Global Change Biology (2006) **12,** 686–702, doi: 10.1111/j.1365-2486.2006.01128.x

The evidence for shrub expansion in Northern Alaska and the Pan-Arctic

KEN TAPE*, MATTHEW STURM† and CHARLES RACINE‡

**Geophysical Institute, University of Alaska-Fairbanks Fairbanks, AK 99775, USA, †USA-CRREL-Alaska Ft., Wainwright, AK 99703, USA, ‡USA-CRREL, Hanover, NH 03755, USA*

Abstract

One expected response to climate warming in the Arctic is an increase in the abundance and extent of shrubs in tundra areas. Repeat photography shows that there has been an increase in shrub cover over the past 50 years in northern Alaska. Using 202 pairs of old and new oblique aerial photographs, we have found that across this region spanning 620 km east to west and 350 km north to south, alder, willow, and dwarf birch have been increasing, with the change most easily detected on hill slopes and valley bottoms. Plot and remote sensing studies from the same region using the normalized difference vegetation index are consistent with the photographic results and indicate that the smaller shrubs between valleys are also increasing. In Canada, Scandinavia, and parts of Russia, there is both plot and remote sensing evidence for shrub expansion. Combined with the Alaskan results, the evidence suggests that a pan-Arctic vegetation transition is underway. If continued, this transition will alter the fundamental architecture and function of this ecosystem with important ramifications for the climate, the biota, and humans.

Keywords: arctic, climate change, greening, shrubs, tundra

Received 29 August 2005; revised version received and accepted 19 October 2005

Introduction

The Arctic has warmed about 2 °C per decade over the last 30 years (Overpeck *et al*., 1997; Serreze *et al*., 2000; ACIA, 2004). This warming has been accompanied by a host of environmental changes (Arendt *et al*., 2002; Hinzman *et al*., 2005), of which the most widely noted is a reduction in sea ice (Rothrock *et al*., 2003; Stroeve *et al*., 2005). The observed 10% reduction in ice extent, paired with a commensurate lessening in ice thickness, has been news-worthy (Overpeck *et al*., 2005) and has had major implications for the heat budget of the Arctic (Sturm *et al*., 2003; Kolbert, 2005).

The terrestrial counterpart has been a shift in land surface vegetation (Chapin *et al*., 1995; Myneni *et al*., 1997; Sturm *et al*., 2001; Zhou *et al*., 2001; Lloyd *et al*., 2003; Stow *et al*., 2004), but it is less clear whether this change has been pan-Arctic in scope or more limited. Documenting the extent and nature of this change is critical because, if it is widespread, the change has probably already begun to alter the heat and carbon budgets of the Arctic by amounts comparable with those associated with changes in sea ice. Without knowledge of the spatial scale of the change, we cannot (a) establish its link to climate conclusively or (b) quantify its feedbacks and effects on the climate and pan-Arctic ecosystem.

The reason for our uncertainty on this important issue is that it is hard to monitor vegetation change using satellites (Fung, 1997; Stow *et al*., 2004). In contrast, monitoring the extent of sea ice change remotely has been at the operational level for more than 30 years (cf., http://pafc.arh.noaa.gov/ice.php). Also, with a wide variety of arctic land surface vegetation types, more than one type of vegetation change has been underway. Sea ice change, on the other hand, can be measured with a single metric. Moreover, the response time to a warming climate is longer for vegetation than for ice.

In this paper, we assemble three lines of evidence for pan-Arctic shrub expansion (Fig. 1a). From *repeat aerial photography* (much of it presented here for the first time), we report on changes in northern Alaska. The photographs allow for unequivocal detection of change and cover a large enough area to allow for regional extrapolation. Unfortunately, suitable photographs for

Correspondence: Ken Tape.

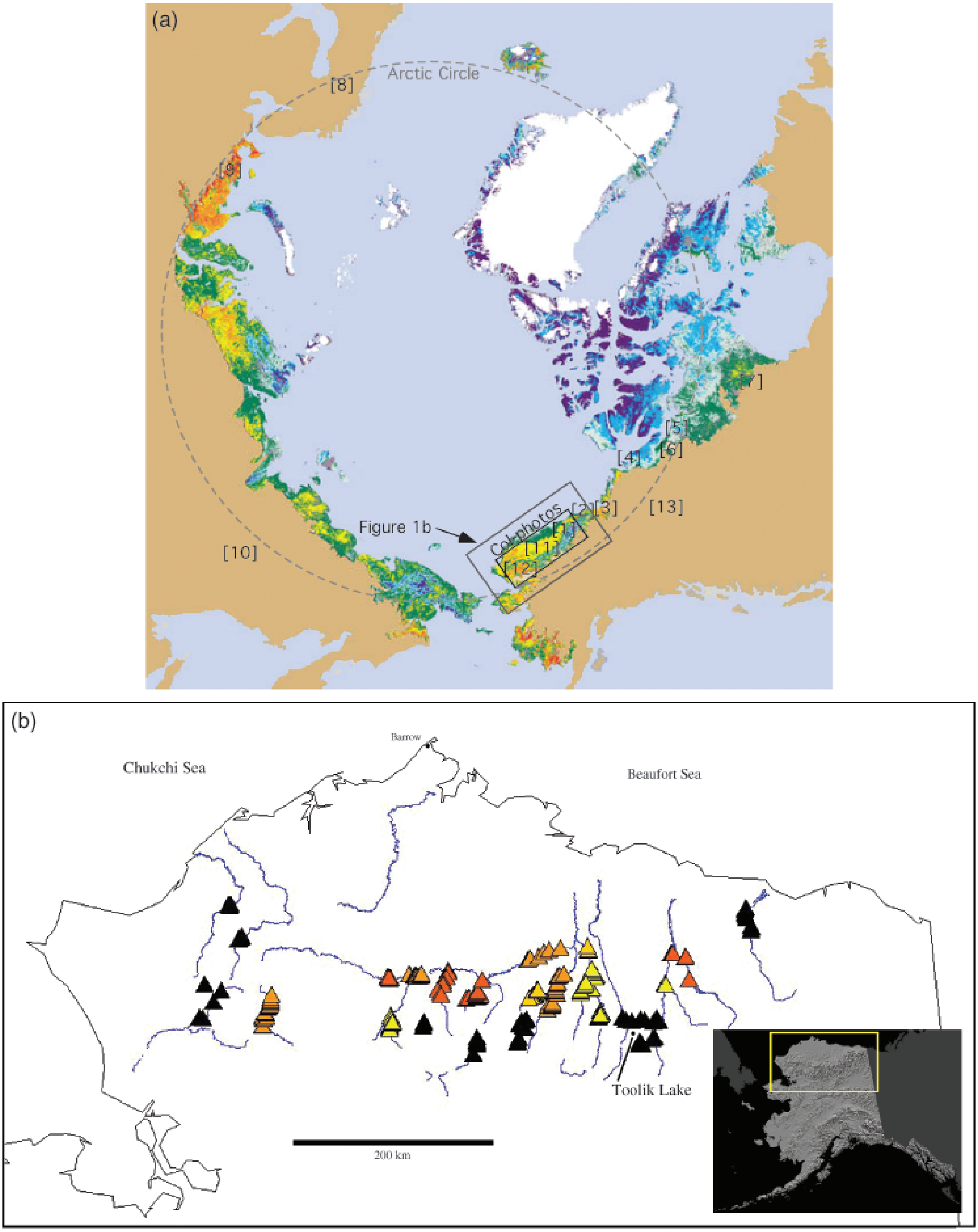

Fig. 1 (a) Location of studies (numbers in brackets) related to shrub expansion in the Arctic. These same numbers in brackets appear in the text associated with relevant studies. The smaller rectangle indicates the area where repeat aerial photography was available (see (b)) (background map: CAVM Team, 2003). (b) The Col photo study area showing the 24 flight lines and 19 river systems along which photos were rephotographed. Color codes indicate relative change in shrub cover (RSC, relative change in shrub cover) (red: RSC = 50–80%; orange: RSC = 30–50%; orange–yellow: RSC = 15–30%; yellow: RSC = 0–15%; black = photos not suitable for this type of analysis). There was almost no negative change (loss of shrubs).

similar analysis are not available outside of Alaska, and even in Alaska the photographic resolution limits the results to detection of changes in larger (>0.5 m tall) shrubs. Using *plot studies* assembled from the literature and provided by colleagues, we find a wealth of detailed information about changes in smaller shrubs, but these data exist at only a few circum-arctic locations. The network of plots is too sparse to allow for meaningful geographic extrapolation at the pan-Arctic scale. S*atellite remote sensing* provides information at both regional and pan-Arctic scales. These data, however, do not provide unambiguous change detection and are most reliable when corroborated using other methods. Fortunately, all three lines of evidence are available in northern Alaska. There they tell a consistent story of change. This consistency improves our confidence when we evaluate changes beyond Alaska where only one or two lines of evidence are available. Using all three lines of evidence, we assess whether a pan-Arctic change in vegetation is underway.

A pan-Arctic shrub expansion has profound implications for arctic ecosystems and the climate. Such a change would alter the surface energy balance of the tundra by reducing the albedo in both summer and winter (Sturm *et al*., 2005), while simultaneously altering the architecture of the boundary layer (McFadden *et al*., 1998; Beringer *et al*., 2005). It would also alter the carbon balance through changes in the above- and belowground production and storage of woody material (Mack *et al*., 2004). Finally, it would change the hydrology by increasing the amount of winter snow trapping, increasing summer transpiration, and changing in an undetermined way the active layer depth and its hydraulic characteristics (Sturm *et al*., 2001). These physical alterations would interact in complex ways that could potentially involve thresholds and nonlinear behavior along with positive amplification of the change. The wholesale alteration of the ecosystem would affect humans and animals alike.

Paper structure

The first section of the paper describes the methods we used to assess change from repeat aerial photography, and the second section describes the results. In 2001 (Sturm *et al*., 2001), we presented preliminary photographic evidence for shrub expansion in Alaska. Here, we greatly expand our coverage, comparing 202 pairs of photographs from a region that spans 620 km (east–west), 350 km (south–north), and exceeds 220 000 km^2. Next, we review published and unpublished results from plot and remote sensing studies. In the Discussion, we combine all three types of studies to answer the question ‘Is a pan-Arctic expansion of shrubs underway?’

Methods

The Col photos and study area

The Col (for Colville River) photo study is based on a remarkable set of oblique black and white photos obtained between 1945 and 1953 for exploration of the Naval Petroleum Reserve Alaska (NPRA) in northern Alaska. Over 4000 large format (18″ × 9″ negative) black and white oblique low-altitude photos were taken in the region bounded by the Brooks Range on the south and the Colville River on the north (Reed, 1958). Taken out of the side door of an airplane that sometimes flew just 50 m off the ground, the photos are of exceptional quality and resolution.

The photographs cover a region of roughly 220 000 km^2 – about the size of Kansas (Fig. 1b) – with two physiographic provinces (Reed, 1958; Wahrhaftig, 1965). The northern province, or Arctic Foothills, is rolling tundra. The southern province, the Brooks Range, is a broad, east–west trending mountain range. The photographs tend to be concentrated along the broad river valleys common in the region. Most of the rivers originate in the Brooks Range and flow north through the Foothills until they join the Colville River. Flat benches, or interfluves, separate one valley system from another. The entire region is underlain by continuous permafrost (Brown *et al*., 1997; Bockheim *et al*., 1998).

The region is blanketed by tundra composed primarily of sedge tussocks, or sedge tussocks and shrubs of various heights (CAVM Team, 2003). The main deciduous shrubs are birch (*Betula nana* and *B. glandulosa*), willow (*Salix alaxsensis*, *S. pulchra*, *S. glauca*) and alder (*Alnus crispa*). Dwarf (<0.5 m) deciduous shrubs are common. Larger (2–7 m high) deciduous shrubs are found throughout the region in the more protected drainages, along water tracks, on stable floodplains, and on terraces adjacent to floodplains. The vegetation of the region is representative of a large part of the vegetated Arctic. Six out of a total of 15 types of vegetation found in the Arctic are represented in the study region. While the region constitutes only about 5% of the total vegetated area of the Arctic, the six types of vegetation found there account for 58% of the mapped vegetation of the Arctic (CAVM Team, 2003).

Repeating the Col photos

We repeated 202 photos between 1999 and 2002. These were selected to provide the widest geographic coverage (Fig. 1a and b) and the greatest likelihood of detecting change. For the latter, we had to be able to see shrubs on the old photos; because of photo

Table 1 Flight lines and river valley systems in study

Photo-line	Location
Anaktuvuk R. (S)	68°N57′, 151°W12′
Anaktuvuk R. (N)	69°N02′, 151°W06′
Atigun Gorge	68°N32′, 149°W03′
Ayiyak R.	68°N54′, 152°W30′
Chandler R.	68°N57′, 151°W54′
Colville R. (W)	68°N52′, 156°W40′
Colville R.	68°N57′, 155°W56′
Colville R. (E)	69°N20′, 152°W21′
Itigaknit R.	68°N43′, 149°W19′
Ivishak R.	69°N22′, 148°W13′
Ivotuk	69°N28′, 155°W44′
Killik R.	68°N20′, 153°W59′
Kiruktagiak Creek	68°N36′, 152°W49′
Kokolik R.	69°N18′, 161°W34′
Kugururok R.	68°N18′, 161°W24′
Kurupa R.	68°N54′, 155°W09′
Lupine R.	69°N05′, 148°W48′
Nanushuk R. (S)	68°N43′, 150°W38′
Nanushuk R. (N)	69°N07′, 150°W49′
Nigu R.	68°N26′, 156°W24′
Nimiuktuk R.	68°N17′, 159°W54′
Oolamnagavik R.	68°N49′, 154°W07′
Sagavanirktok R.	69°N24′, 148°W37′
Utukok R.	68°N60′, 161°W04′

resolution, this meant shrubs taller than 0.5 m. We used a resection technique (Moffitt, 1959), as well as a visual method to determine the map location from which each old photo was taken. A helicopter was used to reoccupy the aerial position. For reasons of cost and efficiency, we used a medium format camera and color film. Old photos and new negatives were then scanned at 4000 dpi and the resulting images were reproduced on a single sheet for comparison. In total, we repeated and analyzed photos from 24 flight lines on 19 separate river valleys (Table 1).

Interpreting the Col photos

Darker areas on the photos are shrub-dominated vegetation. We confirmed this interpretation by field reconnaissance at 10 photo-sites on five rivers (Ayiyak, Chandler, Colville, Sagavanirktok, and Kugururok). At the sites, two people would traverse an area, noting shrub species, heights, diameters, and associated vegetation. They would radio this information back to two other people who observed their position using a spotting scope and recorded the measurements directly on the photos. The field mapping process (1) allowed us to calibrate shrub size (most shrubs were larger than we initially thought) and (2) made us aware of the prevalence of willow and birch in close association with alder. Based on the field mapping, we found we were also able to map smaller, lighter colored shrubs in special cases (i.e., if they were adjacent to rocks or objects against which we could gauge their change in size and abundance).

An example of field mapping is shown in Fig. 2 and Table 2. The upper Chandler River valley has some of the highest shrub coverage of any area in the study. The darkest shrubs in the photo (numbers 15 and 18 on Fig. 2) are green alder (*A. crispa)*, here mixed with birch (*B. glandulosa)* and willow (*Salix sp.*) (6). Willow-dominated patches are visible on the upper slopes (22 and 23) as are patches of birch-dominated shrubs (six and 11). Birch patches appear brown in color photos and have a smooth texture. Willow-dominated patches are typically light gray in the old photos and light green in the new photos.

Detecting change using the Col photos

Most of the photos were of broad valley landscapes (Fig. 3) that can be subdivided into four geomorphic units: (1) broad interfluves, (2) gentle facing slopes and cutbanks, (3) flat river terraces, and (4) active floodplains (Fig. 4). Two methods of photo analysis were used to quantify change in units 2–4. Changes in unit 1 are discussed in the section on remote sensing and plot studies.

Type I photo analysis was applied only to the 86 photo pairs where the new and old photo perspective was close. For this type of analysis, we made a grid of equal-sized cells on a sheet of acetate and placed it over an old photo. This same grid was then transferred to the new photo using tie points (Fig. 3). Because the perspective of the two photos never matched perfectly, the transferred grid was somewhat distorted. Percent shrub cover was visually estimated for each grid cell on both the old and new photos. For those grid cells analyzed (typically on facing slopes), photographic sight lines were close to slope-normal, allowing reasonable ocular coverage estimates.

Type II analysis was applied to 69 pairs of photos not suitable for type I analysis because the perspective of the new photo did not match that of the old. For these photo pairs we made whole-photo ocular estimates of shrub cover in three of the four geomorphic units: slopes, terraces, and floodplains. Type II analysis was also used to evaluate changes in the foreground (terraces and floodplains) of the 86 photos assessed under the type I analysis.

The remaining 47 photographs contained no identifiable shrub forms in either the old or new photos. In general, these tended to be photos of interfluves where

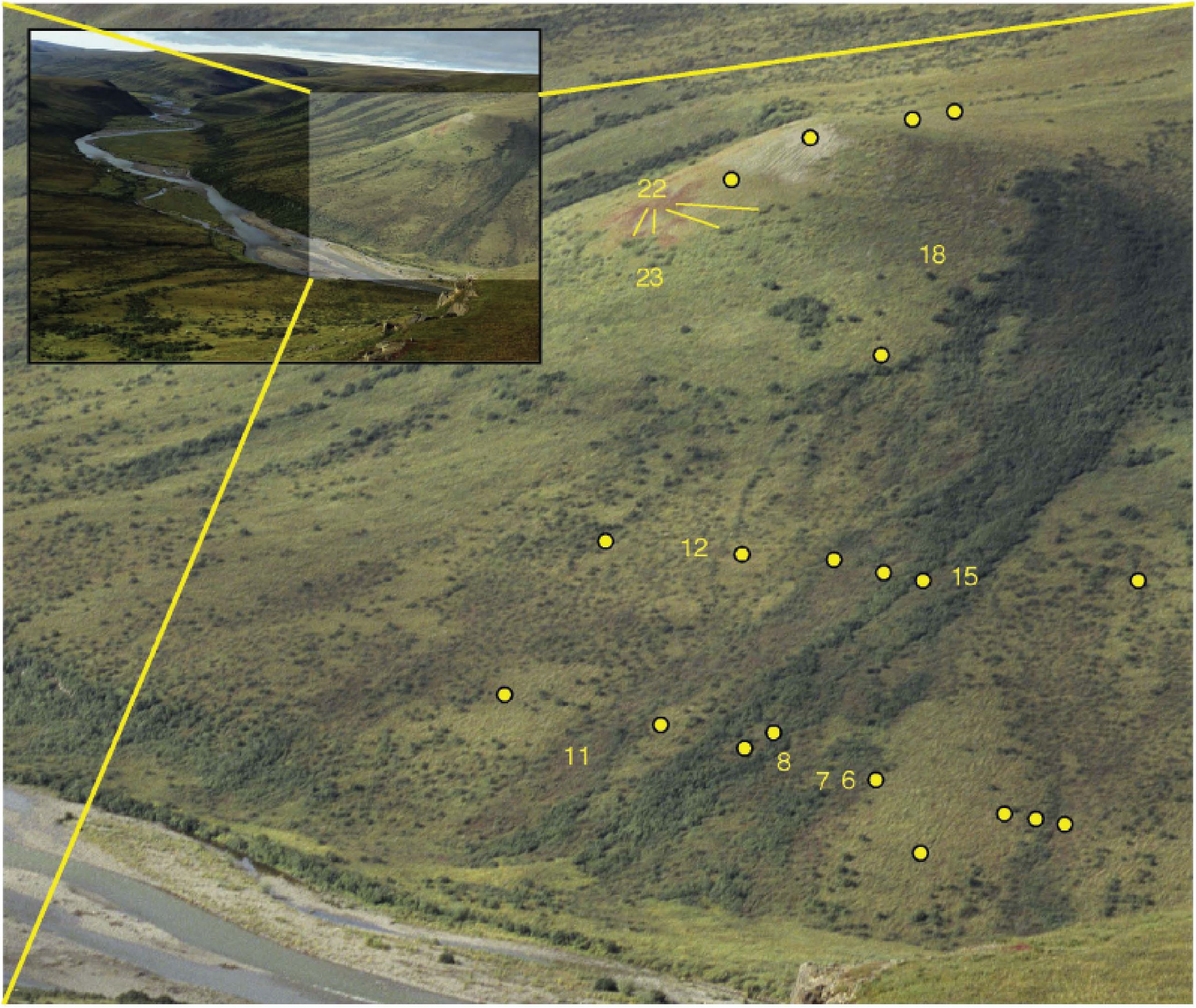

Fig. 2 An example of field mapping of shrubs onto a Col photo. The vegetation at each numbered location is given in Table 2. Photo from the Chandler River located at 68°N49.39′, 152°W00.52′.

Table 2 Vegetation at numbered locations in Fig. 2

Code	Shrub species	Maximum height (m)
6	*Betula glandulosa*, *Salix* sp., *Alnus crispa*	1.5
7	*Salix glauca*	0.6
8	*Betula glandulosa*, *Ledum groenlandica*	0.5
11	*Betula glandulosa*	0.5
12	Alder parkland (scattered alder 2–4 m apart with tussock-shrub tundra)	1.1
15	Alder in drainage channel	3.5
18	Single alder shrub	2.7
22, 23	*Salix* sp.	0.5

there were (and still are) no large shrubs. As our metric of change was shrub cover, these 47 photos were examined, but were not used in our calculations of change. Those calculations were based on the 155 photos we analyzed using types I and II analyses.

We report two measures of change: the change in shrub cover (CSC), which equals the percent shrub cover on a new photo minus the percent shrub cover on an old photo, and the relative change in shrub cover (RSC), which equals the CSC divided by the percent shrub cover in the old photo. For type I analysis, the results for an old-new photo pair are the average of all individual grid cells that could be assessed. The results were also averaged by geomorphic unit (interfluve, slope, terrace, and floodplain) and by river valley. The number of photo pairs used in a river valley average varied from two to 14, according to the number of photos that were available in that location.

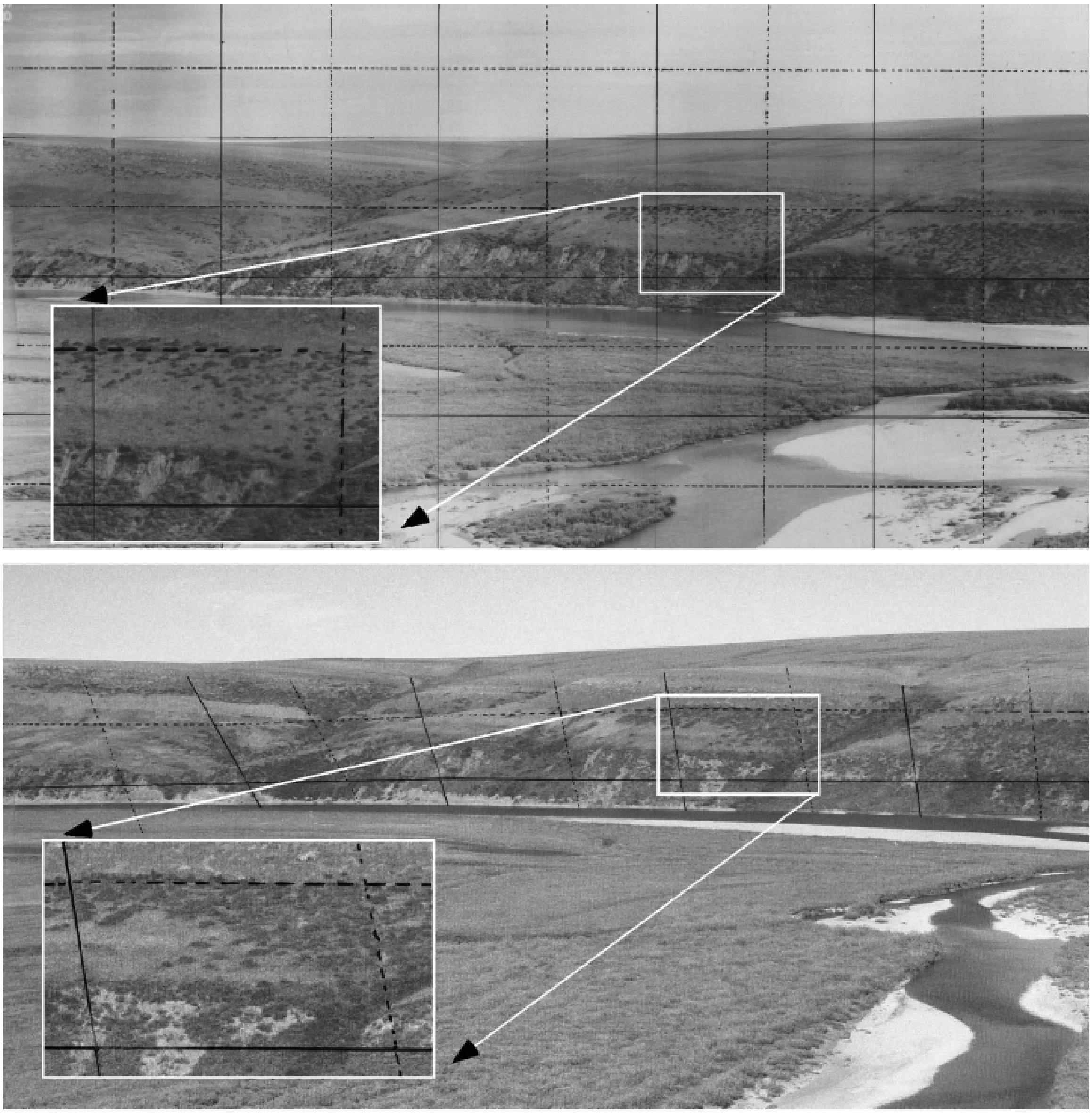

Fig. 3 A typical pair of old and new photos showing initial (rectangular) and final (distorted) grid. The insets show an area where there has been an increase in shrub coverage through patch expansion and in-filling. Photo from the Colville River located at 68°N56.77′, 155°W57.58′: 7/18/1948 and 7/29/2001.

Col photo results

Of the 155 pairs of photographs analyzed, 135 showed a detectable increase in shrubs, while 18 showed no change at all. Only two showed a decrease in shrubs. The increase took place in three ways: (1) shrub patch boundaries expanded, (2) patches filled in, and (3) individual shrubs grew in size. These three types of change typically occurred together (Figs 3 and 5). The expansion varied in magnitude with landscape position (i.e. geomorphic unit: Fig. 4), by river valley (Fig. 1b), and with shrub species.

Variation by landscape

Slopes. On broad slopes leading down to terraces and floodplains along rivers, there was a marked increase in shrub abundance during the last 50 years. Of the 1335 grid cells on 86 photo pairs analyzed under the type I analysis, 894 registered an increase in shrubs, 428 registered no change, and 13 registered a decrease in shrubs. For all 86 photos the average shrub cover increased from 15% to 20%, an RSC of 33% (Table 3). Type II analysis (Table 4) for slopes ($n = 69$) indicated an increase in shrub cover from 22% to 30% for an RSC of

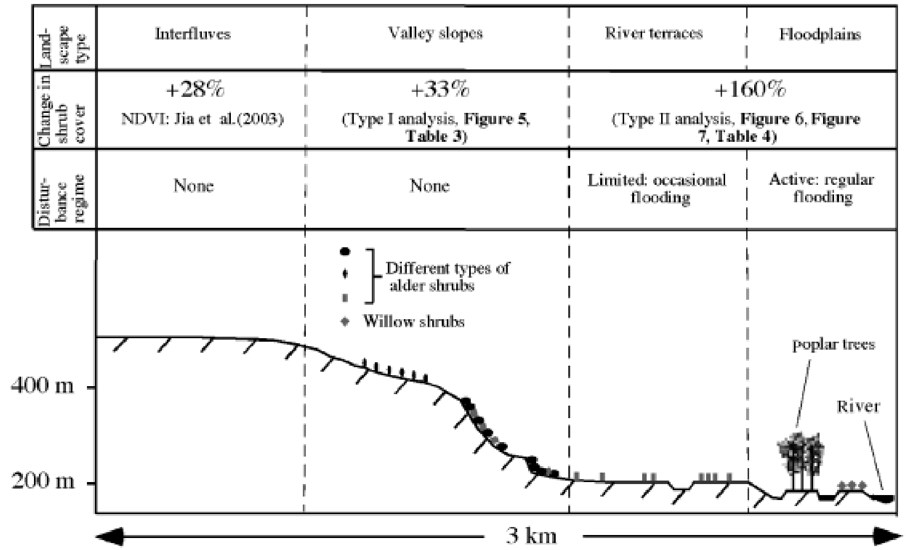

Fig. 4 Cross-section through a typical valley landscape in the study area showing the four geomorphic units, the relative change in shrub cover (RSC) in the unit, and the amount of disturbance common to each unit. Numbers refer to other figures that illustrate these changes. Birch and willow are ubiquitous in many of the landscape locations shown.

36%, consistent with the type I analysis. Based on a two-population analysis of variance (ANOVA), the results from types I and II analyses are statistically the same. Figures 3 and 5 are examples of changes on slopes.

Terraces. The shrubs on the broad, stable terraces that border the floodplains in the study area expanded conspicuously. The soil on these terraces typically shows undisturbed organic layers overlying permafrost, suggesting that minor flooding is the extent of the disturbance regime. Forty-seven out of the 72 photo pairs (types I and II combined) in our set that contained terraces showed shrub expansion, while 25 showed no change. No photo pairs showed negative change. Based on type II analysis for combined flood plains and terraces, there was an average increase in shrub cover from 5% to 13%, an RSC of 160%. The high RSC value reflects the fact that in many cases, the expansion of shrubs on the terraces was new colonization, with initial shrub cover percentages quite low (Fig. 6).

Floodplains. The photo pairs also suggest that the active channels of many rivers in the study area have become shrubbier, more channelized, and more stable. Thirty-eight out of the 49 photo pairs that showed floodplains in the old photos (type II analysis) now have more continuous shrub cover. The water channels themselves appear narrower and more constrained. Gravel and sand bars that were free of vegetation in the old photos now host verdant shrubs (Fig. 7). Active floodplains are, by nature, dynamic so we would expect to see changes in this environment. However, in a stable climate we would have expected to see increases in some floodplain locations counterbalanced by decreases elsewhere, which we did not.

Variation by river valley

As Fig. 1b shows, the magnitude of the shrub increase varied across the study area. The magnitude (RSC) was greater in areas below 400 m elevation and in the deeper valleys. In fact, the area on the North Slope of Alaska with the most abundant shrubs is the set of tributary river valleys south of the Colville and near Umiat (Fig. 1b). Large shrubs are absent on the coastal plain further north and are rare on the upper (western) Colville River and southern Foothills.

Variation by shrub species

The most conspicuous shrubs in the photos were alder (i.e. Figs 3 and 5) but from field mapping and from key photos, a general increase in all deciduous shrubs (alder, birch, and willow) can be inferred. In the field, birch, and willow were always found in close association with alder, although the former shrubs were usually smaller. Rings of birch and willow often surrounded a central alder producing a striking 'halo' (Fig. 8). These halos are probably the result of a favorable combination of snow trapping, modification of soil temperature, and leaf litter rain by the larger shrubs. In 15 locations (for willow) and four locations (for birch), we were able

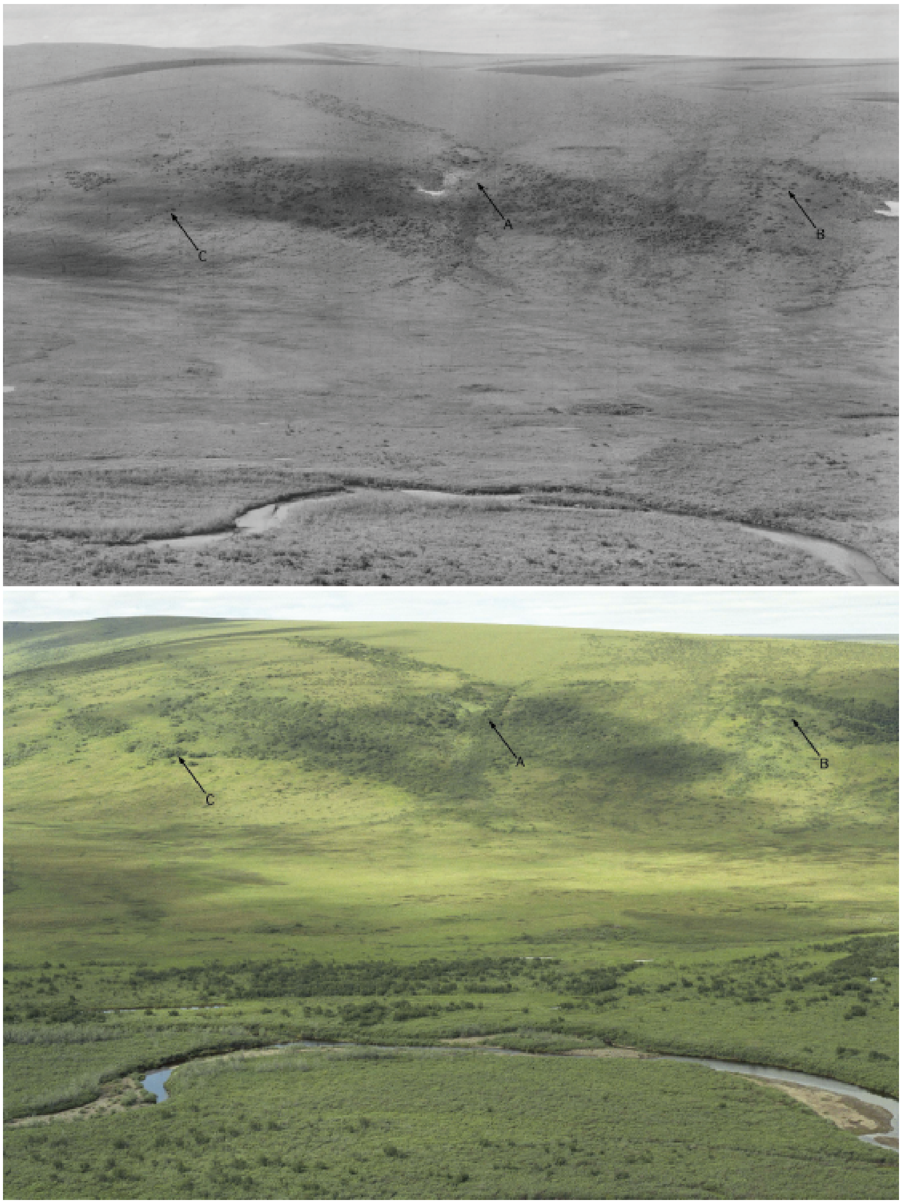

Fig. 5 Three types of shrub expansion. 'A' denotes new colonization, 'B' denotes patch in-filling, and 'C' denotes individuals getting larger. Photo from the Oolamnagavik River located at 68°N52.00′, 154°W08.36′: 8/11/1948 and 7/27/2002.

to unambiguously document an increase in size and abundance, and we are confident that in many other locations birch and willow were expanding but escaped detection. For example, in many photo pairs, what appears to be low-shrub or shrubless tundra in the older photos has a coarser, fuzzier texture in the new photos that is probably a low canopy of new birch and willow (Fig. 8). Elsewhere, large dark alder with distinct canopy forms in the old photos are no longer distinct in the new photos because the willow and birch have grown-up around them.

Plot and remote sensing evidence for shrub expansion

For northern Alaska we can compare the results from plot and remote sensing studies to those from the repeat photography. When we do this, we find that the observed changes are consistent in character, and complementary in location and size of the shrubs. The plot studies indicate that smaller shrubs, those below the detection limit of the photographs, have been increasing. The remote sensing results, the majority of which

Table 3 Type I analyses results for changes in shrub cover ($n = 86$)

Photo-line	Number of photos	% shrub cover (old)	% shrub cover (new)	RSC (%)	Stdev RSC, per photo
Anaktuvuk R. (S)	2	16	18	13	29
Anaktuvuk R. (N)	4	15	18	20	19
Ayiyak R.	2	7	8	14	81
Chandler R.	12	28	38	36	36
Colville R. (W)	6	5	9	80	42
Colville R.	9	18	23	28	30
Colville R. (E)	4	22	28	27	11
Kurupa R.	7	10	15	50	25
Lupine R.	2	6.7	6.9	3	3
Nanushuk R. (S)	4	22	26	18	7
Nanushuk R. (N)	4	17	20	18	14
Nigu R.	3	8	9	13	15
Nimiuktuk R.	14	13	18	38	55
Oolamnagavik R.	10	8	13	63	47
Sagavanirktok R.	3	8	13	63	10
N. Alaska	86	15	20	33	28

RSC, relative change in shrub cover.

Table 4 Type II analyses results for changes in shrub cover ($n = 69$)

		Slopes (%)			Terrace + floodplains (%)		
Photo-line	Number of photos	Old	New	RSC	Old	New	RSC
Anaktuvuk R. (S)	2	18	23	28	3	8	167
Anaktuvuk R. (N)	1	35	40	14	3	10	233
Atigun Gorge	1	20	25	25	15	25	67
Ayiyak R.	11	22	38	73	5	9	80
Chandler R.	6	42	60	43	4	10	150
Colville R.	1	15	17	13	3	3	0
Colville R. (E)	3	43	47	9	18	41	128
Itigaknit R.	4	20	21	5	–	–	–
Ivishak R.	3	22	29	32	0	2	high
Killik R.	5	14	27	93	4	13	225
Kokolik R.	2	18	23	28	–	–	–
Kugururok R.	5	19	21	11	1	8	700
Kurupa R.	2	3	6	100	5	9	80
Nanushuk R. (S)	4	19	27	42	3	6	100
Nanushuk R. (N)	4	20	25	25	11	15	36
Nigu R.	7	18	18	0	–	–	
Nimiuktuk R.	5	30	42	40	3	8	167
Oolamnagavik R.	3	25	40	60	3	14	367
N. Alaska	69	22	30	36	5	13	160

RSC, relative change in shrub cover.

are derived from geomorphic unit 1 (broad interfluves), suggest the same, and allow us to extend the photo results more widely. Collectively, the three lines of evidence provide a coherent picture of a region across which shrubs, both large and small, are increasing in abundance. One of the chief benefits of this consistency is that it gives us increased confidence when we examine changes in tundra outside of northern Alaska, places where two, or sometimes only one, line of evidence is available for the detection of change.

Plot studies

Control plot studies at Toolik Lake (68°36′N, 149°36′W) in northern Alaska (and in the Col photo study area) have shown an increase in dwarf birch between 1983

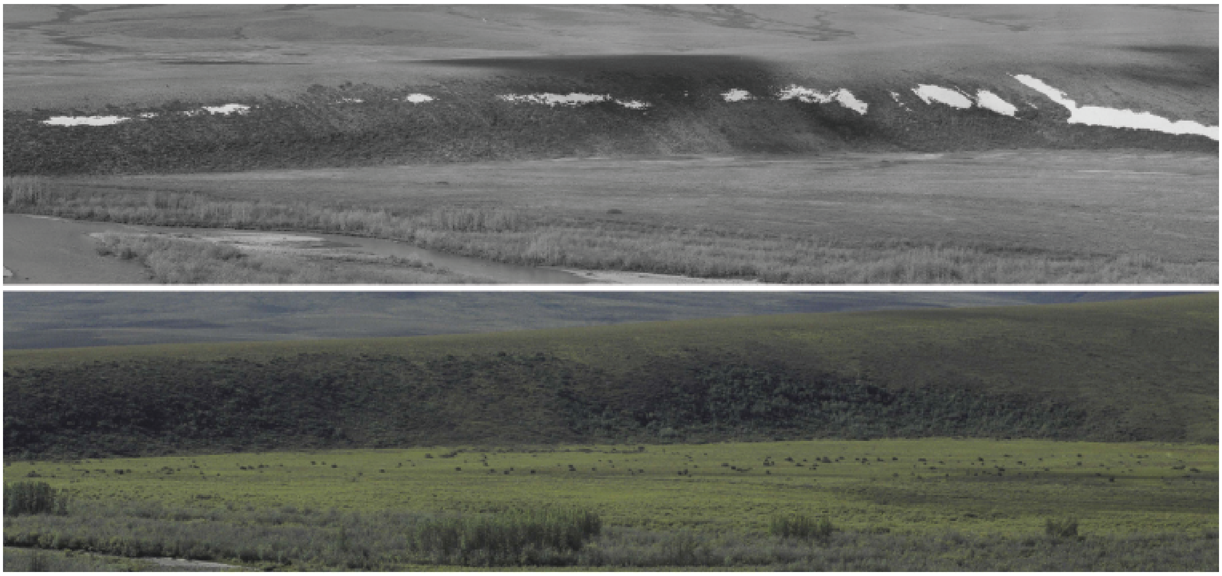

Fig. 6 Large shrubs have colonized a river terrace that was virtually free of large shrubs in 1949. The new shrubs are more than 2 m high. In the foreground are the poplar trees. Photo from the Chandler River located at 68°N48.88′, 151°W58.13′: 7/4/1948 and 7/29/2001.

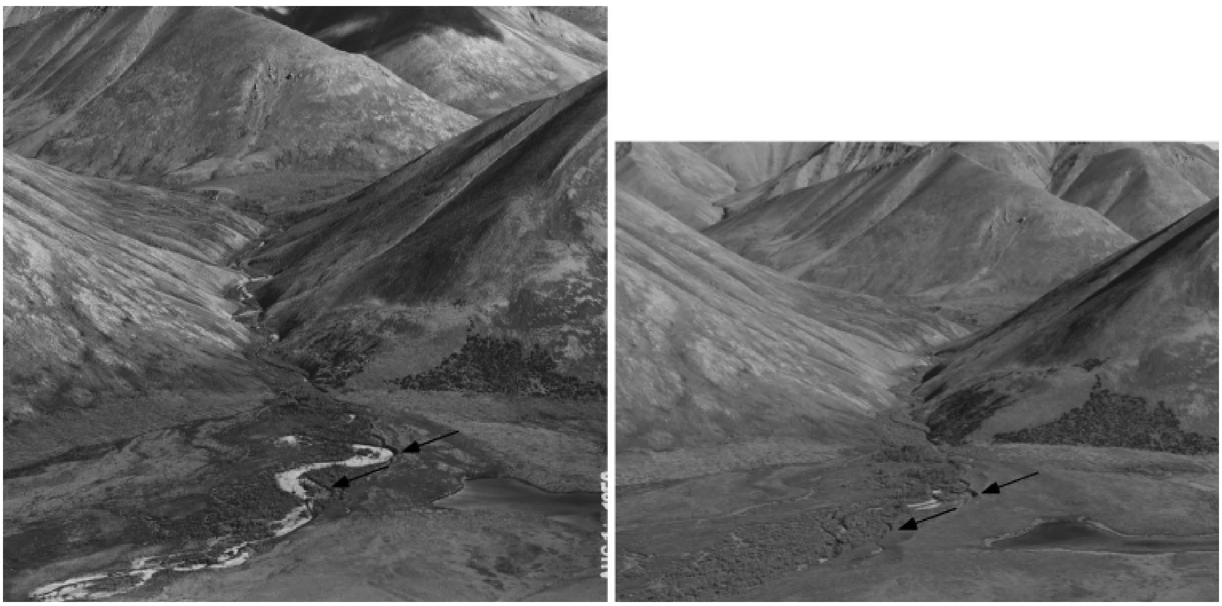

Fig. 7 Active stream channels and gravel bars in 1949 are now colonized by shrubs. Photo from a tributary of the Kugururok River located at 68°N25.14′, 161°W15.24′: 8/1/1950 and 7/10/2000.

and 2004, a period when there was continued climate warming [1] (Chapin *et al*., 1995; Bret-Harte unpublished data; Hollister *et al*., 2005; Wahren *et al*., 2005). In these studies, most, if not all, of the increase is accounted for by the growth of small, intertussock shrubs. The dwarf shrubs (primarily birch) also increased whenever soil temperature was artificially enhanced or nutrients were added. The one exception is a study by [2] Jorgenson & Buchholtz (2005), who found no increase in woody shrubs in an area just north and east of the Col photo study area (~70°N, 147°W) in the 18-year period since 1984.

Outside of Alaska, the results from plot studies are similar. In Canada [3] Lantz & Henry (unpublished

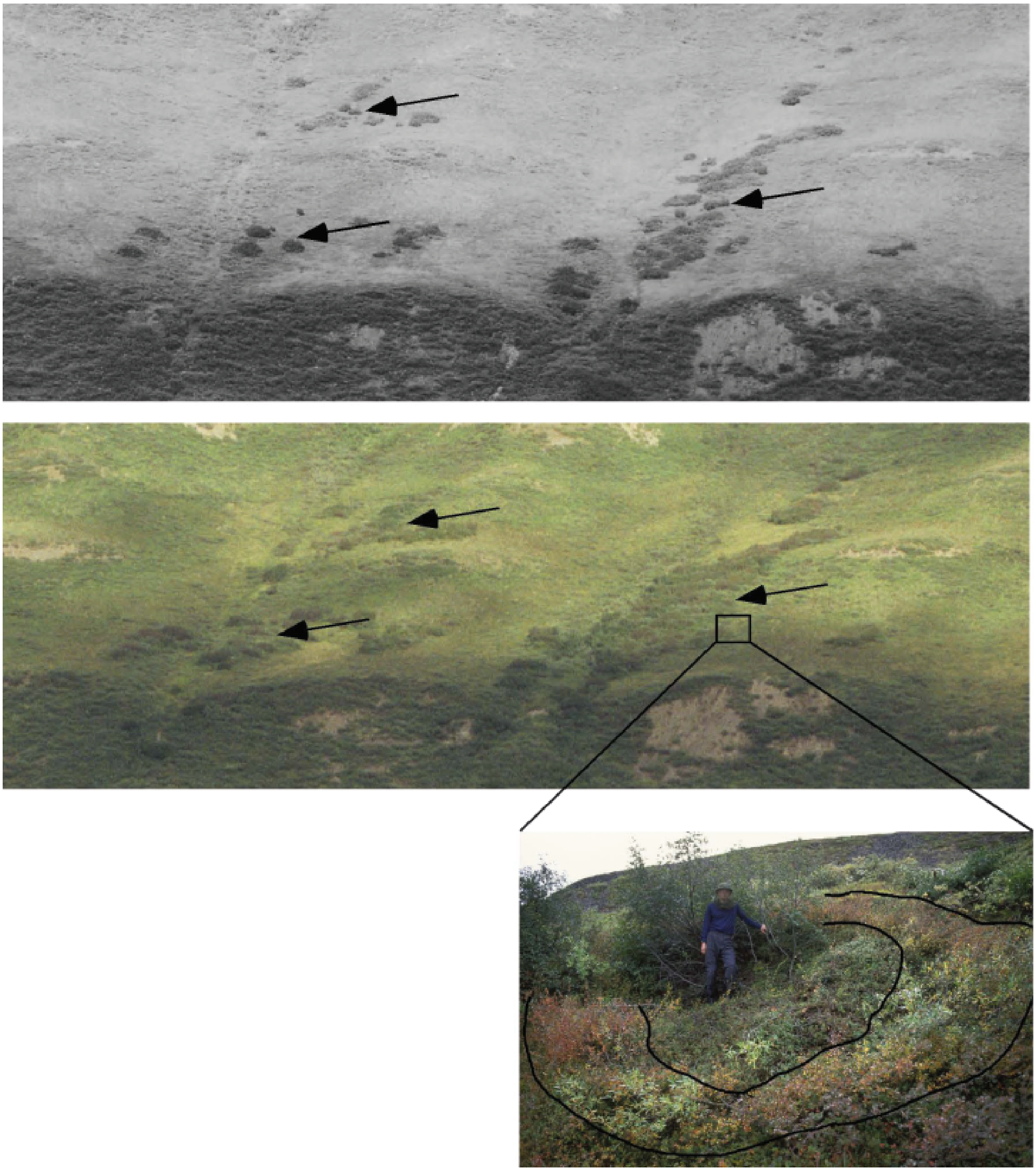

Fig. 8 A 'fuzzy' texture in a new photo suggests birch and willow have increased in size and abundance. The small photo at the bottom shows a halo of birch and willow surrounding an alder that has been cut down. Photo from the Kurupa River located at 68°N47.38′, 155°W09.42′: 7/25/1948 and 7/27/02.

data), using a combination of photographic analysis and plot studies, have preliminary results showing a recent expansion of the shrub cover on the Mackenzie River delta (~ 69°N, 135°W). This expansion is corroborated by anecdotal evidence from [4] Canadian First Nation Elders (Nickels *et al*., 2002). Further east [5], Thorpe *et al*. (2002) find anecdotal evidence for increased birch and willow in western Nunavut (~ 70°N, 107°W). Similarly, there has been an increase in shrubs on floodplains and stream channels in the North–West Territories [6] (65°N, 111.5°W, P. Grogan, personal communication 2005). In eastern Canada [7] (~58°N, 72°W), Gilbert & Payette (1982) and Payette (2005, personal communication) find that alder has increased in conjunction with a northward migration of treeline.

In northern Sweden (68°21′N, 18°30′E), [8] Jagerbrand (2005) observed an increase in dwarf birch in control plots in the last few years, although [8] van Wijk & Clemmensen (2004) found little increase of shrubs in plots that were artificially warmed and/or fertilized. Unfortunately, plot data for the rest of the pan-Arctic is extremely limited. The only relevant study we have found in Russia is that by Shvartsman *et al*. (1999), who found a decrease in the extent of tundra along the Pechora River [9] (~ 66°N, 57°E) between 1960 and 1983, a change they attributed to an increase in trees.

Satellite remote sensing studies

For assessing regional and pan-Arctic shrub expansion, remote sensing is essential because of its broad geographic coverage. The interpretation of the remote sensing results, however, has not been as straightforward as for that of photos and plot studies. The remote sensing has largely been based on the Advanced Very High Resolution Radiometers (AVHRRs) on-board the NOAA-7, -9 and -11 satellites. Using the red visible band (a_V: 0.58–0.68 μm) and the near-infrared band (a_{NIR}: 0.72–1.1 μm), normalized difference vegetation index $(\mathrm{NDVI}) = (a_{NIR} - a_V)/(a_{NIR} + a_V)$ has been computed and used to detect change. This index of leaf area or photosynthetic activity (Tucker & Sellers, 1986; Fung, 1997) correlates well with biomass and productivity, thus indirectly indicating the changing abundance of deciduous shrubs in tundra regions.

Myneni *et al*. (1997, 1998) [10] were the first to report an increase in NDVI in the Arctic. Between 1981 and 1991 they found a 10% increase in the seasonal amplitude of Northern Hemisphere NDVI, with the largest change occurring north of 45°. They attributed the change to a lengthening of the growing season by about 12 days, as did Shabanov *et al*. (2002) and Zhou *et al*. (2001). In Alaska a significant (7%) increase in NDVI was detected for the period 1989–1999 by Stow *et al*. (2003) [11]. Jia *et al*. (2003), analyzing 21 years of data (1981–2001) for the same Alaskan region, found a 17% increase in NDVI, corresponding to a 28% increase in biomass [12]. Their conclusion was based on direct measurements of aboveground biomass coordinated with surface-based measurements of NDVI and was thus attributed to an increase in deciduous shrubs. Both of these Alaskan NDVI studies include the Col photo study area, but they also include the Alaskan Arctic Coastal Plain, which typically has fewer and smaller shrubs than those found in the foothills and Brooks Range. Consequently, the NDVI-based results are likely to be more conservative than the photo-based results. Most recently Goetz *et al*. (2005)[13] have confirmed increasing NDVI values in tundra across the North American Arctic.

There are two key issues related to the interpretation of these NDVI records. The first is whether the long-term records are reliable. Known issues include artifacts because of radiometer drift, atmospheric effects including clouds, and changes from one satellite to another. These effects have been discussed by Fung (1997), Myneni *et al*. (1998), and Stow *et al*. (2003). While the artifact issue is not fully resolved, we find the careful work done by Myneni *et al*. (1998) using data from the Saharan desert as a correction factor, and the multiple correction approach employed by Stow *et al*. (2003) show convincingly that the NDVI record for high latitudes, and Alaska in particular, reflects a real change in surface vegetation. In addition, all of the studies cited above reach a similar result: the seasonal amplitude of NDVI is increasing in the Arctic. While these studies share the same AVHRR source data, they cover different intervals of time, different regions and latitude bands, and have used different methods of data reduction. The consistent nature of the results suggests that the measured changes in NDVI are the result of a real change in arctic vegetation.

The second issue is what that change might mean. Hope *et al*. (1993) and Jia *et al*. (2003) have shown that for tundra an increase in NDVI can be interpreted as an increase in aboveground biomass. In the former study, 51% of the variance in NDVI was explained by biomass change: in the latter study, more than 80%. Increasing tundra biomass does not *a priori* indicate increasing shrubs, but Jia *et al*. (2004, their Fig. 3) found that NDVI values for different tundra types increased consistently and monotonically with the amount of shrubs. Wet tundra, containing virtually no deciduous shrubs, had daily and peak NDVI values that were only about half the value for shrub tundra. There is a striking similarity between the seasonal NDVI curves developed by Myneni *et al*. (1997, their Fig. 2a), Shabanov *et al*. (2002, their Fig. 4), and Zhou *et al*. (2001, their Fig. 4b) and the family of NDVI curves developed for various types of tundra by Jia *et al*. (2004) (Fig. 9). While the change in the seasonal NDVI curves over the last few decades has been explained by changes in growing season length, the same changes (earlier green-up, steeper rise and fall in NDVI during shoulder seasons, higher peak NDVI values in July) can also be explained by the expansion of shrubs on the tundra. We suggest that the observed changes have been a result of both.

Our interpretation, particularly for the Col photo area, is that the increase in NDVI has been primarily the result of an increasing abundance of small, rather than large shrubs. While increases in large shrubs, such

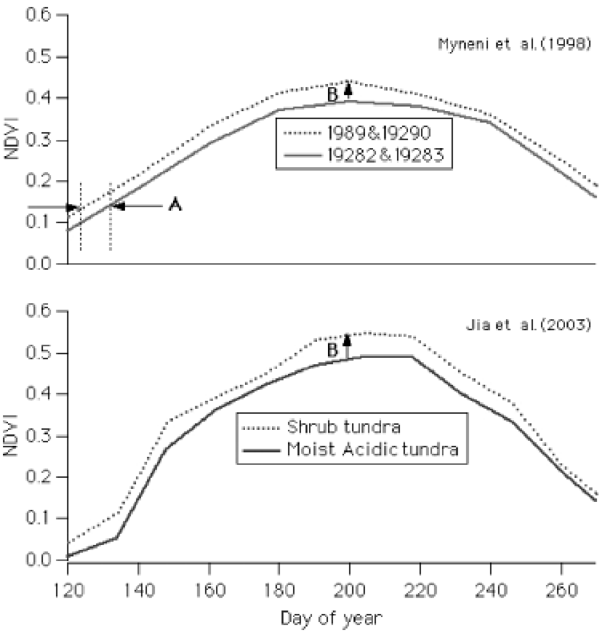

Fig. 9 The shift in normalized difference vegetation index curves between 1982 and 1990 was attributed by Myneni *et al.* (1997) to a longer growing season (a), but as shown by the curves for tundra with more and less shrubs (see Jia *et al.*, 2004), could also be explained by increasing shrub abundance (b).

as those illustrated in Figs 2, 3, 5, 6 and 7, have undoubtedly contributed to the signal, the large shrubs do not cover a sufficient area to have produced widespread changes in NDVI. Most of that change would have to have come from the vast areas of tussock tundra between the valleys where the dwarf shrubs were below the Col photo detection limit.

Discussion

Is a Pan-Arctic expansion of shrubs underway?

Can the case be made for a pan-Arctic expansion of shrubs? Our work, along with the plot and remote sensing studies, establishes that there is ongoing expansion in northern Alaska. Studies also suggest that the expansion extends to western Canada and perhaps Scandinavia. In central Canada, there is limited evidence, but it indicates a positive increase. For the Russian and Siberian sectors of the Arctic, the NDVI data can be interpreted as indicating an expansion, but until direct measurements are available, the trajectory for this sector of the Arctic must remain speculative. Taken together, the data support an ongoing expansion of shrubs that is more than regional in extent, but is it pan-Arctic in scale?

Part of the problem is determining what a pan-Arctic expansion of shrubs would look like. At local and landscape scales such an expansion is likely to produce a bewildering range of shrub cover densities and expansion rates. To demonstrate this, we assume that shrub patch expansion follows a simple logistic growth model (Emmel, 1973; Kingsland, 1982; Conradie, 2003) wherein the rate of increase of a shrub patch is proportional to the amount of shrubs present:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx(1-x). \qquad (1)$$

Here, $x(t)$ is the shrub cover density ($0\% \leq x(t) \leq 100\%$), and r is the intrinsic rate of natural increase of the shrubs (MacArthur, 1972, p. 34).

The value of r depends on the local climate, the quality of the soil, the species composition, and the reproductive biology of the shrubs. It must vary with location, with the amount of competition, and it almost certainly varies with time. As a consequence, adjacent shrub patches can exhibit quite different growth conditions and expansion rates. However, as our goal is to understand the general behavior of shrub patch expansion, we assume for simplicity that r does not vary with time and that for an individual patch there is no competition. We can then solve Eqn (1) for x to get:

$$x(t) = 100\left[1 + \left(\frac{1-x_0}{x_0}\right)e^{-rt}\right]^{-1}, \qquad (2)$$

which produces a family of logistic curves (Fig. 10a) depending on the value of x_0 (the initial shrub cover) and r. Higher initial shrub cover values or higher intrinsic rates of increase produce a greater shrub cover earlier in time. The key point is that with the proper choice of x_0 and r, a wide range of shrub cover values and rates of change can be realized at any point in time since the inception of an expansion. We can almost cover the entire domain shown in Fig. 10a.

Is there any reason to believe the model? An alternate way to plot the family of logistic curves in Fig. 10a is to use Eqn (1) to compute the rate of shrub change ($\mathrm{d}x/\mathrm{d}t$) as function of shrub cover density for a range of x_0 and r values. In Fig. 10b we have done this for the same curves shown in Fig. 10a. The advantage of these latter curves is that they do not explicitly involve time: they relate shrub expansion rates to shrub cover density, both of which can be derived from the Col photos. We have plotted measured shrub expansion rates from all of the Col photo grid cells (our CSC-values divided by the $\sim$50-year interval over which they were measured) against the mean shrub cover percentage for each cell. The data cloud (Fig. 10b) contains a wide range of expansion rates at any particular shrub cover density, consistent with a wide range of x_0 and r values.

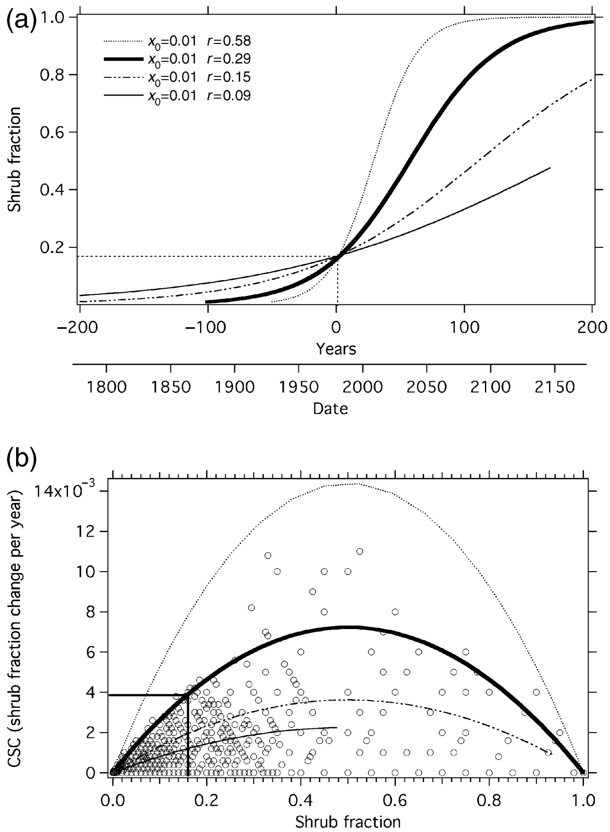

Fig. 10 (a) Logistic growth curves for an initial shrub cover (x_0) of 1% and various shrub expansion rates (r). With appropriate choices of x_0 and r most the plane of the graph could be filled. The heavy curve in the center bounds the Col photo grid cell data best. This data set ($n = 1335$) has a mean shrub cover density of 17% (see text). We have offset the horizontal axis so that time equals 0 at this shrub cover density. The other logistic growth curves have also been offset so that they pass through 17% as well, producing initial times that range from −50 to more than −200 years. (b) Shrub expansion rates (dx/dt) as a function of shrub cover percent for the curves in (a). Data from Col photo grid cells (○) is nicely bounded by the results for the heavy logistic curve ($x_0 = 0.01$, $r = 0.029$) shown in (a). The grid cell data span from ca. 1950 to ca. 2000 with a mid-point date of 1975. At a mean shrub coverage of 17%, the observed rate of change rate was 0.4% yr^{-1}, which suggests an expansion that began ca. 1875.

However, if we look only at the maximum rate at a given shrub cover density, the data cloud is nicely bounded by the distribution curve for x_0 equals 1%, r equals 0.029. In other words, at least for the maximum observed rates of shrub change, we can find a logistic growth curve that matches the data reasonably well. The bulk of the data clusters near 17% cover, with relatively few points at percentages higher than 40%. At 17%, the growth rate is 0.4% per year, a value we will use later.

The key point of the model is that we should expect to observe a wide range of changes during a pan-Arctic shrub expansion because x_0 and r are known to vary greatly across the region. Even in a single watershed, these values might vary enough to produce a large change in one location and little or no change nearby. With this as our perspective, we would argue that a reasonable interpretation of the available data is that a pan-Arctic expansion of shrubs *is* underway. The logistic model tells us that at no point during such an expansion would shrubs everywhere in the Arctic be expanding at detectable levels. It also tells us that there would be no places where the shrub cover was declining. Both facts agree with our current understanding of the changes that are taking place.

Why are shrubs expanding?

The pan-Arctic expansion of shrubs can best be explained by a perturbation operating on a similarly large spatial scale. The most likely cause is a warming arctic climate (Overpeck *et al*., 1997; Serreze *et al*., 2000). Alternate explanations like plant succession following disturbance operate at a much smaller scale. The shrubs, however, are almost certainly being affected by the climate through indirect means, as has been discussed by Weintraub & Schimel (2005) and Sturm *et al*. (2005). Higher temperatures and deeper snow packs promote increased microbial activity, which in turn increases the availability of nutrients. The shrubs are able to utilize these more efficiently than other tundra plants. This temperature-nutrient boost works in both summer and winter.

The landscape pattern of shrub expansion (Fig. 4) lends support to this temperature-nutrient hypothesis. The most dramatic expansion of shrubs has taken place in those geomorphic units that undergo the most disturbance (i.e. channel margins and terraces), and where nutrients are most readily available. Disturbance and nutrient availability are known to be closely related (Chapin & Shaver, 1981; Ebersole & Webber, 1983; Walker & Walker, 1991; Forbes *et al*., 2001; Bockheim *et al*., 2003). With warming affecting all landscape positions in a similar fashion, those landscape positions where there tend to be more nutrients become the locations of the largest increase in shrubs (Fig. 6).

If we knew when the observed expansion of shrubs began, we could determine whether it has been solely the result of the well-documented warming of the last 30 years (Serreze *et al*., 2000), or whether it is part of a longer increasing trend. Unfortunately, plot and NDVI data extend back less than 30 years, and Col photo results provide only the average change over the past 50 years.

However, we can use Eqns (1) and (2) to roughly indicate when the expansion of large shrubs in northern Alaska began. To do this requires an *a priori* assumption as to the initial state of the tundra before the expansion began. We have assumed an initial 1% shrub-cover. A characteristic shared by all the curves in Fig. 10a is that if the slope of the curve is specified for a particular time and shrub fraction, then the initial point of the curve is fixed. In other words, we can use the curve to estimate when the shrub expansion began. The measured rate of expansion for the Col photo grid cells was 0.4%yr^{-1} at the mean shrub cover density of 17%. From Eqn (1), these values indicate that r equals 0.029, and from Eqn (2) and Fig. 10a, that the shrub expansion began about 100 years ago, or ca. 1875 (Fig. 10a, lower time scale). To be more conservative, we could assume that all of the observed change occurred in the latter half of the 50-year interval encompassed by the photo pairs (1950–2000), suggesting an intrinsic growth rate, r, of 0.058. Even in this case, the shrub expansion would have started ca. 1925 (Fig. 10a). In either case, the computations suggest a general expansion that began well before the current warming in Alaska (which started about 1970; see Serreze *et al*., 2000), although they do not preclude an acceleration since 1970. We conclude that the expansion predates the most recent warming trend and is perhaps associated with the general warming since the Little Ice Age (Overpeck *et al*., 1997).

Conclusions

Repeat photography from northern Alaska shows that large shrubs have increased in size and abundance over the past 50 years, colonizing areas where previously there were no large shrubs. Some of these same photographs show that smaller willow and birch shrubs have also been increasing, therefore, indicating an expansion of all major shrubs. A review of plot and remote sensing studies (using NDVI) (a) confirm that shrubs in Alaska have expanded their range and grown in size and (b) indicate that a population of smaller, intertussock shrubs not generally sampled by the repeat photography, is also expanding and growing. Combined these three lines of evidence allow us to infer a general increase in tundra shrubs across northern Alaska. The plot and remote sensing studies indicate shrubs are also expanding across much of arctic Canada and in Scandinavia, and possibly Russia and Siberia. Based on these results, we conclude that a pan-Arctic expansion of shrubs is underway. Disturbance and plant succession operate on a much smaller scale than the observed pan-Arctic expansion leading us to conclude that the change is a response to climate warming. The general expansion (at least in Alaska) seems to predate the recent (last 30 years) warming that has been experienced by much of the North, although this conclusion needs further corroboration. The implications of such a widespread shift in ecosystem architecture are profound, with changes in surface energy budget, carbon budget, hydrology and human activity all possible.

Acknowledgements

We thank our pilots Mike Worlick, Butch Case, and Ken Michaelis who flew us safely around the arctic at low altitude, putting up with multiple passes to 'get the photo right'. We thank VECO-Polar resources for their support, particular Naomi Whitty. Walt and Carl Tape helped in the field and in discussions. George Gryc, who was involved in the original Col photography, generously answered many questions. We thank Jerry Brown for having flight indices made for the photos. Betsy Sturm, Andi Lloyd, Jong Jia and Paul Grogan provided helpful comments on this paper. Two anonymous reviewers helped improve the text substantially. Lastly, we thank the unnamed Navy pilots and photographers who flew countless hours at low altitude to produce the original set of fine-art quality photographs. This work was supported by NSF Grant OPP-0119374.

References

ACIA, (2004) *Impacts of a Warming Arctic: Arctic Climate Impact Assessment*. Cambridge University Press, Cambridge.

Arendt AA, Echelmeyer KA, Harrison WD *et al*. (2002) Rapid wastage of Alaska Glaciers and their contribution to rising Sea level. *Science*, **297**, 382–386.

Beringer J, Chapin III FS, Thompson CD *et al*. (2005) Surface energy exchanges along a tundra-forest transition and feedbacks to climate. *Agricultural and Forest Meteorology*, **131**, 143–161.

Bockheim JG, O'Brien JD, Munroe JS *et al*. (2003) Factors affecting the distribution of *Populus balsamifera* on the north slope of Alaska, U.S.A. *Arctic, Antarctic and Alpine Research*, **35**, 331–340.

Bockheim JG, Walker DA, Everett LR *et al*. (1998) Soils and cryoturbation in moist Nonacidic and Acidic Tundra in the Kuparuk River Basin, Arctic Alaska, U.S.A. *Arctic and Alpine Research*, **30-2**, 166–174.

Bret-Harte S (2005) Tooled Lake plots, unpublished data, May 2005.

Brown J, Ferrians OJ, Heginbottom JA *et al*. (1997) *Circum-Arctic Map of Permafrost and Ground-Ice Conditions*. US Geological survey, Reston.

CAVM Team (2003) *Circumpolar Arctic Vegetation Map*. Scale 1 : 7 500 000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Chapin III FS, Shaver GR (1981) Changes in soil properties and vegetation following disturbance of Alaskan Arctic tundra. *Journal of Applied Ecology*, **18**, 605–617.

Chapin III FS, Shaver GR, Giblin AE *et al*. (1995) Responses of Arctic Tundra to experimental and observed changes in climate. *Ecology*, **76-3**, 694–711.

Conradie JK (2003) Modelling Population Dynamics of Leysera gnaphalodes in Namaqualand, South Africa, Ph.D. Thesis University of Pretoria, Pretoria.

Ebersole JJ, Webber PJ (1983) *Biological Decomposition and Plant Succession Following Disturbance on the Arctic Coastal Plain, Alaska Proceedingsof the fourth International Conference on Permafrost*. National Academy Press, Washington, DC pp. 266–271.

Emmel TC (1973) *An Introduction to Ecology and Population Biology*. Norton, New York.

Forbes BC, Erbersole JJ, Strandberg B (2001) Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems. *Conservation Biology*, **15**, 954–969.

Fung I (1997) A greener north. *Nature*, **386**, 659–660.

Gilbert H, Payette S (1982) Ecologie des populations d'Aulne Vert (*Alnus crispa* (Ait.) Pursh) a la Limite des Forets Quebec Nordique. *Geographie physique et Quaternaire*, **36-1-2**, 109–124.

Goetz SJ, Bunn AG, Fiske GJ *et al*. (2005) Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences*, **102-38**, 13521–13525.

Grogan P (2005) personal communication, April 2005.

Hinzman LD *et al*. (2005) Evidence and implications of recent climate change in Northern Alaska and other arctic regions. *Climatic Change*, **72**, 251–298.

Hollister RD, Webber PJ, Tweedie CE (2005) The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology*, **11**, 525–536.

Hope AS, Kimball JS, Stow DA (1993) The relationship between tussock tundra spectral reflectance properties and biomass and vegetation composition. *International Journal of Remote Sensing*, **14-10**, 1861–1874.

Jagerbrand AK (2005) *Subarctic bryophyte ecology: phenotypic variation and responses to simulated environmental change*. Ph.D. Dissertation, Gotenborg University.

Jia GJ, Epstein HE, Walker DA (2003) Greening of arctic Alaska, 1981–2001. *Geophysical Research Letters*, **30-20**, 2067.

Jia GJ, Epstein HE, Walker DA (2004) Controls over intra-seasonal dynamics of AVHRR NDVI for the Arctic tundra in northern Alaska. *International Journal of Remote Sensing*, **25-9**, 1547–1564.

Jorgenson J, Buchholtz CA (2005) Eighteen years of vegetation monitoring in the Arctic National Wildlife Refuge, Alaska. *Proceedings of the SEARCH Open Science Meeting*, 27–30 October, 2003, Arctic Research Consortium of the US, Fairbanks, AK.

Kingsland S (1982) The refractory model: the logistics curve and the history of population ecology. *Quarterly Review of Biology*, **57**, 29–51.

Kolbert E (2005) The climate of man. The New Yorker Magazine, Issue 2005-05-09.

Lantz T, Henry G (2005) personal communication, May 2005.

Lloyd AH, Rupp TS, Fastie CL *et al*. (2003) Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. *Journal of Geophysical Research*, **108-D2**, Alt 2, 1–15.

MacArthur RH (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Harper & Row, New York.

Mack MC, Shuur EAG, Bret-Harte MS *et al*. (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature*, **431**, 440–443.

McFadden JP, Chapin III FS, Hollinger DY (1998) Subgrid-scale variability in the surface energy balance of arctic tundra. *Journal of Geophysical Research*, **103-22**, 28947–28961.

Moffitt FH (1959) *Photogrammetry*, 2nd edn. International Textbook Company, Scranton, PA.

Myneni RB, Keeling CD, Tucker CJ *et al*. (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **38**, 698–702.

Myneni RB, Tucker CJ, Asrar G *et al*. (1998) Interannual variations in satellite-sensed vegetation index data from 1981 to 1991. *Journal of Geophysical Research*, **103-D6**, 6145–6160.

Nickels S, Furgal C, Castleden J *et al*. (2002) Putting the human face on climate change through community workshops. In: *The Earth is Faster Now: Indigenous Observations of Arctic Environmental Change* (eds Krupnik I, Jolly D), pp. 300–333. ARCUS, Fairbanks, AK.

Overpeck J, Hughen K, Hardy D *et al*. (1997) Arctic environmental change of the last four centuries. *Science*, **278**, 1251–1256.

Overpeck JT, Sturm M, Francis JA *et al*. (2005) Arctic system on trajectory to new, seasonally ice-free state. *EOS, Transactions, American Geophysical Union*, **86**, 1–5.

Payette S (2005) Personal Communication, May 2005.

Reed JC (1958) *Exploration of naval petroleum Reserve no. 4 and adjacent areas: Northern Alaska, 1944–53*. Geological Survey Professional Paper 301.

Rothrock DA, Zhang J, Yu Y (2003) The arctic ice thickness anomaly of the 1990s: a consistent view from observations and models. *Journal of Geophysical Research*, **108-C3**, 28: 1–10.

Serreze MC, Walsh JE, Chapin III FS *et al*. (2000) Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, **46**, 159–207.

Shabanov NV, Zhou L, Knyazikhin Y *et al*. (2002) Analysis of interannual changes in northern vegetation activity observed in AVHRR data from 1981 to 1994. *IEEE Transactions on Geoscience and Remote Sensing*, **40-1**, 115–130.

Shvartsman YG, Barzut VM, Vidyakina SV *et al*. (1999) Climate variations and dynamic ecosystems of the Arkhangelsk. *Chemosphere – Global Change Science*, **1**, 417–428.

Stow D, Daeschner S, Hope A *et al*. (2003) Variability of the seasonally integrated normalized difference vegetation index across the North Slope of Alaska in the 1990s. *International Journal of Remote Sensing*, **24-5**, 1111–1117.

Stow DA, Hope A, McGuire D *et al*. (2004) Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment*, **89**, 281–308.

Stroeve JC, Serreze MC, Fetterer F *et al*. (2005) Tracking the Arctic's shrinking ice cover: another extreme September minimum in 2004. *Geophysical Research Letters*, **32**, 1–4.

Sturm M, Douglas T, Racine R *et al*. (2005) Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research*, **110**, 1–13, doi 10.1029/2005JG000013.

Sturm M, McFadden JP, Liston GE *et al*. (2001) Snow-shrub interactions in Arctic tundra: a hypothesis with climatic implications. *Journal of Climate*, **14**, 336–344.

Sturm M, Perovich DK, Serreze M (2003) Meltdown in the North. *Scientific American*, October, 60–67.

Sturm M, Racine C, Tape K (2001) Increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.

Sturm M, Schimel J, Michelson G *et al*. (2005) Winter biological processes could help convert Arctic Tundra to Shrubland. *Bioscience*, **55-1**, 17–26.

Thorpe N, Eyegetok S, Hakongak N *et al*. (2002) The earth faster now: indigenous observations of Arctic environmental change. In: *Nowadays it is Not the Same* (eds Krupnik I, Jolly D), pp. 200–240. ARCUS, Fairbanks, AK.

Tucker CJ, Sellers PJ (1986) Satellite remote sensing of primary production. *International Journal of Remote Sensing*, **7-11**, 1395–1416.

van Wijk MT, Clemmensen KE (2004) Long-term ecosystem level experiments at Toolik Lake, Alaska and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, **10**, 105–123.

Wahren CHA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after eight years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**, 537–552.

Wahrhaftig C (1965) *Physiographic divisions of Alaska* US Geological Survey Professional Paper 482, US Geological Survey, 52 pp.

Walker DA, Walker MD (1991) History and pattern of disturbance in Alaskan Arctic Terrestrial Ecosystems: a hierarchical approach to analyzing landscape change. *Journal of Applied Ecology*, **28**, 244–276.

Weintraub MN, Schimel JP (2005) Nitrogen cycling and the spread of shrubs control changes in the carbon balance of the arctic tundra ecosystems. *BioScience*, **55**, 408–415.

Zhou L, Tucker CJ, Kaufmann RK *et al*. (2001) Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research*, **106-D17**, 20,069–20,083.