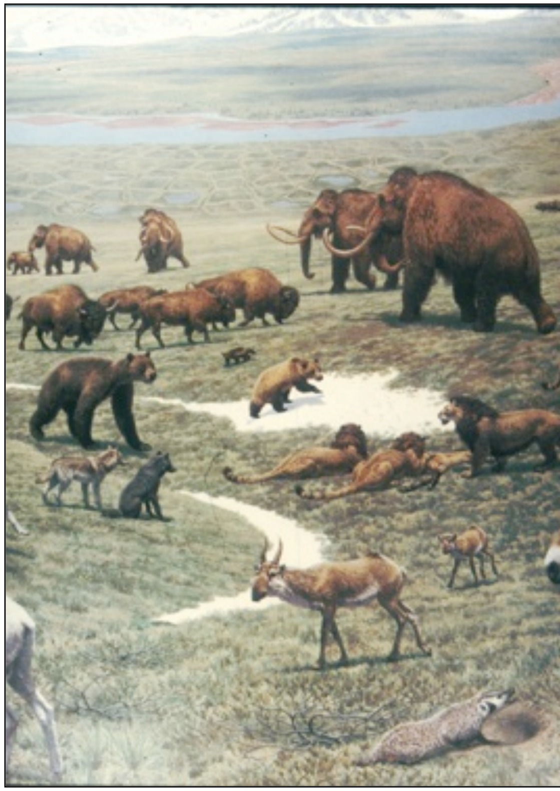
Course Syllabus

Week	Topic	Readings
1	Overview of Arctic Ecosystems: The role of climate, permafrost, and topography	Callaghan et al. 2005. Bliss et al. 1997 Chernov and Matveyeva 1997
2	The role of soil pH in Arctic Vegetation: Loess ecosystems and the Mammoth Steppe	Walker and Everett 1991 Walker, Auerbach et al. 1998; Walker et al. 2001
3	Biocomplexity of patterned ground ecosystems: Interrelationships between climate, geomorphology, permafrost, soils, and vegetation	Walker, Epstein et al. 2008 Walker, Kuss, et al. (in press)
4	Socio-ecological effects of oil and gas development in the Arctic: Comparison of the Prudhoe Bay, Alaska and Bovanenkova, Russia regions	NRC 2003 (look at whole book, focus on chapter 7) Walker, Forbes et al. 2011
5	Greening of the Arctic: Climate change and circumpolar Arctic vegetation	Bhatt et al. 2010
6	Plant to planet mapping of Arctic Vegetation: the Arctic Geobotanical Atlas	Walker, Raynolds et al. 2009 Walker, Raynolds, et al. 2005

Syllabus, description and references and other course materials:
http://www.geobotany.uaf.edu/teaching/CzechArcEcol/index
(Includes pdfs of lecture slides and referenced literature!)



Lesson 2

The role of soil pH in Arctic Vegetation:

Loess ecosystems and

Role of soil pH in vegetation is well studied in Europe...but still not fully understood

- **Ellenberg et al. indicator values (1992), 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’.”**

Journal of Vegetation Science 11: 225-244, 2000

Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements

Schaffers, André P. & Sýkora, Karlè V.

Department of Environmental Sciences, Nature Conservation and Plant Ecology Group, Wageningen Agricultural University, Bornsesteeg 69, NL-6708 PD Wageningen, The Netherlands; Fax +31317484845; E-mail andre.schaffers@staf.ton.wau.nl

Abstract. Ellenberg indicator values for moisture, nitrogen and soil reaction were correlated with measured soil and vegetation parameters. Relationships were studied through between-species and between-site comparisons, using data from 74 roadside plots in 14 different plant communities in The Netherlands forming a wide range.

Ellenberg moisture values correlated best with the average lowest moisture contents in summer. Correlations with the annual average groundwater level and the average spring level were also good. Ellenberg N-values appeared to be only weakly correlated with soil parameters, including N-minerali-

Introduction

The occurrence and abundance of different plant species enables ecologists to make statements about the prevailing environmental conditions. One formalized and extensively used system of indicator values is that of Ellenberg et al. (1992). They assigned indicator values to 2726 Central European vascular plant species, with respect to moisture, soil nitrogen status, soil reaction (acidity/ lime content), soil chloride concentration,

Not so well studied in the Arctic

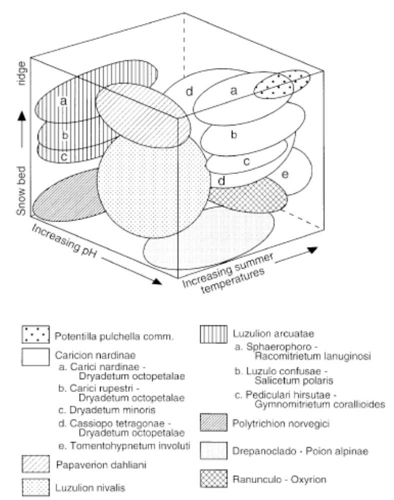
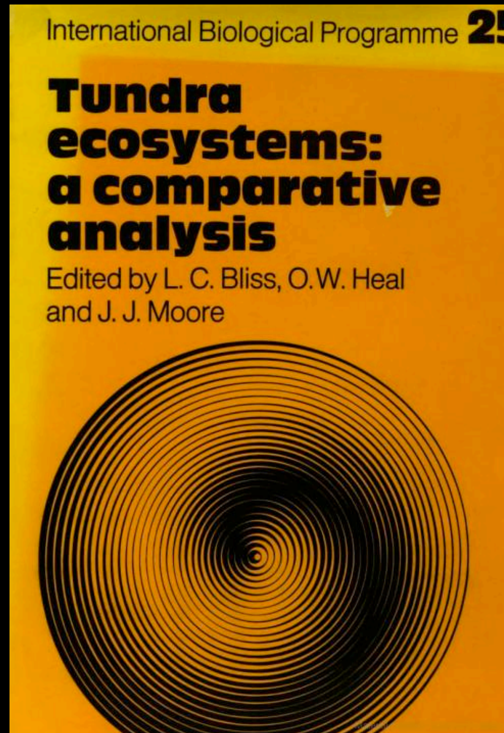


Fig. 3. Positions of syntaxa of exposed ridges, mesic plains/ slopes and snowbeds along three environmental gradients.

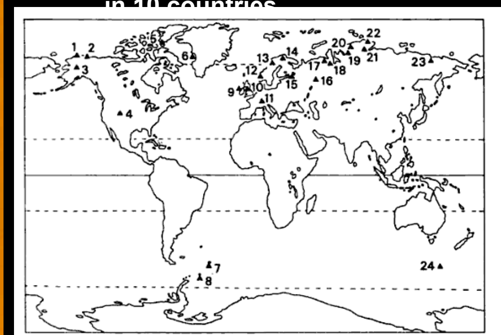
- **Most thorough work is that of Arve Elvebakk (1994) on Svalbard.**
- **Dave Cooper (1986) also recognized the clear differences in communities on limestone and granite in the Arrigetch Mtns., Brooks Range, AK.**
- **Sylvia Edlund (1982) recognized the importance of soil pH in her mapping studies in the Queen Elizabeth Islands, Canada.**

Elvebakk , 1994. A survey of plant associations and alliances from Svalbard, JVS, 5: 791-902

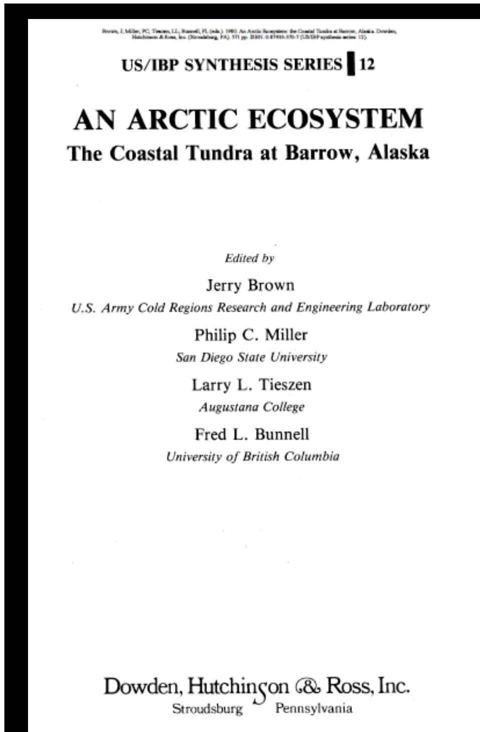


International Biological Programme Tundra Biome (1969-1973)

- IBP: An international effort to examine the Earth's major biomes.
- Tundra biome had study sites in 10 countries



Main U.S. Tundra Biome site at Barrow


US/IBP SYNTHESIS SERIES 12

AN ARCTIC ECOSYSTEM

The Coastal Tundra at Barrow, Alaska

Edited by

Jerry Brown

U.S. Army Cold Regions Research and Engineering Laboratory

Philip C. Miller

San Diego State University

Larry L. Tieszen

Augustana College

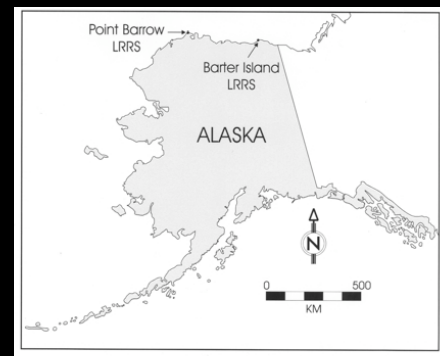
Fred L. Bunnell

University of British Columbia

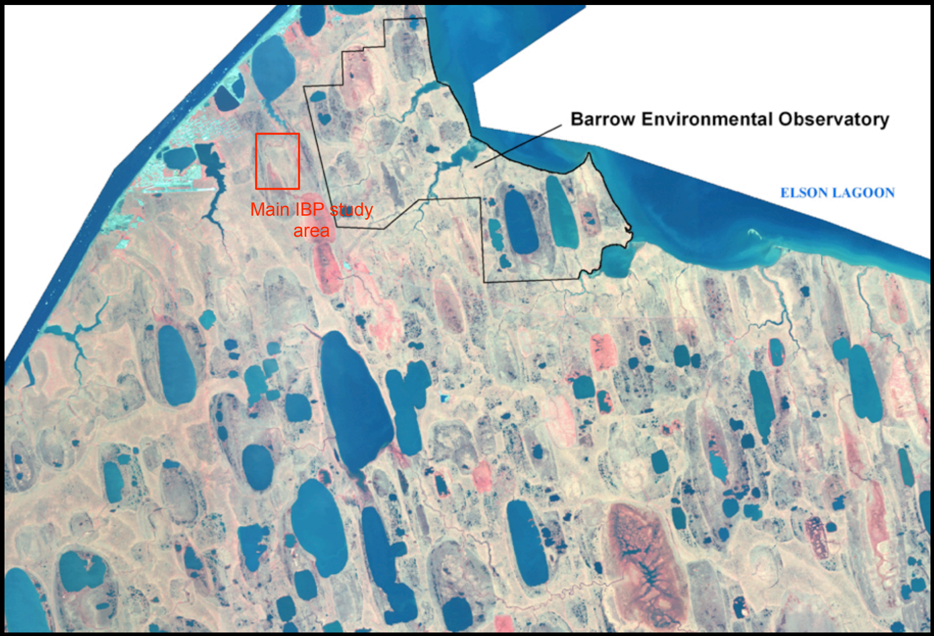
Dowden, Hutchinson & Ross, Inc.

Stroudsburg Pennsylvania

- 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.

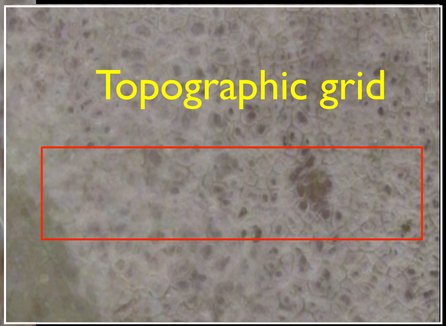


Terrain at Barrow: Wet coastal plain



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

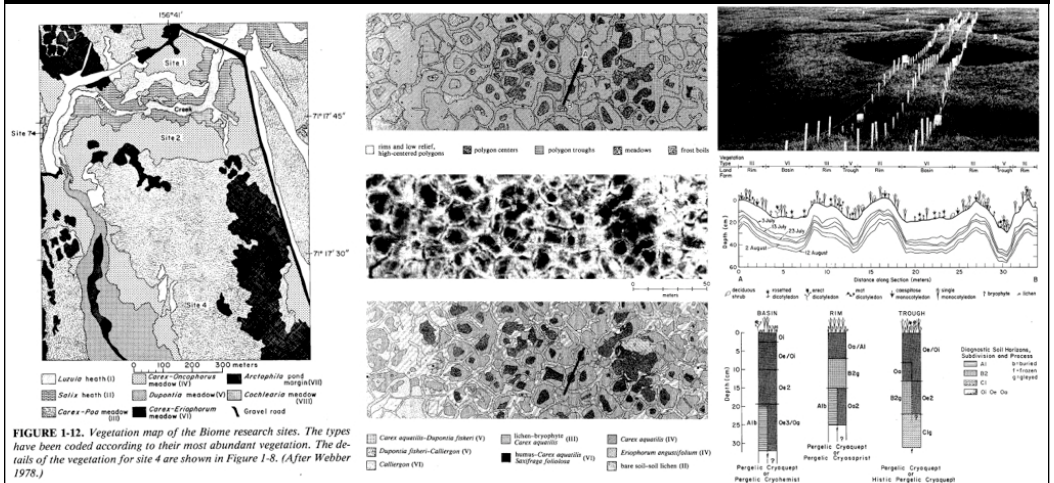


FIGURE 1-12. *Vegetation map of the Biome research sites. The types have been coded according to their most abundant vegetation. The details of the vegetation for site 4 are shown in Figure 1-8. (After Webber 1978.)*

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 Pruhoe Bay mainly to examine the impacts of oil development.
- More interested in tundra contrasts with

Acidic Tundra at Barrow: pH 3.8-5.0

Dry | Moist | Wet

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 very 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

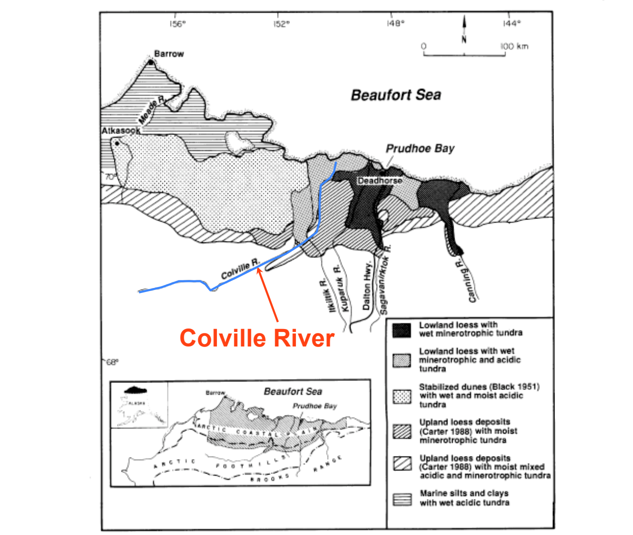


FIG. 1. Extent of minerotrophic and acidic tundras on the Alaskan North Slope based on Carter (1988) and AVHRR satellite-derived imagery. Upland loess occurs in the Arctic Foothills. Lowland loess occurs on the Arctic Coastal Plain.

- **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.**

Surface deposits on the Arctic Coastal Plain

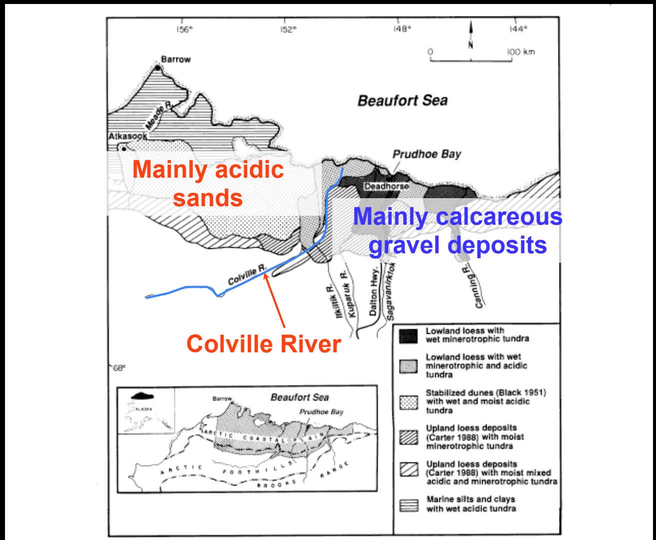


FIG. 1. Extent of minerotrophic and acidic tundras on the Alaskan North Slope based on Carter (1988) and AVHRR satellite-derived imagery. Upland loess occurs in the Arctic Foothills. Lowland loess occurs on the Arctic Coastal Plain.

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

AVHRR image of the North Slope

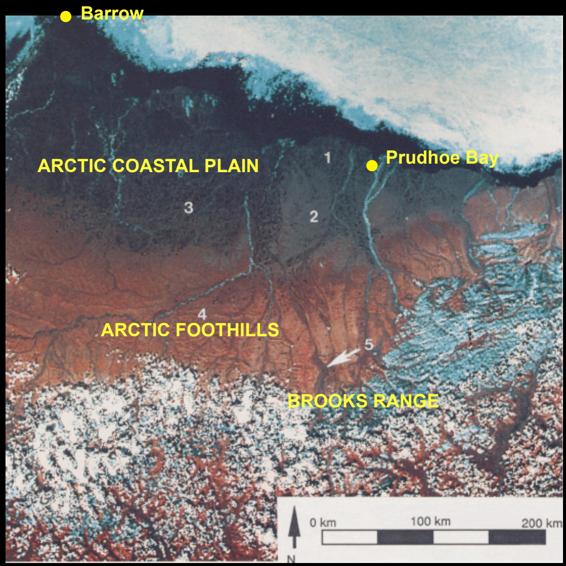
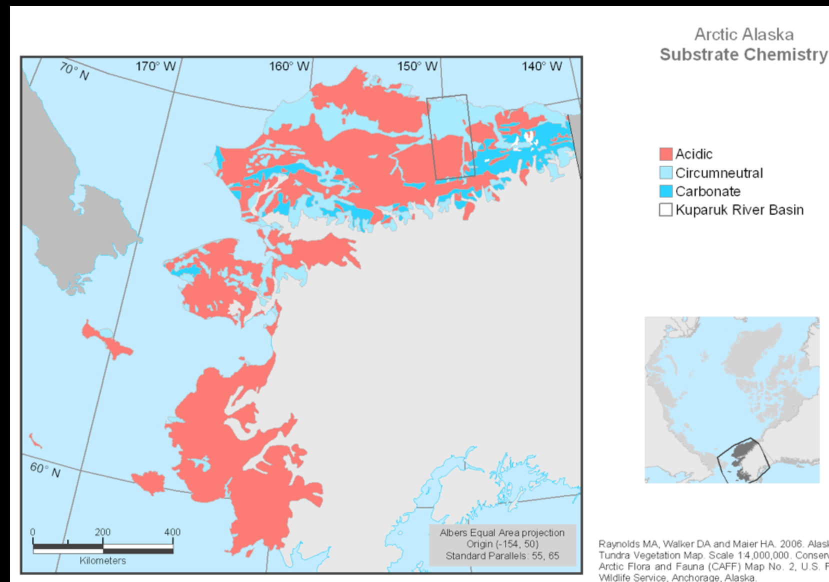


Image courtesy of United States Geological Survey and NASA.

<u>Numbered points</u>:

- Wet nonacidic tundra.
- Moist nonacidic tundra.
- Wet acidic tundra associated with a stabilized sand sea (Carter 1981).
- Moist acidic tundra on old glaciated surfaces in the Arctic Foothills.
- Nonacidic tundra associated with Itkillik-age (late Pleistocene) glacial and glaciofluvial

Distribution of nonacidic substrates in Arctic Alaska



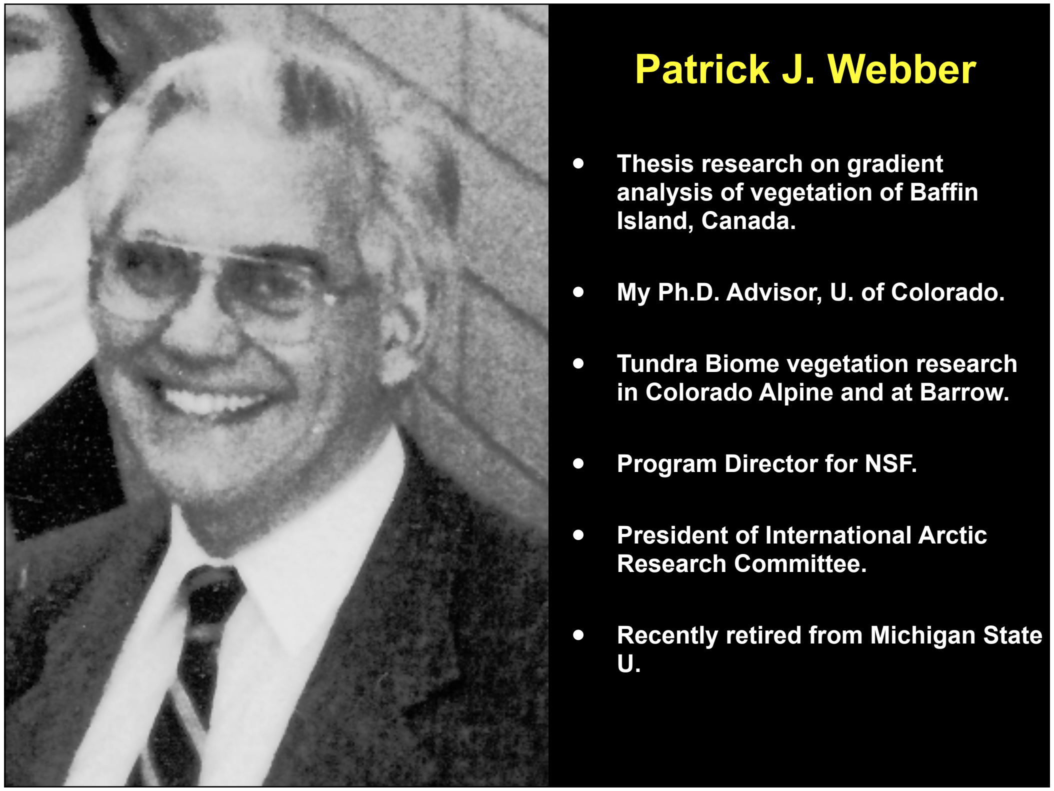
From Raynolds et al. 2005.

Braided rivers flowing out of the Brooks Range: source of modern loess

Sagavanirktok River, northern Alaska

Talk based on 6 key publications

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



Patrick Webber

My Ph.D advisor was Patrick Webber who is now at the Michigan State University.

Pat was a student of Roland Beschel who was a student of Gams, who helped develop the Northern European School of vegetation science.

Webber, however, came to America and was strongly influenced by the Wisconsin School and ordination methods. His thesis focused on applying ordination methods to the vegetation of Baffin Island, Canada.

He has worked most of his career in the Arctic and got me interested in mapping and in the study of disturbed ecosystems.

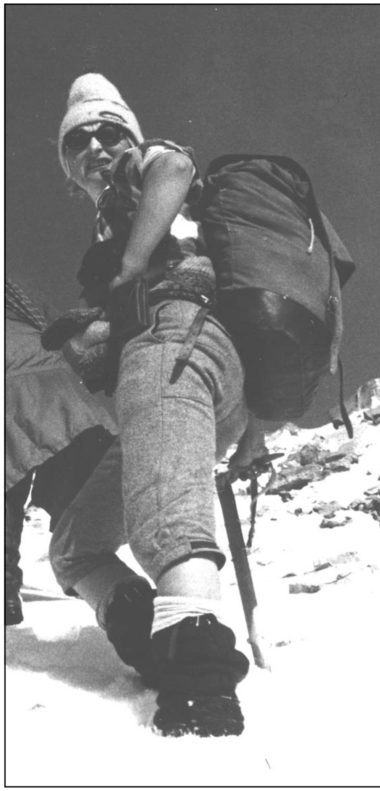
He was involved in the original Tundra Biome research at Barrow and provided me with my introduction to integrated research. I did my master's and Ph.D. theses under Pat Webber. My Master's involved using a scanning densitometer to map vegetation in ice-wedge polygons. My Ph.D. was entitled the Vegetation and Environmental Gradients of the Prudhoe Bay region, Alaska.

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.

Kaye Everett:

This man probably had the biggest influence on my field work. I spent 15 summers in the field with Kaye. Kaye had spent over 30 years in the Arctic and Antarctic. He taught me the importance of the link between soils and vegetation, and I learned an incredible amount about how arctic landscapes function from him.



Vera Komárková
Czechloslovakia-U.S., (1942-2005)

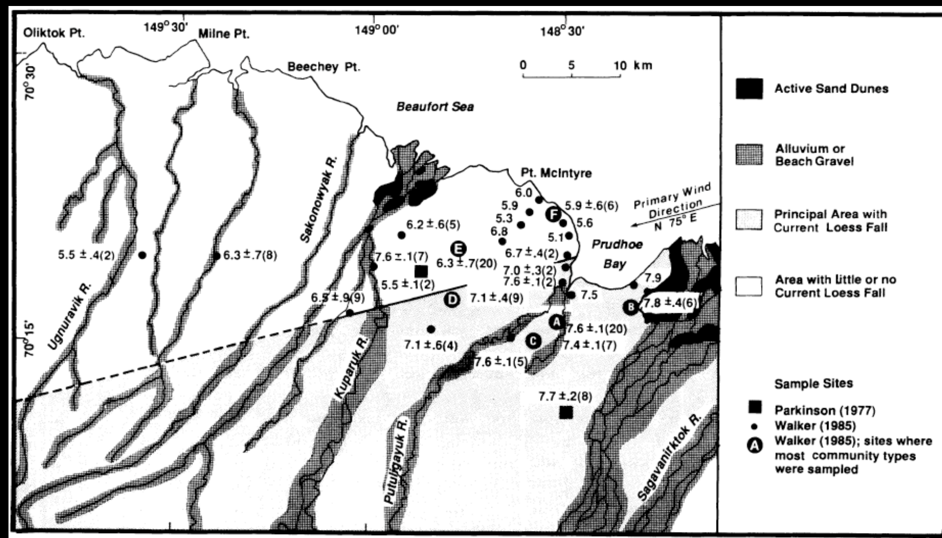
- Plant ecologist educated at Charles U.
- Student of Pat Webber's but she was a mature scientist before coming to the University of Colorado.
- Introduced me to European methods of phytosociology.
- Led first Women's Expedition to Annapurna, and climbed several peaks in the Himalayas over 8000 m.
- Mostly she influeneced 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

Vera Komarkova:

This lady was also a student of Pat Webber's but she was a mature scientist before coming to the University of Colorado. She introduced me to European methods of phytosociology. She is one of the most interesting people I ever met. She was on the first Women's Expedition to Annapurna, and climbed several peaks in the Himalayas over 8000 m.

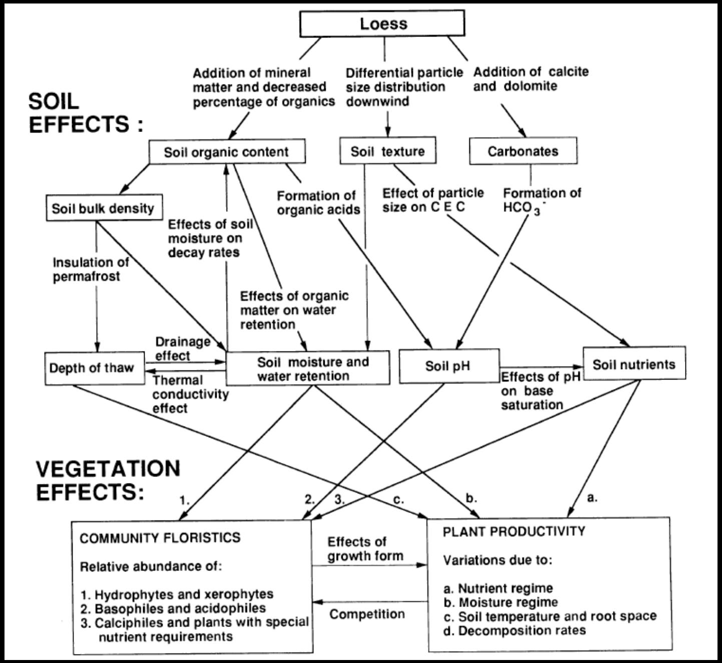
Mostly she influeneced me by her example of extremely hard work in the field and her European training in a wide range of disciplines that are needed to do plant ecological research.

Soil pH gradient downwind of the Sagavanirktok River



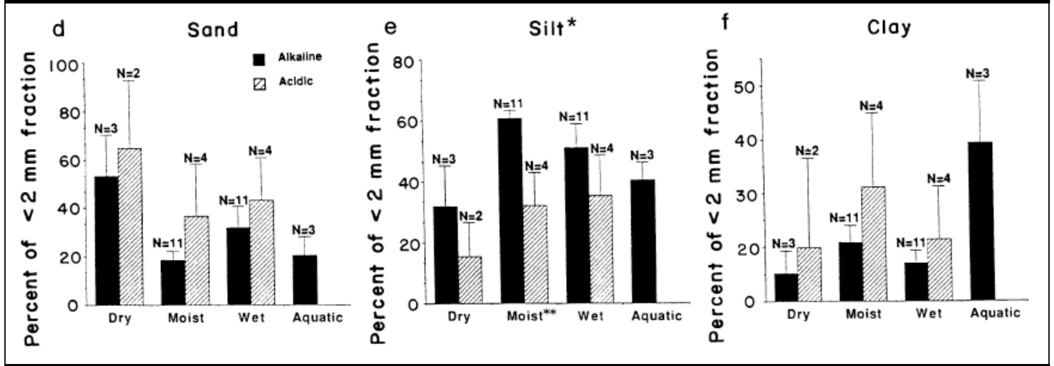
Walker and Everett 1991. Ecol. Monogr.

Effects of loess on soils and vegetation



Walker and Everett 1991. Ecol. Monogr.

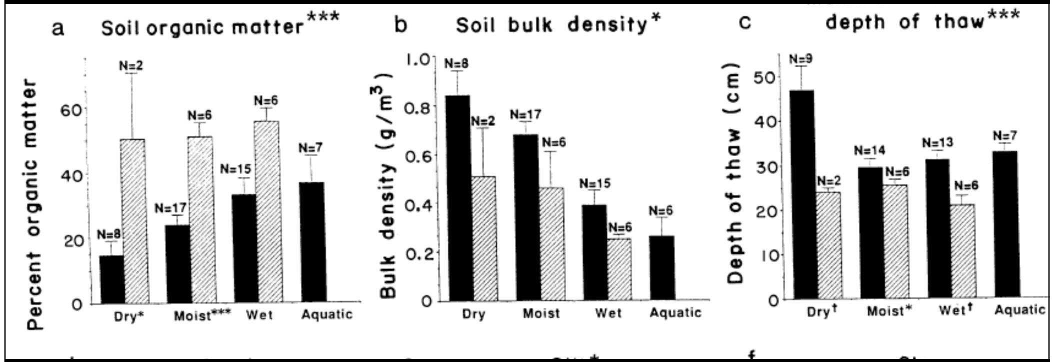
Particle size distribution in acidic and nonacidic soils a Prudhoe Bay



- **Dominance of silt in nonacidic soils.**

Walker and Everett 1991. Ecol. Monogr.

Effect of mineral addition on soil properties

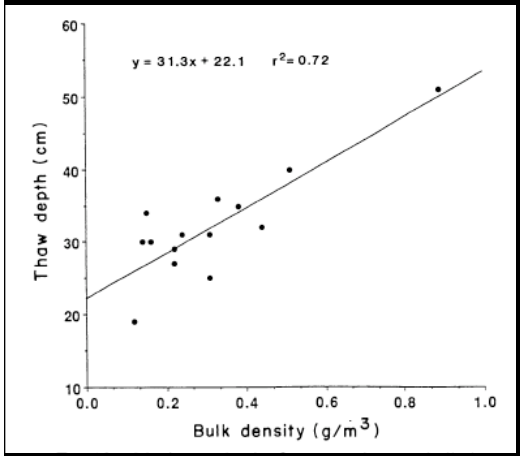


- **Dilution of organic material in peaty soils (decreased soil organic matter and increased soil bulk density)**
- **Decreases the insulative properties of the organic soil horizons, increasing the depth of the Active Layer.**

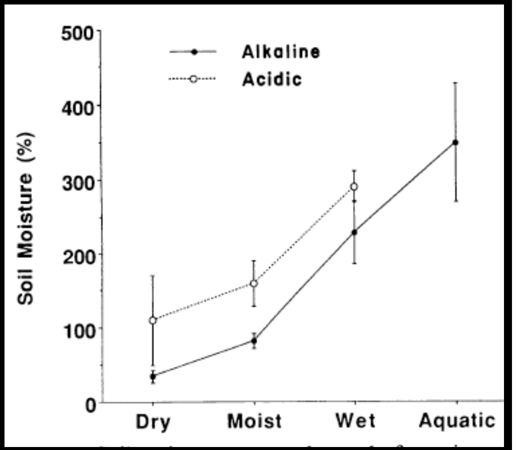
Walker and Everett 1991. Ecol. Monogr.

Effects of mineral matter on thaw depth and soil moisture

Thaw depth vs. bulk density



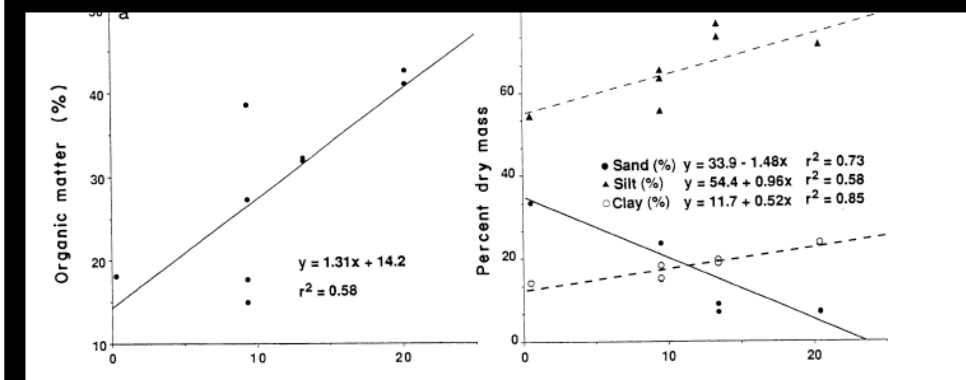
Gravimetric soil moisture vs. subjective moisture class



Walker and Everett 1991. Ecol. Monogr.

Soil properties vs. distance from the Sagavanirktok River

% Organic matter **% Soil texture classes**

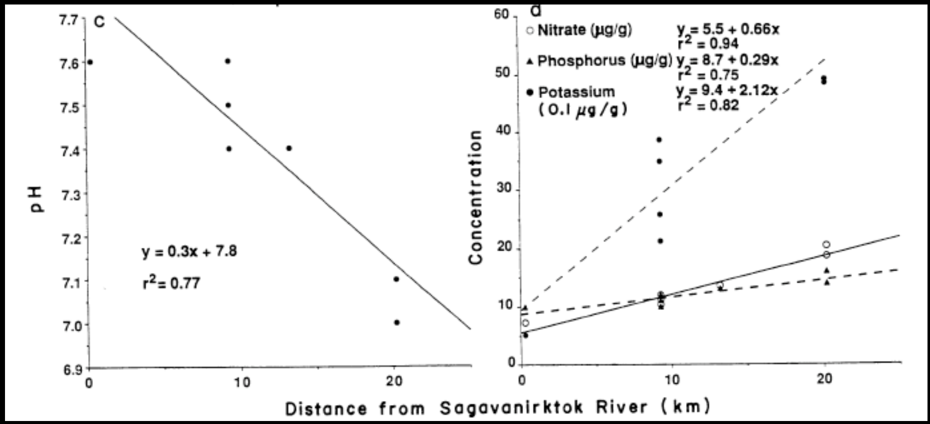


Distance from Sag R. (km) ⟶

Walker and Everett 1991. Ecol. Monogr.

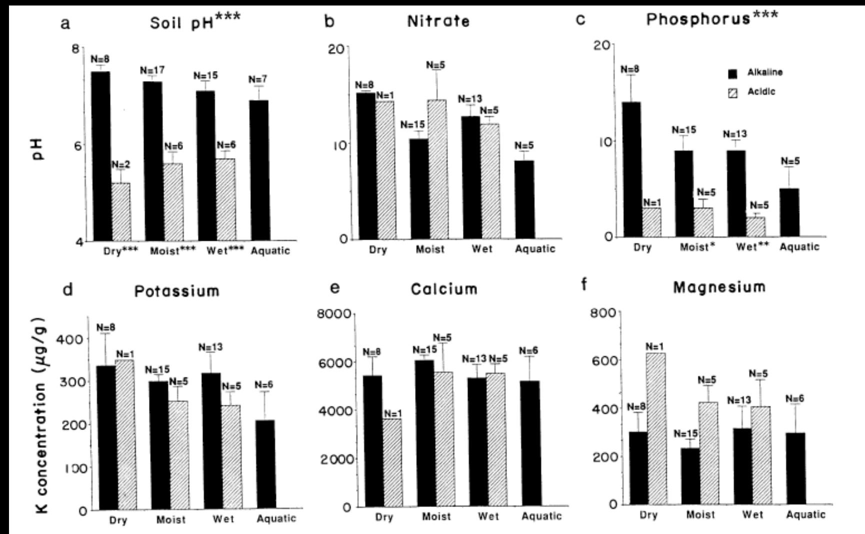
Soil properties vs. distance from the Sagavanirktok River (cont')

Soil pH **Soil nutrients**



Walker and Everett 1991. Ecol. Monogr.

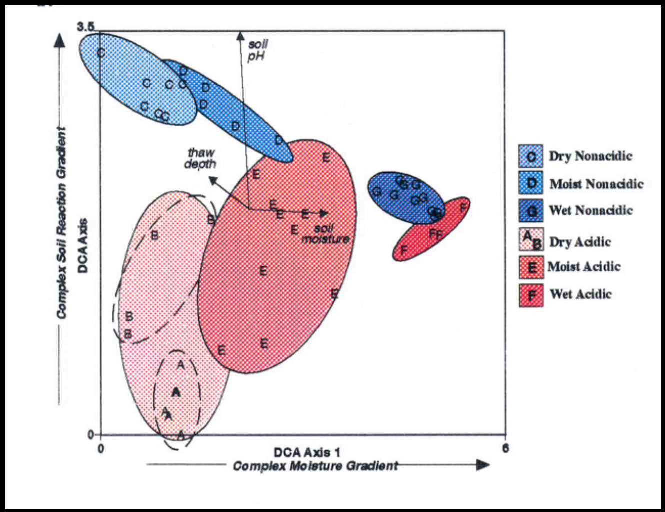
Soil nutrients in nonacidic and acidic tundra



Walker and Everett 1991. Ecol. Monogr.

Generally higher phosphorus in nonacidic soils.

Ordination of releves 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.

Elias, S.A., Short, S.K., Walker, D.A., and Auerbach, N.A., 1996, Historical biodiversity at remote Air Force sites in Alaska, Legacy Project #0742.

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

MAT

Sphagno-Eriophoretum vaginatii

MNT

Dryado-Carici bigelowii

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***

Tussock tundra, Happy Valley, Alaska

Dominant plants in MNT

Carex bigelowii

Dryas integrifolia

- **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: *Tomenthypnum nitens, Hylocomium splendens***
- **Lichens: *Thamnolia* spp., *Cetraria* spp., *Dactylina arctica***

Domninant bryophytes in MAT and MNT

Sphagnum lenense

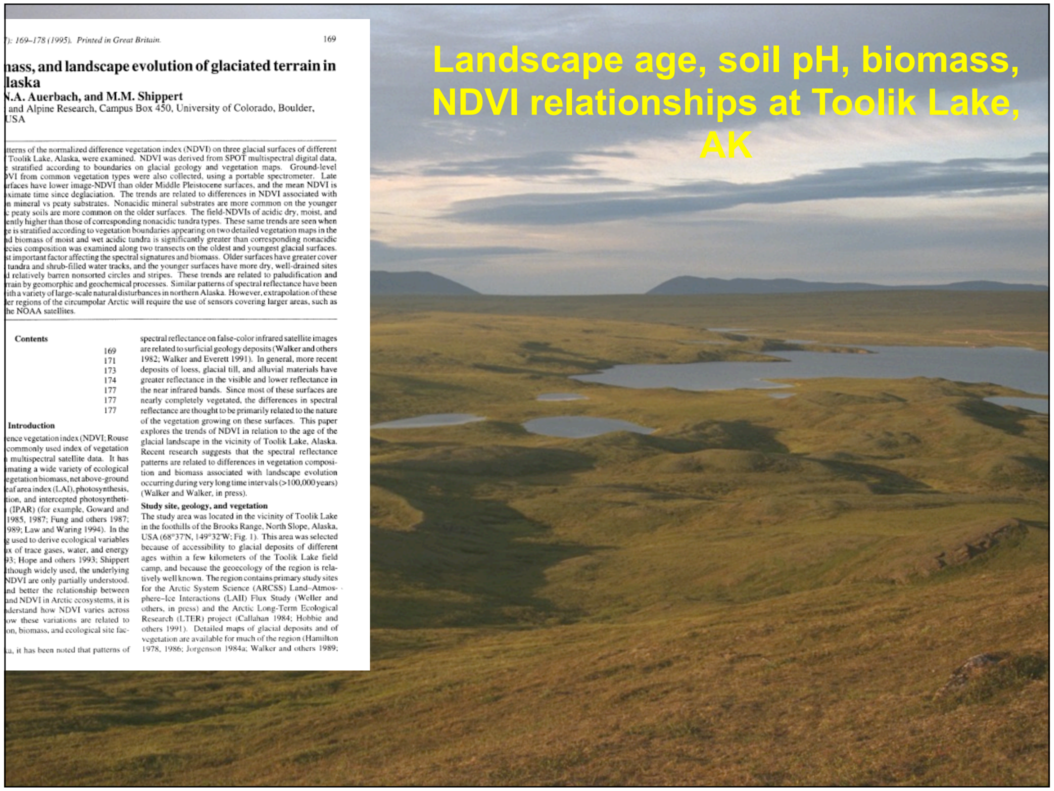
MAT

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

Tomentypnum nitens

MNT

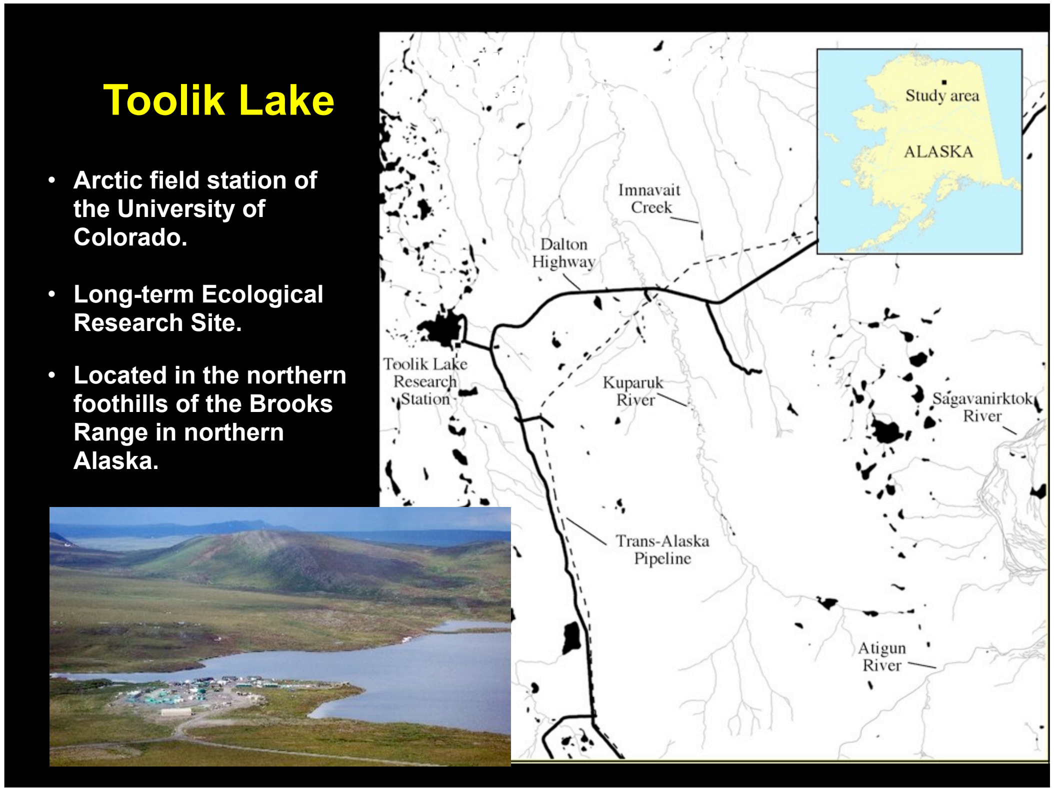
- *Tomentypnum nitens*
- *Ditrichum flexicaule*
- *Distichium capillaceum*
- *Hylocomium splendens*
- *Timmia austriaca*
- *Hypnum bambergeri*
- *Drepanocladus brevifolius*



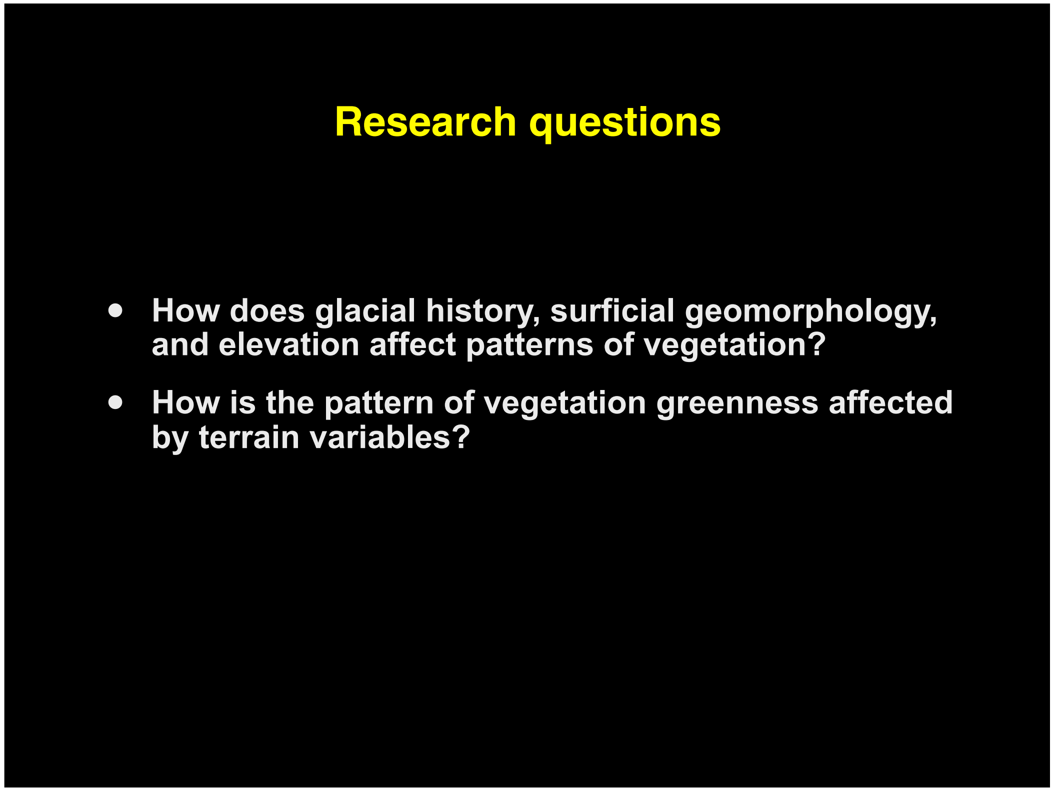
SLIDE 1:

Hi, my name is Hilmar Maier. I am presenting this paper on behalf of Corinne Munger, Skip Walker, and myself who are also coauthors. Corinne and Skip were unable to attend this morning's session because of other commitments.

The title of our talk is "Spatial analysis of glacial geology, surficial geomorpholoy and vegetation in the Toolik Lake region: Relevance to past and future land cover changes"



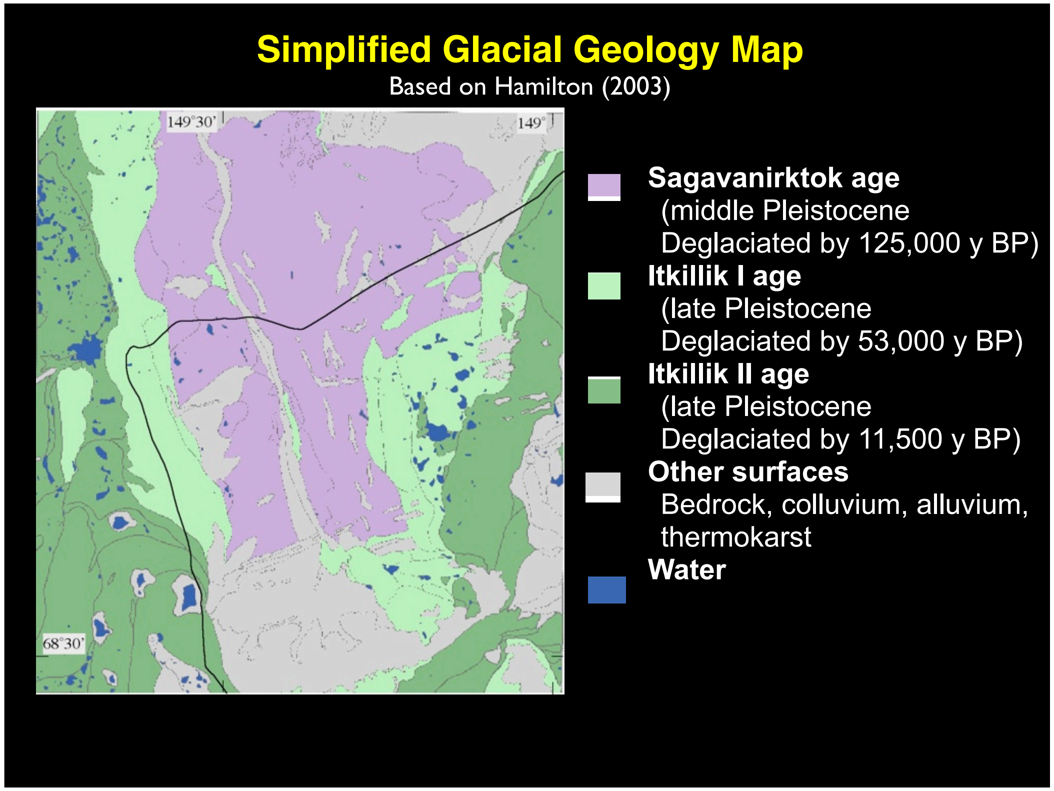
SLIDE 4:
The region of our study was the upper Kuparuk River and Toolik Lake region in northern Alaska.
This area is treeless and is underlain by continuous permafrost 250-300 m thick.



SLIDE 6:

Our primary research questions, used the regional GIS to address three questions related to the spatial and temporal patterns of vegetation:

1. How does glacial history, surficial geomorphology, and elevation affect patterns of vegetation?
2. How is the pattern of vegetation greenness affected by terrain variables?
3. How have the patterns changed during the satellite record?



This is a simplified glacial geology map of the region derived from Tom Hamilton's (2003) map.

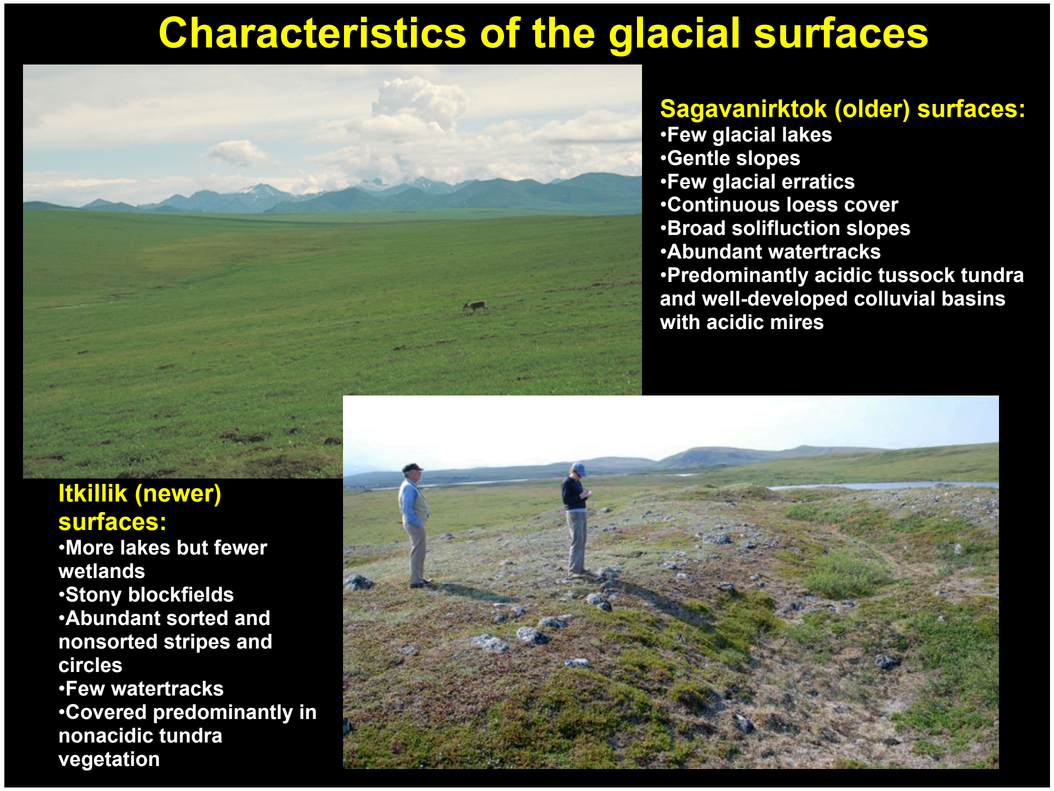
The inset map shows that repeated glacial advances flowed into the region during the mid and late Pleistocene along the major river systems.

The purple areas are mid-Pleistocene-age surfaces that were deglaciated by a glacier along the upper Kuparuk River, and was deglaciated by 125.000 years ago at the latest.

The green areas are late-Pleistocene-age surfaces.

The dark green areas are dated at about about 53,000 year before present,

The light green areas were deglaciated by about 11,500 years before present.

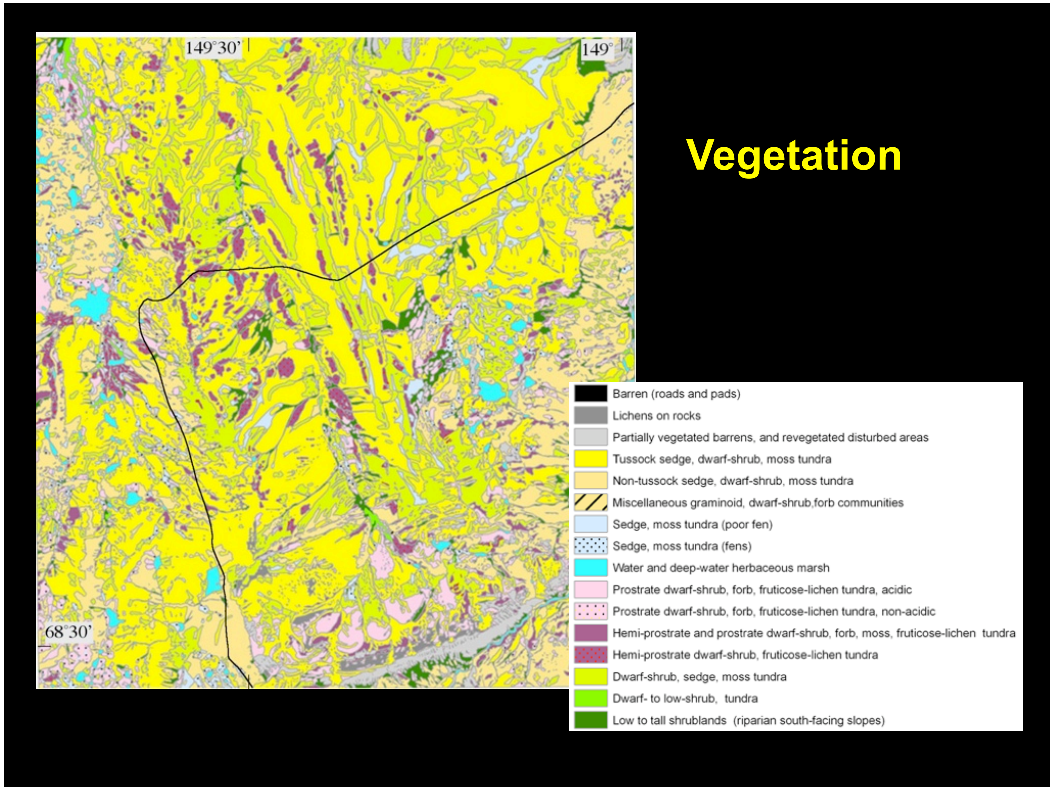


SLIDE 14:

In summary, the spatial analysis of the primary layers in the GIS database revealed these major differences in the glacial surfaces:

The Sagavanirktok-age surfaces have few glacial lakes, gentle slopes with widely dispersed glacial erratics and continuous loess cover and broad sweeping solifluction slopes, abundant water tracks (horsetail drainages), predominantly acidic tussock tundra and well-developed colluvial basins with acidic mires.

The Itkillik-age sufaces have more lakes but fewer wetlands, stony blockfields, abundant sorted and nonsorted stripes and circles, few water tracks, and are covered predominantly in nonacidic tundra vegetation.

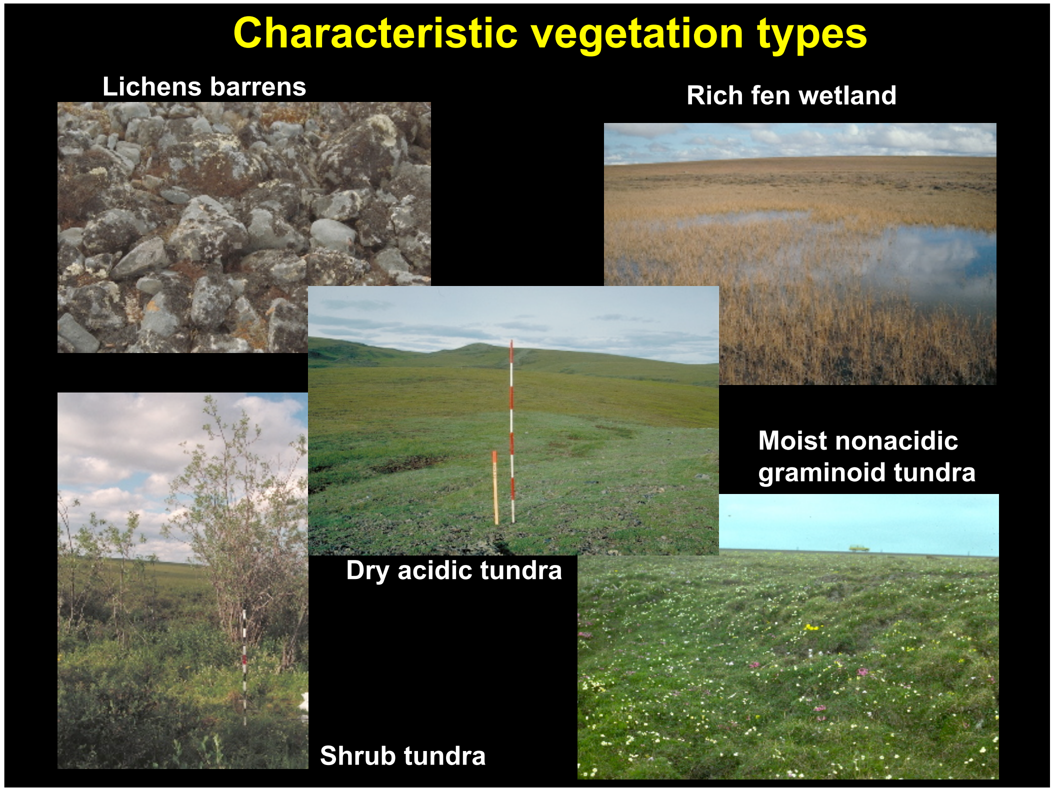


SLIDE 8:

This is the vegetation map of the region.

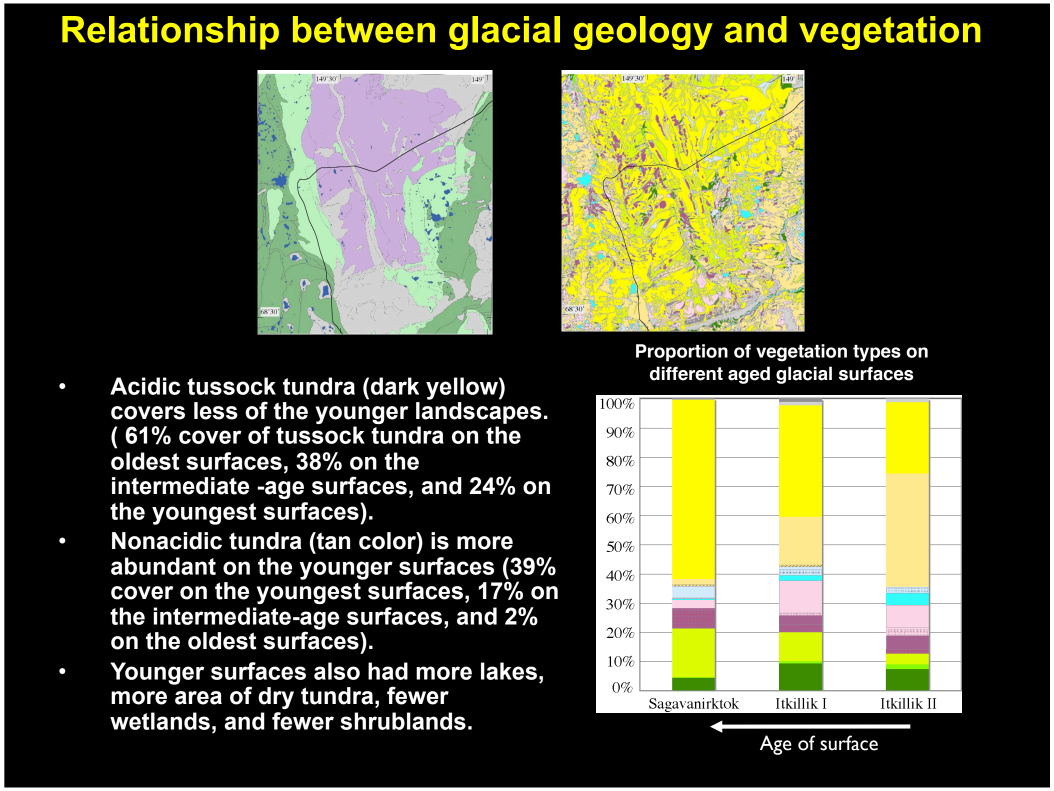
It is based on a detailed vegetation analysis of the region by M.D. Walker. The map has just been published and can be viewed on a poster in today's poster (poster # 2P-3-20).

The background photo and the yellow color on the map is tussock tundra, which the dominant vegetation in the region, and the zonal vegetation of subzone E on the Circumpolar Arctic Vegetation Map.



SLIDE 9:

Other characteristic vegetation types in the region include those shown in this figure.

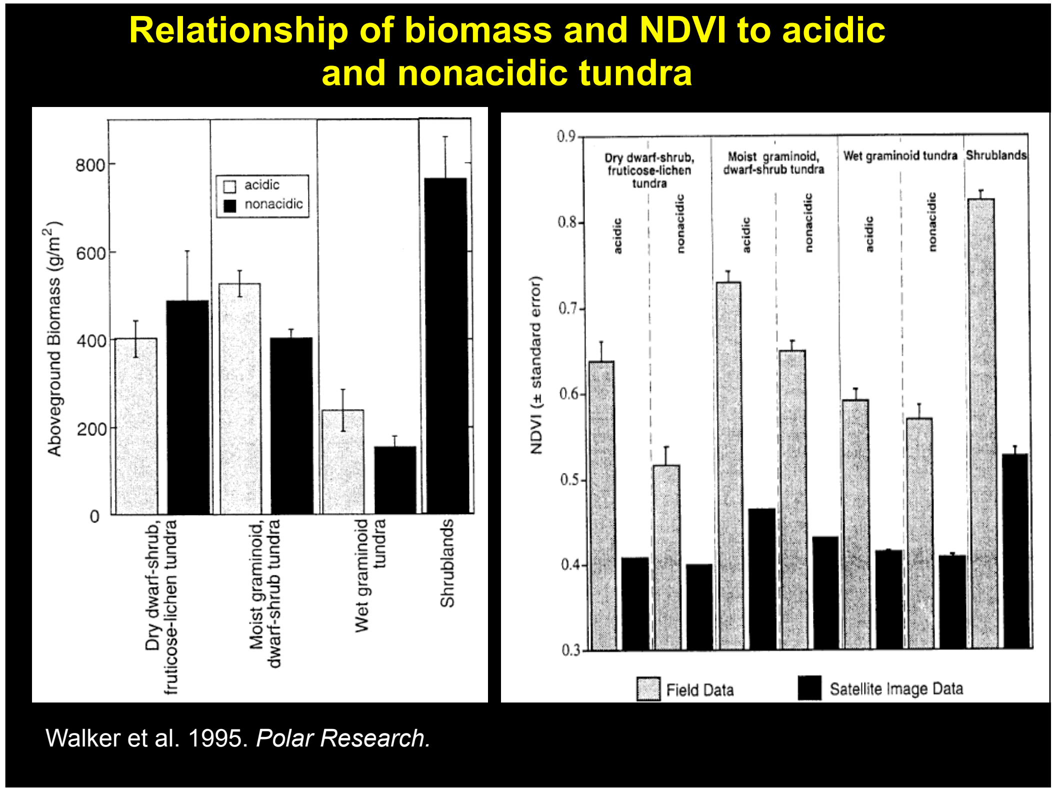


SLIDE 12:

The GIS analysis showed that there were distinctive trends of vegetation with surface age:

1. Acidic tussock tundra (dark yellow) covers less of the younger landscapes. There was 61% cover of tussock tundra on the oldest surfaces, 38% on the intermediate -age surfaces, and 24% on the youngest surfaces.
2. There was a corresponding increase in moist nonacidic tundra (tan areas) on the younger surfaces, with 39% cover on the youngest surfaces, 17% on the intermediate-age surfaces, and 2% on the oldest surfaces

3. Younger surfaces also had more lakes, more area of dry tundra, fewer wetlands, and fewer shrublands.



SLIDE 12:

The GIS analysis showed that there were distinctive trends of vegetation with surface age:

1. Acidic tussock tundra (dark yellow) covers less of the younger landscapes. There was 61% cover of tussock tundra on the oldest surfaces, 38% on the intermediate -age surfaces, and 24% on the youngest surfaces.
2. There was a corresponding increase in moist nonacidic tundra (tan areas) on the younger surfaces, with 39% cover on the youngest surfaces, 17% on the intermediate-age surfaces, and 2% on the oldest surfaces

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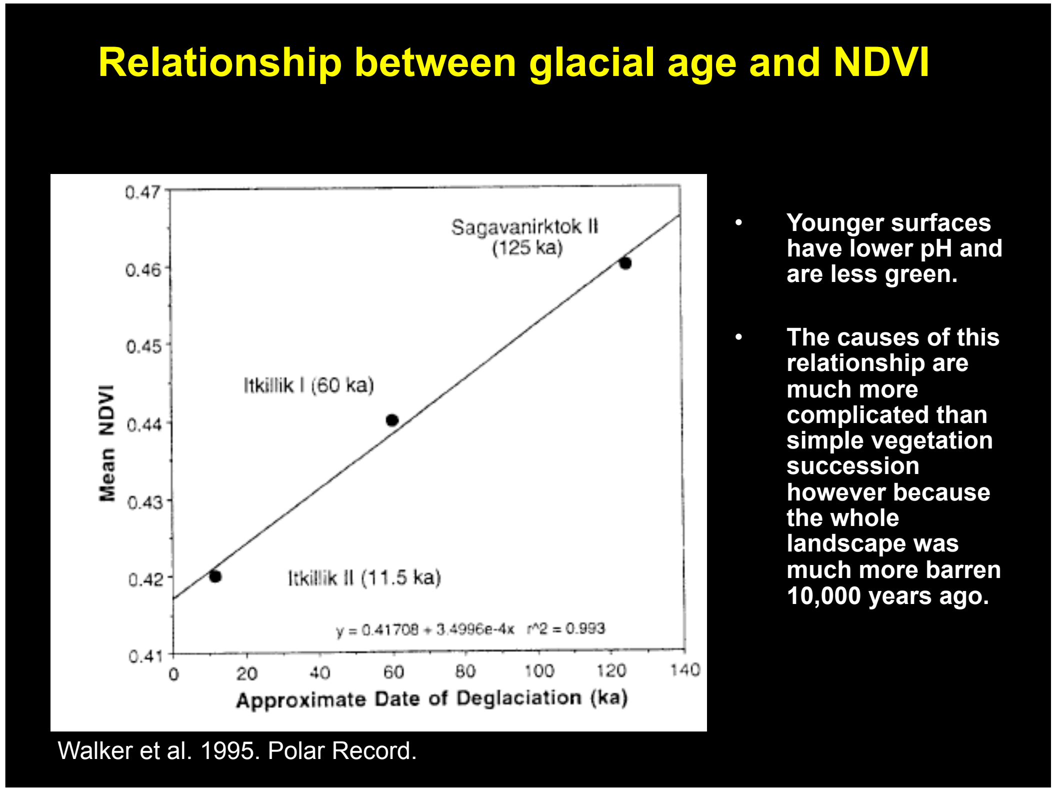

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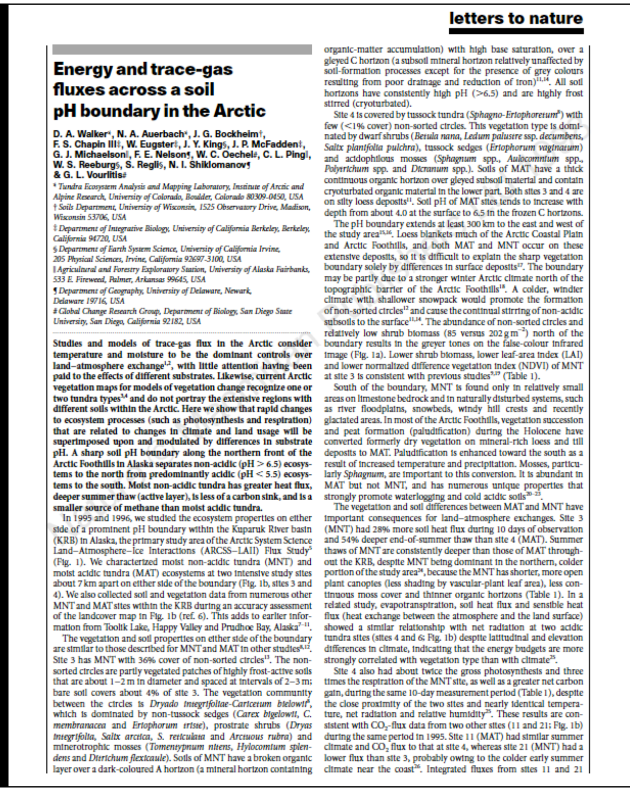


Energy and trace-gas fluxes across a soil pH boundary in the Arctic

D. A. Walker*, N. A. Auerbach*, J. G. Bockheim†, F. S. Chapin III‡, W. Eugster‡, J. Y. King§, J. P. McFadden‡, G. J. Michaelson‖, F. E. Nelson¶, W. C. Oechel#, C. L. Ping‖, W. S. Reeburgh§, S. Regli§, N. I. Shiklomanov¶ & G. L. Vourlitis#

* Tundra Ecosystem Analysis and Mapping Laboratory, Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80309-0450, USA
† Soils Department, University of Wisconsin, 1525 Observatory Drive, Madison, Wisconsin 53706, USA
‡ Department of Integrative Biology, University of California Berkeley, Berkeley, California 94720, USA
§ Department of Earth System Science, University of California Irvine, 205 Physical Sciences, Irvine, California 92697-3100, USA
‖ Agricultural and Forestry Exploratory Station, University of Alaska Fairbanks, 533 E. Fireweed, Palmer, Arkansas 99645, USA
¶ Department of Geography, University of Delaware, Newark, Delaware 19716, USA
# 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 exchange[1,2], 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 types[3,4] and do not portray the extensive regions with different soils 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 superimposed upon and modulated by differences in substrate pH. A sharp soil pH boundary along the northern front of the Arctic Foothills in Alaska separates non-acidic (pH > 6.5) ecosystems to the north from predominantly acidic (pH < 5.5) ecosystems to the south. Moist 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 moist acidic tundra.

In 1995 and 1996, we studied the ecosystem properties on either side of a prominent pH boundary within the Kuparuk River basin (KRB) in Alaska, the primary study area of the Arctic System Science Land–Atmosphere–Ice Interactions (ARCSS–LAII) Flux Study[5] (Fig. 1). We characterized moist non-acidic tundra (MNT) and moist acidic tundra (MAT) ecosystems at two intensive study sites about 7 km apart on either side of the boundary (Fig. 1b, sites 3 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, Alaska[7–11].

The vegetation and soil properties on either side of the boundary are similar to those described for MNT and MAT in other studies[8,12]. Site 3 has MNT with 36% cover of non-sorted circles[13]. The non-sorted circles are partly vegetated patches of highly frost-active soils that are about 1–2 m in diameter and spaced at intervals of 2–3 m; bare soil covers about 4% of site 3. The vegetation community between the circles is *Dryado integrifoliae-Caricetum bigelowii*[8], which is dominated by non-tussock sedges (*Carex bigelowii*, *C. membranacea* and *Eriophorum triste*), prostrate shrubs (*Dryas integrifolia*, *Salix arctica*, *S. reticulata* and *Arctuous rubra*) and minerotrophic mosses (*Tomentypnum nitens*, *Hylocomium splendens* and *Ditrichum flexicaule*). Soils of MNT have a broken organic layer over a dark-coloured A horizon (a mineral horizon containing organic-matter accumulation) with high base saturation, over a gleyed C horizon (a subsoil mineral horizon relatively unaffected by soil-formation processes except for the presence of grey colours resulting from poor drainage and reduction of iron)[11,14]. All soil horizons have consistently high pH (>6.5) and are highly frost stirred (cryoturbated).

Site 4 is covered by tussock tundra (*Sphagno-Eriophoretum*[8]) with few (<1% cover) non-sorted circles. This vegetation type is dominated by dwarf shrubs (*Betula nana*, *Ledum palustre* ssp. *decumbens*, *Salix planifolia pulchra*), tussock sedges (*Eriophorum vaginatum*) and acidophilous mosses (*Sphagnum* spp., *Aulocomnium* spp., *Polytrichum* spp. and *Dicranum* spp.). Soils of MAT have a thick continuous organic horizon over gleyed subsoil material and contain cryoturbated organic material in the lower part. Both sites 3 and 4 are on silty loess deposits[11]. Soil pH of MAT sites tends to increase with depth from about 4.0 at the surface to 6.5 in the frozen C horizons.

The pH boundary extends at least 300 km to the east and west of the study area[15,16]. Loess blankets much of the Arctic Coastal Plain and Arctic Foothills, and both MAT and MNT occur on these extensive deposits, so it is difficult to explain the sharp vegetation boundary solely by differences in surface deposits[17]. The boundary may be partly due to a stronger winter Arctic climate north of the topographic barrier of the Arctic Foothills[18]. A colder, windier climate with shallower snowpack would promote the formation of non-sorted circles[12] and cause the continual stirring of non-acidic subsoils to the surface[11,14]. The abundance of non-sorted circles and relatively low shrub biomass (85 versus 202 $g\,m^{-2}$) north of the boundary results in the greyer tones on the false-colour infrared image (Fig. 1a). Lower shrub biomass, lower leaf-area index (LAI) and lower normalized difference vegetation index (NDVI) of MNT at site 3 is consistent with previous studies[5,19] (Table 1).

South of the boundary, MNT is found only in relatively small areas on limestone bedrock and in naturally disturbed systems, such as river floodplains, snowbeds, windy hill crests and recently glaciated areas. In most of the Arctic Foothills, vegetation succession and peat formation (paludification) during the Holocene have converted formerly dry vegetation on mineral-rich loess and till deposits to MAT. Paludification is enhanced toward the south as a result of increased temperature and precipitation. Mosses, particularly *Sphagnum*, are important to this conversion. It is abundant in MAT but not MNT, and has numerous unique properties that strongly promote waterlogging and cold acidic soils[20–23].

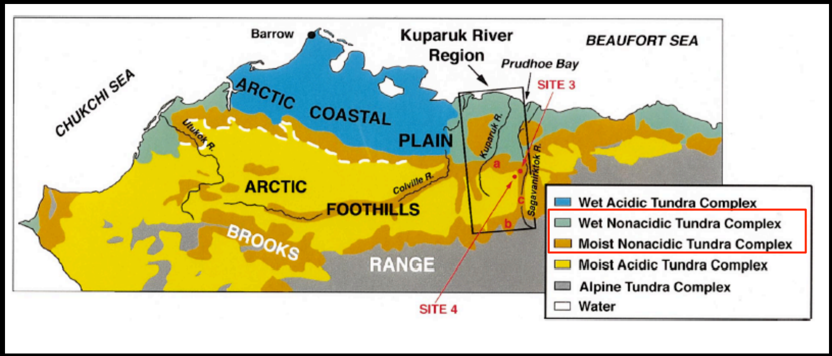
The vegetation and soil differences between MAT and MNT have important consequences for land–atmosphere exchanges. Site 3 (MNT) had 28% more soil heat flux during 10 days of observation and 54% deeper end-of-summer thaw than site 4 (MAT). Summer thaws of MNT are consistently deeper than those of MAT throughout the KRB, despite MNT being dominant in the northern, colder portion of the study area[24], because the MNT has shorter, more open plant canopies (less shading by vascular-plant leaf area), less continuous moss cover and thinner organic horizons (Table 1). In a related study, evapotranspiration, soil heat flux and sensible heat flux (heat exchange between the atmosphere and the land surface) showed a similar relationship with net radiation at two acidic tundra sites (sites 4 and 6; Fig. 1b) despite latitudinal and elevation differences in climate, indicating that the energy budgets are more strongly correlated with vegetation type than with climate[25].

Site 4 also had about twice the gross photosynthesis and three times the respiration of the MNT site, as well as a greater net carbon gain, during the same 10-day measurement period (Table 1), despite the close proximity of the two sites and nearly identical temperature, net radiation and relative humidity[25]. These results are consistent with CO_2-flux data from two other sites (11 and 21; Fig. 1b) during the same period in 1995. Site 11 (MAT) had similar summer climate and CO_2 flux to that at site 4, whereas site 21 (MNT) had a lower flux than site 3, probably owing to the colder early summer climate near the coast[26]. Integrated fluxes from sites 11 and 21

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

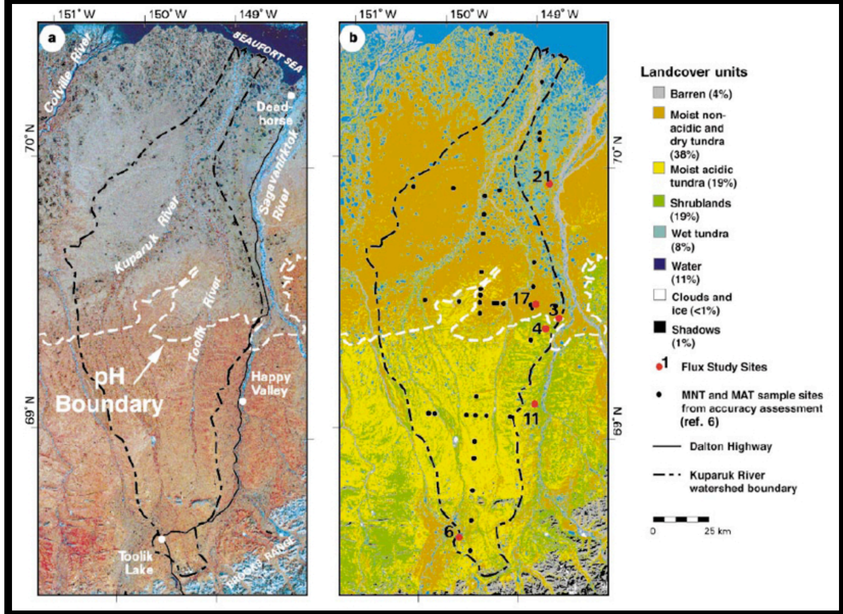
Broader pattern of acidic and nonacidic tundras in northern Alaska



pH boundary within the Kuparuk River watershed

Landsat False CIR image

Landcover classification



Walker et al. 1998. Nature.

Table 1 Comparison of ecosystem properties of MNT and MAT at sites in the Kuparuk River Basin

	Sites 3 and 4			Other sites			
Ecosystem property	MNT	MAT	Significance	MNT	MAT	Significance	Reference
Soil							
pH of top mineral horizon	7.6 [1]	5.5 [1]	n.a.	7.0 ± 0.16 [20]	5.3 ± 0.13 [10]	***	Ref. 14
				6.3 ± 0.1 [14]	4.6 ± 0.1 [33]		Ref. 8†
O-horizon thickness (cm)	9 ± 1 [71]	15 ± 1 [71]	**	11 ± 1.9 [21]	21 ± 1.8 [15]	***	This study‡
Soil moisture of top mineral horizon ($cm^3 cm^{-3}$, Jul 95)	0.37 [1]	0.40 [1]	n.a.				This study
Bare soil (% cover)	4.4 ± 1.6 [6]	0.2 ± 0.0 [6]	***	8 ± 1 [140]	1 ± 0.2 [121]	***	This study§
Vegetation							
Height of plant canopy (cm)	3.9 ± 0.3 [340]	6.5 ± 0.4 [340]	***				This study
Leaf area index	0.50 ± 0.03 [66]	0.84 ± 0.05 [66]	***	0.57 ± 0.06 [7]	0.81 ± 0.08 [11]	**	Ref. 19
NDVI (MSS)	0.23 [1]	0.32 [1]	n.a.	0.28 ± 0.00 [4×10^6]	0.41 ± 0.00 [2×10^6]	n.a.	This study‖
NDVI (Hand-held)				0.62 ± 0.02 [7]	0.71 ± 0.01 [11]	**	Ref. 19
Moss cover (%)	65 ± 4 [12]	79 ± 4 [12]	**				This study
Above ground biomass ($g m^{-2}$)							
Shrubs	85 ± 18 [10]	202 ± 22 [10]	***	127 ± 19 [7]	270 ± 19 [11]	***	Ref. 19
Graminoids	124 ± 12 [10]	112 ± 15 [10]	n.s.	118 ± 22 [7]	118 ± 24 [11]	n.s.	Ref. 19
Forbs	40 ± 22 [10]	10 ± 2 [10]	***	12 ± 4 [7]	12 ± 2 [11]	n.s.	Ref. 19
Mosses, lichens, litter	504	460	n.a.	221 ± 85 [7]	207 ± 33 [11]	n.s.	Ref. 19
Total	753 ± 60 [10]	784 ± 139 [10]	n.s.	447 ± 23 [7]	607 ± 27 [11]	***	Ref. 19
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]	***				This study
Thaw depth (cm)	57 ± 1 [71]	37 ± 1 [71]	***	52 ± 2 [20]	39 ± 2 [14]	***	This study§
				57 ± 5 [14]	36 ± 3 [33]	***	Ref. 8
Evapotranspiration (19–30 Jun 1995, $mm d^{-1}$)	1.16 ± 0.17 [331]	1.06 ± 0.16 [275]	n.a.				This study
10-d gross primary production (19–30 Jun 1995 $g CO_2$-$C m^{-2} d^{-1}$)	0.94 ± 0.14 [331]	1.82 ± 0.27 [275]	n.a.				This study
10-d net CO_2 uptake ($g CO_2$-$C m^{-2} d^{-1}$)	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-d respiration loss ($g CO_2$-$C m^{-2} d^{-1}$)	0.27 ± 0.04 [331]	0.87 ± 0.13 [275]	n.a.				This study
1995 net CO_2 uptake ($g CO_2$-$C m^{-2}$ per season)				27.6 [77]	55.2 [90]	n.a.	This study#
1996 net CO_2 uptake ($g CO_2$-$C m^{-2}$ per season)				3.3 [31]	52.5 [73]	n.a.	This study*
Methane emission ($mg CH_4 cm^{-2} yr^{-1}$)				69 ± 33 [12]	449 ± 301 [15]	*	This study††
Soil organic carbon ($kg C m^{-3}$)	40 [1]	88 [1]	n.a.	56 ± 5 [5]	44 ± 11 [6]	n.s.	Ref. 11
				55 ± 5 [16]	49 ± 4 [7]	n.s.	Ref. 10

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: *$P \leq 0.1$; **$P \leq 0.05$; ***$P \leq 0.01$; 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 aerial 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.

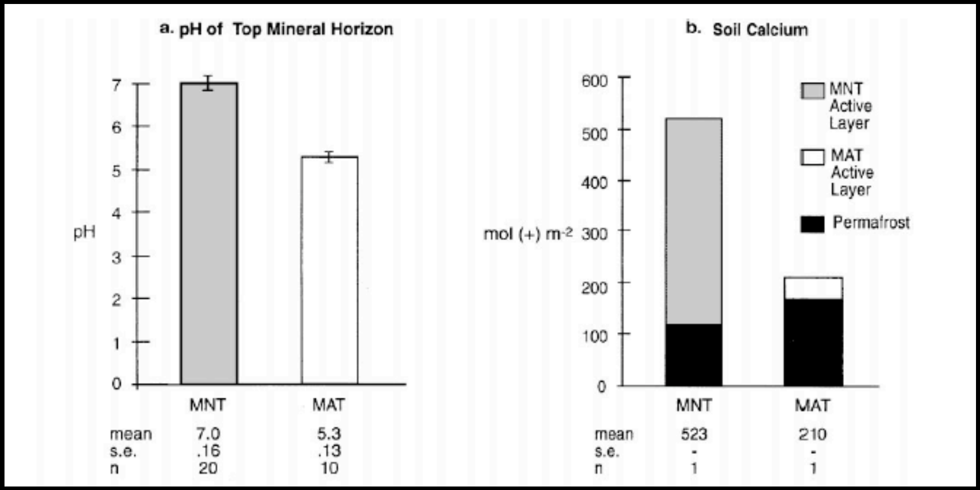
¶ Sites 11 (MAT) and 24 (MNT).

Sites 11 (MAT) and 24 (MNT). Time intervals for measurements: site 11, 1 Jun–31 Aug 1995; site 24, 16 Jun–31 Aug 1995.

* Sites 11 (MAT) and 17 (MNT). Time intervals for measurements: site 11, 6 Jun–31 Aug 1996; site 17, 15 Jun–19 Aug 1996.

†† Methane measurements at 37 plots at Toolik Lake region, Happy Valley and Deadhorse.

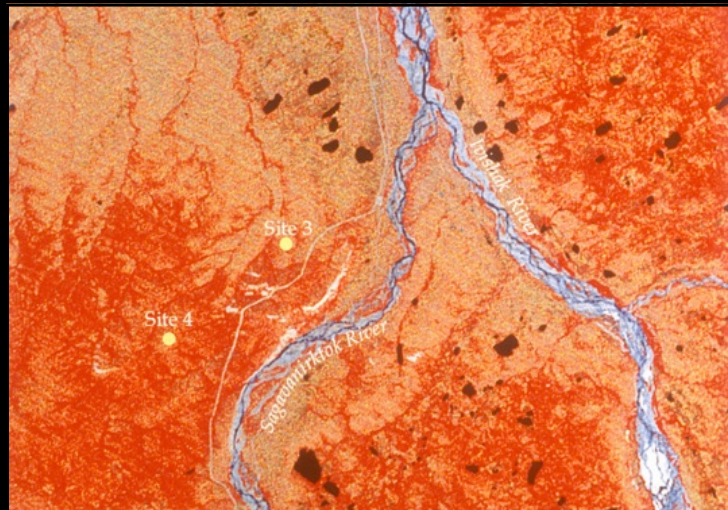
Soil pH and soil calcium



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

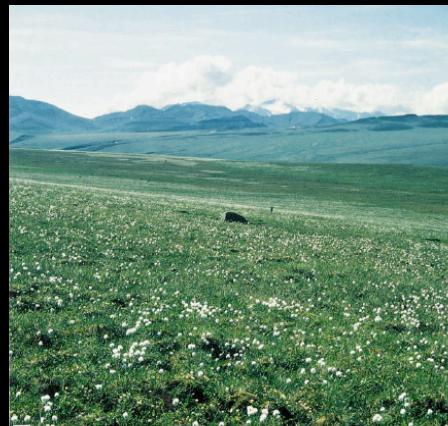


Landsat MSS image of boundary near Sagwon, northern edge of Arctic Foothills, Alaska

- **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.**

Major spectral differences between MAT and MNT

MAT

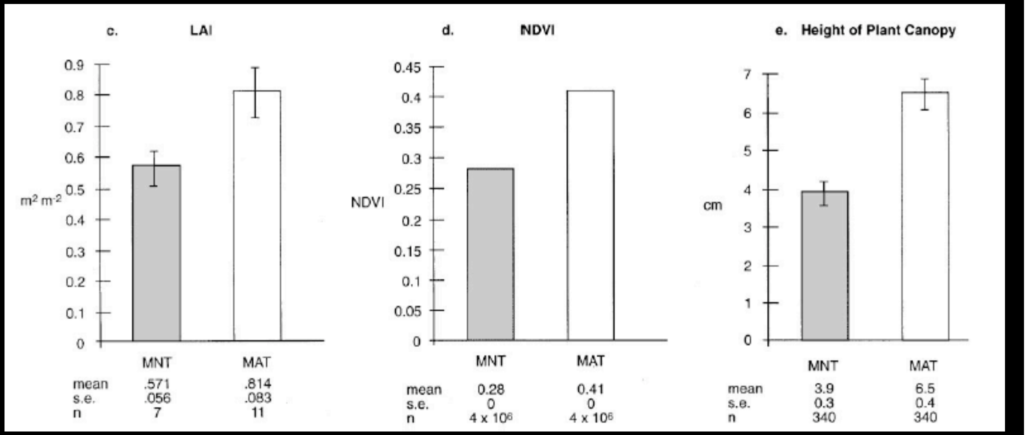


Much greener due to abundance of dwarf shrub (Betula nana, Salix pulchra, Ledum decumbens) and green sedge leaves (*Eriophorum vaginatum*).

MNT

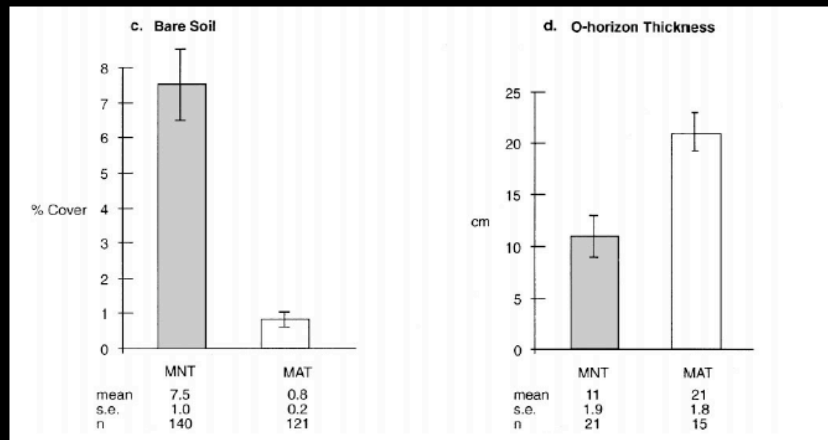
Abundance of dead sedge and *Dryas* leaves, brown mosses (*Tomentypnum nitens, Hylocomium splendens*) and bare soil from frost boils.

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.

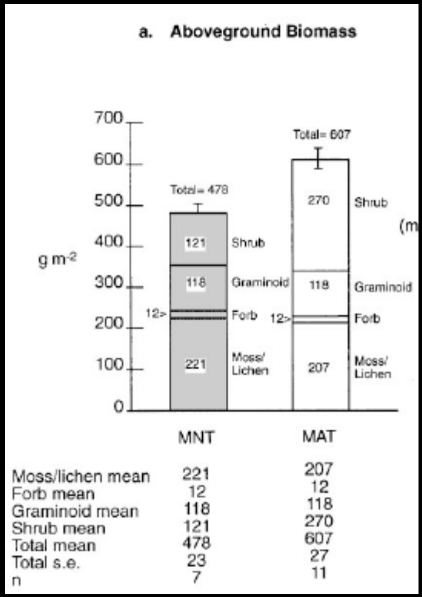
Bare soil and O-horizon thickness from the whole Kuparuk River watershed



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

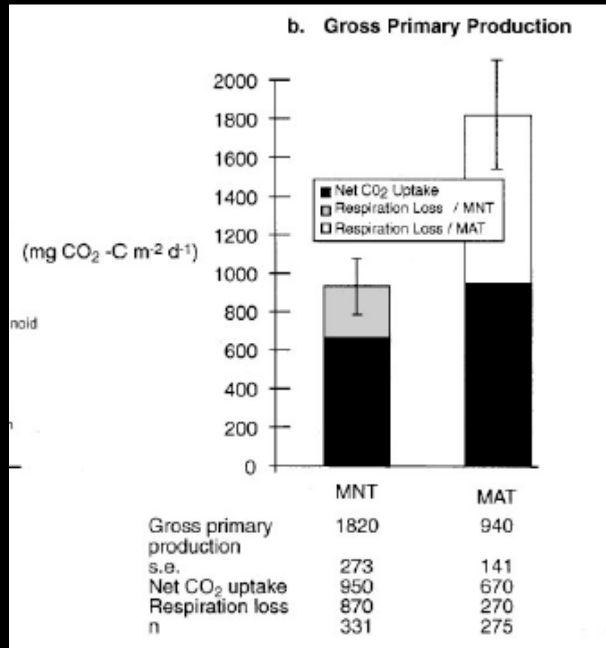
Walker et al. 1998.

d. Measured O-horizon thickness at 37



Aboveground biomass at Sites 3 and 4

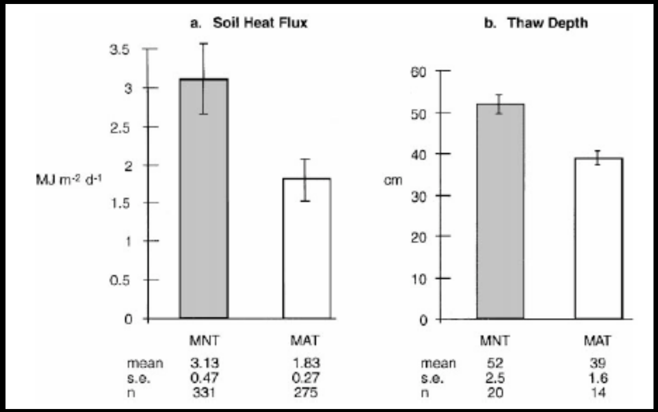
- Much more shrub biomass in the MAT site.
- Measured mainly at Sites 3 and 4.



Gross primary production (respiration + net

- **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



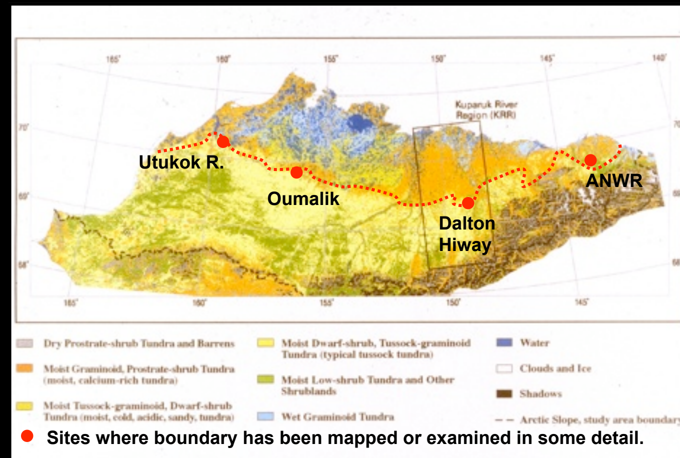
a. Measured at sites 3 and 4.

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**



Moist acidic and nonacidic tundra at Oumalik

MAT

MNT Oumalik, northern Alaska

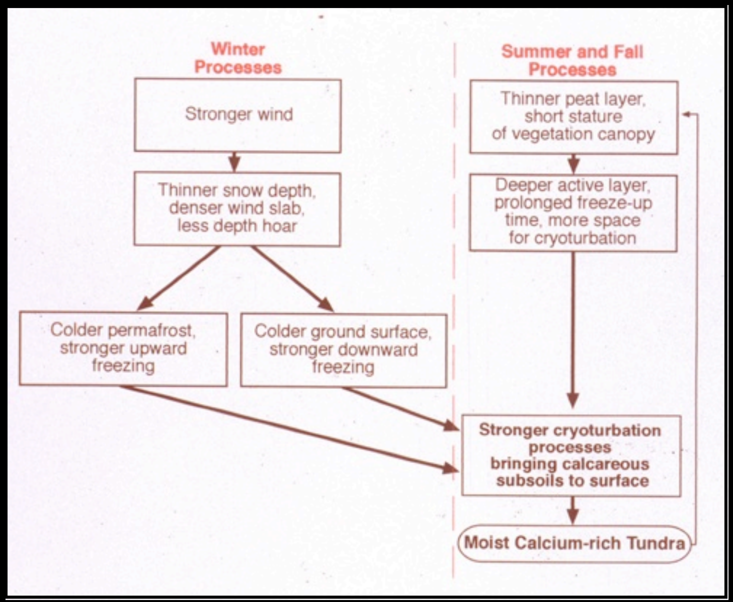
Much of the boundary is distant from modern loess sources, but Northern foothills are areas of ancient loess deposits

Sagavanirktok River, northern Alaska

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.

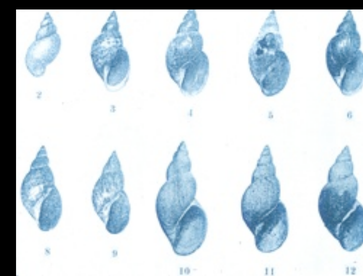
Conceptual model of climate-snow-cryoturbation-MNT hypothesis



Question I'd like to answer: "Is there a relationship between wildlife distribution and MNT?"





PERGAMON

Quaternary Science Reviews 20 (2001) 149–163

QSR

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

D.A. Walker[a,*], J.G. Bockheim[b], F.S. Chapin III[a], W. Eugster[c], F.E. Nelson[d], C.L. Ping[e]

[a]*Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775, USA*
[b]*Soils Department, University of Wisconsin, 1525 Observatory Drive, Madison, WI 53706, USA*
[c]*Department of Integrative Biology, University of California Berkeley, Berkeley, CA 94720, USA*
[d]*Department of Geography, University of Delaware, Newark, DE 19716, USA*
[e]*Agricultural and Forestry Exploratory Station, University of Alaska Fairbanks, 533 E. Fireweed, Palmer, AK 99645, USA*

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

* Corresponding author.
E-mail address: ffdaw@uaf.edu (D.A.Walker).

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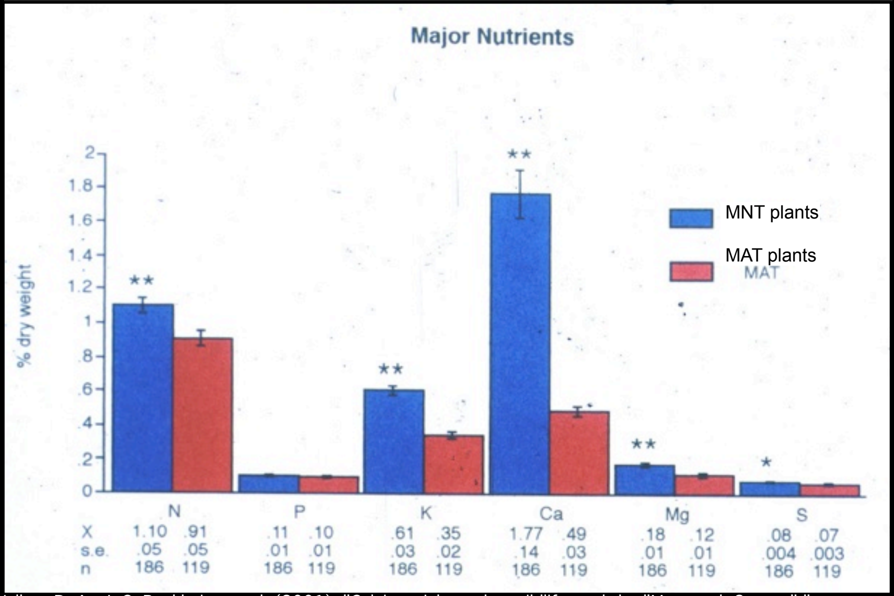
PII: S0277-3791(00)00126-8

Leaf tissue chemistry of MNT and MAT plants

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)

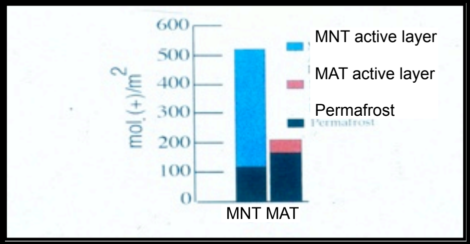
Species	Tissue	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)
Moist nonacidic tundra							
Arctous rubra	Leaves	1.2	0.1	0.39	1.32	0.13	0.06
Arctous rubra	Branches	0.6	0.06	0.16	1.06	0.14	0.06
Carex bigelowii	Aboveground	0.7	0.07	0.3	0.63	0.06	0.06
Cassiope tetragona	Aboveground	0.6	0.06	0.2	1.02	0.08	0.06
Cetraria 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

Leaf tissue chemistry

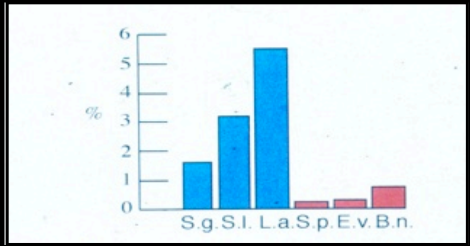


Walker, D. A., J. G. Bockheim, et al. (2001). "Calcium-rich tundra, wildlife, and the "Mammoth Steppe"." Quaternary Science Reviews 20(1-3): 149-163.

Soil calcium



Plant tissue calcium in common forage species



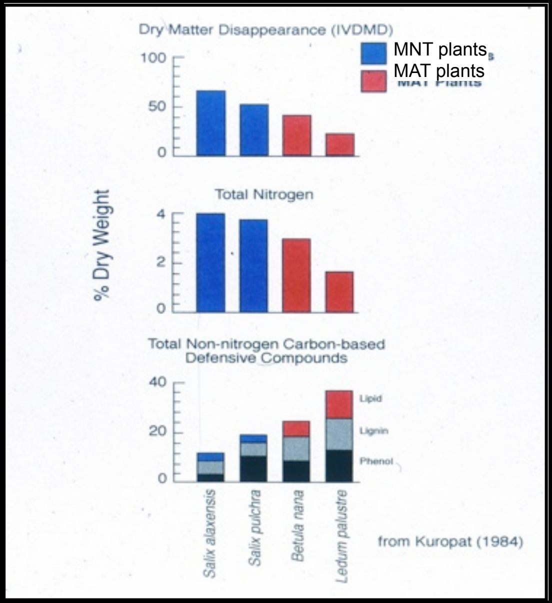
Walker, D. A., J. G. Bockheim, et al. (2001). "Calcium-rich tundra, wildlife, and the "Mammoth Steppe"." Quaternary Science Reviews 20(1-3): 149-163.

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

Betula nana, Ledum decumbens, Rubus chamaemorus

Digestibility, nitrogen and carbon-based defensive compounds in common forage species



Walker, D. A., J. G. Bockheim, et al. (2001). "Calcium-rich tundra, wildlife, and the "Mammoth Steppe"." Quaternary Science Reviews 20(1-3): 149-163.

Common forage species for caribou and grizzly bears upper Utukok River

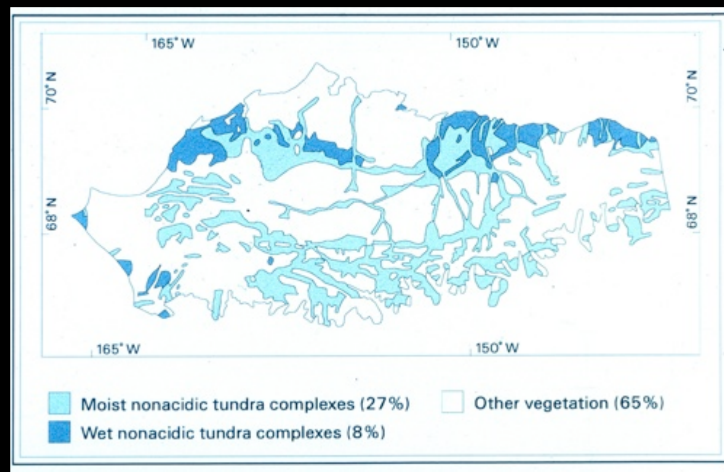
- **Caribou (Kuropat and Bryant 1980)**
  - ***Eriophorum vaginatum* (flowers)**
  - **Salix pulchra**
  - ****Salix alaxensis***
  - ****Salix glauca***
  - ****Equisetum arvense***
  - ****Lupinus arcticus***
  - ****Boykinia richardsonii***
  - ****Oxytropis maydelliana***

Grizzly bear (Hechtel 1985)

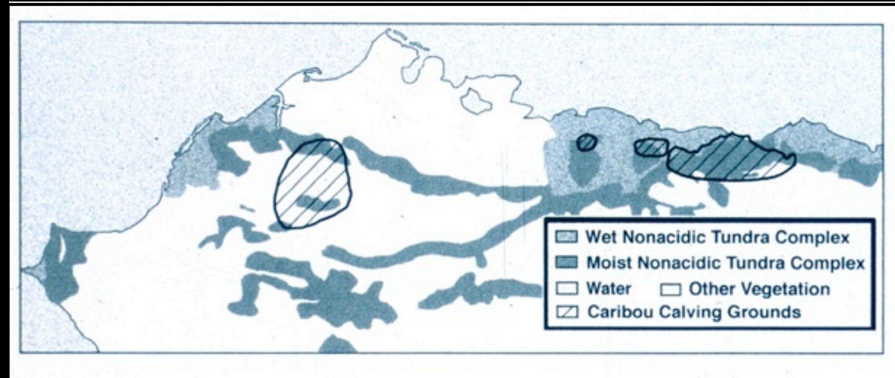
- ****Hedysarum alpinum* roots**
- ****Arctous rubra* berries**
- ****Boykinia richardsonii* leaves and flowers**
- ****Equisetum arvense* young shoots**
- ****Shepherdia canadensis* berries**
- ***Eriophorum vaginatum* flowers**

***Nonacidic species**

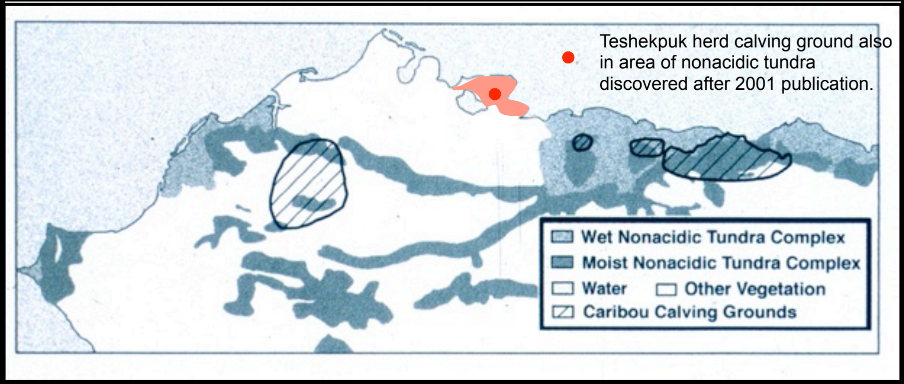
Distribution of nonacidic tundra in northern Alaska



Relationship between known caribou calving grounds and MNT in 1998



Relationship between caribou calving grounds and MNT



Northern Beringia was an arid environment

Pik dunes, northern Alaska

Possible “steppe” tundra analog in dunes along Sagavanirktok River,

Artemisia borealis, Trisetum spicatum, Kobresia myosuroides “steppe”
Sand dunes of the Sagavanirktok River delta

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**

Other key aspects of the "Mammoth Steppe" ecosystem according to Guthrie (1990)

- Fertile soils resulting from continual input of loess.
- Sparse or nonexistent moss carpets (firmer substrates for animal footing).
- Shallow winter snow due to extreme continentality.
- Deep active layers.
- Sparse, but diverse, grass-forb vegetation.
- Rich in nutrients.
- More poorly defended by secondary plant compounds.
- Patchier landscapes with a wider diversity of habitats than present.

Factors that would limit modern animal populations in acidic 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.

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.
- .http://www.carmanetwork.com/download/attachments/1115003/NAC_Herds.mov?version=1

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

Successional sequence downwind from the Sagavanirktok River dunes

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))

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 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

Key points

- Tundra systems can be roughly divided into those that occur on acidic and non-acidic substrates.
- 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, and relatively young landscapes (Walker & Everett 1991, Walker et al. 1995).
- Classification of the acidic and nonacidic tundra was done at Toolik Lake (MD Walker et al. 1994).
- Next to summer temperature and soil moisture, soil pH is a key factor determining species composition and a host of ecosystem properties (Walker et al. 1998).
- The current nonacidic tundra is most likely an intermediate form of vegetation between the steppe-tundra systems of the late

Biomass and LAI vs. total summer warmth index

- **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