 [1]</td>
<td>6.5 [1]</td>
<td>n.a.</td>
<td>7.0 ± 0.16 [20]</td>
</tr>
<tr>
<td>O-horizon thickness (cm)</td>
<td>9 ± 1 [71]</td>
<td>15 ± 1 [71]</td>
<td>**</td>
<td>6.3 ± 0.14 [14]</td>
</tr>
<tr>
<td>Soil moisture of top mineral horizon (cm³ cm⁻³, Jul 95)</td>
<td>0.37 [1]</td>
<td>0.40 [1]</td>
<td>n.a.</td>
<td>11 ± 1.9 [21]</td>
</tr>
<tr>
<td>Bare soil (% cover)</td>
<td>4.4 ± 1.6 [6]</td>
<td>0.2 ± 0.0 [6]</td>
<td>***</td>
<td>8 ± 1 [140]</td>
</tr>
<tr>
<td>Vegetation</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height of plant canopy (cm)</td>
<td>3.9 ± 0.3 [340]</td>
<td>6.5 ± 0.4 [340]</td>
<td>***</td>
<td>0.57 ± 0.06 [7]</td>
</tr>
<tr>
<td>Leaf area index</td>
<td>0.50 ± 0.03 [66]</td>
<td>0.84 ± 0.05 [66]</td>
<td>***</td>
<td>0.28 ± 0.00 [4 × 10⁻⁶]</td>
</tr>
<tr>
<td>NDVI (MSS)</td>
<td>0.23 [7]</td>
<td>0.32 [1]</td>
<td>n.a.</td>
<td>0.82 ± 0.02 [7]</td>
</tr>
</tbody>
</table>

**Energy and trace-gas flux**

| Soil heat flux (19-30 Jun 1995, MJ m⁻² d⁻¹) | 1.39 ± 0.21 [331] | 1.09 ± 0.16 [275] | *** | 52 ± 2 [20] | 39 ± 2 [14] | *** | This study |
| Thaw depth (cm)                         | 57 ± 1 [71] | 37 ± 1 [71] | *** | 57 ± 5 [14] | 36 ± 3 [33] | *** | This study |
| Evapotranspiration (19-30 Jun 1995, mm d⁻¹) | 1.16 ± 0.17 [331] | 1.06 ± 0.16 [275] | n.a. | 52 ± 2 [20] | 39 ± 2 [14] | *** | This study |
| 10-c gross primary production (19-30 Jun 1996, g CO₂-C m⁻² d⁻¹) | 0.94 ± 0.14 [331] | 1.82 ± 0.27 [275] | n.a. | 57 ± 5 [14] | 36 ± 3 [33] | *** | This study |
| 10-c net CO₂ uptake (g CO₂-C m⁻³ d⁻¹) | 0.67 ± 0.10 [331] | 0.95 ± 0.27 [275] | n.a. | 0.27 ± 0.41 [12] | 1.02 ± 0.33 [12] | n.a. | This study |
| 10-c net CO₂ uptake (g CO₂-C m⁻³ per season) | 2.76 [77] | 55.2 [90] | n.a. | 276 [77] | 55.2 [90] | n.a. | This study |
| (g CO₂-C m⁻³ per season)                | 3.3 [31] | 52.5 [73] | n.a. | 69 ± 33 [12] | 449 ± 301 [15] | n.a. | This study† |

Standard error of the mean and number of samples [in brackets] are given for most variables. Probability of significance in all cases was based on two-sample t-test. Significance levels:

* P ≤ 0.1, ** P ≤ 0.05, *** P ≤ 0.01, n.s.: non-significant; n.a.: non-applicable.

* Data are from 47 permanent plots in the Toolik Lake region.

† Measurements at 36 random points within the Kuparuk River basin during accuracy assessment of the land-cover map.

‡ Estimates obtained from RER surveys at 361 sites within the Kuparuk River basin during accuracy assessment of the land-cover map.

§ Mean MSS NDVI values for the land-cover map.

‖ Sites 11 (MAT) and 24 (MNT).


†† Methane measurements at 37 plots at Toolik Lake region, Happy Valley and Deadhorse.
Soil pH and soil calcium

a. Data from 30 sites at Toolik Lake on different-age glacial surfaces.

b. Data from soil pits at sites 3 and 4 at northern edge of the Foothills.
MAT/MNT boundary on false color CIR imagery

- Nonacidic tundra areas are light colored due to abundance of bare standing dead sedges and few erect shrubs.

- Acidic tundra are mainly bright red due to abundance of shrubs.

Landsat MSS image of boundary near Sagwon, northern edge of Arctic Foothills, Alaska
Major spectral differences between MAT and MNT

MAT

Much greener due to abundance of dwarf shrub (Betula nana, Salix pulchra, Ledum decumbens) and green sedge leaves (Eriophorum vaginatum).

Abundance of dead sedge and Dryas leaves, brown mosses (Tomentypnum nitens, Hylocomium splendens) and bare soil from frost boils.

Photos: D.A. Walker
Vegetation LAI, NDVI and mean canopy height

- LAI: Leaf area index measured with point frame.
- NDVI: Normalized Difference Vegetation Index (a measure of vegetation greenness): derived from satellite data, Landsat MSS.
- Plant canopy height: measured with a ruler at random points.
Bare soil and O-horizon thickness from the whole Kuparuk River watershed

**c.** Estimate of cover of bare soil from 161 sites in the Kuparuk R. watershed.

**d.** Measured O-horizon thickness at 37 sites in the Kuparuk R. watershed.

Walker et al. 1998.
Aboveground biomass at Sites 3 and 4

- Much more shrub biomass in the MAT site.
- Measured mainly at Sites 3 and 4.

Biomass and LAI vs. total summer warmth index in acidic and nonacidic systems

- MAT
- LAI shows curvilinear response to temperature
- Due mainly to shrub biomass
- MNT
- LAI shows small response to temperature
- Fewer erect shrubs
- More cover of bare soil due to frost boils

Gross primary production (respiration + net CO$_2$ uptake)

- Twice the GPP in the MAT site.
- 3x respiration in MAT site.
- Measured at sites 3 and 4.
Soil heat flux and thaw depth of MNT and MAT soils

a. Measured at sites 3 and 4.

b. Measured at 34 near Toolik Lake.

Walker et al. 1998.
Effects of Substrate: Distinct vegetation boundary entire Arctic Slope, Alaska caused by acidic/ nonacidic tundra differences

- Separates moist acidic tundra (soil pH<5.5) to the south from moist nonacidic tundra (pH>5.5) to the north across 800 km boundary.

- Possible causes:
  - Geologic differences
  - Loess deposition from the major river systems
  - Climate

Sites where boundary has been mapped or examined in some detail.

Moist acidic and nonacidic tundra at Oumalik

Much of the boundary is distant from modern loess sources, but Northern foothills are areas of ancient loess deposits.
Some evidence to support a climate hypothesis for the MNT/MAT boundary

• The boundary is approximately coincident with transition between the Arctic Foothill and Arctic inland climate subzones.
• Snow depths are deeper south of the boundary.
• Winter winds are greater north of the boundary, and the snow is harder (greater heat flux through the snow).
• Active layers are much thicker north of the boundary.
• Permafrost temperature are much colder north of the boundary.
Conceptual model of climate-snow-cryoturbation-MNT hypothesis
Loess ecosystems and the Mammoth Steppe

D.A. (Skip) Walker
Biol 492/692 Arctic Vegetation Ecology
University of Alaska Fairbanks
“Is there a relationship between wildlife distribution and MNT?”

Photos: D.A. Walker, except bottom right, unknown source.
Calcium-rich tundra, wildlife, and the “Mammoth Steppe”


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*Soil, Water, and Air Laboratory, University of Wisconsin, Madison, WI 53706, USA
*Department of Integrative Biology, University of California Berkeley, Berkeley, CA 94720, USA
*Department of Geography, University of Delaware, Newark, DE 19716, USA
*Arboreal and Forestry Exploration Station, University of Alaska Fairbanks, 333 E. Providence, Palmer, AK 99645, USA

Abstract

Most calcareous tundra has many ecosystem properties analogous to those of the hypothetical “Mammoth Steppe” or steppe tundra of glacial Beringia, and today it is an important range land for arctic wildlife. Most calcium-rich tundra are associated with moderately drained (well-drained) arctic soils with relatively high soil pH. Compared to tussock tundra, most calcareous tundra has 10 times the extractable Ca in the active layer, half the organic layer thickness, and 30% deeper active layer. The vegetation is less shrubby than that of tussock tundra, has twice the vascular-plants species richness, greater habitat diversity at multiple scales, and contains plants with fewer antitoxin-vegetative chemicals and more nutrients (particularly calcium). It has some properties that are unlike the tussock tundra steppe tundra, including abundant sedges and a mossy understory. Most calcium-rich tundra is common to the north of the arctic shrubby tundra in the north of the arctic shrubby tundra in the north of the region and within the range of the species vegetated polar deserts. Successionally, this tundra type occurs between the present-day dry calcareous ecoregion vegetation and tussock tundra. Thus, at least conceptually, most 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. © 2000 Elsevier Science Ltd. All rights reserved.

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 cold 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 what 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, woolly rhinoceros, saiga antelope, steppe bison, and mammoth, could have been supported only by arid, grass- and forb-dominated early systems. These so-called Mammoth Steppes probably had the following general properties: (1) more fertile soils that formed as a result of continuous input of loess, (2) sparse precipitation and shallow winter snow due to the extreme continentality of much of Beringia, (3) summer 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 antitoxin-vegetative 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 investigations have focused on the affinities with Asian steppes (Gitterman and...
## Leaf tissue chemistry of MNT and MAT plants

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

- Mean values for a mix of species in 186 random plant samples from MNT and 119 samples from MAT at the Sagwon MNT/MAT boundary.

- Details of the species collected are in the cited reference Table 2.

Soil calcium

Plant tissue calcium in common forage species

Vascular-plant species richness in acidic and nonacidic tundra of northern Alaska

- Matveyeva (1994) noted very high species richness (130-160 species per 100 m² (including moses and lichens) in the *Carici arctisibiricae-Hylocomietum alaskani* (an nonacidic tundra analogue) on the Taimyr Peninsula, Russia.

MAT plant adaptations to low nutrient environments

- Stress tolerators
- Evergreen leaves
- Small leaves
- Slow growth
- Long-lived perrenials
- Persistent litter
- Lots of secondary metabolites, low palatability to herbivores
- High year-to-year variation in flowering abundance

Acidic tundra, *Betula nana, Ledum decumbens, Rubus chamaemorus*
Photo: N. Werbe
Digestibility, nitrogen and carbon–based defensive compounds in common forage species

Common forage species for caribou and grizzly bears upper Utukok River

**Caribou (Kuropat and Bryant 1980)**
- *Eriophorum vaginatum* (flowers)
- *Salix pulchra*
- *Salix alaxensis*
- *Salix glauca*
- *Equisetum arvense*
- *Lupinus arcticus*
- *Boykinia richardsonii*
- *Oxytropis maydelliana*

**Grizzly bear (Hechtel 1985)**
- *Hedysarum alpinum* roots
- *Arctous rubra* berries
- *Boykinia richardsonii* leaves and flowers
- *Equisetum arvense* young shoots
- *Shepherdia canadensis* berries
- *Eriophorum vaginatum* flowers

*Nonacidic species*
Distribution of nonacidic tundra in northern Alaska
Relationship between known caribou calving grounds and MNT in 1998
Relationship between caribou calving grounds and MNT

Teshekpuk herd calving ground also in area of nonacidic tundra discovered after 2001 publication.
Northern Beringia was an arid environment
Possible “steppe” tundra analog on a pingo at Prudhoe Bay

Artemisia borealis, Trisetum spicatum, Kobresia myosuroides “steppe”
Sand dunes of the Sagavanirktok River delta
Photo: D.A. Walker
Possible “steppe” tundra analogs on Prudhoe Bay Pingo

- Grass and forb-rich communities on south-facing slopes with few mosses or lichens.
- Several Beringian endemic species.
- Soils have deep organic-rich A horizons (Pergelic Cryoborolls, analogous to prairie soils of the midwest).

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 pumelliianus*, *Polemonium acutiyorum*, *Agrpyron boreale* ssp. *hyperarcticum*, *Draba glabella*, *Oxytropis maydelliana*, *Bupleurum triradiatum*, and *Tortula ruralis*. Photos: D.A. Walker.


Nutrient-rich soils and plants of Beringia

• “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 acidic-rich soils of Alaska restrict cation cycling. Theoretically, at least, herbivore diets on the Mammoth Steppe would have been richer in nutrients.”

Guthrie, 1990

• Frozen Fauna of the Mammoth Steppe: The story of Blue Babe
Location of the “Mammoth Steppe”

Resource utilization by common large northern herbivores

Pie diagrams of percentage summaries based on plant tissue samples taken from molars of fossil steppe bison, woolly rhino, muskoxen, caribou, and moose; from fossil horse incisor pits; and from stomach contents of frozen woolly mammoths. Cuticle histological samples were ground and keyed microscopically. Mammoth and woolly rhino samples are from northeastern Asia. All others are from the Fairbanks, Alaska mining district. These represent combined samples of approximately 10 individuals each. A more extensive presentation of this data is to be made in another publication (Guthrie, 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 ).
Key aspects of the “Mammoth Steppe” ecosystem according to Guthrie (1982, 1990, 2001)

• Fertile soils resulting from continual input of loess.
• Preponderance of herbaceous plants, dominated by grass and *Kobresia*.
• Sparse, but diverse, grass-forb vegetation.
• More poorly defended by secondary plant compounds.
• Sparse or nonexistent moss carpets (firmer substrates for animal footing).
• Long growing season.
• Sunny cloud-free summer climate with lots of solar radiation related to continental conditions.
• Shallow winter snow due to extreme continentality, and early spring snow melt.
• Winds in summer and winter (indicated by snow drift adaptations of small mammals, and large mammals who do poorly in snow.)
• Deep active layers.
• Patchier landscapes with a wider diversity of habitats than
Factors that would limit modern animal populations in modern acidic tussock tundra

- Plants have more secondary metabolites (less digestible).
- Less nitrogen and calcium in plant tissues.
- Less diversity of vascular plant species.
- Cold, acidic soils limit nutrient cycling.
- Shallow active layers are poor habitat for burrowing animals.
- Thicker moss carpets and larger tussocks create more difficult footing for migrating mammals.
- Less diversity of habitats in acidic landscapes.

Photo: D.A. Walker
CARMA and Caribou migration animation

• CARMA is a network of researchers, managers and community people who share information on the status of the world's wild Rangifer (reindeer and caribou) populations, and how they are affected by global changes, such as climate change and industrial development.

• An IPY (International Polar Year) project.
MNT: an intermediate tundra type between steppe tundra and MAT?

- Many of the key ecosystem properties are similar to those suggested by Guthrie
- Properties that are different from steppe tundra include:
  - Well developed moss carpets
  - Dominance of sedges
  - Rarity of Artemisia, Kobresia, and other key species
- Successional sequences downwind of dune areas suggest a possible sequence of transitional types between Steppe Tundra and MAT

Moist nonacidic tundra, Oumalik vicinity, Northern Alaska, Photo: D.A. Walker
Successional sequence downwind from the Sagavanirktok River dunes

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

<table>
<thead>
<tr>
<th>Landscape, soil pH (distance from active dunes in km)</th>
<th>Common plant species (Stand type numbers, Walker, 1985)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Active dunes, pH 7.8-8.5 (0 km)</td>
<td>Elymus arenarius, Polemonium boreale (B9)</td>
</tr>
<tr>
<td>2. Partially stabilized dunes, pH 7.8-8.5 (&lt; 0.5 km)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Mesic sites with sandy substrates, pH 7.8-8.0 (1 km)</td>
<td>Carex aquatilis, Dryas integrifolia, Polygonum viviparum, Distichium capillaceum, Salix ovalifolia, Equisetum variegatum</td>
</tr>
<tr>
<td>4. Mesic sites with silty substrates, pH 7.0-7.5 (1-20 km)</td>
<td>Eriophorum vaginatum, Carex membranacea, C. bigelowii, Dryas integrifolia, Salix reticulata, S. arctica, S. lanata, Polygonum viviparum, Senecio atropurpureus, Pedicularis lanata, P. capitata, Papaver macounii, Chrysanthemum integrifolium, Tomentumum nitens, Dittichium flexicaule, Hypnum bambergeri, Orthothecium chryseum, Mesia uliginosa, Thamnola subuliformis, Ceraria spp., Dactylina arctica, Peligeran spp. (U2 = Dryado integrifoliatum-Caricetum bigelowii (Walker et al., 1994))</td>
</tr>
<tr>
<td>5. Mesic tussock tundra sites on the coastal plain with silty substrates, pH 6.0-7.0 (20-70 km)</td>
<td>Eriophorum vaginatum, Cassiope tetragona, Polygonum bistorta, Salix planifolia spp. pulchra, Carex bigelowii, Eriophorum vaginatum, Dryas integrifolia, Salts reticulata, Carex visidens, Tomenclum nitens, Hylocomium splendens, Ptilidium ciliare, Distichium capillaceum, Dittichium flexicaule, Orthothecium chryseum, Oxyrolepis wahlenbergii, Aulacomnium turgidum, A. palustre, Cladonia gracilis, Thamnola subuliformis (U1).</td>
</tr>
</tbody>
</table>

Photos: D.A. Walker
Relationship of MNT to humans on the Arctic Slope

• Paludification of Beringia caused constriction of areas of nutritious forage during the Holocene, possibly affecting the extinction of some of the Pleistocene mammals.

• Evidence from the Mesa site (Kunz & Reiner 1996) suggests that Paleoindian habitation on the Arctic Slope ceased at about the time of regional paludification about 8500 years ago.

• Modern distribution of game species may be also be related to MNT distribution patterns.

Mesa archeological site
Photo: Kunz and Rienier 1996
Past, present and future of moist nonacidic tundra

• Past
  – MNT was intermediate, transitional, ecosystem between the Steppe Tundras and the present-day moist acidic tundras

• Present
  – Occurs on:
    • Colder, windier, less snowy areas, mostly to the north
    • Areas with disturbance regimes (aeolian, glacial, cryoturbation)
    • Calcareous bedrock
  – An important habitat for a wide variety of organisms

• Future
  – Global warming and long-term vegetation succession could reduce the extent of MNT.
Take Home Points

- Next to summer temperature and soil moisture, soil pH is the key factor determining species composition and a host of ecosystem properties in Arctic tundra vegetation (Walker et al. 1998).
- Acidic and nonacidic tundra systems have been described in Svalbard (Elvebakk), Canada (Edlund) and Alaska (Walker), but the mechanisms responsible for such different acidic and nonacidic tundra ecosystems are still poorly understood.
- In the Low Arctic, the zonal vegetation tends to be acidic because of the accumulation of peat and organic acids.
- Nonacidic tundra occurs in relationship to a wide variety of circumstances including carbonate bedrock, glacial loess, recent glaciations, and relatively young landscapes (Walker & Everett 1991, Walker et al. 1995).
- High Arctic tundra in North America tends to be nonacidic because of very dry climates and abundance of carbonate bedrock.
- Classification of the acidic and nonacidic tundra was done at Toolik Lake (MD Walker et al. 1994).
- The moist acidic tundra (MAT)/moist nonacidic tundra (MNT) boundary in the at the northern boundary of the Arctic Foothills is used to describe and contrast the differences between these two important systems.