PERMAFROST AND PERIGLACIAL PROCESSES
Permafrost Periglac. Process. **14**: 103–123 (2003)
Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/ppp.452

Vegetation-Soil-Thaw-Depth Relationships along a Low-Arctic Bioclimate Gradient, Alaska: Synthesis of Information from the ATLAS Studies

D. A. Walker,[1]* *G. J. Jia,*[2] *H. E. Epstein,*[2] *M. K. Raynolds,*[1] *F. S. Chapin III,*[1] *C. Copass,*[1] *L. D. Hinzman,*[3] *J. A. Knudson,*[1] *H. A. Maier,*[1] *G. J. Michaelson,*[4] *F. Nelson,*[5] *C. L. Ping,*[4] *V. E. Romanovsky*[6] *and N. Shiklomanov*[5]

[1] Institute of Arctic Biology, University of Alaska-Fairbanks, Fairbanks, Alaska, USA
[2] Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia, USA
[3] Water and Environmental Research Center, University of Alaska-Fairbanks, Fairbanks, Alaska, USA
[4] Palmer Research Center, University of Alaska-Fairbanks, Palmer, Alaska, USA
[5] Department of Geography, University of Delaware, Newark, Delaware, USA
[6] Geophysical Institute, University of Alaska-Fairbanks, Fairbanks, Alaska, USA

ABSTRACT

Differences in the summer insulative value of the zonal vegetation mat affect the depth of thaw along the Arctic bioclimate gradient. Toward the south, taller, denser plant canopies and thicker organic horizons counter the effects of warmer temperatures, so that there is little correspondence between active layer depths and summer air temperature. We examined the interactions between summer warmth, vegetation (biomass, Leaf Area Index, Normalized Difference Vegetation Index), soil (texture and pH), and thaw depths at 17 sites in three bioclimate subzones of the Arctic Slope and Seward Peninsula, Alaska. Total plant biomass in subzones C, D, and E averaged 421 g m^{-2}, 503 g m^{-2}, and 1178 g m^{-2} respectively. Soil organic horizons averaged 4 cm in subzone C, 8 cm in subzone D, and 14 cm in subzone E. The average late-August thaw depths in subzones C, D, and E were 44 cm, 55 cm, and 47 cm respectively. Non-acidic soils in equivalent climates generally have shorter-stature sedge-dominated canopies and many frost boils, and consequently have thicker active layers than acidic soils. The trends reported here are useful for palaeo-ecological reconstructions and predictions of future ecosystem changes in the Low Arctic. Climate change will not lead to uniform thickening of the active layer, and could lead to shallower active layers in some presently dry areas due to paludification. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: active layer; NDVI; biomass; soil pH; frost boils; bioclimate subzones

INTRODUCTION

A major concern in Arctic climate change research is that, with warming, active layers will deepen, possibly eliminating permafrost in some areas, and releasing stored carbon to the atmosphere. Deeper active layers would also release more water to the Arctic Ocean, dry the tundra, cause erosion and damage to infrastructures, and change arctic systems considerably (Kane *et al*., 1991; Jorgenson *et al*., 2001; Nelson *et al*., 2001). Current evidence indicates that permafrost has already warmed during the recent record in some parts of the Arctic (Lachenbruch

* Correspondence to: Dr D. A. Walker, Institute of Arctic Biology, University of Alaska - Fairbanks, Fairbanks, Alaska 99775, USA. E-mail: ffdaw@uaf.edu

Received 29 January 2003
Revised 15 April 2003
Accepted 15 April 2003

and Marshall, 1986). Understanding the interactions among vegetation, soils and active layers along natural climate gradients can aid in developing circumpolar maps of active layer depths, and will help in predictions of how climate change will affect Arctic systems.

The studies summarized here were part of a multidisciplinary project called Arctic Transitions in the Land-Atmosphere System, or ATLAS (McGuire *et al.*, 2003). Previous studies in the FLUX project (Weller *et al.*, 1995) focused on the 27 278 km^2 Kuparuk River region, central Arctic Slope, Alaska, where researchers developed regional approaches to map and model arctic vegetation, soils, active-layers, hydrology, and trace-gas fluxes. The ATLAS studies combined the information from the FLUX studies with new information from sites in western Alaska and the Seward Peninsula to achieve an understanding of the controls over fluxes across a broader area of the Arctic. One ATLAS goal was to examine changes in the system at major transitions or boundaries in the arctic system. The purpose of the studies reported in this paper is to examine how vegetation, soils, and thaw depth vary across the arctic bioclimate gradient in northern Alaska (inset to Plate 1). One objective was to determine if the patterns of vegetation and active layers observed in the Kuparuk River basin could reasonably be extended across the Arctic Slope and expanded to the warmer tundra on the Seward Peninsula as a step towards developing a circumpolar map of active layer thickness.

The Effect of Vegetation and Soils on the Active Layer

Changes to the active layer caused by climate change are likely to be affected by simultaneous changes to the vegetation and soils. Numerous studies have demonstrated the clear linkages between climate, vegetation, soils, and the active layer, but the details of these linkages are not well understood (Benninghoff, 1966; Klene *et al.*, 2001; Shiklomanov and Nelson, 2002, 2003, Vasiliev *et al.* 2003). For modelling purposes, the thermal effects of vegetation and a host of edaphic variables affecting thaw have been lumped into an 'edaphic parameter', E, in the equation, $ALT = E^{*}SQRT(DDT)$, where ALT is the active layer thickness and DDT is the degree days of thawing (Anisimov *et al.*, 2002). At present, the complex effect of vegetation and soil on the edaphic parameter is understood only in general terms. Vegetation shades the soils and provides a blanket of insulation that reduces summer heat flux. Moss and organic matter in the soil increase the water holding capacity affecting the hydrological properties. Thick moss carpets and organic soil horizons decrease active layer thickness, consequently decreasing the depth to which water is able to drain because of the presence of permafrost (Kane, 1997). This process of waterlogging, or *paludification*, is thought to be the driving mechanism behind long-term vegetation succession and changes in the active layer thickness in the Low Arctic (Walker and Walker, 1996; Mann *et al.*, 2002).

Palaeodata show that major changes in arctic vegetation have occurred during past climate changes (Mann *et al.*, 2002, Bigelow *et al.*, 2003), and major changes are expected in the future under a warming climate (Chapin III *et al.*, 2000; Kittel *et al.* 2000; McGuire *et al.*, 2000; Cramer, 1997; Kaplan *et al.*, 2003). There is also good evidence that some changes have already occurred to the vegetation in the recent past. For example, during the last 50 years, shrub cover has increased over large areas of northern Alaska (Silapaswan *et al.*, 2001, Sturm *et al.*, 2001b). This may be responsible for a relatively rapid greening observed over 20 years of satellite observations from arctic Alaska (Jia, 2002, submitted). These changes are expected to have an effect on the regional energy balances and carbon budgets (Oechel *et al.*, 1997) and would also affect active layer thickness and permafrost regimes. Regional estimates of trace-gas flux can be linked to the spatial variation of active layer thickness over large regions (Goulden *et al.*, 1998).

Vegetation is known to change in predictable ways across the north-to-south arctic temperature gradient (Figure 1). This is the principal basis for several approaches to arctic bioclimate zonation (Alexandrova, 1980; Elvebakk *et al.*, 1999; Walker *et al.*, 2002). Mapping and modelling of numerous ecosystem variables in the Kuparuk River basin of Alaska have shown strong correspondence between climate, vegetation, active layer patterns, and regional trace-gas fluxes (Hinzman *et al.*, 1998; Muller *et al.*, 1998; Nelson *et al.*, 1998a; Reeburgh *et al.*, 1998; Oechel *et al.*, 2000; Shiklomanov and Nelson, 2002, 2003). A 13-year active layer mapping program in the Kuparuk River region of northern Alaska demonstrated that, although thaw depths can exhibit substantial inter-annual variations in response to climatic forcing, vegetation type is an important component of procedures used to model spatial variation in active-layer thickness. Moreover, the ranking of active-layer

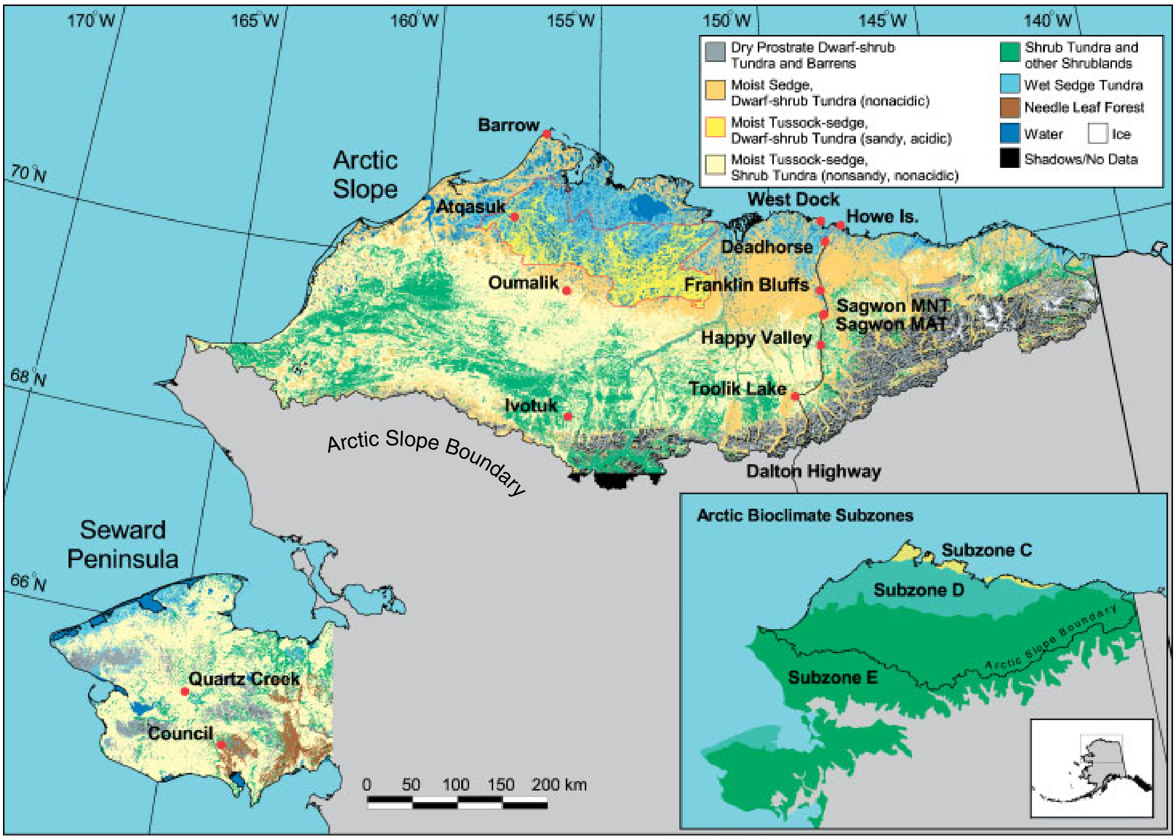

Plate 1 Location of the study sites with respect to broad vegetation types and bioclimate subzones. The vegetation map of the Arctic Slope is modified from Muller *et al*. (1999). The map of the Seward Peninsula is modified from an unpublished map (Thayer-Snyder, 2000). The inset map shows the bioclimate subzones of the Arctic Zone in northern Alaska based on Walker *et al*. (2003). Red boundary outlines the area of the sand sea.

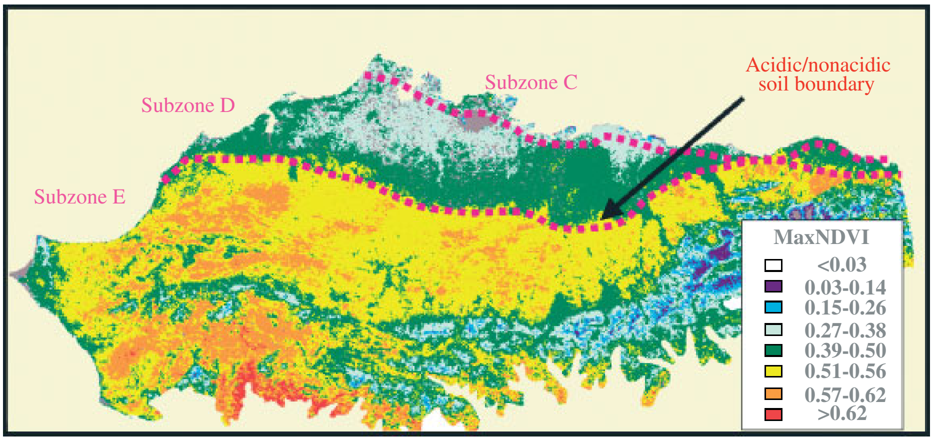

Plate 2 Map of the Max NDVI in northern Alaska derived from AVHRR composite images. The image consists of pixels (1 × 1-km picture elements) with highest NDVI among biweekly images from 1993 and 1995. The southern border of the image is clipped at tree line. The boundary between the yellow and green colours (arrow) is the boundary between primarily acidic tundra to the south and non-acidic tundra to the north. This boundary approximately coincides with a physiographic boundary separating the Arctic Foothills from the Arctic Coastal Plain, and a bioclimate boundary separating subzones D and E. The yellow areas are mainly tussock tundra. The green areas are less shrubby and dominated by graminoid plants. The light blue (lower NDVI) colours on the northern portion of the coastal plain are caused primarily by the abundance of lakes, which have low NDVI. The dark orange and red areas are shrubbier areas, and the darker blue colours are mainly barren areas in the Brooks Range.

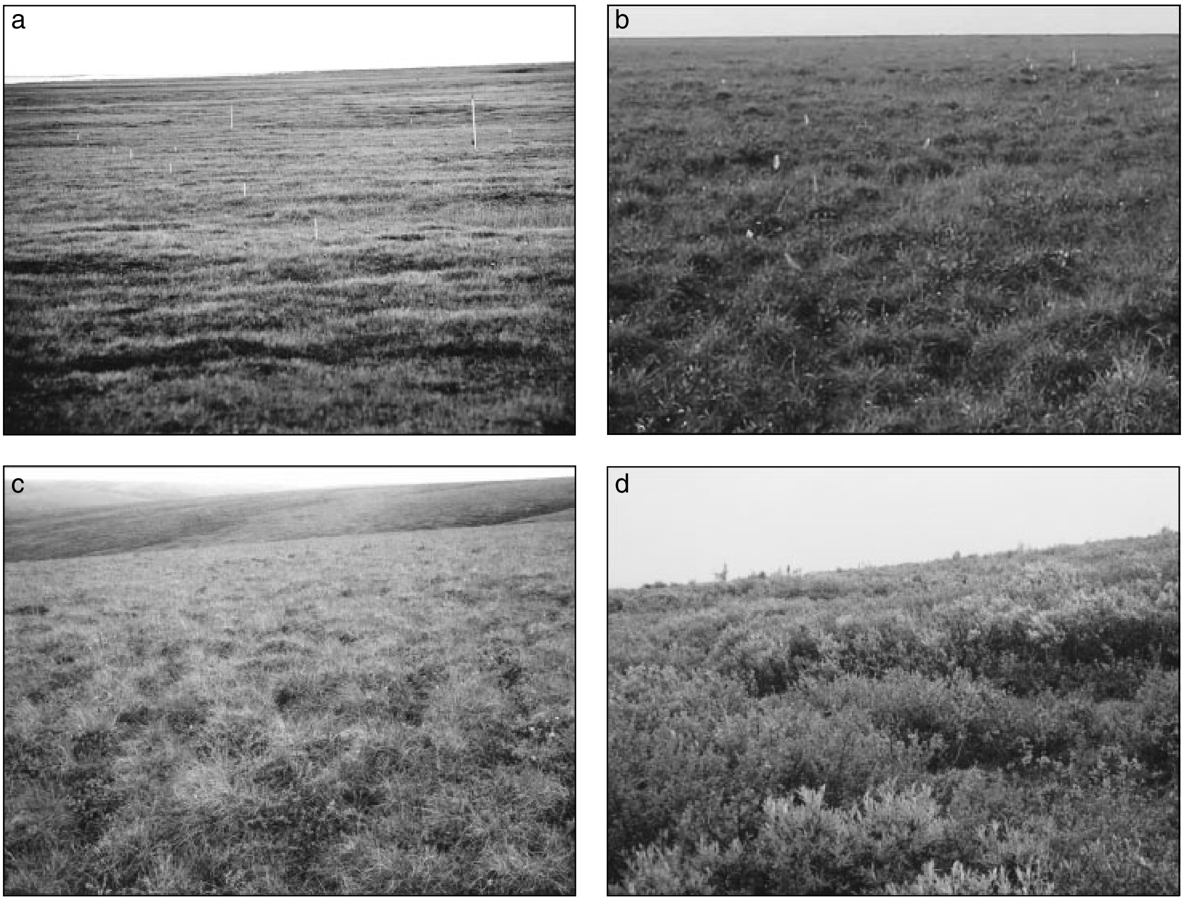

Figure 1 Typical vegetation in each subzone. (a) Moist acidic coastal tundra at Barrow (subzone C). Note the lack of any erect shrubs and the dominance of graminoid plants (mostly *Carex aquatilis* ssp. *stans, Eriophorum angustifolium, Dupontia fisheri, Poa arctica).* (b) Moist non-acidic tundra at Franklin Bluffs (subzone D). Note the scattered erect dwarf shrubs (mostly Richardson's willow (*Salix richardsonii*) and dominance of graminoid plants *(Carex bigelowii, C. membranacea, Eriophorum triste*). (c) Moist acidic tundra at Quartz Creek (subzone E). Note the dominance of tussock cotton grass (*Eriophorum vaginatum*) and erect shrubs (*Betula nana, Ledum palustre* ssp. *decumbens, Rubus chamaemorus*). (d) Shrub tundra near Council (warm maritime subzone E). Council is at tree line. The dominant shrubs are about 1.5 m tall and include *Betula glandulosa* and *Salix glauca*.

thickness among vegetation classes remains consistent from year to year (Shiklomanov and Nelson, 2002).

We were also interested in the transitions associated with different soil properties, particularly soil pH and soil texture. Studies across the Kuparuk River basin have noted strong correlations among soil pH, active layer thickness, and a wide variety of ecosystem variables (Bockheim *et al*., 1996). These correlations were attributed to the different nature of the vegetation growing on acidic versus non-acidic soils (Walker *et al*., 1998; 2001) (Figure 2). The studies noted a boundary separating large regions of acidic and non-acidic tundra at the northern edge of the Arctic Foothills (Plate 2). South of the boundary, there were higher values of the Normalized Difference Vegetation Index (NDVI) caused by greener vegetation. North of the boundary, there were more standing dead vegetation and barren frost boils, which contributed to low NDVI values. Studies near the boundary at Sagwon found that the soil pH of the upper mineral horizon averaged 5.2 south of the boundary and 6.9 north of the boundary (Walker *et al*., 1998). The amount of bare soil was 10 times greater north of the boundary, and active layers were 33% thicker (52 cm vs. 39 cm). Other studies found greater heat flux, higher diversity of plants, less of a carbon sink, and a smaller source of methane north of

Figure 2 (a) Moist acidic tundra at the Oumalik MAT site. Note the abundance of dwarf shrubs. *Eriophorum vaginatum* (cotton grass) is the dominant sedge (white inflorescences). The dominant shrubs are dwarf birch *(Betula nana*), Labrador tea *(Ledum decumbens* ssp. *palustre*), and diamond-leaved willow *(Salix pulchra*). (b) Moist non-acidic tundra near the Sagwon MNT site. Note the abundance of flowering forbs and standing dead grasses, mostly *Arctagrostis latifolia*, and relatively few erect deciduous shrubs. The dominant forbs include *Lupinus arcticus, Oxytropis maydelliana,* and *Hedysarum alpinum.* Other common plants include the sedges, *Carex bigelowii, C. membranacea, C. scirpoidea,* and *Eriophorum triste*, the prostrate dwarf shrubs, *Dryas integrifolia, Salix reticulata,* and *Arctous rubra,* and the moss *Tomentypnum nitens.* Numerous frost boils are hidden by the plant cover.

the boundary in the non-acidic soils (Eugster *et al*., 1997; Reeburgh *et al*., 1998; Oechel *et al*., 2000). Snow depths and winter ground surface temperatures also change at this boundary (Liston and Sturm, 2002; Taras *et al*., 2002). We were particularly interested in seeing if the boundary between acidic and non-acidic tundra observed near Sagwon extended across the entire Arctic Slope as suggested by the NDVI image in Plate 2, and if it had the same effect on vegetation, soils, and thaw depths.

Soil texture is also known to affect vegetation and active-layer thickness. Much of the non-mountainous portions of northern Alaska are covered by fine-grained soils associated with windblown loess deposits. An exception is a large sand sea west of the Colville River (Carter, 1981) (see Plate 1, moist tussock-sedge, dwarf-shrub tundra (sandy, acidic)). One of our study sites, Atqasuk, was located within this region. Previous studies in this region provided baseline information on the vegetation and soils (Komárková and Webber, 1980; Everett, 1980). Other very large regions of sandy tundra occur on the Yamal and Gydan peninsulas, Russia, and in coastal river deltas and glaciofluvial outwash deposits throughout the Arctic.

Zonal Variation in Microscale Patterns of Vegetation and Active-layer Thickness

Small-scale differences in microrelief, soil moisture, and openness of the plant canopy and a host of other microscale factors can cause major differences in thaw depth. One important source of variation is patterned-ground, such as ice-wedge polygons and frost boils. Frost boils are common on most Arctic zonal surfaces and are, therefore, particularly relevant to this study. Frost boils (also known as frost scars, mud boils and mud circles) are small 1–3 m diameter patterned ground forms with a dominantly circular outline that lack a border of stones (van Everdingen, 1998) (Figure 3). Frost boils are abundant in silty soils such as those of northern Alaska. Numerous modes of their formation have been suggested (Washburn, 1956). The size and character of frost boils changes across the Arctic bioclimate gradient (Chernov and Matveyeva, 1997; Matveyeva, 1998). One of our goals was to examine how the patterns of vegetation and active layers on and between frost boils change from subzone C to subzone E.

METHODS

Study Sites

Our data came from 17 grids located at 12 sites spread across the Arctic Slope and Seward Peninsula (Plate 1). The studies were done on grids and transects of various sizes that were erected as part of the FLUX and ATLAS studies. Many of the sites were

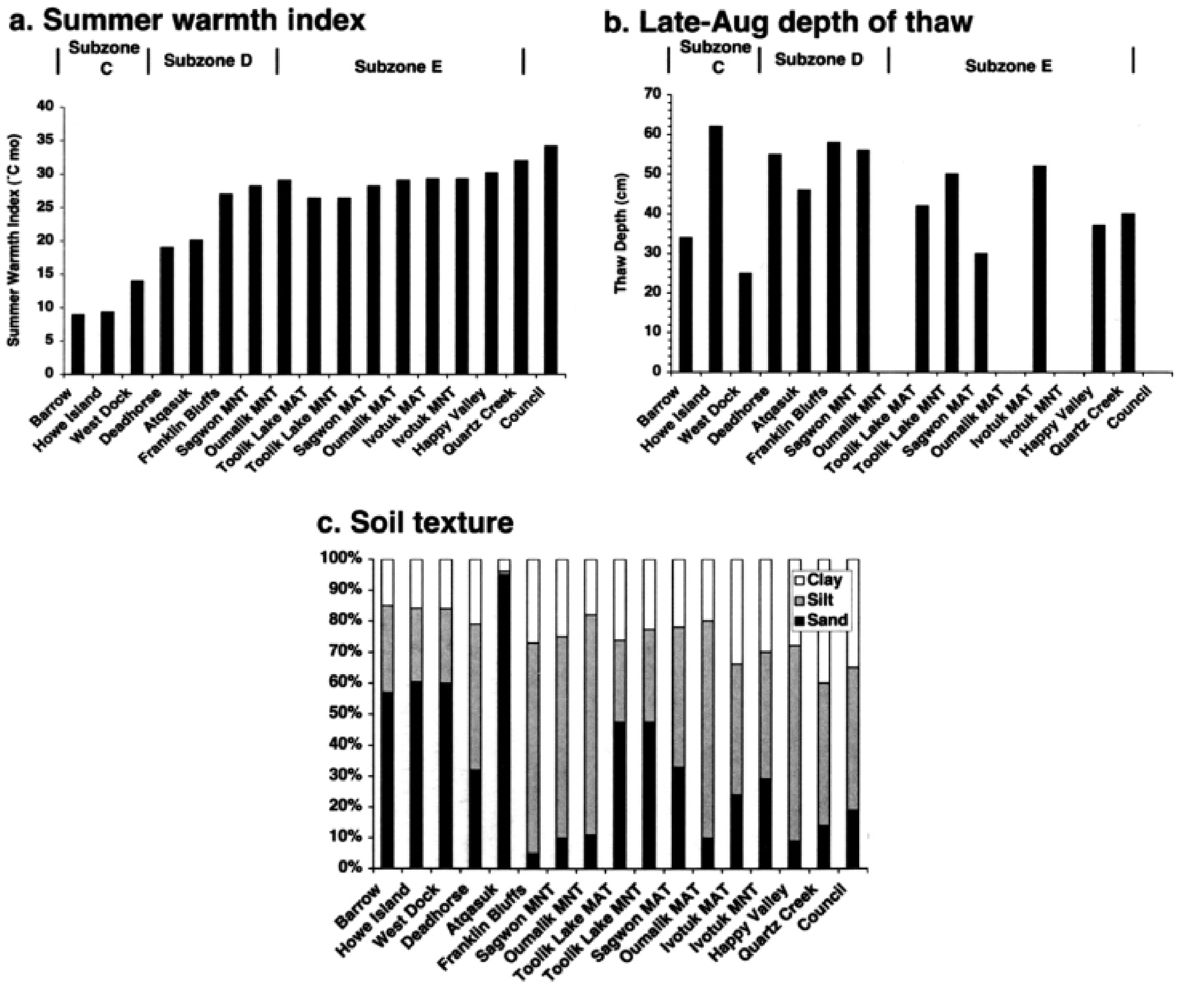

Figure 3 Comparison of physical variables for the study sites arranged by subzone. (a) SWI, (b) late-August depth of thaw, and (c) soil texture. Gaps in (b) are due to either missing data (Oumalik MNT and MAT), or rocky soils (Ivotuk MNT), or have no permafrost (Council).

located within or near 1 × 1-km grids that were used for eddy-correlation tower studies of trace-gas and energy fluxes, and which are now part of the Circumpolar Active Layer Monitoring (CALM) program (Brown *et al*., 2000) (Barrow, West Dock, Atqasuk, Happy Valley, Ivotuk). The eight sites in the western portion of the region (Barrow, Atqasuk, Oumalik MNT (moist non-acidic tundra), Oumalik MAT (moist acidic tundra), Ivotuk MNT, Ivotuk MAT, Council, and Quartz Creek) had 100 × 100-m grids with 10-m grid-point spacing. These grids were established in 1998–1999. The vegetation, soils, and climate were described and monitored at all these locations. Each site had a climate station where air and ground temperatures were monitored. Seven locations near the Dalton Highway (Howe Island, West Dock, Deadhorse, Franklin Bluffs, Sagwon MAT, Sagwon MNT, Happy Valley) had 10 × 10 m grids with 1-m grid point spacing. These grids were established in 2000–2001. The smaller grid size was used to examine high-frequency spatial variation in active layers, vegetation and soils associated with frost boils. For Toolik Lake, we used data from permanent vegetation plots established in 1989 and 1990.

We used the bioclimate subzones of the Pan Arctic Flora and Fauna project (Elvebakk *et al*., 1999), and the Circumpolar Arctic Vegetation Map (CAVM) (Walker *et al*., 2002a, b) as a framework for the study (see inset to Plate 1 and photographs in Figure 1).

Zonal vegetation and soils occur on flat or gently sloping plains or hills with fine-grained soils and no extremes of snow, soil moisture, soil chemistry, or disturbance (Vysotsky 1927). The sites were chosen subjectively to represent zonal vegetation wherever possible. Exceptions occurred at Atqasuk, which had a sandy soil, and Howe Island, which had a dry wind-swept surface, more typical of zonal subzone C sites in the Canadian High Arctic.

Bioclimate subzone C, the coldest subzone, occurs in a narrow strip along the northern coast of Alaska. Subzone D covers most of the Arctic Coastal Plain and the northwest portion of the Seward Peninsula, and subzone E covers most of the Foothills and most of the non-forested portion of the Seward Peninsula. Barrow, West Dock, and Howe Island are in subzone C. Deadhorse, Franklin Bluffs, Sagwon MNT, Atqasuk, and Oumalik MNT are in subzone D. Sagwon MAT, Oumalik MAT, Happy Valley, Toolik Lake, Ivotuk, Quartz Creek, and Council are in subzone E. The low-shrub site at Council was selected as representative of the zonal tundra situation at the Arctic tree line; shrublands are abundant on the majority of mesic gentle slopes in the region. Wherever possible, we also selected sites on acidic and non-acidic soils within the same climate regime to examine the effects of soil pH. This situation occurred at Sagwon, Oumalik, and Ivotuk.

The Dalton Highway is the only road that traverses the area from north to south. Nine of the study sites were located at seven locations along this road (Plate 1). Most of the other sites are located near remote airstrips. Four study sites were located in each of the bioclimate subzones along a western transect from Barrow to Ivotuk. The most remote location, Oumalik, 100 km southeast of the nearest airstrip at Atqasuk, was accessed by helicopter. It was chosen because it is located on the western extension of the acidic/non-acidic boundary, and it has a history of nearby vegetation and permafrost research (Ebersole, 1985). The Quartz Creek and Council sites are on the Seward Peninsula in a warmer climate than anywhere on the Arctic Slope. Discontinuous permafrost is present over much of the peninsula (Brown *et al.*, 1997). Quartz Creek is in a hilly tussock-tundra region similar to the Foothills of northern Alaska, and provides a possible example of how the Arctic Slope might respond to a few degrees of summer warming.

Summer Warmth Index (SWI)

Climate data came from several sources. The National Weather Service data were available for Barrow, Nome, and Umiat. Howe Island data came from the Endicott site established by the Minerals Management Service Beaufort Sea Meteorological Monitoring and Data Synthesis project (http://www.resdat.com/mms/index.cfm). The Toolik Lake data were from the Arctic Lake Long Term Ecological Research site. The rest of the data came from sites established by investigators in the ATLAS project. A mean SWI was calculated for each site. SWI is the sum of the mean monthly temperatures greater than 0 °C (thawing-degree months). We chose the SWI over an index based on thawing-degree days (TDD) because SWI is readily derived from monthly climate summaries and does not require daily information, a significant advantage in this study, which used climate data from several sources.

Thaw Depth

The thaw measurements were taken from three different years in mid- to late-August. Data from most of the Dalton Highway sites (Howe Island, West Dock, Deadhorse, Franklin Bluffs, Sagwon, and Happy Valley) were collected in late-August 2001. The Toolik Lake data were from permanent plots sampled in late-August 1989 (Walker and Barry, 1991). Data from Barrow, Atqasuk, Oumalik, Ivotuk, Quartz Creek, and Council were collected from 1999. At Barrow, Atqasuk, and Quartz Creek (also called Kougarok) we used data from the nearby CALM grids (Brown *et al.*, 2000). Thaw depths at Oumalik, although they are reported here, were collected too early in the season to be useful for this study. Since we were interested in broad geographic differences in zonal thaw depths and not small inter-annual differences, it was reasonable to use data from different years, especially since the standard deviation of mean end-of-summer thaw is 6 cm or less at all 12 northern Alaska sites in the CALM network (Brown *et al.*, 2000).

The thaw depth was monitored using a blunt tipped steel probe that was inserted into the soil to the point of contact with hard frozen soil. Measurements were taken at 10 m intervals on the 100 × 100-m grids (121 measurements per grid), and at 0.5 m intervals on the 10-m grids (441 measurements per grid). The high density of sample points on the 10-m grids was for resolving the pattern of thaw associated with frost boils in each grid. On the permanent plots at Toolik Lake, 10 measurements were taken within each 10-m^2 study plot. More recent information indicates that the thawed layer can continue to deepen into September or even October; so our measurements should be considered 'late-August thaw depth' and not necessarily the full thickness of the active layer. To maintain this distinction, we use the term 'thaw depth' in subsequent sections of this paper.

Vegetation Data

Biomass.

Clip harvests were collected from 20 × 50-cm (0.1 m^2) plots at all sites except Council, where biomass was collected from 1 × 1-m plots. In the 100 × 100-m grids at Barrow, Atqasuk, Oumalik, Ivotuk, Council, and Quartz Creek, samples were collected from 10 random grid points within the grids. For the 10 × 10-m grids in the vicinity of the Dalton Highway (Howe Island, West Dock, Deadhorse, Franklin Bluffs, Sagwon, and Happy Valley) samples were collected from two 50-m transects located adjacent to the grids. Three clip harvest samples were collected from each transect at 5 m, 25 m and 45 m points along the transects. The Toolik Lake data were obtained in permanent vegetation plots that were clipped in 1993; three replicates were obtained from five moist non-acidic sites (15 clip harvests) and four acidic plots (12 clip harvests).

The vascular plants were clipped at the top of the moss layer, or at the base of the green herbaceous shoots. Mosses were clipped at the base of the green portion of the mosses. All the clip harvests were partially sorted in the field according to major plant functional types (shrubs, graminoids, forbs, mosses, and lichens). They were frozen and sorted into finer categories (live and dead, deciduous and evergreen shrubs, foliar and woody) at a later time. After sorting, the samples were dried at 50 °C to constant weight and stored for later nutrient analysis.

Leaf Area Index (LAI).

LAI was measured using a LI-COR LAI-2000 Plant Canopy Analyzer. The instrument gave an indication of canopy cover based on differences in diffuse radiation above and below the plant canopy. At each sample point, an above-canopy reading was followed by four below-canopy readings taken above the moss layer. The average of the four readings was retained for the data analysis. A 90° field-of-view shield was used to prevent interference from the observers. All measurements were taken facing away from the sun. The LAI readings should be taken on cloudy days to prevent problems with reflections in the plant canopy. This was not always possible, so on sunny days a sun shield was used to shade the sensor from direct sunlight while at the same time providing an unobstructed view of the sky. We collected LAI data from 33 random points within the grids of the six western sites. For the eastern transect, we collected LAI at 2-m intervals along two 50-m transects (total of 50 points for each location). At Council, LAI readings were taken at 121 points in the 100 × 100-m grid, with one up and one down measurement at each point. A mean LAI value was calculated for each grid (N = 33) and each transect (N = 50). We did not make direct comparisons of the optical LAI values with destructive measures of leaf area. A previous study of LAI using the LI-COR 2000 instrument in arctic vegetation showed generally good correspondence between LAI, NDVI, and biomass, especially when examined across broad biomass gradients (Shippert *et al.*, 1995). Because the sites were chosen to be centrally located within large homogeneous zonal landscapes, we assumed that the means of the LAI and biomass were representative of a larger area comparable to a remotely-sensed 1-km pixel. This assumption, however, was not tested.

NDVI.

NDVI is an index of vegetation greenness. NDVI = (NIR − R)/(NIR + R), where NIR is the spectral reflectance in the near-infrared band (0.725–1.1 μm), dominated by light scattering from the plant canopy, and R is reflectance in the red, chlorophyll-absorbing, portion of the spectrum (0.58–0.68μm) (Markon *et al.*, 1995). The NDVI data were derived from Advanced Very High Resolution Radiometer (AVHRR onboard National Oceanographic and Aeronautical Administration (NOAA) satellites) images. AVHRR-derived NDVI time-series data for 1995–1999 were obtained from the US Geological Survey (USGS) Alaska Data Center on CD-ROMs. These data were based on 14-day composite periods to match the processing of global data sets. We used the portion of the data between 1 April and 31 October, which consistently brackets the snow-free period in northern Alaska and covers the greenup-to-senescence phase of the vegetation (Markon, 1999). Only the portion covering northern Alaska and the Seward Peninsula was used for the analysis. The original data were converted into a GRID coverage using ARC/INFO GRID software. Cloud and snow contamination were minimized using the Best Index Slope Extraction adaptive filter (Viovy, 2000). The filter is also designed to minimize registration errors that induce short-lived NDVI peaks, which may occur in the compositing process.

We used 1 : 60 000-scale colour-infrared aerial photographs (acquisition dates, 1978 and 1982) to delineate 202 areas of homogeneous vegetation on acidic and non-acidic parent material in the vicinity of the climate stations. This was the same data set used for the analysis of intra-seasonal patterns of NDVI in relation to the climate record (Jia *et al.*, 2002). Polygons were drawn around these areas on mylar transparent overlays. The aerial photographs and polygons were then digitized and geo-registered to the AVHRR imagery using ARC/INFO software. To register the photographs to the AVHRR image, we used 127 control points from 1 : 63 360-scale USGS topographic maps. Of the 202 polygons on the aerial photographs, 91 were large enough to locate on the AVHRR image. Although the dates of acquisition for the photographs and the satellite images were different, we assumed that the broad vegetation patterns had not changed, especially within large areas of homogeneous zonal vegetation selected for this study. The mean maximum NDVI (MaxNDVI) for each polygon was calculated from the set of annual maximum NDVI values for all pixels within the polygon. These MaxNDVI values were then used for the correlation analyses with SWI, phytomass, and LAI. The temporally-integrated NDVI (Integrated NDVI) is the sum of all the biweekly NDVI values during the green period. Green days are the number of days during which the NDVI exceeds 0.9, and is the period during which most plants are photosynthetically active.

Soils Data

At each site, a soil pit of about 1×1 m^2 was excavated to 1 m depth with shovels and a gas-powered jackhammer. Soil morphological properties were described according to the *Soil Survey Manual* (Soil Survey Staff, 1993). Soil samples were taken from each horizon and shipped to either the Palmer Research Center Laboratory or the National Soil Survey Laboratory for characterization analysis according to standard USDA procedures (Soil Survey Staff, 1993). Soil pH was measured in distilled water. Soil pH, sand, silt, and clay values used in this analysis are from the top mineral horizon. Particle size distribution was determined with a hydrometer in the Palmer Laboratory.

Mapped Data

Aerial photographs were taken of each grid from a helicopter at about 30 m elevation for the 10×10-m grids, and about 300 m elevation for the 100×100-m grids. Detailed vegetation maps of all the 10×10-m grids and some of the 100×100-m grids were made based on ground surveys. Maps of vegetation, snow cover, and active-layer thickness were made for the 10×10-m grids based on the measured values at the grid points for snow cover, and at 0.5 m intervals for the active-layer measurements.

Data Analysis

The climate, soil and vegetation data were assembled into a matrix (Table 1). The sites were grouped according to their bioclimate subzones and SWI. Mean values for each variable were calculated for the subzones and soil reaction classes. Regression analysis was done on a full set of the variables to examine the strength of the relationships.

RESULTS

Summer Warmth

SWI varied from 8.9 °C months at Barrow to 34.2 °C months at Council (Figure 3a). Three sites, Barrow, Howe Island, and West Dock are in bioclimate subzone C with summer warmth indices less than 15 °C months. There are five sites in subzone D. Sagwon and Oumalik are on the boundary between subzones D and E. The MNT sites at both of these locations are in subzone D, and the MAT sites are in subzone E. Toolik Lake is a high elevation (cooler) site within subzone E. The mean values for summer warmth were 10.8 °C months in subzone C, 24.6 °C months in subzone D, and 29.5 °C months in subzone E (Figure 4a). The acidic tundra areas were somewhat warmer than the non-acidic tundra areas (26.5 °C months vs. 23.1 °C months) because most of the non-acidic sites are subzones D and C, whereas the MAT sites are mainly in subzone E.

Thaw Depth

Late-August thaw depth ranged from 25 cm at West Dock to no permafrost at Council (Figure 3b). The average thaw depth values were 44 cm in subzone C, 55 cm in subzone D, and 47 cm in subzone E, excluding the Council site, where there was no permafrost (Figure 4c). Non-acidic tundra areas had generally deeper thaw than the acidic tundra areas (54 cm vs. 45 cm).

Soils

Soil pH ranged from 4.3 at the Toolik MAT sites to 7.9 at Howe Island. The break between the acidic and non-acidic soils was considered to be at pH 5.5 (Bockheim *et al.*, 1998). There were eight locations with non-acidic soils, and nine with acidic soils.

Table 1 Summary of bioclimate, NDVI, thaw depth, biomass, and soil information for the study sites. Vegetation types are MAT (moist acidic tundra). MNT (moist non-acidic tundra), SMAT (sandy MAT). SMNT (sandy MNT), SDNT (sandy dry non-acidic tundra), SAT (shrubby acidic tundra). SWI is the sum of the mean monthly temperatures greater than 0 °C (°C months). Green days are the number of days in which the NDVI value is greater than 0.09. Soil O is the thickness of the organic horizons.

Site	Sub zone	Veg type	SWI (°C) months	Thaw depth (cm)	Max NDVI	Integrated NDVI	Green days	Biomass (g/m2) Total	Lichen	Moss	Shrub	Graminoid	LAI	Soil pH	Soil O (cm)	Soil H_2O (% vol)	Sand (%)	Silt (%)	Clay (%)
Barrow	C	SMAT	8.94	34*	0.418	2.51	88	452	103	267	25	55	0.75	5.2	7	20	57	28	15
Howe Island	C	SDNT	9.33	62	0.259	1.42	72	183	14	59	109	1	0.01	7.9	1	36	61	24	16
West Dock	C	SMNT	14.0	25	0.280	1.71	77	389	21	104	59	204	0.61	7.6	6	46	60	24	16
Deadhorse	D	MNT	19.0	55	0.342	2.15	87	412	6	86	84	221	0.89	7.5	10	28	32	47	21
Atqasuk	D	SMAT	20.1	46*	0.392	2.73	97	357	99	96	60	101	1.1	4.8	10	47	95	1	4
Franklin Bluffs	D	MNT	27.0	58	0.462	3.14	92	544	24	237	120	157	0.81	7.5	11	29	5	68	27
Sagwon MNT	D	MNT	28.2	56	0.477	3.56	102	658	46	483	58	70	0.49	7.5	8	32	10	65	25
Oumalik MNT	D	MNT	29.1	(27)**	0.491	3.17	102	488	45	217	178	26	0.61	6.2	5	45	11	71	18
Toolik Lake MAT	E	MAT	26.4	42****	0.511	4.01	116	583	18	92	283	175	0.77	4.3	14	32	47	26	26
Toolik Lake MNT	E	MNT	26.4	50****	0.444	3.30	114	429	45	115	145	106	0.37	6.2	20	40	46	29	22
Sagwon MAT	E	MAT	28.2	30	0.534	4.23	108	932	59	515	268	84	1.5	5.0	16	32	33	45	22
Oumalik MAT	E	MAT	29.1	(19)**	0.556	3.78	105	904	38	148	465	251	1.65	4.9	15	32	10	70	20
Ivotuk MAT	E	MAT	29.3	52***	0.543	3.96	112	839	31	145	358	302	2.15	4.9	29	30	24	42	34
Ivotuk MNT	E	MNT	29.3	rocks	0.529	3.86	111	647	5	415	101	94	0.49	6.8	33	72	29	41	30
Happy Valley	E	MAT	30.2	37	0.527	4.19	109	813	68	262	272	208	1.48	5.1	10	36	9	63	28
Quartz Creek	E	MAT	32	40*	0.482	3.71	136	793	18	17	427	326	2.9	4.8	15	43	14	46	40
Council	E	SAT	34.2	no permafr.	0.539	3.79	141	2420	43	204	2135	25	2.27	6.0	13	47	19	46	35

* Thaw from nearby CALM grid (Brown *et al*. 2000). ** Thaw taken in early July, data not used in analysis. *** Ivotuk data from late Aug 2000, data used in the analysis. **** Toolik Lake data obtained from permanent plots in 1989, late Aug (Walker and Barry, 1991) data used in the analysis.

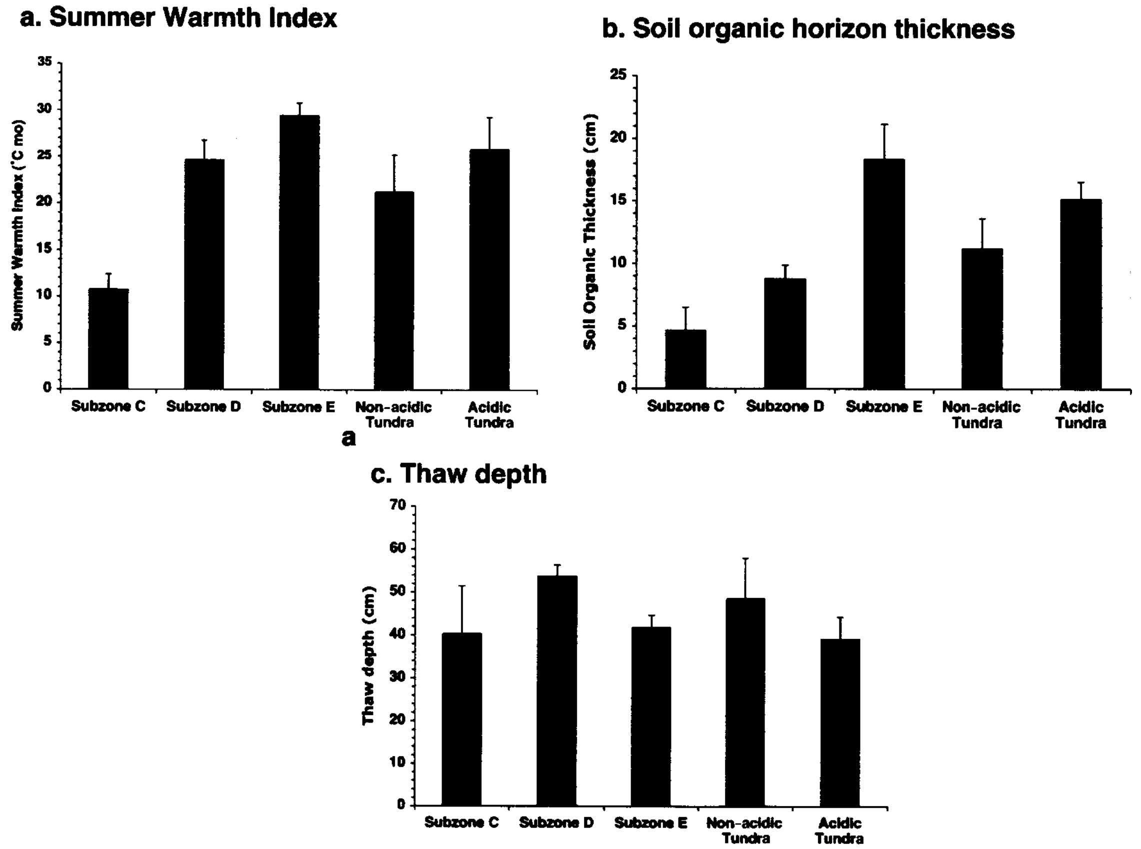

Figure 4 Summary of means (± standard errors) for three key physical variables by bioclimate subzone and acidic and non-acidic tundra: (a) SWI, (b) soil organic horizon thickness, and (c) late-August thaw depth.

Soil textures were predominantly silts and silt loams except for the coastal sites at Barrow, West Dock, Howe Island, and Toolik Lake, which had sandy loams, and Atqasuk which had sandy soils (Figure 3c).

Soil organic horizons varied from less than 1 cm at Howe Island to 33 cm at the Oumalik MAT site. The mean values for the organic thickness were 4 cm in subzone C, 8 cm in subzone D, and 17 cm in subzone E (Figure 4b). Acidic tundra areas had on average thicker organic horizons than non-acidic tundra (14 cm vs. 10 cm).

Volumetric soil moisture values were all in the range from 20 to 47%, except for the Ivotuk MNT site with 72%, which was caused by drainage from a nearby snowbed.

Phytomass and LAI

Above-ground phytomass varied from 183 g m^{-2} at Howe Island to 2420 g m^{-2} at Council (Figure 5a). The very low phytomass at Howe Island was much less than the subzone C sites at Barrow and West Dock, which had moister soils and more plant cover and biomass close to 400 g m^{-2}.

Mean zonal phytomass was 341 g m^{-2} in subzone C, 482 g m^{-2} in subzone D, and 1050 g m^{-2} in subzone E (Figure 6a). Graminoid plants showed a steady increase across the subzones, 87 g m^{-2} in subzone C, 113 g m^{-2} in subzone D, and 184 g m^{-2} in subzone E. In subzones C and D, graminoid biomass exceeded shrub biomass. This was true at all coastal plain sites except Howe Island, where the dominant plants were prostrate dwarf shrubs (*Dryas integrifolia*). In subzone E and all acidic tundra sites except Atqasuk, shrub biomass exceeded graminoids. Atqasuk is in subzone D and graminoids were dominant at this site. Most of the large amount of phytomass in subzone E was due to the shrub biomass (Figure 6b). There was 64 g m^{-2} of shrubs in subzone C, 102 g m^{-2} in subzone D, and 575 g m^{-2}

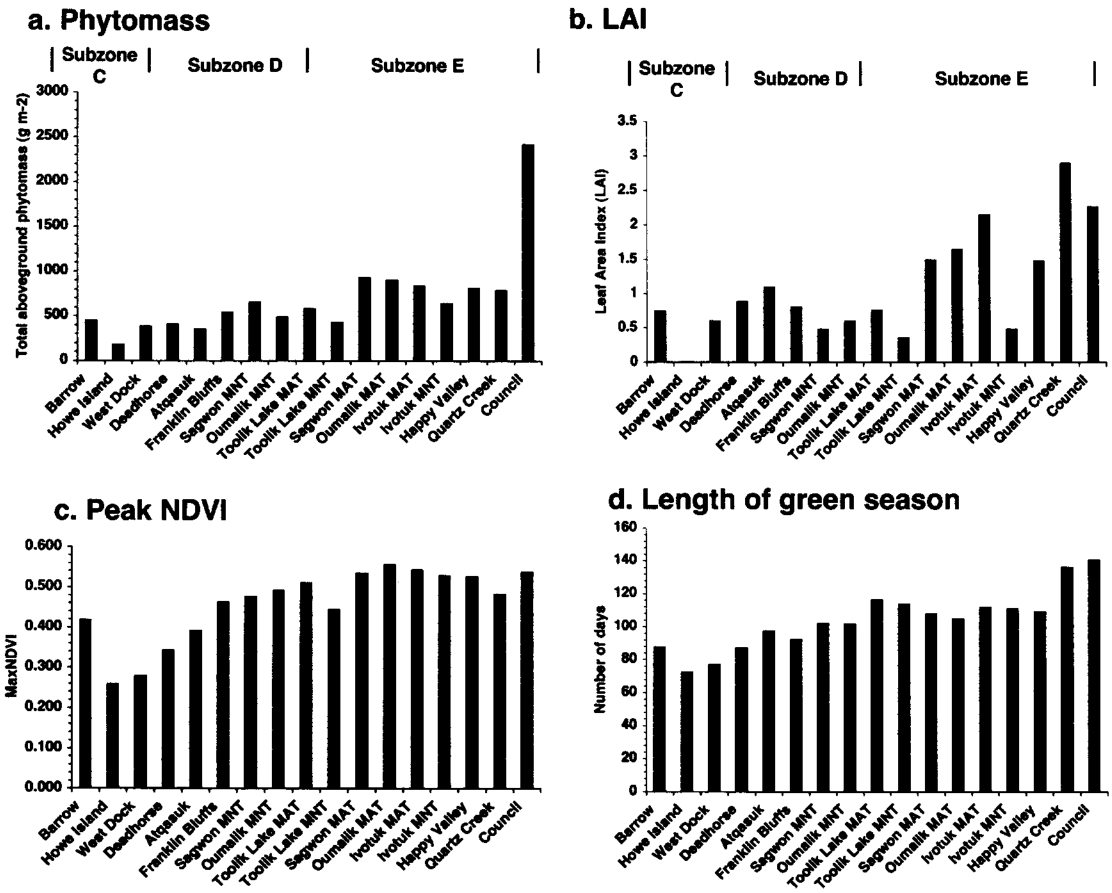

Figure 5 Summary of (a) phytomass, (b) LAI, (c) peak NDVI, and (d) length of green season at the study sites.

in subzone E. Moss biomass averaged 143 g m^{-2} of moss in subzone C, 221 g m^{-2} in subzone D, and 243 g m^{-2} in subzone E (Figure 6c). Lichens showed the opposite trend with 46 g m^{-2} in subzone C, 36 g m^{-2} in subzone D, and 37 g m^{-2} in subzone E. There was twice as much phytomass on average in the acidic plots as there was in the non-acidic plots (939 g m^{-2} vs. 471 g m^{-2}) (Figure 6a), and this was also due primarily to the difference in shrubs (501 g m^{-2} in the acidic sites vs. 103 g m^{-2} in the non-acidic sites; Figure 6b).

LAI varied from 0.01 at Howe Island to 2.27 at Council (Figure 5b). The trends in LAI along the bioclimate gradient closely reflected the trends in total above-ground phytomass. The average LAI was 0.68 in subzone C, 0.92 in subzone D, and 1.65 in subzone E (Figure 6d). Acidic sites averaged twice the LAI of the non-acidic sites, 1.61 vs. 0.8.

NDVI

Highest Peak NDVI occurred at the Oumalik MAT site (0.56) and the lowest NDVI was at Howe Island (0.26) (Figure 5c). The onset of greening varied from late April on the Seward Peninsula to early June at the Arctic coastal sites of Barrow, West Dock, Howe Island, Barrow and Deadhorse (Figure 5d). Integrated-NDVI values were 1.88 in subzone C, 3.00 in subzone D, and 3.87 in subzone E. The trends in both MaxNDVI (not shown) and time-integrated NDVI (Figure 6e) follow the trends in total above-ground phytomass and LAI but do not show such a large increase from subzone D to E as phytomass and LAI. Acidic tundra had higher Integrated NDVI values than non-acidic tundra averaging 3.66 vs. 2.85.

One cause of the much larger biomass in subzone E is the longer growing season (Figure 6d). Council has nearly twice the number of green days as Howe Island (141 vs. 72 days). Quartz Creek,

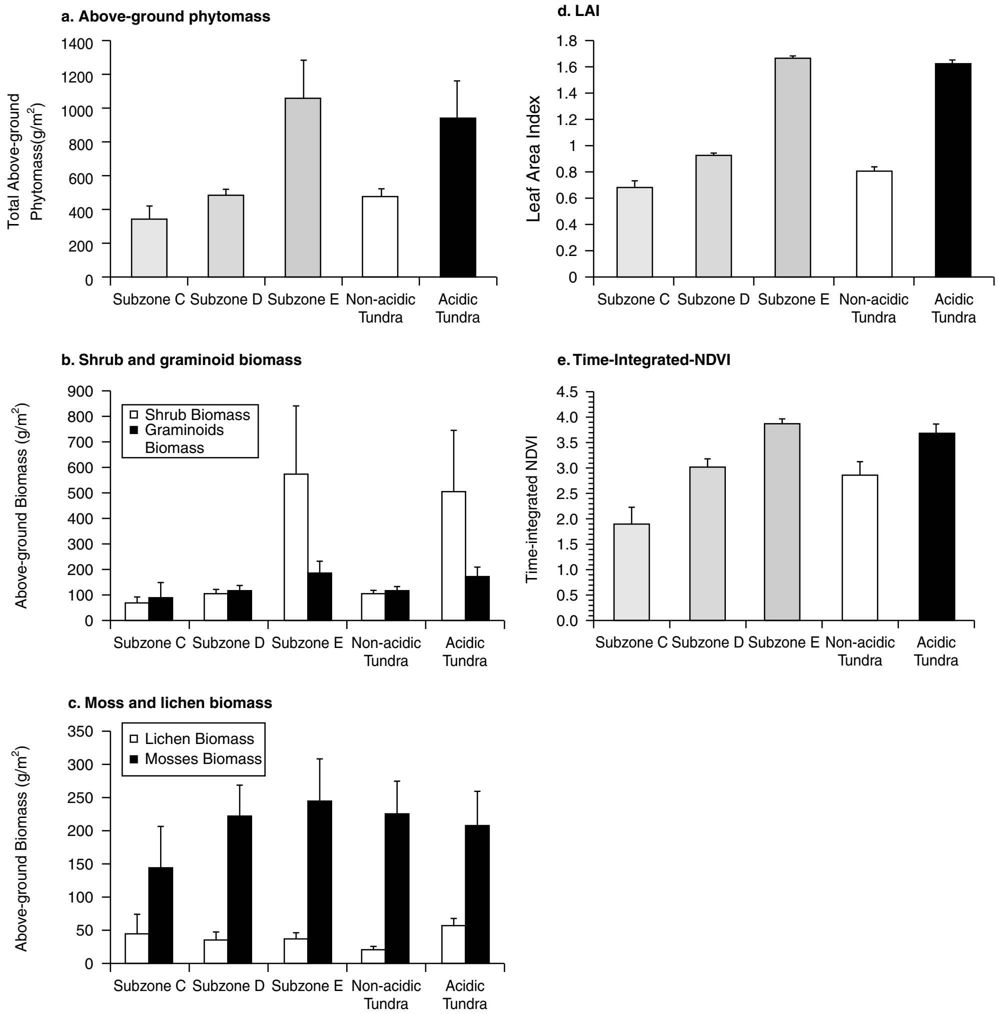

Figure 6 Summary of means (± standard errors) for key biological variables by bioclimate subzones and soil reaction class: (a) above-ground phytomass, (b) shrub and graminoid phytomass, (c) moss and lichen phytomass, (d) LAI, and (e) total Integrated NDVI.

also on the Seward Peninsula had 136 green days. The next highest number of green days was Toolik Lake with 116. The Arctic Slope data show the annual trend in greenup, which starts in the southern foothills at Toolik Lake (116 green days) and spreads northward to Ivotuk, Happy Valley, Sagwon. Franklin Bluffs, Atqasuk, Deadhorse, Barrow, West Dock, and Howe Island (72 green days) (Figure 5d).

Trends of Vegetation Along the Summer-warmth Gradient

Total biomass and LAI increased with temperature in acidic tundra, but showed a weaker relationship in non-acidic tundra (Figures 7a–c). Organic layer thickness and Integrated NDVI showed a stronger relationship in non-acidic tundra than in acidic tundra (Figures 7d, e). The stronger NDVI relationship in non-acidic tundra may be partially due to saturation of the AVHRR sensors at higher NDVI values (Shippert *et al.*, 1995). Also acidic areas with high biomass do not have corresponding higher NDVI values or LAI because much of the biomass is non-green woody tissue. Acidic sites had generally higher values than non-acidic sites for phytomass, LAI, shrub biomass, and NDVI under comparable climate regimes. A notable exception was the sandy nutrient-poor site at Atqasuk, which had relatively less phytomass than the colder site at Barrow (357 g m^{-2} vs. 452 g $^{-2}$).

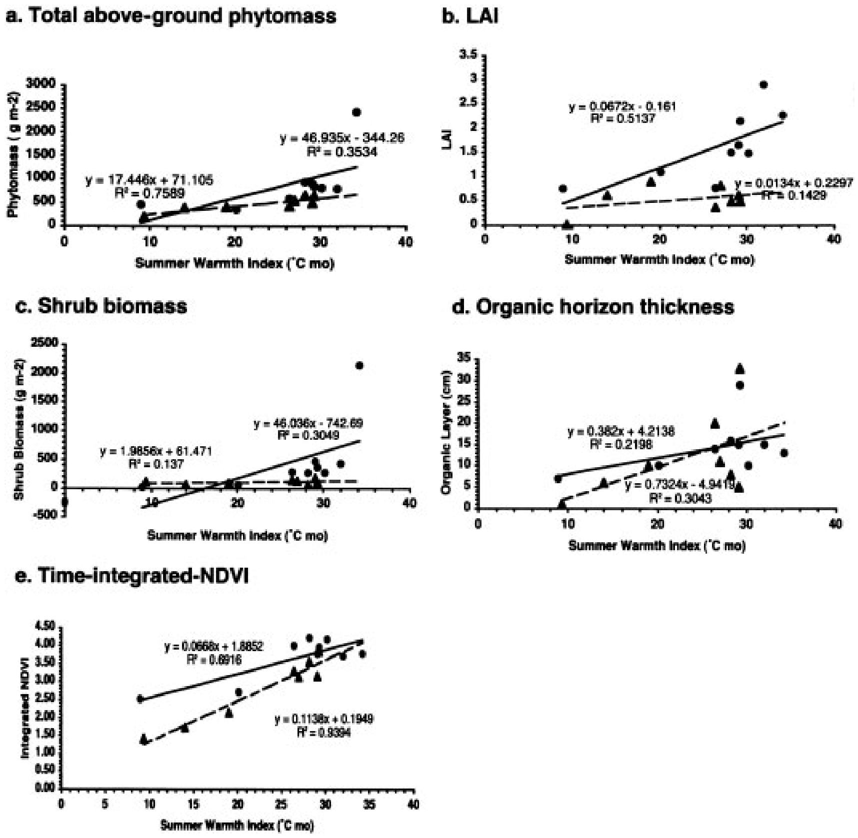

Figure 7 Trends in five vegetation-related variables along the summer warmth gradient: (a) total phytomass, (b) LAI, (c) shrub biomass, (d) organic horizon thickness, and (e) Integrated NDVI. Circles and solid lines are acidic sites, and triangles and dashed lines are non-acidic sites.

Trends of Thaw Depth Along Major Gradients

The non-acidic sites generally had deeper thaw than the acidic sites along gradients of moisture, warmth, NDVI, and organic-layer thickness (Figure 8). Late-August thaw depth did not show significant ($p < 0.05$) trends with the SWI, NDVI or organic-layer thickness (Figure 8a, b, d). Thaw in non-acidic sites showed a significant negative trend with soil moisture, likely due to drier near-surface soil horizons in deeply thawed areas (Figure 8c).

Zonal Variation in Microscale Patterns of Vegetation and Thaw Depth Associated with Frost Boils

The details of trends in frost-boil plant communities along the bioclimate gradient are presented in another paper (Walker *et al*., 2003, in press). The general trends are: (1) from north to south there is a trend of less bare soil, and more well-vegetated frost boils. (2) The character of the frost boils change from large nearly totally barren patches in subzone C to more heterogeneous mixes of bare soil and sparse plant communities in subzone D, to completely vegetated hummock features in subzone E. (3) The inter-frost-boil areas change from sparse dry prostrate dwarf-shrub plant communities in subzone C, to well-vegetated graminoid, dwarf-shrub, moss tundra typical of moist non-acidic tundra in subzone D, to tussock-graminoid, erect-dwarf shrub, moss plant communities typical of moist acidic tundra in subzone E. Figure 9 illustrates the differences in frost boils between Howe Island, a High-Arctic site on mineral soils in subzone C, and Kurishka, Russia, a Low-Arctic site with a well-developed vegetation in subzone D.

Thaw depth on the sparsely vegetated subzone C site at Howe Island was quite deep (Table 2). In late August, 2002, thaw averaged 68 cm on the frost boils and 61 cm between the frost boils. In subzone

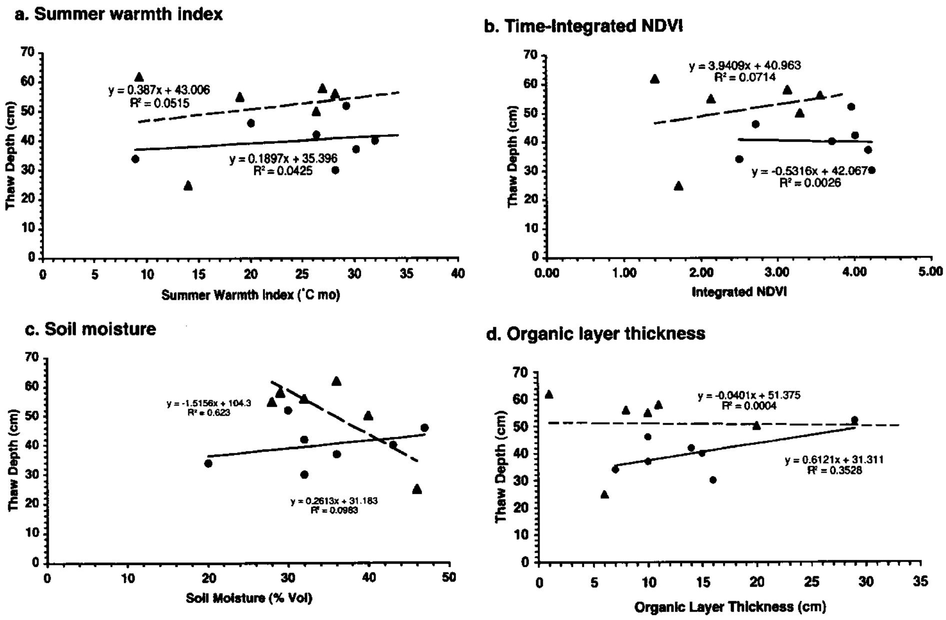

Figure 8 Trends in thaw depth with (a) SWI, (b) Integrated NDVI, (c) soil moisture, and (d) organic horizon thickness. Circles and solid lines are data from acidic sites, and triangles and dashed lines are from non-acidic sites.

Figure 9 (a) Frost boils in subzone C, Howe Island. Note the nearly barren frost boils. The sparse vegetation between the frost boils consists primarily of the prostrate dwarf-shrub, *Dryas integrifolia*, and crustose lichens. (b) Frost boils in subzone D, near Kurishka, Kolyma River, Russia. The frost boils are partially barren with many prostrate dwarf shrubs, lichens and mosses. The inter-frost boil areas are well vegetated with prostrate and erect dwarf shrubs (*Betula exilis, Ledum palustre* ssp. *decumbens, Salix sphenophylla, S. pulchra, Vaccinium vitis-idaea)*, sedges (mostly *Carex arctisibirica*) and mosses (*Dicranum* spp., *Aulacomnium turgidum* and *Hylocomiium splendens*).

D, thaw on the frost boils was consistently deep (68 cm at Deadhors, and 66 cm at Franklin Bluffs and Sagwon MNT), whereas thaw between the frost boils was shallower (55 cm at Deadhorse, and 58 cm at Franklin Bluffs, and Sagwon MNT). In subzone E, the thaw on the frost boils was 46 cm at Sagwon MAT, and 48 cm at Happy Valley. Thaw between the frost boils was 30 cm at Sagwon MAT, and 37 cm at Happy Valley. The area covered by frost boils was greater in subzones C and D, varying from 21% at

Table 2 Thaw in frost boils and inter-boil areas for the Dalton Highway grids: mean, sample size (N), and standard deviation (s.d.), Aug 16–26, 2002. Area of frost boils is determined by dividing the N of frost boils by the N of the entire plot.

Location	Frost boil thaw depth		Inter-boil thaw depth		Entire Plot		Area of Frost Boils (%)
	Mean (cm)	(N) s.d.	Mean (cm)	(N) s.d.	Mean (cm)	(N) s.d.	
Howe Island	68	(48) 4	61	(73) 6	64	(121) 5	39.7
West Dock	No frost boils				25	(441) 2	0
Deadhorse	68	(167) 4	55	(274) 4	60	(441) 8	37.8
Franklin Bluffs	66	(143) 4	55	(298) 4	60	(441) 8	32.4
Sagwon MNT	66	(95) 5	56	(346) 10	58	(441) 10	21.5
Sagwon MAT	46	(26) 9	30	(415) 8	32	(441) 9	5.9
Happy Valley	48	(53) 10	37	(388) 9	38	(441) 10	12

Sagwon MNT to 40% at Howe Island, compared to 5–12% in the acidic subzone-E sites at Sagwon MAT and Happy Valley.

DISCUSSION

Effects of Summer Warmth on Plant Growth and Thaw Depth

The summer insulative effect of the vegetation mat clearly affects the depth of thaw on zonal sites along the bioclimate gradient. Towards the south, taller, denser plant canopies shade the soil and thick moss carpets and thicker soil organic horizons counter the effect of warmer air temperature, so that the thaw depth across the gradient shows little correspondence with air temperature. The study region has a strong summer warmth gradient that directly and indirectly affects plant production. The SWI increased about 3.8 times from 8.9 °C months at Barrow to 34.2 °C months at Council. Aboveground phytomass increased about six fold from about 400 g m^{-2} at Barrow and West Dock to about 2400 g m^{-2} at Council. Thaw depths, on the other hand, showed only a weak relationship to summer warmth. Some of the deepest thaw depths were actually near the Arctic coast at Howe Island and Deadhorse (62 and 55 cm respectively). In general, increased plant biomass along the bioclimate gradient acts as a negative feedback to increases in thaw depth, because of the insulative effects of vegetation and highly organic soil horizons. This relation underscores the importance of vegetation on development of the active layer (Nelson *et al.*, 1997; Hinkel and Nelson, 2003).

Studies from the Mackenzie River corridor also have shown little correspondence between latitude and active-layer thickness (Brown *et al.*, 2000). However, other studies using the CALM data have shown strong relationships between thawing-degree days and active-layer thickness (Nelson *et al.*, 1997; Hinkel and Nelson, 2003). The strong correlations in these studies are related to several factors. First, the 1 × 1 km CALM grids are much larger than our 10 × 10-m plots. Our plots specifically focus on zonal vegetation, whereas the CALM grids cover broad landscapes with a variety of vegetation types. Other research has shown that the thaw depth in many intrazonal vegetation types, such as wetlands, snowbeds, and dry areas, especially those with thin insulative organic layers do show strong correlations with temperature (Vasiliev *et al.*, 2003).

The zonal vegetation in subzones D and E, except at Council, is primarily tussock-tundra that occurs on high-ice permafrost soil that is well insulated from thaw by the vegetation mat, and like peatlands shows only a weak trend of increasing thickness of the active layer with increases in regional temperature (Vasiliev *et al.*, 2003). The trend of the active layer with summer temperature in our study is strongly affected by changes at the northern end of our gradient where the soils rapidly change from mineral soils with no or thin organic layers to thick organic layers (recall the deeper thaw in subzone D than in subzone E in Figure 4c).

It also points to the important control of the active layer on vegetation properties. For example, no permafrost was encountered in the very shrubby tundra at Council. Tundra with dense shrubs over 150 cm tall, such as at the Council site, is not typical of zonal areas with continuous permafrost, but does occur in areas of discontinuous permafrost, such as the southern Seward Peninsula, the northern portions of the Yukon-Kuskokwim River delta, and the

European Russian Arctic west of the Ural Mountains. It is possible that these dense, relatively tall shrub communities require soils without permafrost, as was the case at Council. Alternatively, the taller shrub cover may develop primarily in areas with relatively deep winter snow cover that insulates the soil in winter and prevents the formation of permafrost (Sturm *et al*., 2001a). National Weather Service data indicate that winter snow cover is much deeper on the southern Seward Peninsula (average of 156 cm of snowfall at Nome vs. 82 cm at Umiat, and 77 cm at Barrow).

Most of the increase in phytomass along the gradient was due to shrubs, which increased about 20-fold, from less than 100 g m^{-2} at the coast to about 2100 g m^{-2} at Council. Graminoid and moss biomass showed a smaller increase and lichens decreased, possibly because competition and shading from the taller shrubs limited growth of the sedges and cryptogamic plants. The steepness of the phytomass-SWI relationship was distorted by the very large phytomass at Council, which had 2.6 times greater above-ground phytomass than the next largest phytomass value at the Sagwon MAT site. If Council is excluded from the data, phytomass increased by a factor of about two from Barrow to Quartz Creek. Very cold summer temperatures near the Beaufort Sea severely limit the amount of plant production that can be allocated to woody support tissues. Other work has shown a strong increase in the height and biomass of woody shrubs inland from the Arctic coast (Walker, 1987).

Reflections on the Interactions Between Permafrost and Zonal Tundra

Consideration of permafrost-vegetation interactions on zonal arctic sites can help us interpret how changes in regional climate could affect arctic ecosystems. The zonal concept, which originated with Dokuchaev in 19th century Russian soil science (Vysotsky, 1927), provides a means to subdivide the great diversity of Earth's vegetation into a manageable number of categories, which can then be used for a variety of scientific applications, such as computer simulations of vegetation and ecosystem response to climate change (Cramer, 1997). Zonal vegetation is the climatic climax that develops under the prevailing climate on 'placor' sites. Placors are generally flat or gently sloping sites with fine-grained soils and no extremes of soil moisture, snow, soil chemistry, soil texture or disturbance regimes.

Tussock-tundra has traditionally been considered to be the zonal vegetation in subzones D and E in much of northern Alaska, northwestern Canada, and northeast Siberia (Beringia) (Alexandrova, 1980; Yurtsev, 1994). Recently, this has been challenged because the high-ice-content permafrost of these regions results in saturated soils, which is not a normal characteristic of zonal sites (Razzhivin, 1999). Well-developed zonal tussock-tundra occurs extensively on very old terrain that was not glaciated during the last glacial episode. Tussock-tundra is widely distributed across subzones D and E, with some variation in species composition or structure. The differentiation between the zones is based more on differences in intrazonal sites such as streamsides, wetlands, and warmer microsites. This led Razzhivin to suggest that instead of looking for zonal vegetation on flat sites, we should look to moderate slopes with well-drained soils. Using this approach in subzone D, the zonal vegetation would consist of erect dwarf-shrub tundra, and in subzone E it would consist of taller shrubs, like that at Council.

In theory, this approach helps to isolate the effect of summer warmth from the effects of soil drainage. However, in practice it is difficult to find such representative slopes. For example, in the Arctic Foothills of northern Alaska, most gentle slopes have the same ice-rich permafrost as flat sites. Even moderate slopes of the Arctic Foothills are classified as 'wetlands' according the US Fish and Wildlife Service wetland classification system (Cowardin *et al*., 1979; Walker *et al*., 1989). Furthermore, vegetation on slopes is complicated by other factors, including redistribution of snow and differences in total incident radiation, so it seems unwise to use different criteria for selecting zonal sites in some parts of the Arctic than are used in other zones of the globe. It may be better to keep the topographic position of the placor consistently on flat or gently sloping terrain, and accept that permafrost is a unique arctic phenomenon that influences a suite of sites factors affecting zonal vegetation.

We can get some idea of the vegetation that develops in the absence of near-surface, ice-rich permafrost at both ends of the bioclimate gradient in northern Alaska. In subzone C, Barrow and West Dock are typical of maritime sites along the coast, with moist, ice-rich soils, relatively high biomass (about 400 g m^{-2}) and shallow thaw depths (<40 cm) (see Figure 1a). In contrast, the Howe Island site (Figure 9a) is more typical of large areas of subzone C in the High Arctic of Canada, where drier soils prevail with more open plant canopies, low biomass (<200 g m^{-2}) and deep active layers (65 cm). So at the northern extreme of the gradient, zonal sites with thick active layers have much less biomass than sites with thin active layers.

The opposite situation occurs in the southern parts of subzone E. Here, zonal sites with ice-rich soils and thin active layers develop tussock-tundra; whereas zonal sites with thick active layers have dense shrub-tundra. This vegetation occurs on extensive areas of discontinuous permafrost, such as the southern Seward Peninsula, the northern portions of the Yukon-Kuskokwim River delta, and the European Russian Arctic west of the Ural Mountains. It is likely that dense, relatively tall shrub communities require warm soils. Snow is a likely contributing factor to warmer winter soil conditions because it insulates the soil in winter and prevents the formation of permafrost. For example, winter snow cover is much deeper on the southern Seward Peninsula (average of 156 cm of snowfall at Nome vs. 82 cm at Umiat, and 77 cm at Barrow).

Understanding the interaction between permafrost and zonal vegetation types is key to predicting their linked response to climate change. In High-Arctic subzone C, where well-drained mineral soils prevail, we might expect that climate warming would promote conditions more similar to the Low Arctic (subzones 4 and 5) (Walker and Walker, 1996). Warmer high-arctic ecosystems would produce more plant biomass; more extensive moss layers, and thicker soil organic horizons. Paludification would increase soil moisture, and active layers would become less thick. At the other end of the bioclimate gradient in subzone E, especially near the tree line, we might expect that climate warming would increase the active-layer thickness, and that permafrost would become more discontinuous, resulting in patchier landscapes with areas of shrub-tundra or even forests developing on sites without permafrost.

Effects of Soil pH and Frost Boils on Tundra Ecosystem Properties and Relevance to Climate Change

The results of this study support the conclusions of earlier studies that showed generally deeper thaw in non-acidic soils (Nelson *et al*., 1998). Observations at Oumalik indicate that the acidic/nonacidic boundary observed near Sagwon extends all along the northern front of the Arctic Foothills. The cause of the boundary is still not fully understood, but the major physiographic break at the Foothills boundary coincides with a major climate boundary (Zhang *et al*., 1996). The Foothills appear to affect the mean position of the Arctic Front and affect a major change in the wind regimes. Generally, windier, colder, drier conditions occur north of the boundary resulting in shallower, denser snowpacks during winter and colder soil surface temperatures (Liston and Sturm, 2002; Taras *et al*., 2002), and less precipitation and higher evapotranspiration during the summer. The net result is that south of the boundary there are moister soils, more plant production, thicker organic soil horizons, and thinner active layers.

Plant communities on either side of the boundary at Oumalik were similar to those found at Sagwon, and thaw depths followed a similar pattern, with deeper thaw north of the boundary. Compared to moist acidic tundra, moist non-acidic soils generally supported lower amounts of biomass, higher plant diversity, lower NDVI, and more frost boils. Moist non-acidic tundra generally has open plant canopies that permit more solar radiation to reach the soil surface. The trend of increasing soil organic horizons from north to south reflects the general increase in the biomass of the moss layers. Non-acidic tundra moss layers increased substantially toward the southern end of subzone D. For example, there was about 100 g m^{-2} or less of moss in the non-acidic sites near Howe Island, West Dock and Deadhorse. At Franklin Bluffs, there was 237 g m^{-2} of moss, and 437 g m^{-2} at Sagwon MNT. The largest increase in moss biomass occurs within subzone D and is caused mostly by increases in the brown moss *Tomentypnum nitens*. This moss forms luxuriant carpets in the inter-frost-boil areas at the southern boundary of subzone D at both Sagwon and Oumalik. These thick carpets of *Tomentypnum* appear to have a distinct limiting effect on the thaw depths.

This observation has implications for past climate change on the Arctic Slope. Palaeoenvironmental studies in northern Alaska indicate that forb- and grass-rich ecosystems prevailed during the last glacial maximum. Paludification of arctic Alaskan landscapes followed the last cold interval, and by 8500 years BP, moist acidic tundra was dominant in large regions of the Foothills (Mann *et al*., 2002). Shifts in soil moisture toward a wetter system were responsible for the dramatic ecosystem changes that occurred during this period. Paludification resulted from linked vegetation-permafrost responses. Before *Sphagnum* and other acidophilous mosses became established, basiphilous mosses must have caused the initial trend toward wetter more acidic conditions. It appears likely from observations along the present-day climate gradient that *Tomentypnum nitens* was a primary precursor of acidophilous mosses. Where *Tomentypnum* forms thick carpets, it changes the thermal and hydrological properties of the site in a manner similar to that of *Sphagnum*. Eventually, without continual input of base cations from, for example, loess deposition or through cryoturbation, the system eventually becomes leached of base cations, and acidic tussock-tundra becomes established. More detailed examination of the boundary near Sagwon may help in determining how the switch from non-acidic to acidic tundra occurred over large areas of northern Alaska at the end of the last glacial maximum and could help predict how this boundary between subzones D and E might respond to future climate change.

Feasibility of a Circumpolar Active-Layer Model and Map

In the absence of a means to directly determine the permafrost table using remote sensing, modelling approaches, in combination with landcover maps, are the most promising for mapping active layer depth (Nelson *et al*., 1997). Mapping the active layer requires spatial information for several factors that influence the thermal properties of the soil, including soil density, soil water, soil texture, thickness of the organic layer, topographic position, and number of thawing degree days (Shiklomanov and Nelson, 2003, submitted; Klene *et al*., 2001, 2002). It is very difficult to obtain spatially distributed estimates of all these variables for very large areas. However, plant biomass and vegetation type are also functions of some of these same properties (for example, soil type, soil water, TDD). Vegetation can therefore be used in combination with other key spatial data sets, including soils maps and topography maps, to compile active-layer maps. This paper provides insights regarding climate effects on specific components of the zonal vegetation in the Low Arctic and how these are related to changes in thaw depth. Other studies have also emphasized the dependence of the active layer on vegetation and landscape type (Vasiliev *et al*., 2003, in press; Shiklomanov and Nelson, 2003, in press). Extrapolation to the circumpolar region still requires obtaining more substantive information for common substrate and terrain types in the circumpolar Arctic that were not examined with sufficient replication in this study if at all (e.g., sandy substrates, rocky terrain, High Arctic climates, zonal shrub tundra, wetlands). Six key circumpolar maps are now available as ancillary data to help in making a circumpolar active layer map: the Circumpolar Arctic Vegetation Map and circumpolar NDVI maps (Walker *et al*., 2002a, 2002b, CAVM Map Team, 2003), the Circumpolar Soils Map (Tarnocai *et al*., 2003), the Circum-Arctic map of Permafrost and Ground-Ice Conditions (Brown *et al*., 1997), and the global digital elevation model (Gesch *et al*., 1999). These can provide a first approximation of the variables at coarse scales. Coordinated studies, such as in the ATLAS project, involving soil scientists, permafrost specialists, vegetation, and remote-sensing specialists at many sites across the Arctic bioclimate gradient are the best hope to gain sufficient empirical data to develop the circumpolar models and maps.

CONCLUSIONS

1. Zonal vegetation is strongly linked to active-layer regimes across the summer climate gradient in northern Alaska. Active layers are affected by two opposing trends along the climate gradient. Warmer air temperatures promote deeper thaw, but the insulation provided by more dense plant canopies and thicker soil organic horizons counter this trend. There was little overall increase in thaw depth on zonal sites despite nearly a four-fold increase in the amount of summer warmth. The biomass of tussock-tundra growing in bioclimate subzones D and E on high-ice-permafrost soils did not increase as strongly with temperature as might be expected in the absence of permafrost. The biomass of tussock-tundra appears to be limited more by cold wet soils than by air temperature. In the absence of ice-rich permafrost, other vegetation types replace tussock-tundra on zonal sites, including dwarf-shrub tundra in subzone D and low-shrub tundra in subzone E.
2. The increased warming associated with climate change will not necessarily lead to uniform thickening of the active layer. In some portions of subzone C that currently have mineral soils and deep active layers, warmer temperatures could cause thicker moss layers and more dense plant cover and reduce active layer thicknesses. Near the boundary between subzones D and E, warming could lead to a decrease in active layer variability due in part to colonization of frost boils. In warmer parts of subzone E, expansion of shrub-tundra with thicker active layers could result in patchier landscapes with discontinuous permafrost.
3. Soil pH strongly influences plant community production, and indirectly influences the active layer thickness. Acidic tundra in bioclimate subzones D and E had consistently greater phytomass, LAI, and NDVI and shallower thaw depths than non-acidic tundra. The distinctive spectral boundary observed near Sagwon in

previous studies extends across all of the Arctic Slope and is caused by different vegetation on acidic and non-acidic soils on either side of the boundary. The microsite variability associated with frost boils is an important cause of the generally deeper thaw depths in non-acidic soils.
4. Good information exists from northern Alaska that could be used to extrapolate the biomass, and active layer results to the Low Arctic of much of the circumpolar region. More soil/vegetation/active layer information from a broader suite of terrain types and bioclimate subzones is needed to develop a circumpolar active layer map.

ACKNOWLEDGEMENTS

This manuscript was prepared under National Science Foundation grant OPP-0120736 and OPP-9908829. This work was performed under several NSF grants to the participating investigators.

REFERENCES

Alexandrova VD. 1980. *The Arctic and Antarctic: Their Division into Geobotanical Areas*. Cambridge University Press: Cambridge.

Anisimov OA, Shiklomanov NI, Nelson FE. 2002. Variability of seasonal thaw depth in permafrost regions: a stochastic modeling approach. *Ecological Modeling* **53**: 217–227.

Benninghoff WS. 1966. Relationships between vegetation and frost in soils. In *Proceedings of Permafrost: First International Conference*. National Academy of Sciences, Purdue University: Lafayette, IN; 9–13.

Bigelow NH, Brubaker LB, Edwards ME, Harrison SE, Prentice IC, Anderson PM, Andreev AA, Bartlein PJ, Christensen TR, Cramer W, Kaplan JO, Lozhkin AV, Matveyeva NV, Murray DF, McGuire AD, Razzhivin VY, Ritchie JC, Smith B, Walker DA, Igarashi AD, Kremenetskii KV, Paur A, Pisaric MFJ, Volkova VS. 2003. Climate change and Arctic ecosystems I: Vegetation changes north of 55 °N between the last glacial maximum, mid-Holocene and present. *Journal of Geophysical Research*. In press.

Bockheim JG, Walker DA, Everett LR. 1996. Soil carbon distribution in non-acidic and acidic soils of arctic Alaska. In *Advances of Soil Science*, Lal R, Kimble JM, Follett RF, Stewart BA (eds). Proc. Internat. Symp. on Carbon Sequestration in Soil. CRC Press, Ohio State University: Columbus; 143–155.

Bockheim JG, Walker DA, Everett LR, Nelson FE, Shiklomanov NI. 1998. Soils and cryoturbation in moist non-acidic and acidic tundra in the Kuparuk river basin, arctic Alaska, U.S.A. *Arctic and Alpine Research* **30**: 166–174.

Brown J, Ferrians OJ, Heginbottom JA, and Melnikov ES. 1997. Circum-arctic map of permafrost and ground-ice conditions. US Geological Survey Map CP-45, scale 1 : 10 000 000.

Brown J, Hinkel KM, Nelson FE. 2000. The circumpolar active layer monitoring (CALM) program: research designs and initial results. *Polar Geography* **24**: 165–258.

Carter LD. 1981. A Pleistocene sand sea on the Alaskan Arctic Coastal Plain. *Science* **211**: 381–383.

CAVM Map Team. 2003. Circumpolar Arctic Vegetation Map, Conservation of Arctic. Flora and Fauna (CAFF) Map No. 1. US Fish and Wildlife Service, Anchorage, AK. Scale 1 : 75 000 000.

Chapin FS III, McGuire AD, Randerson J, Pielke R, Baldocchi D, Hobbie SE, Roulet N, Eugster W, Kasischke E, Rastetter EB, Zimov SA, Running SW. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology* **6**: 211–223.

Chernov YL, Matveyeva NV. 1997. Arctic ecosystems in Russia. Wielgolaski FE (ed). *Polar and Alpine Tundra*. Elsevier, Amsterdam: 361–507.

Cowardin LM, Carter V, Golet FC, LaRoe ET. 1979. Classification of wetlands and deep water habitats of the United States. US Government Printing Office FWS/OBS-79/31, US Fish and Wildlife Service.

Cramer W. 1997. Modeling the possible impact of climate change on broad-scale vegetation structure: examples from northern Europe. In Oechel WC, Callaghan T, Gilmanov T, Holten JI, Maxwell B, Molau U, and Sveinbjörnsson B (eds) *Global Change and Arctic Terrestrial Ecosystems*. Springer, New York: 312–329.

Ebersole JJ. 1985. Vegetation disturbance and recovery at the Oumalik Oil Well, Arctic Coastal Plain, Alaska. Ph.D. Thesis University of Colorado, Boulder.

Elvebakk A, Elven R, and Razzhivin VY 1999. Delimitation, zonal and sectorial subdivision of the Arctic for the Panarctic Flora Project. In Nordal I, Razzhivin VY (eds). *The Species Concept in the High North—A Panarctic Flora Initiative*. The Norwegian Academy of Science and Letters, Oslo: 375–386.

Eugster W, McFadden JP, Chapin FS III. 1997. A comparative approach to regional variation in surface fluxes using mobile eddy correlation towers. *Boundary-Layer Meteorology* **85**: 293–307.

Everett KR. 1980. Distribution and variability of soils near Atkasook, Alaska. *Arctic and Alpine Research* **12**: 433–446.

Gesch DB, Verdin KL, Greenlee SK. 1999. New land surface digital elevation model covers the Earth. *EOS Transactions, American Geophysical Union* **80**: 69–70.

Goulden ML, Wofsy SC, Harden JW, Trumbore SE, Sutton DJ, Bazzaz A, Munger JW. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* **279**: 214–217.

Hinkel KM, Nelson FE. 2003. Spatial and temporal patterns of active layer thickness at circumpolar active layer monitoring (CALM) sites in northern

Alaska, 1995–2000. *Journal of Geophysical Research-Atmospheres*. **108**: 2. DOI: 10.1029/2001JD000927.
Hinzman LD, Goering DJ, Kane DL. 1998. A distributed thermal model for calculating soil temperature profiles and depth of thaw in permafrost regions. *Journal of Geophysical Research* **103**: 28 975–28 992.
Jia GJ, Epstein HE, Walker DA. 2002. Spatial characteristics of AVHRR-NDVI along latitudinal transects in northern Alaska. *Journal of Vegetation Science* **13**: 315–326.
Jorgenson MT, Racine CH, Walters JC, and Osterkamp TE. 2001. Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change* **48**: 551–579.
Kane DL. 1997. The impact of hydrologic perturbations on arctic ecosystems induced by climate change. In Oechel WC, Callaghan T, Gilmanov T, Holten JI, Maxwell B, Molau U, and Sveinbjörnsson B, (eds) *Global Change and Arctic Terrestrial Ecosystems*. Springer, New York: 63–81.
Kane DL, Hinzman LD, Zarling JP. 1991. Thermal response of the active layer to climatic warming in a permafrost environment. *Cold Regions Science and Technology* **19**: 111–122.
Kaplan JO, Bigelow NH, Bartlein PJ, Christensen TR, Cramer W, Harrison SP, Matveyeva NV, McGuire AD, Murray DF, Prentice IC, Razzhivin VY, Smith B, Walker DA, Anderson PM, Andreev AA, Brubaker LB, Edwards ME, Lozhkin LV, Ritchie JC. 2003. Climate change and Arctic ecosystems II: Modeling, paleodata-model comparisons, and future projections. *Journal of Geophysical Research-Atmospheres*. In press.
Kittel TFG, Steffen WL, Chapin FS. III. 2000. Global and regional modelling of Arctic-boreal vegetation distribution and its sensitivity to altered forcing. *Global Change Biology* **6**: 1–18.
Klene AE, Nelson FE, Shiklomanov NI, Hinkel KM. 2001. The n-factor in natural landscapes: Variability of air and soil-surface temperatures, Kuparuk River basin, Alaska. *Arctic, Antarctic, and Alpine Research* **33**: 140–148.
Klene AE, Nelson FE, Shiklomanov NI. 2002. The N-factor as a tool in geocryological mapping seasonal thaw in thaw in the Kuparuk River Basin, Alaska. *Physical Geography* **22**: 449–466.
Komárková V, Webber PJ. 1980. Two Low Arctic vegetation maps near Atkasook, Alaska. *Arctic and Alpine Research* **12**: 447–472.
Lachenbruch AH, Marshall BV. 1986. Changing climate: geothermal evidence from permafrost in the Alaskan arctic. *Science* **234**: 689–696.
Liston G, Sturm M. 2002. Winter precipitation patterns in arctic Alaska determined from a blowing-snow model and snow-depth observations. *Journal of Hydrometeorology* **3**: 646–659.
Mann DH, Peteet DM, Reanier RE, Kunz ML. 2002. Responses of an arctic landscape to Late glacial and early Holocene climatic changes: the importance of moisture. *Quaternary Science Reviews* **21**: 997–1021.
Markon CJ. 1999. Characteristics of the Alaskan 1-km Advanced Very High Resolution Radiometer data sets used for analysis of vegetation biophysical properties. USGS Open File Report 99–088, US Geological Survey.
Markon CJ, Fleming MD, Binnian EF. 1995. Characteristics of vegetation phenology over the Alaskan landscape using AVHRR time-series data. *Polar Record* **31**: 179–190.
Matveyeva NV. 1998. *Zonation in Plant Cover of the Arctic*. Russian Academy of Sciences, Proceedings of the Komarov Botanical Institute, Russian Academy of Science, Moscow, No. 21. (In Russian).
McGuire AD, Clein JS, Melillo JM, Kicklighter DW, Meier RA, Vorosmarty CJ, Serreze MC. 2000. Modelling carbon responses of tundra ecosystems to historical and projected climate: sensitivity of pan-Arctic carbon storage to temporal and spatial variation in climate. *Global Change Biology* **6**: 141–159.
McGuire AD, Sturm M, Chapin FS. III. 2003. Arctic transitions in the Land-Atmosphere system (ATLAS): Background, objectives, results, and future directions. *Journal of Geophysical Research - Atmospheres*. **108**: 2. DOI: 10.1029/2001JD000236.
Muller SV, Walker DA, Nelson F, Auerbach N, Bockheim J, Guyer S, and Sherba D. 1999. Accuracy assessment of a land-cover map of the Kuparuk River basin, Alaska: considerations for remote regions. *Photogrammetric Engineering & Remote Sensing* **64**: 619–628.
Nelson FE, Shiklomanov NI, Mueller GR, Hinkel KM, Walker DA, Bockheim JG. 1997. Estimating active-layer thickness over a large region: Kuparuk River Basin, Alaska. *Arctic and Alpine Research* **29**: 367–378.
Nelson FE, Hinkel KM, Shiklomanov NI, Mueller GR, Miller LL, Walker DA. 1998. Active-layer thickness in north-central Alaska: systematic sampling, scale, and spatial autocorrelation. *Journal of Geophysical Research-Atmospheres* **103**: 28 963–28 973.
Nelson FE, Anisimov OA, Shiklomanov NI. 2001. Subsidence risk from thawing permafrost. *Nature* **410**: 889–890.
Oechel WC, Callaghan T, Gilmanov T, Holten JI, Maxwell B, Molau U, and Sveinbjörnsson B, (eds). 1997. *Global Change and Arctic Terrestrial Ecosystems*. Springer, New York.
Oechel WC, Vourlitis GL, Verfaillie J Jr, Crawford T, Brooks S, Dumas E, Hope A, Stow D, Boynton B, Nosov V, Zuleta R. 2000. A scaling approach for quantifying the net CO2 flux of the Kuparuk River Basin, Alaska. *Climate Change Biology* **6**: 160–173.
Razzhivin VY. 1999. Zonation of vegetation in the Russian Arctic. In Nordal I, Razzhivin VY. (eds). *The Species Concept in the High North - A Panarctic Flora Initiative*. The Norwegian Academy of Science and Letters, Oslo: 113–130.
Reeburgh WS, King JY, Regli SK, Kling GW, Auerbach NA, Walker DA. 1998. A CH4 emission estimate for the Kuparuk River basin, Alaska. *Journal of Geophysical Research-Atmospheres* **103**: 29 005–29 014.
Shiklomanov NI and Nelson FE. 2002. Active-layer mapping at regional scales: a 13-year spatial time series for the Kuparuk Region, north-central Alaska. *Permafrost and Periglacial Processes* **13**: 219–230.

Shiklomanov NI and Nelson FE. 2003. Statistical representation of landscape-specific active-layer variability. *Proceedings of the International Permafrost Conference*, Zurich, Switzerland, Swets & Zeitlinger, The Netherlands. In press.

Shippert MM, Walker DA, Auerbach NA, Lewis BE. 1995. Biomass and leaf-area index maps derived from SPOT images for Toolik Lake and Imnavait Creek areas, Alaska. *Polar Record* **31**: 147–154.

Silapaswan CS, Verbyla D, McGuire AD. 2001. Land cover change on the Seward Peninsula: The use of remote sensing to evaluate potential influences of climate change on historical vegetation dynamics. *Journal of Remote Sensing* **5**: 542–554.

Soil Survey Staff. 1993. *Soil Survey Manual*, USDA Handbook No. 18. US Government Printing Office, Washington, DC.

Sturm M, Racine C, Tape K. 2001a. Increasing shrub abundance in Arctic. *Nature* **411**: 547–548.

Sturm M, McFadden JP, Liston GE, Chapin FS III, Racine CH, Holmgren J. 2001b. Snow-shrub interactions in arctic tundra: a hypothesis with climatic implications. *Journal of Climate* **14**: 336–344.

Taras B, Sturm M, Liston GE. 2002. Snow-ground interface temperatures in the Kuparuk River Basin, Arctic Alaska: measurements and model. *Journal of Hydrometeorology* **3**: 377–394.

Tarnocai CJ, Kimble J, Waltman S, Swanson D, Goryachkin S, Naumov YM, Stolbovoi V, Jakobsen, Broll G, Montanarella L, Arnoldussen O, Arnalds O, Yli-Halla M. 2003. *Northern Circumpolar Soils*. Research Branch, Agriculture and Agri-Food Canada, Ottawa, Canada. 1 : 10,000,000-scale map.

Thayer-Snyder C. 2000. A preliminary Landsat MSS-derived land-cover map of the Seward Peninsula, Alaska: Classification methods, and comparison with existing data sets. Poster presented at the ARCSS LAII Science Workshop, Seattle, WA, 23–26 Feb 2000.

van Everdingen ROe. 1998. *Multi-language Glossary of Permafrost and Related Ground-Ice Terms*. University of Calgary, Calgary.

Vasiliev AA, Moskalenko NG, Brown J. 2003. A new approach for interpreting active layer observations in the context of climate change: a West Siberian example. *Proceedings of the International Permafrost Conference*, Zurich, Switzerland, Swets & Zeithinger, The Netherlands. In press.

Viovy N. 2000. Automatic classification of time series (ACTS): a new clustering method for remote sensing time series. *International Journal of Remote Sensing* **21**: 1537–1560.

Vysotsky GN. 1927. Theses on soil and moisture (conspectus and terminology). In Lesovedenie (ed). Sbornik Lesnogo Obschestva v Leningrade, Leningrad: 67–79 (In Russian).

Walker DA. 1987. Height and growth-ring response of *Salix lanata* ssp. *richardsonii* along the coastal temperature gradient of northern Alaska. *Canadian Journal of Botany* **65**: 988–993.

Walker DA and Barry NC. 1991. Toolik Lake permanent vegetation plots: site factors, soil physical and chemical properties, plant species cover, photographs and soil descriptions. Data report to the Department of Energy R4D Program, Institute of Arctic and Alpine Research, University of Colorado, Boulder, 48 pp + appendices.

Walker DA and Walker MD. 1996. Terrain and vegetation of the Imnavait Creek Watershed. In Reynold JF and Tenhunen JD (eds). *Landscape Function: Implications for Ecosystem Disturbance, a Case Study in Arctic Tundra*. Springer-Verlag, New York: 73–108.

Walker DA, Auerbach NA, Bockheim JG, Chapin FS III, Eugster W, King JY, McFadden JP, Michaelson GJ, Nelson FE, Oechel WC, Ping CL, Reeburgh WS, Regli S, Shiklomanov NI, Vourlitis GL. 1998. Energy and trace-gas fluxes across a soil pH boundary in the Arctic. *Nature* **394**: 469–472.

Walker DA, Bockheim JG, Chapin FS III, Eugster W, Nelson FE, Ping CL. 2001. Calcium-rich tundra, wildlife, and the ''Mammoth Steppe''. *Quaternary Science Reviews* **20**: 149–163.

Walker DA, Gould WA, Maier HA, Raynolds MK. 2002. The Circumpolar Arctic Vegetation Map: AVHRR-derived base maps, environmental controls, and integrated mapping procedures. *International Journal of Remote Sensing* **23**: 2552–2570.

Walker DA, Epstein HE, Jia GJ, Copass C, Edwards EJ, Gould WA, Hollingsworth J Knudson J, Maier H, Moody A, Raynolds MK. 2003. Phytomass, LAI, and NDVI in northern Alaska: relationships to summer warmth, soil pH, plant functional types and extrapolation to the circumpolar Arctic. *Journal of Geophysical Research—Atmospheres*. **108**: 2. DOI: 10.1029/2001JD0098.

Walker MD, Walker DA, Everett KR. 1989. Wetland soils and vegetation, Arctic Foothills, Alaska. US Fish and Wildlife Service Report 89 (7).

Washburn AL. 1956. Classification of patterned ground and review of suggested origins. *Geological Society of America Bulletin* **67**: 823–866.

Weller G, Chapin FS, Everett KR, Hobbie JE, Kane D, Oechel WC, Ping CL, Reeburgh RS, Walker D, Walsh J. 1995. The Arctic Flux Study: a regional view of trace gas release. *Journal of Biogeography* **22**: 365–374.

Yurtsev BA. 1994. Floristic division of the Arctic. *Journal of Vegetation Science* **5**: 765–776.

Zhang T, Osterkamp TE, Stamnes K. 1996. Some characteristics of the climate in Northern Alaska, U.S.A. *Arctic and Alpine Research* **28**: 509–518.