Article Title: NDVI, biomass, and landscape evolution of glaciated terrain in northern Alaska

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NDVI, biomass, and landscape evolution of glaciated terrain in northern Alaska

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ABSTRACT. The patterns of the normalized difference vegetation index (NDVI) on three glacial surfaces of different ages in the vicinity of Toolik Lake, Alaska, were examined. NDVI was derived from SPOT multispectral digital data, and the images were stratified according to boundaries on glacial geology and vegetation maps. Ground-level measurements of NDVI from common vegetation types were also collected, using a portable spectrometer. Late Pleistocene glacial surfaces have lower image-NDVI than older Middle Pleistocene surfaces, and the mean NDVI is correlated with approximate time since deglaciation. The trends are related to differences in NDVI associated with vegetation growing on mineral vs peaty substrates. Nonacidic mineral substrates are more common on the younger landscapes, and acidic peaty soils are more common on the older surfaces. The field-NDVI of acidic dry, moist, and wet tundra are consistently higher than those of corresponding nonacidic tundra types. These same trends are seen when the SPOT NDVI image is stratified according to vegetation boundaries appearing on two detailed vegetation maps in the region. Above-ground biomass of moist and wet acidic tundra is significantly greater than corresponding nonacidic types. Vegetation species composition was examined along two transects on the oldest and youngest glacial surfaces. Shrub cover is the most important factor affecting the spectral signatures and biomass. Older surfaces have greater cover of shrub-rich tussock tundra and shrub-filled water tracks, and the younger surfaces have more dry, well-drained sites with low biomass and relatively barren nonsorted circles and stripes. These trends are related to paludification and modification of the terrain by geomorphic and geochemical processes. Similar patterns of spectral reflectance have been noted in association with a variety of large-scale natural disturbances in northern Alaska. However, extrapolation of these results to much broader regions of the circumpolar Arctic will require the use of sensors covering larger areas, such as the AVHRR aboard the NOAA satellites.

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Introduction
The normalized difference vegetation index (NDVI; Rouse and others 1973) is a commonly used index of vegetation activity derived from multispectral satellite data. It has proven useful for estimating a wide variety of ecological variables, including vegetation biomass, net above-ground primary production, leaf area index (LAI), photosynthesis, respiration, transpiration, and intercepted photosynthetically active radiation (IPAR) (for example, Goward and others 1985; Sellers 1985, 1987; Fung and others 1987; Running and others 1989; Law and Waring 1994). In the Arctic, NDVI is being used to derive ecological variables for estimating the flux of trace gases, water, and energy (Stow and others 1993; Hope and others 1993; Shipert and others 1995). Although widely used, the underlying physical controls of NDVI are only partially understood. In order to understand better the relationship between biophysical controls and NDVI in Arctic ecosystems, it is important first to understand how NDVI varies across large regions and how these variations are related to vegetation composition, biomass, and ecological site factors.

In northern Alaska, it has been noted that patterns of spectral reflectance on false-color infrared satellite images are related to surficial geology deposits (Walker and others 1982; Walker and Everett 1991). In general, more recent deposits of loess, glacial till, and alluvial materials have greater reflectance in the visible and lower reflectance in the near infrared bands. Since most of these surfaces are nearly completely vegetated, the differences in spectral reflectance are thought to be primarily related to the nature of the vegetation growing on these surfaces. This paper explores the trends of NDVI in relation to the age of the glacial landscape in the vicinity of Toolik Lake, Alaska. Recent research suggests that the spectral reflectance patterns are related to differences in vegetation composition and biomass associated with landscape evolution occurring during very long time intervals (>100,000 years) (Walker and Walker, in press).

Study site, geology, and vegetation
The study area was located in the vicinity of Toolik Lake in the foothills of the Brooks Range, North Slope, Alaska, USA (68°37'N, 149°32'W; Fig. 1). This area was selected because of accessibility to glacial deposits of different ages within a few kilometers of the Toolik Lake field camp, and because the geocology of the region is relatively well known. The region contains primary study sites for the Arctic System Science (ARCSS) Land–Atmosphere–Ice Interactions (LAI) Flux Study (Weller and others, in press) and the Arctic Long-Term Ecological Research (LTER) project (Callahan 1984; Hobbie and others 1991). Detailed maps of glacial deposits and of vegetation are available for much of the region (Hamilton 1978, 1986; Jørgenson 1984a; Walker and others 1989;
Fig. 1. (Opposite. (a) Glacial geology of the Toolik Lake vicinity (adapted from Hamilton 1978). (b) NDVI map of the study area derived from a portion of the SPOT multispectral satellite image, acquisition date 28 July 1989. White lines indicate boundaries of glacial geology units as in (a). Darkening shades of gray indicate progressively higher NDVI values. Black areas have low NDVI (<0.25) associated with water bodies and barren areas such as roads and gravel pads.

Walker and Walker, in press).

Hamilton (1986) described and mapped the glacial deposits of the Brooks Range. Deposits dating from the Middle (Sagavanirktok II) and Late (Iktlik I and II) Pleistocene occur within the study area (Fig. 1). The younger Iktlik II surfaces have more irregular topography, stony surfaces, steeper slopes, deranged drainage systems, and more heterogeneous vegetation cover. In contrast, the Sagavanirktok surfaces are generally more highly eroded with smooth slopes, broad hill crests, few glacial erratics, mature drainage systems, and more extensive tussock tundra (Hamilton 1978, 1986). Complexes of nonsorted stripes and vegetation and dry heath vegetation are more common on younger surfaces, and moist tussock tundra and bog vegetation are more common on the older surfaces (Jorgenson 1984a, 1984b; Walker and others 1989; Walker and Walker, in press).

The vegetation of the Arctic foothills physiographic province (Wahrhaftig 1965) has been broadly divided into four major physiognomic categories, defined on the basis of site moisture and dominant plant growth forms (Walker and others 1989; Walker and Walker, in press; Walker and others 1994a):

1. Dry dwarf-shrub, fruticose-lichen tundra is dominant on exposed sites and well-drained snowbed areas;
2. moist graminoid, dwarf-shrub tundra is dominant on most moderately drained upland surfaces;
3. wet graminoid tundra occurs in fens, bogs, marshes, and poorly drained habitats; and
4. shrublands, dominated by species of dwarf birch, alder, and willow, occur along streams, water tracks, and south-facing slopes.

These broad physiognomic categories are subdivided into groups of vegetation community types that occur on acidic and nonacidic soils (Shipert and others 1995; Fig. 2). The terms acid and nonacid are roughly equivalent to their usage in the US soil taxonomy (Soil Taxonomy Survey 1975). Soils with pH <5.0 are considered acidic, and soils with pH ≥5.0 are considered nonacidic. This study focuses on the differences in moist acidic and nonacidic tundra because these units dominate the largest portion of the foothills region.

Although the physiognomies of moist acidic and nonacidic tundra are similar, there are different species associated with each habitat. For example, moist acidic tundra includes tussock tundra, which is the zonal vegetation of stable mesic slopes throughout the foothills. It contains plant-community types dominated by mesophytic, acidophilous plant species (for example, Eriophorum vaginatum, Betula nana, Salix planifolia ssp. pulchra, Vaccinium uliginosum, V. vitis-idaea, Rubus chamaemorus, Ledum palustre ssp. decumbens, Sphagnum spp., Dicranum spp., Polytrichum strictum, Aulacomnium turgidum, A. palustre, Cladina arbuscula, C. rangiferina, and Cladonia amaurocraea). In contrast, moist nonacidic tundra types are found in areas with high soil pH or minerotrophic ground water, and basophilous plant species are dominant in these types (such as Dryas integrifolia, Salix reticulata, S. arctica, Eriophorum triste, Lagotis glauca, Tofieldia pusilla, Rhododendron lapponicum, Pedicularis oederi, Equisetum variegatum, Saussurea angustifolia, Tomentypnum nitens, Orchothecium chryseum, and Ditrichum flexicaule).

Methods

NDVI of glacial surfaces

The trends in NDVI on each of the glacial surfaces were examined by digitally overlaying a glacial geological map (scale 1:250,000; Hamilton 1978) on a SPOT-1 High Resolution Visible (HRV) sensor multispectral (XS) image (28 July 1989; location: column 437, row 207). This was done using an ARC/INFO geographic information system. The methods for processing the SPOT data are presented in Shipert and others (1995). Some of the areas of the map were reclassified based on new information (T.D. Hamilton, personal communication). NDVI was calculated for each pixel (20 x 20 m picture element) using equa-
where \( NIR \) and \( R \) are the reflectances in the SPOT near-infrared and red bands. Chlorophyll in green vegetation absorbs strongly in the red wavelengths and reflects strongly in the \( NIR \) wavelengths, and the ratio of the two is commonly used as an index of green biomass (for example, Colwell 1973; Rouse and others 1973; Tucker 1979; Tucker and Sellers 1986). NDVI distribution curves were plotted for each of the three glacial surfaces using all of the pixels in the study area, excluding water and barren surfaces. Water and barren pixels (roads and gravel pads) with NDVI <0.25 were eliminated because the authors were interested in the NDVI of vegetated surfaces. The skewness and kurtosis of the curves were calculated using the \( g_1 \) and \( g_2 \) statistics (Sokal and Rohlf 1979). The remaining pixels were grouped into 45 NDVI classes, each class being 0.01 NDVI units. The mean NDVI was calculated for each glacial surface. These numbers are the true means without error, because all the pixels on each vegetated glacial surface were included in the analysis.

**NDVI of mapped vegetation units**

The NDVI of mapped vegetation types was determined by overlaying detailed (1:5000 scale) vegetation maps of the Toolik Lake and Innvavait Creek regions (Walker and others 1989) on the SPOT image, using an ARC/INFO geographic information system software. A one-pixel buffer zone was generated around each polygon boundary to minimize the influence of mixed pixels occurring on the boundaries between two vegetation units. Mean NDVI and standard error of the mean were calculated for each vegetation community type on the maps. The values were also grouped according to larger vegetation categories used for this analysis (acidic and nonacidic dry, moist, wet, tundra, and shrublands).

**Field measurements of NDVI and biomass**

The controls of vegetation parameters on spectral reflectance were examined by measuring reflectance spectra and above-ground biomass on 60 permanently marked study plots. The sampling was done on plots near Toolik Lake and Innvavait Creek, Alaska, between 25 July and 10 August 1993. These plots were a subset of the 180 plots used for the vegetation classification of the region (Walker and others 1994a). They were chosen to represent acidic and nonacidic vegetation types in the four major physiognomic categories of vegetation (dry dwarf-shrub, fruticose lichen tundra; moist graminoid, dwarf-shrub tundra; wet graminoid tundra; and shrublands). Three 20 x 50 cm subsamples were located within the confines of each of the 60 permanent plots (180 subsamples total).

Reflectance spectra were collected on the 180 subsamples using a PS-II portable spectrometer manufactured by Analytical Spectral Devices, Inc. The instrument operates in the 350–1050 nm portion of the spectrum at approximately 2–3 nm resolution, giving essentially a continuous spectrum of reflectance. Reflectance values were calculated for broader red (630–690 nm) and near-infrared bands (760–900 nm) so that the reflectance could be compared to the satellite-derived data. Three replicate spectral-reflectance samples were collected from each of the 180 subsamples and grouped according to vegetation type and by acidic and nonacidic dry, moist, wet, and shrubland vegetation categories. Mean field-NDVI was calculated for each vegetation category. More detailed descriptions of the sampling methods are presented in Shippert and others (1995).

Each subplot was then harvested by clipping all the vegetation above the dead part of the moss layer. The harvests were frozen and later sorted according to growth form, live and dead foliar, and woody components. The sorted components were dried at 105°C, weighed, and the results converted to dry weight per m². Mean biomass was calculated for the same categories as the NDVI (Shippert and others 1995).

**Soil, vegetation, and NDVI on Sagavanirktok-age and Itkillik-age hillslopes**

Another approach to examining NDVI-vegetation relationships took advantage of previously collected vegetation and soil information from toposequence transects on the youngest and oldest glacial surfaces (Walker and others 1989; Walker and Barry 1991). Soil pH and growth-form cover values were compared to mean SPOT-derived NDVI along these transects. A preliminary hypothesis was that the lower NDVI values of the younger surfaces should correspond to one or more of the following factors: less shrub cover, more cover of bare soil, and/or more standing dead vegetation.

Two broad hillslopes were compared: a Sagavanirktok-age slope at Innvavait Creek and a Itkillik II-age hillside near Toolik Lake. Both toposequences followed interfluves and avoided vegetation in drainages. The vegetation data came from numerous 10 m transects parallel to the elevation contours on each hillside in order to sample the hill crest, shoulder, backslope, and footslope areas adequately. Five sample plots were located at 2 m intervals along each transect. Twelve transects (60 plots) were placed along the Sagavanirktok-age hillside, and 8 transects (40 plots) were placed along the Itkillik II-age hillside. At each transect one soil sample was collected from the top of the mineral horizon and analyzed for pH (saturated-paste method: Page and others 1982). The vegetation was sampled using a 50 x 100 cm point quadrat containing 50 grid points spaced at 10-cm intervals (Walker and Walker 1991). The top plant species in the vegetation canopy intersecting each grid point was recorded. A total of 3000 point samples were collected from the Sagavanirktok-age hillside and 2000 points from the Itkillik II-age hillside. These data were grouped to examine percentage cover of six growth forms (broad-leaf deciduous shrubs, evergreen shrubs, graminoids, forbs, mosses, and lichens) and total dead (erect dead plus litter).

The mean NDVI for each hillside along swaths from the hill crests to the footslopes in the vicinity of the toposequences was calculated using the SPOT image. Three pixel-wide (60 m-wide) rectangles from each
Table 1. NDVI frequency distribution curve information for Fig. 2. Itkilik II is skewed to the right and is leptokurtic. Itkilik I and Sagavanirktok are skewed to the left and are leptokurtic. *P < 0.001.

<table>
<thead>
<tr>
<th>Statistic</th>
<th>Itkilik II</th>
<th>Itkilik I</th>
<th>Sagavanirktok</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean NDVI</td>
<td>0.42</td>
<td>0.44</td>
<td>0.46</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.05</td>
<td>0.06</td>
<td>0.05</td>
</tr>
<tr>
<td>Standard error</td>
<td>0.00018</td>
<td>0.00013</td>
<td>0.00008</td>
</tr>
<tr>
<td>Minimum</td>
<td>0.25</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td>Maximum</td>
<td>0.59</td>
<td>0.7</td>
<td>0.7</td>
</tr>
<tr>
<td>Skewness (g1)</td>
<td>0.618*</td>
<td>-0.132*</td>
<td>-0.057*</td>
</tr>
<tr>
<td>Kurtosis (g2)</td>
<td>1.244*</td>
<td>0.078*</td>
<td>0.037</td>
</tr>
<tr>
<td>Median</td>
<td>0.41</td>
<td>0.44</td>
<td>0.46</td>
</tr>
</tbody>
</table>

hillslope were extracted and the mean NDVI for each hillslope was calculated.

**Results**

**Image-NDVI of glacial units**

The three glacial surfaces had distinctive frequency distributions of NDVI (Fig. 2; Table 1). None of the distributions was normal. All were leptokurtic (more peaked than a normal distribution) with NDVI values concentrated toward the mean and tails of the curves and relatively few in the intermediate regions. The Sagavanirktok surfaces had more high NDVI values (skewed to the left), and the Itkilik II surfaces had more low NDVI values (skewed to the right), indicating a greater proportion of areas with high biomass on the older surfaces than on the younger surfaces. Mean image-NDVI of the Sagavanirktok, Itkilik I, and Itkilik II were 0.46, 0.44, and 0.42, respectively. The regression of the mean NDVI for each surface vs the approximate time since deglaciation yielded a linear relationship ($r^2 = 0.993$; Fig. 3). Although the regression contained only three points, it suggested that vegetation biomass evolves in conjunction with terrain evolution over periods of time exceeding 100,000 years.

**Image-NDVI of mapped vegetation units**

Mean image-NDVI of the mapped acidic dry (0.41), moist (0.47), and wet (0.42) vegetation units was consistently higher than those of corresponding nonacidic units (0.4, 0.43, and 0.41, respectively; Fig. 4).

**Field-NDVI of vegetation units**

This same trend occurred with the field NDVI values obtained with the portable spectrometer, but with even stronger differences between acidic and nonacidic types (Fig. 4). Image-NDVI values were about 40% of the field-NDVI values, most likely due to factors associated with geometry of the satellite-sensor viewing angle and the solar incidence angle (Shipper and others 1995). The NDVI is highest in moist acidic vegetation and is relatively low in dry and wet vegetation. Shrub vegetation of water tracks and streamside areas have the highest NDVI values.

**Biomass of vegetation units**

Acidic moist tundra has significantly higher above-ground biomass than nonacidic moist tundra (512 ± 26 g m$^{-2}$ vs 403 ± 21 g m$^{-2}$; Fig. 5). There is also a significant difference in the biomass of the wet tundra types (wet acidic = 238 ± 49 g m$^{-2}$, wet nonacidic = 154 ± 25 g m$^{-2}$). There is no significant difference in biomass of dry acidic and nonacidic vegetation types (358 ± 41 g m$^{-2}$ for dry acidic and 488 ± 115 g m$^{-2}$ for dry nonacidic). Shrublands have the greatest biomass (735 ± 90 g m$^{-2}$).

Shaver and Chapin (1991) reported mean values of 319 g m$^{-2}$ in dry tundra, 708 g m$^{-2}$ in moist (tussock) tundra, 178 g m$^{-2}$ in wet tundra, and 1934 g m$^{-2}$ in shrublands. This study’s lower value for moist tundra (overall mean for moist acidic and nonacidic was 466 ± 39 g m$^{-2}$) may be due to the larger range of moist vegetation types included. This sample included four different moist tundra community types, whereas Shaver and Chapin included only one. This study also measured relatively low biomass in the shrub communities compared to Shaver and Chapin. Numerous dwarf-shrub communities that were included in this category were sampled, but the taller shrub communities were not because of the difficulty of obtaining reflectance spectra and clip harvests in these types.

The biomass trends generally correspond to the trends in NDVI, except for the relatively high biomass of dry tundra types, which have relatively low NDVI values. These types have large amounts of prostrate shrubs (such as Dryas octopetala and D. integrifolia), with large amounts of nongreen woody stems and dead, attached leaves that contribute to the biomass without a corresponding contribution to the NDVI values. A similar explanation has been proposed for the unexpected high biomass of dry alpine-tundra vegetation types (Walker and others 1994b).

**Vegetation and soil characteristics on Sagavanirktok-age and Itkilik II-age hillslopes**

Mean soil pH on the Sagavanirktok-age and Itkilik II-age
hillslopes were 4.08 ± 0.09 and 6.5 ± 0.12, respectively (Table 2). Mean SPOT-image-derived NDVIs were 0.48 ± 0.04 (n = 96 pixels) for the Sagavanirktok slope and 0.39 ± 0.02 (n = 36 pixels) for the Itkillik II slope. Deciduous shrubs had greater cover on the Sagavanirktok-age hillslope (23.1 ± 1.8% cover vs 8.8 ± 1.1) (Fig. 6). Forsults had greater cover on the Itkillik II-age hillslope (6.9 ± 1.7% vs 1.8 ± 0.5). Total cover of vascular plants was somewhat greater on the Sagavanirktok-age hillslope (67 vs 60%). Unfortunately, the samples did not distinguish between green and woody cover of shrubs, so the total cover of green vegetation could not be compared. The measurements also recorded only the plant species at the top of the vegetation canopy and did not consider the stature of the canopy nor the total green-leaf area of the two slopes. Other studies have shown larger leaf area index (LAI) values in moist acidic tundra types than in moist nonacidic tundra (0.815 ± 0.053 vs 0.586 ± 0.044) and a strong correlation between LAI and NDVI (r² = 0.85) (Shipert and others 1995). There was no significant difference in the amount of standing dead and litter on the two hillslopes (29.1 ± 2.3% vs 28.1 ± 1.2%). The greater shrub cover appeared to be the primary cause of the higher NDVI values on the older surfaces.

Discussion
Remote sensing of landscape evolution patterns
The strong correlation between NDVI and landscape age (Fig. 3) indicates that large-scale patterns of vegetation biomass are related to landscape evolution occurring over time periods exceeding 10,000 years. Such extended time intervals for landscape evolution is probably partially related to the slow rate of biological, geochemical, and geomorphic processes in the cold Arctic climate. The patterns of NDVI and biomass make sense in light of geocological studies. Acidic moist tussock tundra, which has relatively high NDVI and biomass (Figs 4 and 5) is more abundant on the older surfaces. Jorgenson (1984a) recorded about 78% cover by tussock tundra types on Sagavanirktok-age surfaces, compared to 62% on Itkillik I surfaces, and only 21% on Itkillik II surfaces. Well-developed tussock tundra is found primarily on old stable hillslopes in portions of Beringia that were not glaciated during the Late Pleistocene (Aleksandrova 1980). Paleo-environmental reconstruction of northern Alaskan vegetation during the last 30,000 years suggests that the tundra was generally arid during the last glacial and was warmer and wetter during the early Holocene. Tussock tundra appears to have become widely established in northern Alaska sometime during the mid-Holocene climatic cooling (6000–5000 BP; Eisner and Colhoun 1990). C14 dates from the base of modern peat deposits on hillslopes range from about 8000 to 2000 years across much of the foothills region (Everett and Brown 1982; Marion and Oechel 1993), and peat in foothill wetlands is somewhat older (for example, >11,000 BP in the Innivait Creek headwaters; Eisner 1991). The patterns of vegetation on the present-day landscapes thus do not represent a true successional sequence spanning >100,000 years. Instead, it appears that peat development started on all the glacial surfaces during the mid- to late-Holocene and that tussock tundra became established more readily and extensively.

Fig. 4. Image- and field-NDVIs of major tundra vegetation categories in the Toolik Lake region (mean ± standard error). Image-NDVI of vegetation map units were determined from SPOT satellite imagery stratified according to vegetation map-unit boundaries (Walker and others 1989; Walker 1991). Field-NDVI of vegetation units were determined from the permanent plots used for the vegetation classification of the region. Field-NDVI values are about 40% greater than the image values due to a combination of factors (Shipert and others 1995).
shrub-rich vegetation types: NDVI of dry heath < wet sedge tundra < tussock tundra < shrub-filled water tracks. These trends match the trend of field- and image-NDVI values in this study. Hope and others (1995) could not demonstrate a strong correlation between NDVI and either photosynthetic or nonphotosynthetic biomass within a relatively narrow range of NDVI values; however, Shipper and others (1995) have shown a strong correlation between total biomass and NDVI across a somewhat broader range of NDVI values and when samples are lumped into broader vegetation types.

The greater deciduous-shrub cover on the older acidic hillslopes is probably due in part to more water being held in the rooting zone on slopes with Sphagnum-rich peat layers. Slopes with non-peaty vegetation types become drained of water during the dry summer months, but peaty slopes remain relatively wet through the summer due to higher water-holding capacity, lower heat flux, and shallower depth of summer thaw (Jorgenson 1984b; Walker and Barry 1991).

The relative abundance of shrub-filled water tracks and barren areas also contributes to the different spectral signatures of the young and old landscapes. Hillslope water tracks are shallow narrow drainage channels that are spaced tens of meters apart. They are common features on the mid- to lower portions of most moist acidic hillslopes, particularly on the older glaciated surfaces (Chapin and others 1988; Walker and Walker, in press). These drainage channels are usually densely filled with low willows (Salix planifolia ssp. pulchra) and dwarf birch (Betula nana) and have high NDVI values (Fig. 4). Nonsorted circles are patterned ground features composed of regularly spaced circular patches of bare ground with diameters 0.5–3.0 m, which are formed by frost heaving of the soil (Washburn 1980). Nonsorted stripes are another type of patterned ground feature that have a striped pattern oriented down slopes. They are apparently caused by a combination of cryoturbation, erosion, and gelification (Washburn 1980). The stripes are dominated by patches of bare soil and dry dwarf-shrub, fruticose-lichen tundra. Nonsorted circles and stripes are most common on hill crests and shoulders of younger landscapes (Walker and others 1989). Jorgenson (1984b) reported more than 40% cover of nonsorted stripes on Itkililik II glacial surfaces compared to less than 5% on Itkililik I and Sagavanirktok surfaces. Vegetation growing on nonsorted circles (community type Anthelia juratskana-Luzula arctica) has the lowest field-NDVI of any of the communities sampled in this study (see Shipper and others 1995; Fig. 2).
Table 2. Information from two gentle toposequences on Itkilik II and Sagavanirktok surfaces.

<table>
<thead>
<tr>
<th>Glacial surface</th>
<th>Hillslope length (m)</th>
<th>Aspect</th>
<th>Average slope (%)</th>
<th>pH mean ± s.e.</th>
<th>NDVI mean ± s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Itkilik II</td>
<td>400</td>
<td>West</td>
<td>8.75</td>
<td>6.5 ± 0.12</td>
<td>0.39 ± 0.02</td>
</tr>
<tr>
<td>Sagavanirktok</td>
<td>650</td>
<td>Southeast</td>
<td>9.2</td>
<td>4.08 ± 0.09</td>
<td>0.48 ± 0.04</td>
</tr>
</tbody>
</table>

The older landscapes are generally moister due to more subdued slopes, fewer barren areas, clay-rich soils, better developed moss carpets on hillslopes, better developed mires in basins between hills, and the presence of better integrated stream networks with many shrub-filled water tracks (Walker and Walker, in press; Walker and others 1994a). Vegetation succession occurs in conjunction with terrain modification by geomorphic hillslope processes operating over geologic time scales. Several factors lay the foundation for colonization and eventual dominance by mesophytic acidophilous plant communities, including gradual erosion of steeper glacial terrain features, accumulation of colluvial materials on the lower slopes, leaching of mineral-rich soils, the accumulation of finer soil particles, the transformation to peat-rich soils, and the creation of water-track and stream networks.

The presence of fine-grained soils is important in maintaining the presence of Eriophorum vaginatum, the dominant plant in most tussock tundra communities. Most of the older surfaces have old eolian deposits overlying glacial deposits (Kreig and Reger 1982). E. vaginatum depends on fine-grained mineral soils for seedling germination (Gartner 1982). Cryoturbation within the nonsorted circles constantly stirs the soils of tussock tundra landscapes and continually creates the small-scale disturbances necessary to maintain the presence of Eriophorum vaginatum. In the absence of cryoturbation, it is likely that the tussocks would eventually be eliminated and the community would evolve into a Sphagnum-ericaceous shrub heath, similar to that found in many colluvial basins on deep organic substrates.

General relevance to Arctic landscape evolution
Nonacidic tundra is associated with a variety of naturally disturbed landscapes that cover large areas of Arctic Alaska. For example, Walker and Everett (1991) examined the vegetation patterns occurring on loess deposits in the Prudhoe Bay region. Circumneutral to basic soils (pH >7.5) occur near the major rivers. They documented a gradient of soil pH and corresponding vegetation communities from alkaline tundra types near the river to acidic tussock tundra at 60 km downwind of the Sagavanirktok River. Compared to areas far downwind from the river, soils near the river have comparatively shallow organic horizons, higher bulk density, deeper annual thaw, less water-holding capacity, and less nutrient availability (due to the coarser soil textures). Walker and others (1982) also noted a relationship between soil pH and the spectral signatures of the vegetation on the Arctic coastal plain. NDVI is generally higher for vegetation growing on acidic substrates than vegetation on nonacidic substrates. A small amount of clip-harvest data from Prudhoe Bay also suggests less vegetation production in nonacidic areas (Walker and Everett 1991).

Similar patterns of low NDVI and high soil pH also occur in association with old stabilized river bars of large braided floodplains that cover large areas of the Arctic coastal plain. Chronic disturbances, such as loess deposition, cryoturbation, and floods, act to maintain the nonacidic soils and prevent the colonization by Sphagnum. Sphagnum is a key species in landscape evolution because its presence can radically change hydrological, geochemical, and thermal properties of a site (Auer 1928; Lawrence 1958; Heinseelman 1970; Klinger 1989, 1990). Paludification is a process whereby formerly dry habitats become waterlogged through the advent of mosses (particularly Sphagnum); it has been shown to be important in the conversion of boreal forest ecosystems to

Fig. 6. Mean cover of growth forms on Sagavanirktok-age and Itkilik II-age hillslopes in the Toolik Lake region.
bogs. Viereck (1966) also described paludification on stabilized outwash gravel leading to Sphagnum-rich tussock-tundra in Denali National Park.

Conclusions
NDVI is strongly correlated with estimated time since deglaciation within the Toolik Lake and Innvaat Creek region. Glaciated landscapes of Middle Pleistocene age have higher NDVI and greater amounts of biomass than Late Pleistocene landscapes.

The soils on the younger glacial surfaces are primarily nonacidic and support basophilous plant communities, whereas the older surfaces have acidic soils and support acidophilous plant communities. The relatively high cover of deciduous shrubs in the acidophilous communities appears to account for much of the difference in NDVI values. The relatively greater shrub cover in acidic tundra types is likely due in part to the greater water-holding capacity of the Sphagnum-rich moss carpets on the older hillslopes.

Other factors contributing to the difference in NDVI on the different glacial surfaces include a greater abundance of dry, well-drained sites on the younger surfaces, more nonsorted circles and stripes on the younger hillslopes, and more shrub-rich water tracks on the older landscapes.

Landscape/vegetation evolution on glaciated landscape in the Arctic foothills is closely tied to geomorphic and geochemical processes, and spans time periods exceeding 100,000 years. The development of tussock tundra landscapes requires a combination of geomorphic and vegetation successional processes, including weathering, colluviation, eolian deposition, and paludification.

Additional sampling at other sites is needed to determine if the NDVI-landscape age trends of this study have broader relevance to the entire glaciated region of the North Slope and to other regions of natural disturbance in the circumpolar Arctic. Similar studies using other sensors (such as AVHRR) would help in extending these findings to broader regions.

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References


Jorgenson, M.T. 1984b. The response of vegetation to landscape evolution on glacial till near Toolik Lake, Alaska. In: Inventorying forest and other vegetation of the high altitude regions: proceedings of an interna-
tional symposium. Fairbanks; Society of American For-
Klinger, L.F. 1989. Global patterns in community succe-
sion: bryophytes and forest decline. Memoirs of the
Torrey Botanical Club 23.
Klinger, L.F. 1990. Global patterns in community succe-
sion: bryophytes and forest decline. Memoirs of the
summary of landform and soil properties along the
route of the trans-Alaska pipeline system. Anchorage:
Alaska Division of Geological and Geophysical Sur-
veys (Geologic Report 66).
sensing and climatic data to estimate net primary pro-
duction across Oregon. Ecological Applications 4: 717–
728.
Lawrence, D.B. 1958. Glaciers and vegetation in south-
carbon balance in Arctic Alaska and its implications for
of soil analysis, part 2: chemical and microbiological
properties. Madison, WI: American Society of Agronomy
and Soil Science Society of America (Agronomy Series
9).
1973. Monitoring vegetation systems in the great plains
with ERTS. In: Proceedings of the third ERTS sympos-
Running, S.W., R.R. Nemani, D.L. Peterson, L.E. Band,
D.F. Potts, L.L. Pierce, and M.A. Spanner. 1989. Map-
ing regional forest evapotranspiration and photosyn-
thesis by coupling satellite data with ecosystem simu-
Sellers, P.J. 1985. Canopy reflectance, photosynthesis
and transpiration. International Journal of Remote Sens-
ing 6: 1395–1372.
and transpiration, II: the role of biophysics in the linearity
of their interdependence. Remote Sensing of the
relationships and element cycling in contrasting Arctic
Shippert, M.M., D.A. Walker, N.A. Auerbach, and B.E.
Lewis. 1995. Biomass and leaf area index maps de-
uced from SPOT images for the Toolik Lake and Imnava-
Soil Taxonomy Survey. 1975. Soil taxonomy, a basic
system of soil classification for making and interpreting
and practice of statistics in biological research. San Fran-
Stow, D.A., A.S. Hope, and T.H. George. 1993. Reflect-
ance characteristics of Arctic tundra vegetation from
airborne radiometry. International Journal of Remote
combinations for monitoring vegetation. Remote Sens-
ing of Environment 8: 127–150.
Tucker, C.J., and P.J. Sellers. 1986. Satellite remote sens-
ing of primary production. International Journal of Re-
on gravel outwash of the Muldrow Glacier, Alaska.
Reston, VA: US Geological Survey (Geological Survey
Professional Paper 482).
vegetation plots: site factors, soil physical and chemical
properties, plant species cover, photographs, and soil
descriptions. Unpublished report for the Department of
Energy R4D program and the Joint Facility for Regional
Ecosystem Analysis, Institute of Arctic and Alpine Re-
search.
Walker, D.A., E. Binnian, B.M. Evans, N.D. Lederer, E.
Nordstrand, and P.J. Webber. 1989. Terrain, vegeta-
tion and landscape evolution of the R4D research site,
Brooks Range Foothills, Alaska. Arctica Ecolology 12:
238–261.
northern Alaska: regional gradient and toposequence at
Prudhoe Bay. Ecological Monographs 61 (4): 437–
464.
Brown, and P.J. Webber. 1982. Landsat-assisted envi-
ronmental mapping in the Arctic National Wildlife Ref-
uge, Alaska. Hanover, NH: US Army Cold Regions
Research and Engineering Laboratory (CRREL Report
82-27).
of disturbance in Alaskan Arctic terrestrial ecosystems:
a hierarchical approach to analysing landscape change.
Walker, D.A., and M.D. Walker. In press. Terrain and
vegetation of the R4D Imnavait Creek intensive re-
search site. In: Reynolds, J.F., and J.D. Tenhunen
(editors). Landscape function: implications for ecosys-
tem response to disturbance, a case study in Arctic
Vegetation of a tussock tundra landscape, Brooks
Range Foothills, Alaska. Journal of Vegetation Science
1994b. Effects of interannual climate variation on
aboveground phytomass in alpine vegetation. Ecology
75: 393–408.
processes and environments. New York: Halsted Press,
John Wiley and Sons.
Weller, G., and nine others. In press. The Arctic Flux Study:
a regional view of trace gas release. Global Ecology
and Biogeography Letters.

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