

Effects of deglaciation on circumpolar distribution of arctic vegetation

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Abstract. An understanding of the factors controlling the distribution of arctic vegetation will allow better prediction of the effects of climate change. This study examines the effect of the age of landscapes on the distribution of arctic vegetation. We compared time since deglaciation with the distribution of vegetation types and Advanced Very High Resolution Radiometer (AVHRR) satellite measures of greenness (normalized difference vegetation index, NDVI). Most of the older arctic landscapes occur between the Taimyr Peninsula in Russia and the Mackenzie River in Canada. The vegetation types most commonly associated with the oldest landscapes include tussock-sedge, dwarf-shrub, moss-tundra, and sedge-shrub wetlands. Most of the Arctic, including most bioclimate subzones and most vegetation types, showed increasing NDVI with increasing landscape age. Landscapes showed rapid increases in NDVI during the first several thousand years after deglaciation. Relatively low NDVI values occurred on landscapes 5000 – 15 000 years old, as on the Canadian Shield. Higher NDVI values occurred on landscapes older than 20 000 years. Landscape age accounted for 34% of the variation in NDVI for landscapes younger than 900 000 years. The coldest parts of the Arctic (subzone A) and vegetation types that grow primarily in these areas did not show any trend with landscape age.

Résumé. Une compréhension des facteurs qui contrôlent la distribution de la végétation arctique permettra une meilleure prédiction des effets du changement climatique. Cette étude examine l'effet de l'âge du paysage sur la distribution de végétation arctique. Nous avons comparé la période de déglaciation des surfaces avec la distribution des formations végétales, et des mesures satellitaires de verdure (NDVI, « normalized difference vegetation index ») par AVHRR (« Advanced Very High Resolution Radiometer »). La majorité des anciens paysages arctiques se rencontrent entre la péninsule de Taimyr en Russie et la rivière Mackenzie au Canada. Les formations végétales principalement associées aux paysages les plus anciens comprennent la toundra à laïche-monticule, buisson-nain, mousse et à laïche-buisson des zones humides. La majeure partie de l'Arctique, incluant la plupart des sous-zones bio-climatiques et des types végétaux, montre des augmentations rapides de NDVI durant les premiers millièmes d'années après le départ des glaciers. Les valeurs de NDVI relativement basses sont fréquentes sur les paysages datés de 5000 – 15 000 ans, comme le Bouclier Canadien. Les valeurs plus élevées de NDVI sont associées aux paysages datés de plus de 20 000 ans. L'âge du paysage comptait pour 34 % dans la variation du NDVI pour les paysages plus jeunes que 900 000 ans. Les parties les plus froides de l'Arctique (la sous-zone A) et les types végétaux présents principalement dans ces endroits, ne montraient pas de relation avec l'âge du paysage.

Introduction

Recent concern about climate change has focused on the Arctic. This concern is appropriate based on records of past climate changes, which document the amplification of global changes at high latitudes, and evidence of recent amplification in warming in the Arctic (Hassol, 2004). The dramatic reduction of summer sea ice in the Arctic Ocean in the last several years is a highly visible symptom of these changes, with repercussions for global climate systems (Comiso et al., 2008).

Vegetation in the Arctic is also responding to climate change, though not as dramatically as sea ice (Bhatt et al., in preparation). Twenty-five-year satellite records show an increase in vegetation greenness over tundra areas (Jia et al., 2007) and also show that spring is coming sooner, lengthening the growing season (Goetz et al., 2005). Fifty-year photographic

comparisons document shrubs expansion in the tundra (Tape et al., 2006), a trend that is corroborated by the results of international experiments which showed that deciduous shrubs and graminoid plants increased in height in response to warming treatments (Walker et al., 2006).

Although arctic tundra plants are extraordinarily responsive to changes in air temperature, plant production can also be limited by a wide variety of other site factors, such as nutrient and water availability, cold soil temperatures, short growing seasons, and winter desiccation and abrasion. In fact, most arctic plants are so well adapted to cold temperatures that factors other than temperature often limit their distribution (Billings, 1997). A better understanding of these limiting factors will help predict where and how arctic vegetation will respond to climate change. This study focuses on the importance of time since deglaciation, which is related to soil

Received 12 September 2008. Accepted 17 December 2008. Published on the Web at <http://pubs.nrc-cnrc.gc.ca/cjrs> on 25 May 2009.

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development and nutrient and moisture regimes, in controlling the distribution of arctic vegetation.

Glacial effects in the Arctic are recent and obvious in many locations. Almost all of the Canadian Arctic was glaciated during the Last Glacial Maximum 20 000 years ago and deglaciated within the last 10 000 years (the Holocene) (Ehlers and Gibbard, 2004). Earlier glaciations that occurred during the Pleistocene are evident in other parts of the Arctic, with the largest ones centered around 70 thousand years ago (kya), 200 kya, 600 kya, and 800 kya (Ehlers and Gibbard, 2004). Unlike the adjacent boreal forest, where trees mask the landscape and fire is a major source of patterning, vegetation differences as a function of landscape age are relatively apparent in the Arctic. In this study, we investigated how arctic vegetation is related to landscape age, with the goal of understanding how time since deglaciation will influence the Arctic's response to climate change.

Methods

Landscape age since emergence

Glaciers not only covered land with ice but also depressed the surface of the earth with their weight. As the ice melted, the weight was released and the land surface rose again, a process called isostatic rebound. Sea level was also lowered during the glacial intervals due to the large amount of water tied up in the continental ice sheets. Deglaciation was accompanied by worldwide sea-level rises, which occurred more quickly than isostatic rebound. The combination of depressed land surfaces and rising sea levels caused marine transgressions, where ocean water covered low-elevation land. Glaciers also dammed rivers, especially north-flowing rivers, and created large proglacial lakes. All these factors made land unavailable for plant colonization, so we consider the time since emergence, whether it was from ice, ocean, or lake.

The age of most recent deglaciation, emergence from the sea, or drainage of proglacial lakes was obtained from a compilation of Quaternary glaciations, available in digital format (Ehlers and Gibbard, 2004). Supplemental data provided in some of the regional chapters were especially useful (Astakhov, 2004; Barendregt and Duk-Rodkin, 2004; Duk-Rodkin et al., 2004; Dyke, 2004; Funder et al., 2004; Kaufman and Manley, 2004). Although landscape age estimates are bound to change as research continues, the compilation used in this study includes the best available current estimates and provides a relatively robust dataset for analysis at a circumpolar scale.

All dates in this study are in calendar years. Dates for Canada were converted from ^{14}C years to calendar years (Dyke, 2004). Data for glaciations in southwest Alaska and the Seward Peninsula were supplemented by Brigham-Grette (2001), and those for the North Slope by Hamilton (2003). Data for the Mackenzie River area were from Murton et al. (2005) and Andrews and Dunhill (2004). Data for the Queen Elizabeth Islands were supplemented by England et al. (2006) and Atkinson (2003). Briner et al. (2003; 2005) found that areas of

northeast Baffin Island had been glaciated much more recently than previously thought, by nonerosive ice sheets that formed on top of older deposits (the source of previous dating). Data for eastern Canada were supplemented by Occhietti et al. (2004).

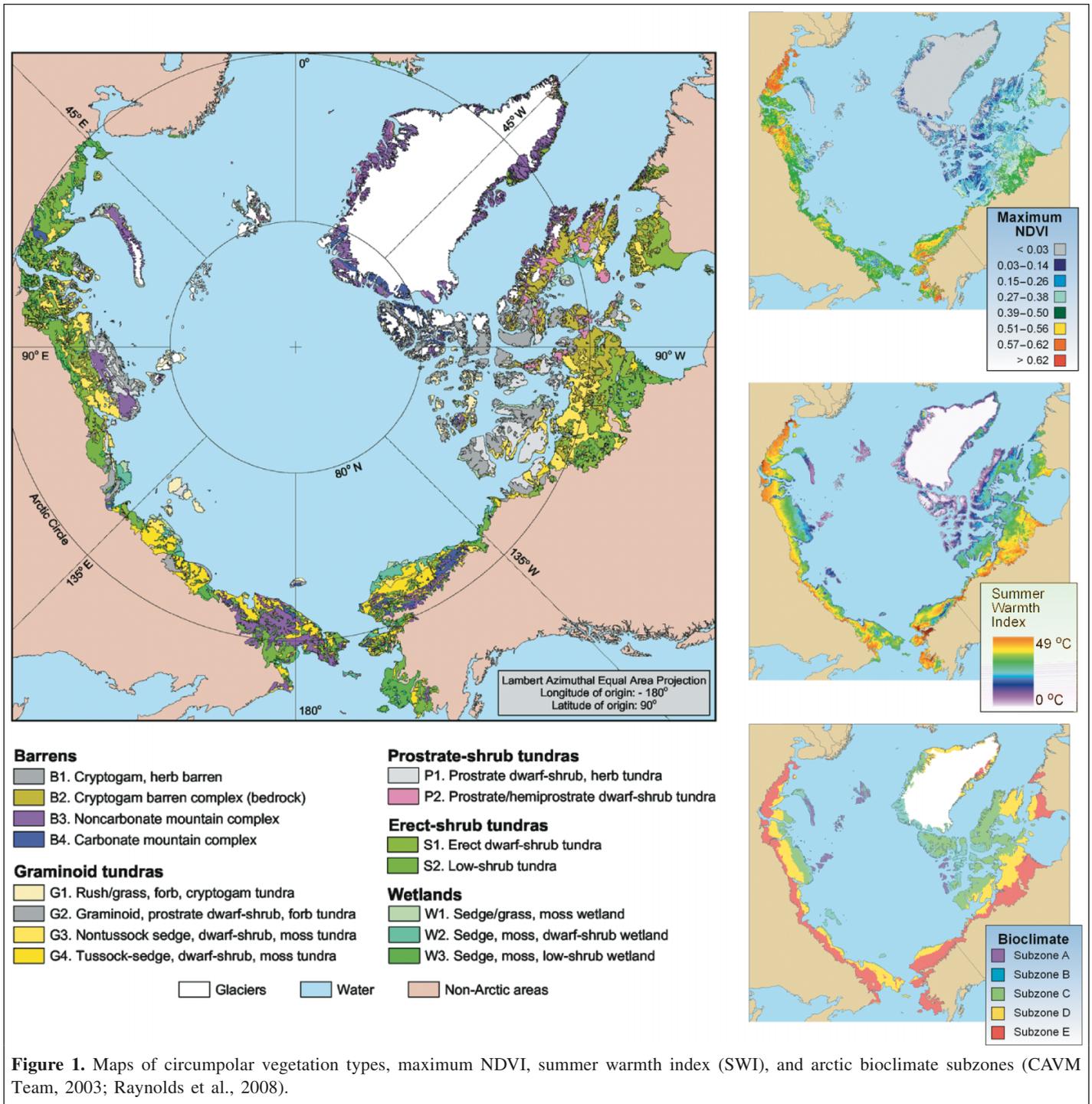
Details for the Disko Bay area were obtained from Lloyd et al. (2005) and Long et al. (2003). Dates for northeastern Greenland were confirmed by Cremer et al. (2008), and those for Svalbard, Franz Josef Land, and Novaya Zemlya were from Forman et al. (2004). In European Russia, the date of Quaternary maximum glaciation was estimated at 140 kya (Astakhov, 2004), with deglaciation of the Kanin Peninsula around 60–50 kya (Paus et al. 2003). Raab et al. (2003) showed evidence of marine transgression on the islands of Severnaya Zemlya and evidence of earlier deglaciation (~45 kya) on these islands than that shown by Ehlers and Gibbard (2004) (25 kya). The work of Mangerud et al. (2004) was used to map the extent of proglacial lakes in European Russia. A continual record of Quaternary deposits on the New Siberian Islands (Schirrmeyer et al., 2002) confirmed the lack of glaciation mapped by Ehlers and Gibbard (2004). Similarly, evidence from Wrangel Island showed minor glaciation on the north coast during the Pleistocene (Gualtieri et al., 2003). The work of Brigham-Grette and Gualtieri (2004) supported the mapping by Ehlers and Gibbard of mountain glaciations in Chukotka during the Pleistocene.

Circumpolar Arctic Vegetation Map (CAVM)

In this study we used the bioclimate definition of the Arctic adopted for the Circumpolar Arctic Vegetation Map (CAVM Team, 2003). It is the region north of the arctic treeline with tundra vegetation and an arctic climate (**Figure 1**). The map was created at a scale of 1 : 7 500 000, with a minimum polygon diameter of 8 km, and is available digitally as a vector map (www.arcticatlas.org/atlas/cavm). The integrated vegetation mapping approach used to create the vegetation map was based on the principle that a combination of environmental characteristics controls the distribution of vegetation. Vegetation-type boundaries were drawn on an Advanced Very High Resolution Radiometer (AVHRR) false-color infrared base map, based on existing ground data and vegetation maps, bioclimate (tundra subzones A–E), floristic regions, landscape categories, elevation, percent lake cover, substrate chemistry, and surficial and bedrock geology. The distribution of 15 arctic vegetation types was mapped and described on the CAVM (**Figure 1**), using a unifying circumpolar legend that enables analysis of the entire Arctic (CAVM Team, 2003; Walker et al., 2005).

Normalized difference vegetation index (NDVI) data

The normalized difference vegetation index (NDVI) is a measure of relative greenness, calculated as $\text{NDVI} = (\text{NIR} - R)/(\text{NIR} + R)$, where NIR is the spectral reflectance in the near-infrared where reflectance from the plant canopy is dominant, and R is the reflectance in the red portion of the spectrum where chlorophyll absorbs maximally. NDVI has a theoretical



maximum of 1, and its relationship to vegetation characteristics such as biomass, productivity, percent cover, and leaf area index (LAI) is asymptotically nonlinear as it approaches 1. As a result, NDVI is less sensitive to ground characteristics at higher values and begins to show signs of saturation for LAI > 1 (van Wijk and Williams, 2005). This is not a severe problem in the Arctic, where vegetation is often sparse and patchy: the mean NDVI for arctic land areas in the dataset used in this study was 0.32, well below the saturation point (Raynolds et al., 2006).

NDVI values in the Arctic increase with an increase in the amount of vegetation as measured by LAI, phytomass, and productivity (Shippert et al., 1995; Riedel et al., 2005). NDVI values correlate well with ground characteristics of arctic vegetation and can be used to distinguish between vegetation types (Hope et al., 1993; Stow et al., 1993).

A 1-km-resolution maximum-NDVI dataset was used for this study (Figure 1). These data were derived from the US Geological Survey Earth Resources Observation Systems

(EROS) AVHRR polar composite of NDVI data for 1993 and 1995 (Markon et al., 1995; CAVM Team, 2003). Daily data were collected by AVHRR sensors onboard National Oceanic and Atmospheric Administration (NOAA) satellites for channel 1, red (0.50–0.68 μm), and channel 2, near-infrared (0.725–1.100 μm). Satellite measurement of NDVI is affected by a variety of conditions, especially cloud cover, viewing angle, and seasonal variation, that can be compensated for by compositing data over time (Goward et al., 1991; Riedel et al., 2005). Daily NDVI values were composited into 10-day maxima. The maximum values of these composited data during two relatively cloud free summers (11 July – 31 August in 1993 and 1995) were used to create an almost cloud free dataset of maximum NDVI for the circumpolar Arctic in the early 1990s.

Analysis

Digital maps from Ehlers and Gibbard (2004) were converted into the same projections as the CAVM, so the maps could be overlaid. A landscape age was assigned to each CAVM integrated terrain-unit map polygon, and new polygons were created where CAVM boundaries did not match the glacial emergence data. Data from more recent references were incorporated in the deglaciation map.

The spatial distribution of different CAVM categories was analyzed using geographical information system (GIS) software, and the results were summarized graphically. Means were calculated using an area-weighted average of polygon data. The NDVI data were analyzed by calculating the average NDVI value for landscapes with different emergence ages. Lakes and glaciers were assigned an emergence age of zero, since they are still not available for plant colonization, and were excluded from analyses of land area. Areas that had not been glaciated during the Pleistocene (age > 900 kya or unknown) were excluded from any analysis involving a mathematical calculation using age.

To further investigate the relationship between NDVI and emergence age, landscapes were stratified by CAVM categories. Landscape age data were transformed using a logarithmic transformation, as the dates of more recent deglaciations are known much more precisely than older ones. Linear regressions were run between the transformed data and NDVI (R Development Core Team, 2006). General linear models (GLMs) were used to determine the importance of emergence age in a suite of characteristics known to be important in controlling NDVI in the Arctic (R Development Core Team, 2006; Reynolds et al., 2006). Attributes mapped as characteristics of the CAVM polygons, weighted by area, were used as input data. These attributes included summer warmth index (SWI = sum of monthly mean temperatures > 0 °C) (Figure 1), tundra bioclimate subzone (A–E, cold to warm) (Figure 1), elevation, and percent lake cover (CAVM Team, 2003).

Results

The glaciation data were used to create a map of landscape age since emergence from Quaternary ice, marine transgressions, or proglacial lakes (Figure 2). Much of the Arctic is still under ice (27% of land area), including 1.7 million km^2 in the Greenland Ice Cap. Most of the ice-free land area (65%) was deglaciated since the Last Glacial Maximum (LGM, 20 kya, during the Late Wisconsinan period of the Late Pleistocene). The most common age category is 8–7 kya, during the Holocene, and includes most of the Canadian Arctic (Figure 3; blue areas in Figure 2). Large areas of European Russia and parts of Alaska (24% of the Arctic) were glaciated at some point in the Late Pleistocene but earlier than the LGM. Chukotka, Novaya Zemlya, and the Kanin Peninsula were deglaciated during the Late Wisconsinan (35–10 kya). Western Siberia was deglaciated or emerged from extensive marine transgressions or proglacial lakes during the Middle–Early Wisconsinan (80–35 kya). Parts of the Brooks Range in northern Alaska and Banks Island in the southwest Canadian Arctic Archipelago were deglaciated in the Middle Pleistocene (900–200 kya). There is no evidence of glaciations over large areas of Yakutia and low-elevation areas in Chukotka and Alaska, so these areas are assumed to have been ice-free for over 900 kya (12% of the Arctic). The oldest areas are east of the Taimyr Peninsula and west of Canada's Mackenzie River. The youngest areas are on Baffin Island, the Ungava Peninsula, and parts of Greenland.

Comparing only those areas of the Arctic that were glaciated during the Pleistocene, the oldest landscapes are in subzone E, the warmest bioclimate subzone, where the average emergence is over 120 kya (Figure 4). The contrast between subzone E and the colder subzones is striking. This effect could be due to the combination of the warmer climate and greater distance from oceanic sources of moisture resulting in less frequent glaciation of subzone E compared with the other four subzones.

The areas with the fewest lakes are also the oldest (Figure 5). There is a large contrast between the age of areas with <2% lake cover and areas with >2% lake cover. A comparison of different vegetation types shows that tussock-sedge, dwarf-shrub, moss tundra (G4) is much older than most other vegetation types (Figure 6). Carbonate mountain complexes (B4) are generally older than noncarbonated mountain complexes (B3) because the carbonate mountains occur mostly in the oldest areas of Pleistocene glaciation, such as the Brooks Range of Alaska.

Figure 7 shows low NDVI on arctic landscapes for the first several thousand years after glacial emergence as plant colonization occurs. There is a quick rise in NDVI to about 0.20 in the first 4000 years, followed by several thousand years of slightly declining NDVI, from around 4000 to 14 000 years, after which NDVI climbs to a level around 0.40–0.45. The low NDVI values for the 26–50 kya age category are because the only arctic areas of these ages are located in northern Taimyr and the offshore islands of Severnaya Zemlya, mostly in the coldest subzones A and B, which have very low NDVI.

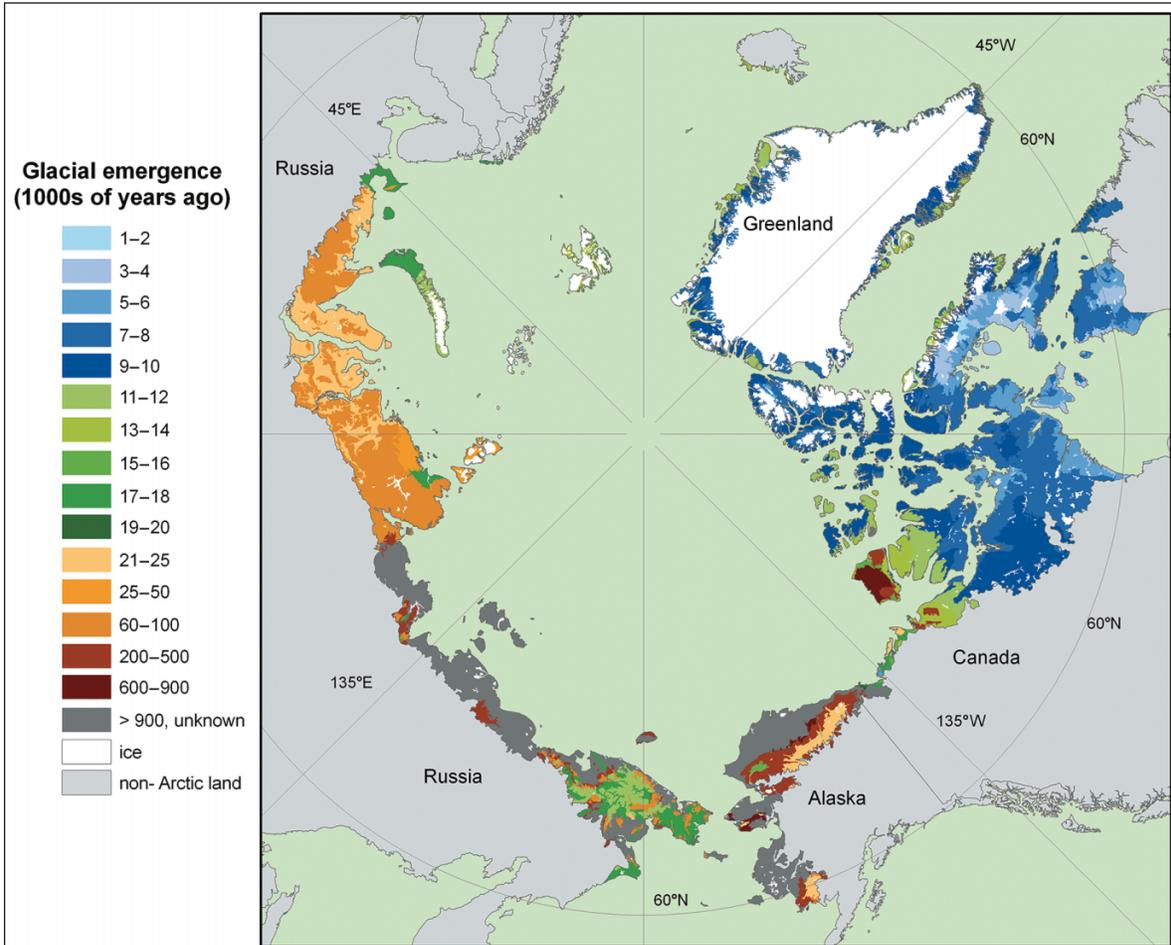


Figure 2. Map showing time since emergence of arctic landscapes from Pleistocene glaciation, marine transgressions, or proglacial lakes.

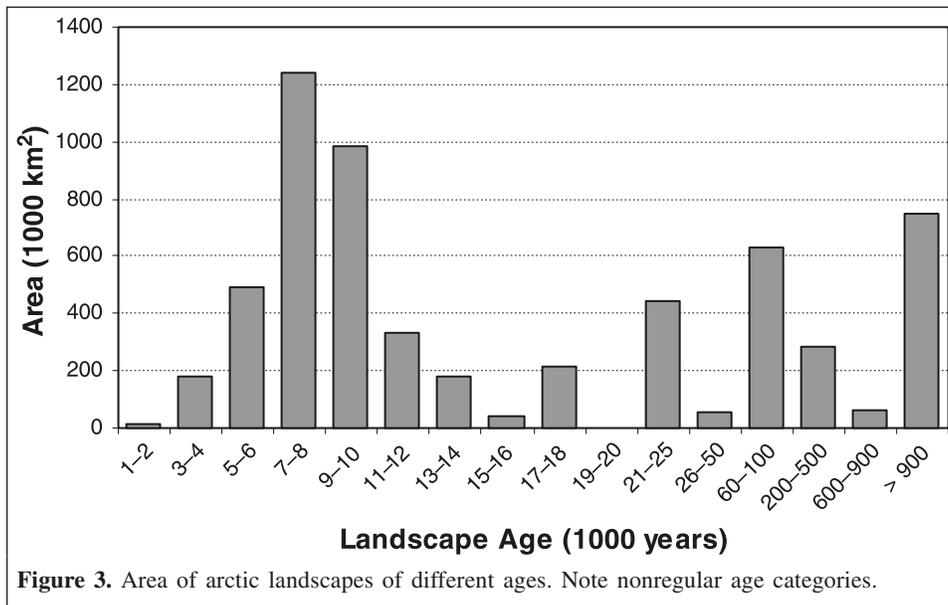
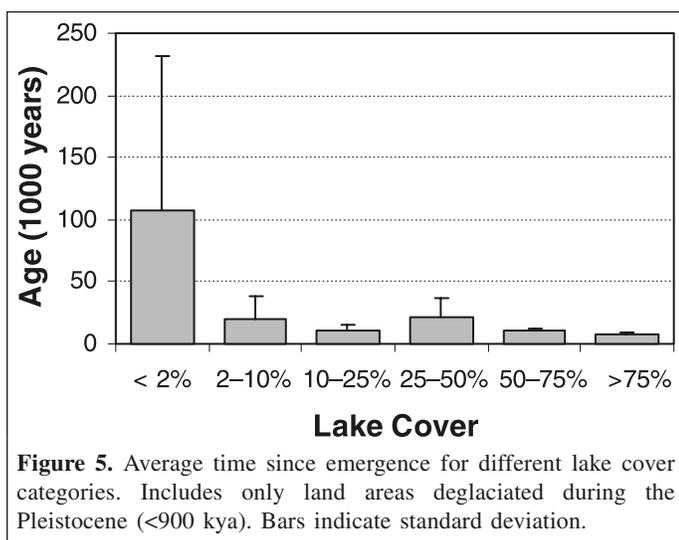
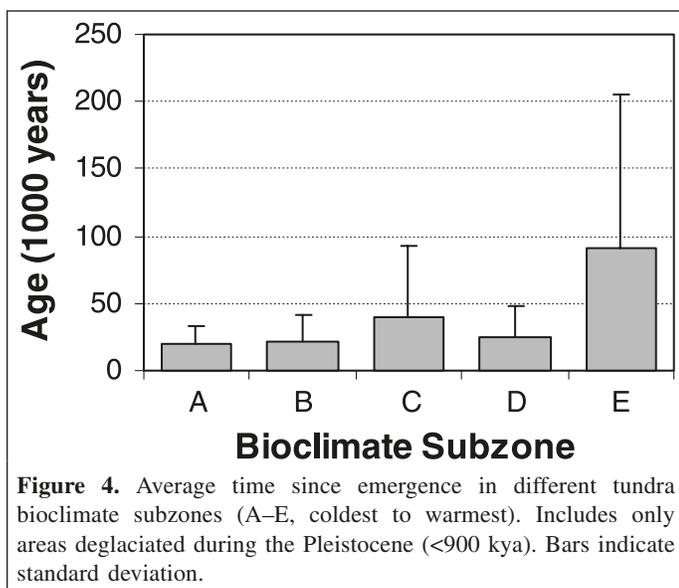


Figure 3. Area of arctic landscapes of different ages. Note nonregular age categories.



The results from linear regression showed the relationship between age of landscape emergence and NDVI was positive and accounted for 34% of the variation in NDVI between polygons in the whole Arctic. NDVI generally increased with age over the length of the Pleistocene, with a linear relationship with the logarithm-transformed age and an intercept very close to zero (**Table 1**). The coldest parts of the Arctic (subzone A) and vegetation types that grow primarily in these areas (G1, P2) did not show a significant trend in NDVI with landscape age. There was also no trend for vegetation type B2, the cryptogam barren complex that grows on recently glaciated bedrock, because all of this type has a similar, recent age (**Figure 6**). The regression relationships accounted for the most variation in carbonate mountain complexes (B4), nontussock sedge, dwarf-shrub moss tundra (G3), and erect dwarf-shrub tundra (S1) (**Table 1**).

In a general linear model including summer warmth index and the logarithm-transformed age of emergence, the summer

Table 1. Results of linear regression of NDVI by logarithm-transformed landscape age for all of the Arctic, tundra bioclimate subzones, and vegetation types.

	Slope	Intercept	R^2	Significance, p
All Arctic	0.2047	0.0215	0.3418	$<2 \times 10^{-16}***$
Subzone A	-0.0133	0.0745	0.0034	0.4154
Subzone B	0.2410	-0.1447	0.3688	$<2 \times 10^{-16}***$
Subzone C	0.1793	-0.0023	0.2569	$<2 \times 10^{-16}***$
Subzone D	0.2588	-0.0034	0.4013	$<2 \times 10^{-16}***$
Subzone E	0.0908	0.2993	0.2918	$<2 \times 10^{-16}***$
Type B1	0.0404	0.0253	0.0318	0.00423**
Type B2	-0.0561	0.2175	0.0105	0.109
Type B3	0.2480	-0.1156	0.3658	$<2 \times 10^{-16}***$
Type B4	0.2104	-0.1182	0.7013	$<2 \times 10^{-16}***$
Type G1	0.0286	0.0866	0.0121	0.103
Type G2	0.1291	0.1219	0.2558	$<2 \times 10^{-16}***$
Type G3	0.1564	0.1860	0.4777	$<2 \times 10^{-16}***$
Type G4	0.0619	0.3569	0.3955	$4.06 \times 10^{-15}***$
Type P1	0.1691	-0.0282	0.2839	$<2 \times 10^{-16}***$
Type P2	0.0239	0.1320	0.0020	0.5721
Type S1	0.1540	0.1834	0.4368	$<2 \times 10^{-16}***$
Type S2	0.0729	0.3821	0.1841	$<2 \times 10^{-16}***$
Type W1	0.0851	0.1670	0.1290	$5.93 \times 10^{-6}***$
Type W2	0.1194	0.2382	0.2199	$1.45 \times 10^{-6}***$
Type W3	0.0729	0.3601	0.2085	$2.94 \times 10^{-8}***$

Note: See **Figure 1** for full names of vegetation types. Includes only land areas deglaciated during the Pleistocene (<900 kya). **, $p < 0.01$; ***, $p < 0.001$.

warmth index accounted for 63% of the variation in NDVI, and the age of the landscape accounted for 8.3% (**Table 2**). The interaction was significant, meaning that the effect of landscape age on NDVI varies with climate. Within bioclimate subzones, landscape age accounts for 13.4%–20.1% of the variation in NDVI. Variation in summer warmth index was most important within subzones B, C, and D, and percent lake cover was most important in subzone E (**Table 2**).

Discussion

The results show that NDVI did not increase with time in the coldest subzones. Although initial plant colonization occurred, the short summers provided little time for vegetation growth and reproduction. Plant community development is also hindered by how few plants can survive in subzone A, which is characterized by its depauperate vascular flora (Elvebakk, 1999). Soil-development processes are also slow due to cold temperatures. Even during the short summer, temperatures are not much above 0° C.

However, the perception that plant colonization and the formation of arctic plant communities is slow, taking millennia, has proven to be false. Arctic plants are actually well adapted to changing geographic ranges, as they have had to migrate due to glacial cycles throughout the last several million years. Between 3 and 1 million years ago, glacial cycles occurred every 41 000 years, with smaller 23 000 year cycles. Since about 900 kya, larger glacial cycles have occurred approximately

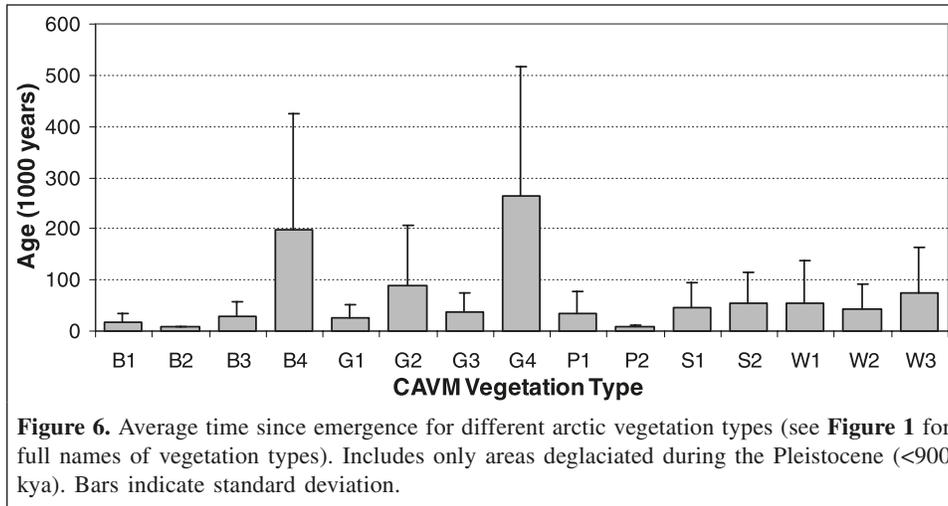
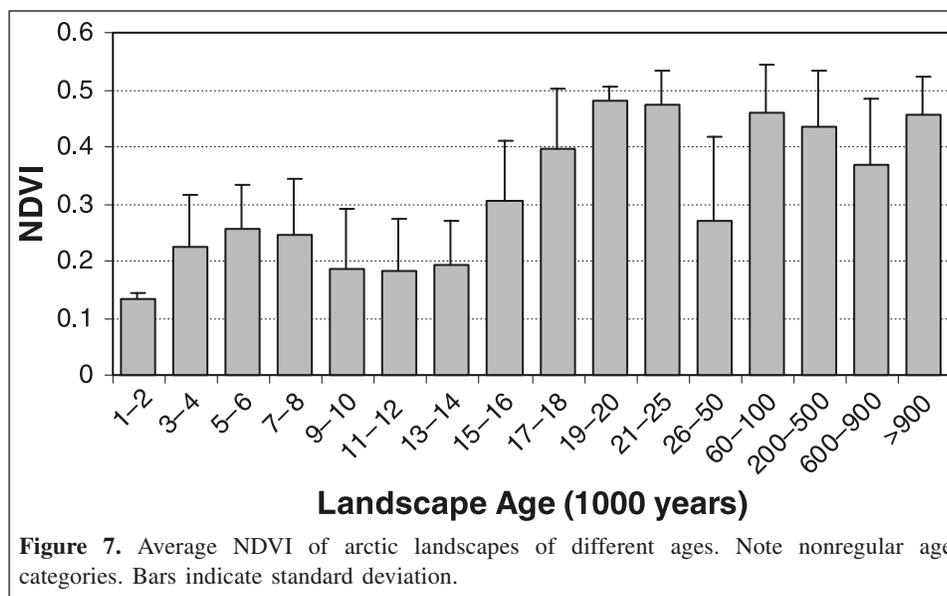


Figure 6. Average time since emergence for different arctic vegetation types (see **Figure 1** for full names of vegetation types). Includes only areas deglaciated during the Pleistocene (<900 kya). Bars indicate standard deviation.

Table 2. Results of a general linear model of NDVI and age of landscape emergence for circumpolar Arctic.

Variable	Deviance	% total deviance	Significance, <i>p</i>
All Arctic (n = 5921): NDVI ~ SWI × log(age)			
SWI	133.472	63.1	<2×10 ⁻¹⁶ ***
Log(age)	17.649	8.3	<2×10 ⁻¹⁶ ***
SWI × log(age)	1.547	0.7	<2×10 ⁻¹⁶ ***
Subzone A (n = 271): NDVI ~ SWI + log(age) + elevation + lake cover			
SWI	0.12764	14.0	1.88×10 ⁻¹⁰ ***
Log(age)	0.12216	13.4	2.22×10 ⁻³ **
Elevation	0.07842	8.6	1.74×10 ⁻¹³ ***
Lake cover	0.07943	8.7	4.11×10 ⁻¹⁰ ***
Subzone B (n = 693): NDVI ~ SWI + log(age) + elevation + lake cover			
SWI	3.8206	38.4	<2×10 ⁻¹⁶ ***
Log(age)	1.6048	16.1	<2×10 ⁻¹⁶ ***
Elevation	0.3195	3.2	1.45×10 ⁻¹³ ***
Lake cover	0.0266	0.3	3.66×10 ⁻² **
Subzone C (n = 1505): NDVI ~ SWI + log(age) + elevation + lake cover			
SWI	13.1398	42.1	<2×10 ⁻¹⁶ ***
Log(age)	4.5508	14.6	<2×10 ⁻¹⁶ ***
Elevation	1.2472	4.0	<2×10 ⁻¹⁶ ***
Lake cover	1.6006	5.1	<2×10 ⁻¹⁶ ***
Subzone D (n = 1549): NDVI ~ SWI + log(age) + elevation + lake cover			
SWI	18.1920	44.5	<2×10 ⁻¹⁶ ***
Log(age)	5.4990	13.5	<2×10 ⁻¹⁶ ***
Elevation	0.5130	1.3	<2×10 ⁻¹⁶ ***
Lake cover	6.5850	16.1	<2×10 ⁻¹⁶ ***
Subzone E (n = 1872): NDVI ~ SWI + log(age) + elevation + lake cover			
SWI	6.4670	18.7	<2×10 ⁻¹⁶ ***
Log(age)	6.9330	20.1	<2×10 ⁻¹⁶ ***
Elevation	0.0004	0.0	<2×10 ⁻¹⁶ ***
Lake cover	11.0840	32.1	<2×10 ⁻¹⁶ ***

p* < 0.01; *p* < 0.001.



every 100 000 years (Ruddiman, 2001). The glacial climate cycles are extreme enough in the Arctic to completely change the vegetation, even in areas not directly affected by glacial ice.

Despite cold climates, revegetation of fresh surfaces in the Arctic happens relatively quickly. In Svalbard, areas deglaciated since the Little Ice Age (in the last 150 years) have vegetation covering most of the surface, with mature tundra species replacing colonizing species (Moreau et al., 2005). Change continues at a rapid rate, resulting in measurable changes in community composition over 30 years (Moreau et al., 2009). In a study looking at the likelihood that arctic plants persisted in refugia in the North Atlantic through the LGM, Brochmann et al. (2003) concluded that the fossil evidence shows no sign of refugia but does show high migration rates and very rapid recolonization of deglaciated areas, even in the coldest areas. This trend is seen in the spatial analysis presented in this study, with the rapid rise in circumpolar Arctic NDVI shown within the first several thousand years after deglaciation.

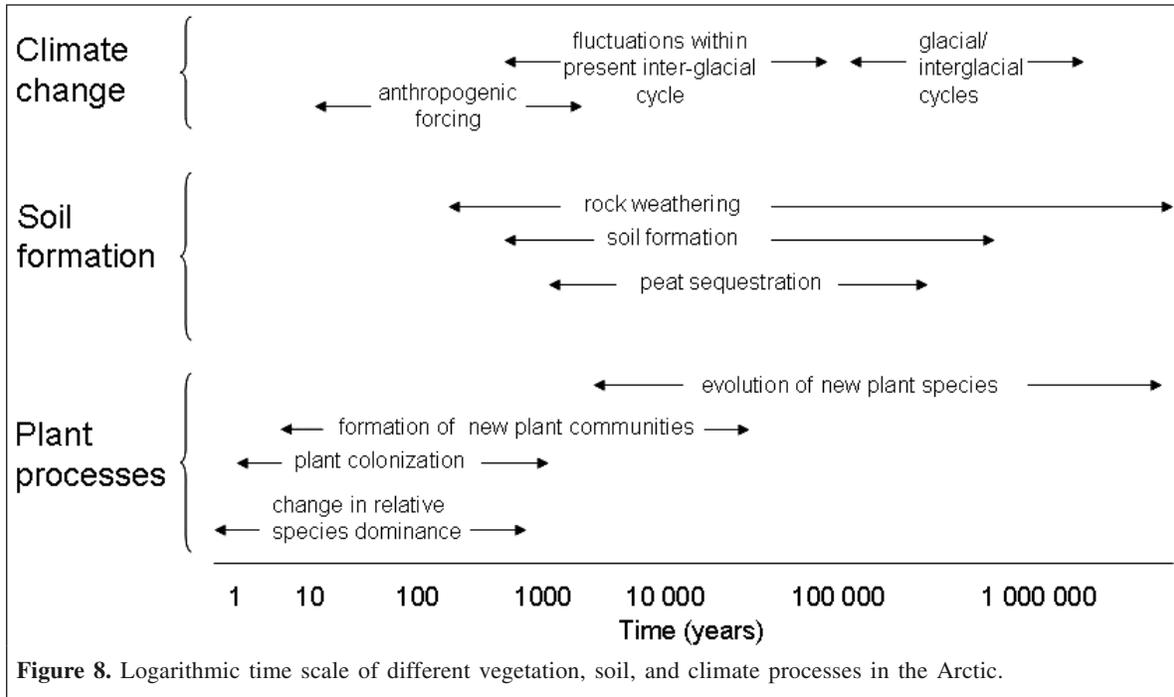
After the initial rise in NDVI for newly deglaciated areas, NDVI stays relatively constant for areas deglaciated 2000 to 20 000 years ago (Figure 7). This is the time scale at which paludification and peat accumulation occur (Figure 8). Paludification is the process of wetland formation on previously well drained terrain. In the Arctic, paludification involves the accumulation of organic material, which insulates the soil, reduces the active layer, restricts soil drainage, and transforms formerly dry mineral soils to wet peaty soils (Walker and Walker, 1996; Mann et al., 2002; Walker et al., 2003; Shur and Jorgenson, 2007). Soils become progressively colder and more acidic, which in turn favors peat-producing species like sphagnum mosses and tussock sedges, in a positively reinforcing cycle. This can have a wide variety of ecosystem consequences, including reduction of soil heat flux, increased carbon sequestration in the soils, and increased methane flux (Walker et al., 1998). Extensive peatlands developed remarkably recently in deglaciated areas,

sequestering 180–445 Pg of carbon since the LGM (MacDonald et al., 2006). Peatland initiation generally occurred 1000–2000 years after deglaciation and peaked 7–8 kya (Gorham et al., 2007).

For landscapes older than 18–20 kya, landscapes not glaciated during the LGM, there is a big jump in NDVI values (Figure 7). These landscapes are old enough for a whole different set of processes to become significant, characterizing the differences between the younger landscapes of the Canadian Arctic and the older glaciated landscapes of Alaska and Russia. Tens of thousands of years is the time frame required for soil development in the Arctic (Birkeland, 1978). It is also long enough for lakes to fill with sediments and vegetation (Figure 5) (Campbell et al., 1997). The ages of the oldest landscapes are due to erosional and depositional processes, rather than glaciation.

Pollen records from unglaciated areas in the southern Arctic show changes from cold, dry, herb-dominated steppe tundra in glacial periods to warmer, wetter, shrub-dominated tundra in the interglacial periods (Bigelow et al., 2003). Pollen cores from a lake in Chukotka record four glacial cycles over about 300 000 years, represented by repeating cycles in pollen assemblages. Researchers recognized three assemblages, namely shrub dominated, mixed herb and shrub dominated, and herb dominated, and attributed the changes in pollen composition to changes in species abundance and spatial distribution (Lozhkin et al., 2007). The vegetation type with the oldest average landscape age is tussock tundra (Figure 6), which consists of a group of plants that are well adapted to wet, acidic soils resulting from (and contributing to) paludification. Through repeated glacial cycles, these areas would revegetate in the interglacial periods with similar acidophilic species such as tussock sedges, dwarf-shrub birch and ericaceous shrubs, and sphagnum moss, resulting in tussock tundra.

Pollen data show major changes in vegetation from climate fluctuations, even within the most recent interglacial (the last



20 000 years), such as the cool Younger Dryas event (12.8–11.5 kya; Peteet, 1995). Other studies show changes in tree and shrub distribution since the Little Ice Age, 150 years ago (Suarez et al., 1999; Tape et al., 2006). Thus existing arctic plant communities are not stable, climax communities, but rather what we see now is one moment in the continually changing mix of arctic plant species. The communities we see today result from a continual process of adaptation to changing conditions, including relatively recent climate changes and older geologic events (see **Figure 8** for time scales). On older landscapes, vegetation communities have come and gone with climate fluctuations, and their effects on the soil are superimposed on the much slower process of soil development through chemical and physical weathering.

On regional and local scales, the effects of glaciation are very heterogeneous. Glaciations not only killed vegetation by covering the land with year-round ice, they also eroded landscapes and left deposits including unsorted moraines and till, sorted glaciofluvial deposits and eskers, and ice blocks that created countless kettle ponds. In addition to this spatial heterogeneity, glacial landscapes also show evidence of glaciations from many different time periods. It has even been shown that relatively recently melting ice sheets can uncover much older, uneroded landscapes (Briner et al., 2005). These cold-bottomed glaciers reset the clock for plant community development, but only stopped the clock for soil development. As a result, a small area can include large differences in types of glacial deposits and can have adjacent glaciations of very different ages (Hamilton, 1986). The present distribution of communities reflects differences between substrates of varying glacial ages and types (Walker et al., 1995). Whether the soil is scraped to bedrock, whether an underlying soil is left intact,

and whether the glacier deposits fresh till or sorted sands all have effects on plants and can be as important as whether the glaciation that caused these effects was 10 or 10 000 kya.

An examination of the importance and relative time scales of the various processes affecting arctic vegetation distribution shows that recent climate change in the Arctic will impact plants on several different time scales. Temperature is the most important factor affecting NDVI of vegetation types in all but the warmest parts of the Arctic (Bunn et al., 2005; Raynolds et al., 2008). Annual fluctuations in NDVI in response to temperature are superimposed on the longer term trends of increasing NDVI and temperature (Jia et al., 2003). These longer term trends will change relative species dominance in communities, such as the increase in shrubs seen in the southern Arctic (Tape et al., 2006). The changes that we have seen in arctic vegetation since the 1970s match this understanding that changes in plant community composition and structure will show up on the decadal scale at the earliest. Warming will also accelerate processes that are happening on the geologic scale because chemical processes occur more rapidly at warmer temperatures, but this acceleration in rock weathering, soil formation, and peat sequestration will not be evident for decades or hundreds of years.

Conclusions

This study presents a map of landscape age in the circumpolar Arctic based on time that landscapes have been available for plant colonization and community development since they emerged from glacial ice, sea, or lake. A large portion (38%) of the Arctic was deglaciated relatively recently (7–10 kya), mostly Arctic Canada, the site of the Laurentide Ice

Sheet. Russian and Alaskan arctic landscapes are much older, with the oldest areas remaining unglaciated throughout the whole Pleistocene. The vegetation types most commonly associated with the oldest landscapes include tussock-sedge, dwarf-shrub, moss-tundra, and sedge-shrub wetlands.

Most of the Arctic, including most bioclimate zones and most vegetation types, showed increases in the normalized difference vegetation index (NDVI) with an increase in landscape age. Landscapes showed rapid increases in NDVI during the first several thousand years after deglaciation. Landscapes 5000 – 15 000 years old, the age of the most rapid peat accumulation, had relatively low levels of NDVI. Landscapes older than 20 000 years had higher NDVI levels. These landscapes are old enough to show the effects of soil development and infilling of lakes and are much more common in the less frequently glaciated southern Arctic than in the north.

Landscape age accounted for 34% of the variation in NDVI for landscapes younger than 900 000 years. The coldest parts of the Arctic (subzone A) and vegetation types that grow primarily in these areas did not show any trend with landscape age. This could change due to anthropogenic warming, as the difference between subzone A and subzone B is about 2 °C in mean July temperatures, a level of change we are likely to see occur in the Arctic (Hassol, 2004). Warming in subzone A would increase vegetation colonization, succession, and soil-formation processes, which over time would lead to increases in vegetation cover and NDVI.

Acknowledgements

Research for this publication was supported by a University of Alaska International Polar Year (IPY) graduate fellowship through the Cooperative Institute for Arctic Research (CIFAR) with funds from NOAA under cooperative agreement NA17RJ1224 and National Science Foundation (NSF) grants ARC-0531180 and ARC-0425517.

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