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Recent expansion of erect shrubs in the Low Arctic: evidence from Eastern Nunavik

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Abstract
In order to characterize shrub response near the treeline in Eastern Nunavik (Québec), a region under extensive warming since the 1990s, we compared two series (1964 and 2003) of vertical aerial photos from the vicinity of Kangiqsualujjuaq. Our study revealed a widespread increase in erect woody vegetation cover. During the 40 years spanning the two photo series, erect shrub and tree cover increased markedly on more than half of the land surface available for new colonization or infilling. Within the 7.2 km^2 analysed, areas with dense shrub and tree cover ($>90\%$) increased from 34% to 44% whereas areas with low cover ($<10\%$) shrank from 45% to 29%. This increase in cover of trees and shrubs occurred throughout the landscape regardless of altitude, slope angle and exposure, although to varying extents. The main shrub species involved in this increase was *Betula glandulosa* Michx. (dwarf birch), which was present in 98% and dominant in 85% of the 345 plots. In addition, numerous seedlings and saplings of *Larix laricina* (Du Roi) K Koch (eastern larch) were found above the treeline (25% of the plots), suggesting that the altitudinal treeline might shift upslope in the near future. Sites that remained devoid of erect woody vegetation in 2003 were either characterized by the absence of a suitable seedbed or by harsh local microclimatic conditions (wind exposure or excessive drainage). Our results indicate dramatic increases in shrub and tree cover at a Low Arctic site in Eastern Nunavik, contributing to a growing number of observations of woody vegetation change from various areas around the North.

Keywords: shrub expansion, repeat photography, *Betula glandulosa*, *Larix laricina*, forest–tundra ecotone, climate warming

1. Introduction

Land cover change is a major response of arctic and subarctic terrestrial ecosystems to climate warming (Levis *et al* 1999, Kittel *et al* 2000, Beringer *et al* 2005). Under warmer temperatures, open-tundra ecosystems will likely be colonized by tree and shrub species (Euskirchen *et al* 2009). In a recent review, Harsch *et al* (2009) found evidence of latitudinal or altitudinal treeline shifts in more than half of the sites monitored since the beginning of the 20th century. However, *in situ* evidence of erect shrub species expansion in response to climate is scarce, even though they represent one of the dominant functional vegetation groups in the Low Arctic.

Shrub expansion was first reported by Sturm *et al* (2001a) who compared different series of vertical photos taken about 50 years apart in Alaska. Since then, quantitative data on the extent and on the species associated with shrub cover increase in North America were reported for Alaska (Tape *et al* 2006, Dial *et al* 2007), Yukon (Myers-Smith 2011, Myers-Smith *et al* 2011), Mackenzie Delta Region, Northwest Territories

(Lantz *et al* 2009), western Nunavik (subarctic Québec, Ropars and Boudreau 2012) and the High Arctic (Hudson and Henry 2009, Hill and Henry 2011). In addition, decadal scale increased greenness at high latitudes has been documented by Normalized Difference Vegetation Index (NDVI) studies (Silapaswan *et al* 2001, Jia *et al* 2004, Verbyla 2008, Forbes *et al* 2010, Olthof and Pouliot 2010, Fraser *et al* 2011). However, these coarse scale approaches cannot distinguish between growth forms (shrubs or graminoids) or processes responsible for such changes.

The expansion of shrub species has been shown to be associated with climate warming or release from grazing pressure (Myers-Smith 2011). Several dendrochronological studies identified positive correlations between shrub radial growth and summer temperatures (Bär *et al* 2006, Forbes *et al* 2010, Hallinger *et al* 2010, Myers-Smith 2011, Blok *et al* 2011, Boudreau and Villeneuve-Simard 2012) while others identified winter temperature and snow cover as the most important climatic variables (Schmidt *et al* 2006, 2010, Rixen *et al* 2010, Hallinger *et al* 2010). Shrub species were also shown to respond positively to experimental warming (Chapin *et al* 1995, Chapin and Shaver 1996, Hobbie and Chapin 1998, Bret-Harte *et al* 2001, 2002, Van Wijk 2003, Jonsdottir *et al* 2005, Wahren *et al* 2005, Walker *et al* 2006, Elmendorf *et al* 2012). On the other hand, browsing and grazing are known to have notable impacts on shrub vegetation in Arctic Canada (Henry and Gunn 1991, Manseau *et al* 1996, Post *et al* 2009) and Fennoscandia or Siberian tundra (Speed *et al* 2011, Hofgaard *et al* 2010, Pajunen 2009). In fact, changing levels of browsing could inhibit shrub expansion (Olofsson *et al* 2009).

An increased shrub cover and stature (from prostrate or dwarfed to erect or tall) in arctic and subarctic regions could have consequences on many ecological factors (reviewed in Naito and Cairns 2011, Myers-Smith 2011). For example, shrub expansion could result in lower albedo (Chapin *et al* 2005, Sturm *et al* 2005a, Loranty *et al* 2011, Blok *et al* 2011), greater snow accumulation, deeper active layer and higher summer evapotranspiration (Sturm *et al* 2001a, Liston *et al* 2002, Pomeroy *et al* 2006, Strack *et al* 2007, Marsh *et al* 2010). Soil nutrient cycling could also be altered through changes in production and accumulation of woody material (carbon sequestration), through higher retention of windblown organic debris (Fahnestock *et al* 2000) and through warmer soil winter temperatures (Sturm *et al* 2001a, Myers-Smith *et al* 2011). Such changes could enhance decomposition (Grogan and Chapin 2000, Schimel *et al* 2004, Sturm *et al* 2005b) which could promote further shrub expansion.

To date, the nature and extent of erect shrub cover increase remains unknown for most of the arctic and subarctic regions of North America, and gaining actual knowledge of land cover change is essential to understand how high-latitude ecosystems will respond to current and future climate changes. In this letter, we quantified land cover change over the last 40 years in Eastern Nunavik (Low Arctic Québec). We compared erect woody vegetation cover (which includes both shrub and tree species) on old (1964) and recent (2003) vertical aerial photos of areas surrounding the village of Kangiqsualujjuaq. Vegetation surveys in the field were conducted to validate the results of the aerial photo analysis and to identify and characterize the shrub and tree species associated with the shrubification process.

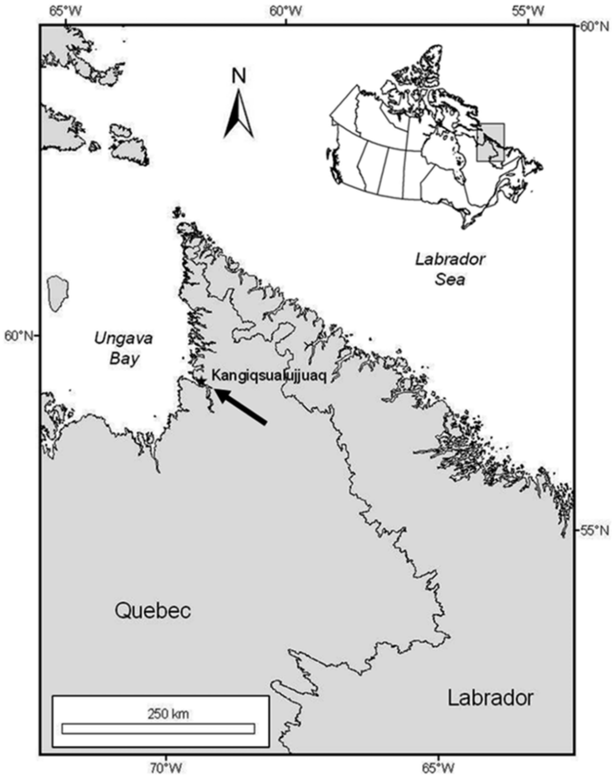

Figure 1. The study site near Kangiqsualujjuaq in Nunavik, (Low Arctic Québec, Canada).

2. Methods

The study was conducted near Kangiqsualujjuaq (58°42′39″ N–65°59′43″ W) in Eastern Nunavik (figure 1), a community located on the southeast side of Ungava Bay, about 25 km upstream from the mouth of the George River. We chose a study site in the forest–shrub tundra transition zone to investigate recent vegetation change, because changes in plant communities in response to climate change are expected to happen first in ecotones (Silapaswan *et al* 2001). All shrub growth forms are common in this region from prostrate species such as some berry producing plants to tall shrub species such as *Salix planifolia* Pursh. Two tree species are common, *Larix laricina* (du Roi) K Koch and *Picea mariana* (Mill.) BSP, but they are mainly restricted to valley bottoms.

Long-term climatic data (1948–2008) from the nearest available meteorological station at Kuujjuaq (160 km to the southwest) indicate a mean annual temperature of about −5.5 °C and mean annual precipitation of greater than 500 mm (Environment Canada 2011). A strong warming trend was recorded in the region over the last two decades (figure 2), consistent with observations from several other Canadian Eastern Arctic sites (Allard *et al* 2007). Short-term data available for the study area (1993–2008) are well correlated to those from Kuujjuaq (Pearson correlation coefficient of 0.98),

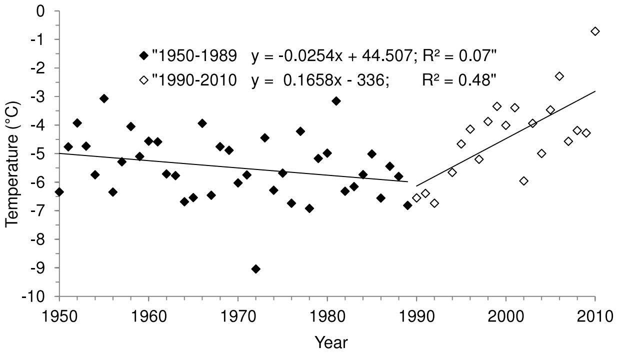

Figure 2. Mean annual temperatures recorded in Kuujjuaq (Québec, 58°06′ N–68°25′ W) for the period 1950–2010 (Environment Canada 2011).

with a difference in mean annual temperature of $<0.5\,^{\circ}\mathrm{C}$ between the two locations.

The landscape of the study area is dominated by steep sided flat-topped hills which do not exceed 300 m of altitude. Bedrock is archaean gneiss, with some quartzites and amphibolites (Paradis and Parent 2002). Vegetation varies greatly with altitude, grading from boreal–subarctic on protected lowlands to arctic on mid slopes and hilltop plateaus. Small expanses of closed-crown coniferous forests are found on valley bottoms and lower parts of hillsides, where trees as high as 20 m grow. At higher altitudes, tree density and height decrease progressively. Local treeline is generally found at 80 m asl, but on some well protected and favourably exposed valley sides, it may reach 150 m.

2.1. Erect woody vegetation change analysis

2.1.1. Aerial vertical photograph analysis. Comparative analysis was conducted on two series of vertical aerial photographs covering the community of Kangiqsualujjuaq and the surrounding area (5–6 km radius). The first series of aerial photographs date back to 6th August 1964. Monochrome contact prints at 1:15 000 and 20 000 scales were obtained from the National Air Photo Library of Natural Resources Canada. Additional 1964 photographs of the area are available mostly at 1:40 000 scale. The recent aerial photographs were taken 24th July 2003 and are at a 1:10 000 scale. Monochrome orthophotographs at a 0.25 m resolution of these 2003 photos were obtained from the Géoboutique Québec of the Ministère des Ressources naturelles et de la Faune, Québec. Digital orthorectified files of the 1964 prints were created at a 0.5 m resolution based on the georeferenced 2003 orthophotographs and a digital elevation model at a 2 m resolution (1 pixel = 4 m^2) generated using the vectorial data of the 1:50 000 maps of the area (24I12, 24I13, 24J09, 24J16). Third order polynomials and local spline adjustments were used to correct the image. Total area of overlap of the two photo series was 17 km^2, of which 14.3 km^2 was land surface and 13.2 km^2 were undisturbed by human activities and available for vegetation change analyses. More than half (55%) of this undisturbed area (7.2 km^2) was analysed for erect woody vegetation cover on the two photo series representing at least 30% of each environmental parameter class (see below). Shrub-covered areas on the orthophotos can be detected visually by their darker shade and distinct texture created by the foliage and the roundish aspect of each shrub seen from above (figure 3, figure A.1). Trees are easily detected by the triangular shape of their projected shade. However, in this study, we did not separate the increase of shrub cover from the increase in tree cover. As a consequence, the term erect woody vegetation cover will be used hereafter.

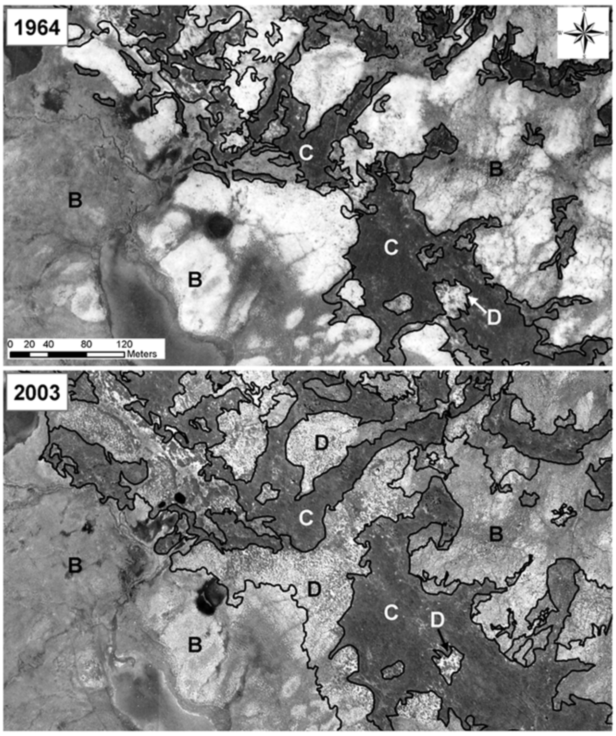

Figure 3. Portions of the 1964 and 2003 orthophotos showing examples of erect shrub cover for the three cover types: $<10\%$ (B for barren), discontinuous (D) and continuous (C). Darker shade of erect shrubs is easily seen in discontinuous and continuous areas, but distinct texture is most evident in the continuous cover polygons. Dark grey tones in the $<10\%$ erect shrub cover (barren) areas correspond to wet vegetation (fens) with dense mosses, herbs and prostrate shrub cover and some exposed gravel and boulders on better drained microsites. Top panel reprinted with permission from Natural Resources Canada 2012, courtesy of the National Air Photo Library (A18324-19 (1964-08-06)). Bottom panel reproduced with permission from Géoboutique Québec, Minstère des Ressources naturelles et de la Faune (24I12-1602 and 1702 (2003-07-23); © Government of Québec).

During analyses with ArcGIS (version 9.2 from ESRI), we used a stretched symbology with standard deviations as stretch type (‘n’ values between 1.5 and 2.5) for orthophoto display. Images were analysed by one observer and contours of surfaces covered by erect woody vegetation were traced, delimiting them inside polygons. Minimum area for these surfaces to be considered was fixed at 100 m^2 and contours were traced in order to encompass them in the smallest possible polygons. Analysis was thus kept at the smallest scale above the minimum area, enclosing the least possible non-shrub/tree-covered land inside the polygons. With this method, analysis was generally made at a view scale between 1:400 and 1:800. At first, surfaces covered by erect woody vegetation were classified in three vegetation types according

Table 1. Classes of environmental parameters as determined for the purpose of this study.

Environmental parameter	Class	Description
Altitude (m)	0–20	Coastal areas
	20–70	Valley bottoms and lower part of slopes
	70–120	Mid to upper slopes
	>120	Upper slopes and hilltop plateaus
Slope (deg)	0–5	Flatland to lowly inclined slopes
	5–15	Medium slopes
	15–30	Steep slopes
	>30	Very steep slopes and cliffs
Exposure	N	Northwest to northeast (315°–360° and 0°–45°)
	E	Northeast to southeast (45°–135°)
	S	Southeast to southwest (135°–225°)
	W	Southwest to northwest (225°–315°)

to observed cover patterns. Those with 90% cover or more were classified as 'continuous cover'. They presented dense shrubland and/or woodland with essentially no possibility of total cover increase (figure 3). Surfaces with cover between 10% and 90% were classified as 'discontinuous cover', displayed on the photos as patchy shrubs or shrub thickets and isolated or aggregated trees, all with a heterogeneous spatial distribution (figure 3). Surfaces that contained no erect woody vegetation or only very isolated individuals were classified as $<10\%$ shrub cover. We classified the limits of the discontinuous cover classes in such a way because of the difficulty in evaluating cover inside larger polygons with irregular contours.

To evaluate cover changes at a finer scale within the discontinuous cover zones, polygons were randomly selected for the following situations: (i) areas with a discontinuous erect woody vegetation cover in 2003 that were assigned to the $<10\%$ erect woody vegetation cover class in 1964 (50 polygons), (ii) erect woody vegetation cover change in areas assigned to the discontinuous cover class in both 1964 and 2003 (50 polygons each year) and (iii) areas with a discontinuous erect woody vegetation cover in 1964 that were assigned to the $>90\%$ cover class in 2003 (50 polygons). In each of these polygons, cover was evaluated in a randomly located 40 m × 40 m (1600 m^2) quadrat and categorized into one of four narrower cover classes spanning the whole interval of the discontinuous cover class: 10–30%, 30–50%, 50–70% and 70–90%. Mid cover class values were used to calculate mean cover per type. A Welch Two Sample *t*-test was performed to compare vegetation cover in discontinuous polygons in 1964 that remained discontinuous in 2003 (R Development Core Team 2011).

To identify the landscape types in which changes in erect woody vegetation occurred, we used the following variables: altitude, slope and exposure. The digital elevation model previously created was used to generate raster datasets of slope and exposure with ArcGIS. Four classes were created for each environmental variable. The four cardinal points were used as centroid of exposure classes (90° each). In the case of altitude and slope, the boundaries of the classes were fixed based on the natural breaks of the distribution of values as plotted with ArcGIS, and on their ecological significance (table 1). Raster datasets of these variables were extracted for each erect woody vegetation cover category ($<10\%$, discontinuous and continuous cover). The sum of pixels in each variable class was multiplied by pixel size (4 m^2) to obtain net surface occupied by erect woody vegetation and vegetation cover type in each class.

2.1.2. Field surveys. Prior to field sampling, areas where erect woody vegetation cover had changed was determined by superimposing and uniting the 1964 and 2003 polygons to extract new polygons. The three new polygon categories included: a change from the $<10\%$ erect woody vegetation cover class in 1964 to either discontinuous or continuous cover in 2003, or from discontinuous cover in 1964 to continuous cover in 2003, hereafter referred to as infilled areas. Each of these polygons was attributed values of altitude, slope and exposure based on mean value of these variables' classes within a given polygon.

A stratified random selection of the different new polygons was conducted for ground-truthing to ensure that each combination of vegetation cover types and environmental parameters was represented. All polygons located 20 m or less from disturbed areas were excluded from the sampling. The centroid of each polygon selected was computed with ArcGIS and used as the field plot location. To provide information on habitats which had not been colonized by erect woody vegetation, ten plots were randomly positioned inside areas assigned to the lower cover class on both 1964 and 2003 orthophotos. Each 78.5 m^2 ground-truthing circular plot (5 m radius) was described (general habitat, drainage, soil, natural and anthropogenic disturbance); height, cover and presence of seedlings, saplings and suckers were determined for each erect woody species and close-up photos were taken. Ground-truthing took place during the summer of 2008, from 17th July to 2nd September.

3. Results

3.1. Aerial vertical photograph analysis

In 1964, 325 ha of the study area was essentially devoid of erect woody vegetation while discontinuous and continuous cover occupied 149 and 246 ha (table 2). From 1964 to

Table 2. Changes in erect woody vegetation cover in the vicinity of Kangiqsualujjuaq (Nunavik, Québec) from 1964 to 2003 detailed by environmental parameter classes. Cover values represent analysed area occupied by either <10% cover, discontinuous (10–90%) or continuous (>90%) erect woody vegetation. (Note: 1964: cover evaluated on the 1964 aerial picture; 2003: cover evaluated on the 2003 aerial picture; Δ: percentage of change of the area occupied by the cover classes from 1964 to 2003; New: area assigned to the <10% cover in 1964 that was reassigned to either discontinuous or continuous cover; Lost to cont. or Gained from disc.: area assigned to the discontinuous cover in 1964 that was reassigned to a continuous cover in 2003.)

		<10% cover			Discontinuous					Continuous				
	Area (ha)	1964 (ha)	2003 (ha)	Δ (%)	1964 (ha)	New (ha)	Lost to cont. (ha)	2003 (ha)	Δ (%)	1964 (ha)	New (ha)	Gained from disc. (ha)	2003 (ha)	Δ (%)
Altitude (m)														
0–20	111	30	12	−60.0	15	12	−9	18	20.0	66	6	9	81	22.7
20–70	361	122	72	−41.0	78	42	−30	90	15.3	161	8	30	199	23.5
70–120	123	77	50	−35.1	31	22	−11	42	35.3	15	5	11	31	106.6
>120	125	96	77	−19.8	25	19	−3	41	64.0	4	0	3	7	75.0
Slope (deg)														
0–5	332	118	76	−35.6	63	37	−21	79	25.3	151	5	21	177	17.1
5–15	292	153	99	−35.3	65	45	−24	86	32.3	74	9	24	107	44.7
15–30	85	47	31	−34.0	19	12	−7	24	25.9	19	4	7	30	57.6
>30	11	7	5	−28.6	2	1	−1	2	0.0	2	1	1	4	100.0
Exposure														
North	105	42	28	−33.3	26	13	−7	32	23.0	37	1	7	45	21.9
South	306	148	92	−37.8	56	43	−25	74	32.2	102	13	25	140	37.5
East	82	47	36	−23.4	18	9	−6	21	16.4	17	2	6	25	47.3
West	227	88	55	−37.5	49	30	−15	64	30.6	90	3	15	108	20.2
Overall	720	325	211	−35.1	149	95	−53	191	28,1	246	19	53	318	29.5

2003, erect woody vegetation expanded substantially in the study area. New colonization was observed on land previously assigned to the lowest cover class. In fact, 95 and 19 ha of the <10% cover class in 1964 were reassigned respectively to discontinuous and continuous cover in 2003. As a result, the area occupied by the <10% cover class shrank to 211 ha over the period, now covering 29% of the study area compared to 45% in 1964 (figure 4). Newly colonized surfaces that were reassigned to the discontinuous cover class had a mean cover value of 37 ± 14%. Surfaces still devoid of erect woody vegetation in 2003 contained boulder fields, rock outcrops, exposed hilltop plateaus with abundant boulders and bare soil and sedge fens found mainly on valley floors and hillside nivation terraces.

Infilling occurred on surfaces for which erect woody vegetation cover was classified as discontinuous on the 1964 aerial photos. From 1964 to 2003, the area occupied by a discontinuous cover increased from 149 to 191 ha, even though 53 ha of the studied area classified as discontinuous in 1964 was re-classified as continuous in 2003 (table 2). The 1964 discontinuous cover surfaces that have remained in this cover class in 2003 have undergone partial infilling, with a significant increase in cover from 47 ± 18% in 1964 to 62 ± 12% in 2003 ($t_{86.684} = -4.7866$, $P < 0.001$). Finally, the area occupied by a continuous cover increased from 246 to 318 ha between 1964 and 2003. This increase resulted mainly from the infilling of sites initially classified as discontinuous (53 ha with a mean cover of 59 ± 18% in 1964), although new continuous cover (19 ha) was observed on previously shrubless and treeless surfaces.

Decreases in erect woody vegetation cover between 1964 and 2003 were observed infrequently (<10) on <1 ha surfaces. These decreases in cover were mostly associated with geomorphological disturbances such as landslides on steep talus along the George River.

3.2. *Cover change and altitude, slope and aspect*

The increase in erect woody vegetation cover was not spatially uniform at the landscape level. New colonization and infilling occurred for all environmental parameter classes, although to various extent (table 2). Decreases in the surfaces assigned to the lowest cover class (<10%) between 1964 and 2003 were inversely proportional to the altitude. For example, such areas shrunk by 60% in the lower altitudinal class compared to 20% in the higher one. Areas assigned to a discontinuous or continuous cover increased from 1964 to 2003 for all altitudinal classes with the relative increase being greater for both cover classes at higher altitudes (>70 m). Surfaces assigned to the lowest cover class (<10%) of erect woody vegetation showed similar relative decrease from 1964 to 2003, from 29% to 36%, for the different slope classes (table 2). Areas with a discontinuous cover increased from 1964 to 2003 for all slope classes but the steeper one, whereas areas with a continuous cover expanded for all slope classes, the increase being relatively higher as the slopes got steeper. Finally, new colonization and infilling of surfaces with an erect woody vegetation cover <10% was observed on all slope exposures, although it was somewhat lower on east-facing slopes (23%, table 2). Relative increase of areas with a discontinuous cover between 1964 and 2003 occurred mainly on south (32%) and west-facing slopes (31%), while the relative increase was higher on south (38%) and east-facing slopes (47%) for areas with a continuous cover.

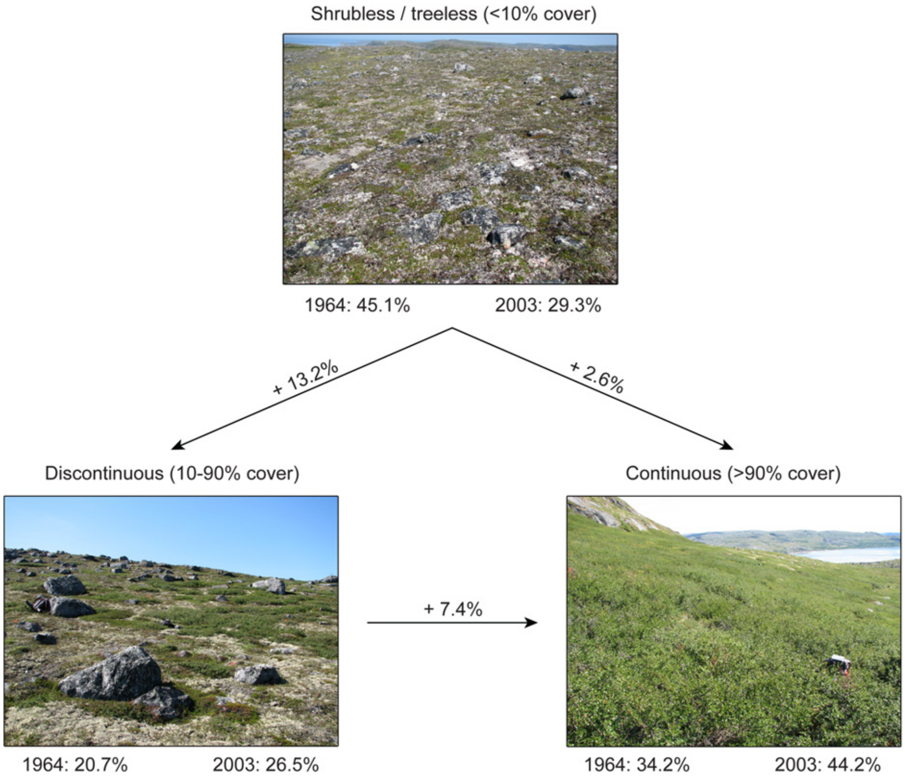

Figure 4. Changes in erect woody vegetation cover in the vicinity of Kangiqsualujjuaq (Nunavik, Québec) from 1964 to 2003 detected through comparative analysis of past and recent aerial vertical orthophotos. All values are in per cent and represent proportions of studied area. Arrows show direction of change from one vegetation cover type to another, accompanied by amount of change indicated above.

3.3. Field surveys

Field surveys revealed that cover increases detected by repeat photography were mostly due to shrub new colonization or infilling. *Betula glandulosa* Michx. (dwarf birch) was the most common and abundant erect shrub species in areas where changes were detected. This species was recorded in 98% of the 345 plots, dominated (highest cover value) the erect woody vegetation cover in 85% of the plots and had an average cover of 48% (figure 5). In fact, it was the only erect woody species found in 22% of the plots. Aside from *B. glandulosa*, *Salix planifolia* Pursh (diamondleaf willow), *Salix glauca* L. var. *cordifolia* (Pursh) Dorn (grayleaf willow), *Larix laricina* (Du Roi) K Koch (eastern larch) and *Rhododendron groenlandicum* (Oeder) Kron & Judd (Labrador tea) were also frequently observed (>20% of plots) but their mean cover was lower (<20%, figure 5).

Overall, more than 41% of the plots contained erect shrub seedlings, suggesting that the increase of erect woody vegetation cover might continue. Seedlings of *B. glandulosa* were recorded in more than 37% of the field survey plots (figure 6) and were usually found on bare mineral soil exposures related to cryoturbation such as frost boils. However, some seedlings were also observed through dense lichen cover (on palsas) or on wet brown moss beds over mixed organic and loam deposits (in fens). The only other shrub species for which seedlings were frequently observed was *R. groenlandicum* (>12% of the plots).

Seedlings and saplings of *L. laricina*, one of the dominant tree species at the landscape level, were found in about 25% of the plots (figure 6), with densities greater than 1 seedling m^{-2} in some plots. Most of the recruits were observed at low to mid-altitude sites (0–70 m) in valley sides above the current altitudinal treeline or in lowland openings (palsa summits). In comparison, seedling and sapling abundance of *Picea mariana* (Mill.) BSP (black spruce), the only other tree species present at the study site, was much lower and was recorded in <4% of the plots, all located at low altitude.

4. Discussion

Comparative analysis of old and recent aerial vertical photos of land surface surrounding the village of Kangiqsualujjuaq indicates a substantial increase of erect woody vegetation cover between 1964 and 2003. These findings are consistent with regional-scale NDVI analysis (Fraser *et al* 2011, McManus *et al* 2012) and other studies using repeated pairs of aerial vertical or oblique photographs in different regions of subarctic North America (Sturm *et al* 2001a, Tape *et al* 2006, Ropars and Boudreau 2012). However, the processes underlying the observed *shrubification* are still unclear because several changes in the abiotic or biotic environments could have triggered this phenomenon. Here, we first compare our results to other studies which have looked at recent shrub expansion in subarctic and arctic ecosystems before discussing the potential role of climate change and large herbivores on the phenomenon.

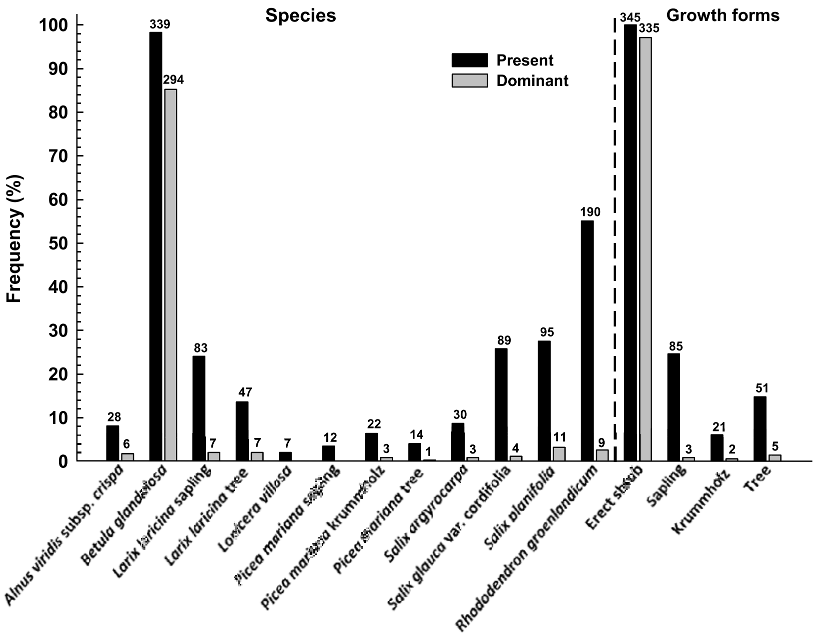

Figure 5. Proportion of total ground-truthing plots ($n = 345$) where each erect shrub and tree species is present, and where each species dominate the erect woody vegetation cover. Proportions are also shown by growth form (erect shrub, krummholz, tree) and stage (sapling). Straight *Picea mariana* ≥ 2.5 m high (Lescop-Sinclair and Payette 1995) and *Larix laricina* > 5 m high are considered as trees; they are considered as saplings below these values. *L. laricina* does not form krummholz in the study area. Number of plots is given above bars.

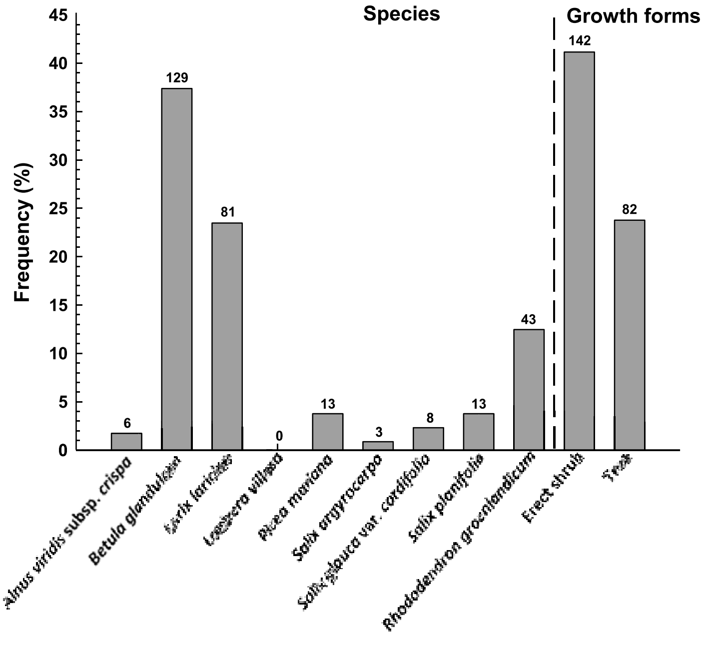

Figure 6. Proportion of total ground-truthing plots ($n = 345$) where seedlings of erect shrub species as well as seedlings and/or saplings of tree species occur. Proportions are also shown by growth form. Height for *Picea mariana* to be considered as a sapling was ≤ 2.5 m with a straight growth and ≤ 5 m for *Larix laricina*. Number of plots is given above bars.

4.1. *Betula glandulosa: a key species for shrub expansion near Kangiqsualujjuaq*

Field surveys have shown that the recent increase of erect woody vegetation reported in this study was associated with the expansion of *B. glandulosa*, which is probably the most abundant erect shrub in the Canadian Eastern Low Arctic. Ropars and Boudreau (2012) also reported an increase of this species in the Boniface River area in western Nunavik. *B. glandulosa* was previously identified by Tape *et al* (2006) as one of the key species in the pan-arctic shrub densification. It has a wide ecological niche, occurring in all types of habitats, from wet and peaty to dry, rocky and exposed environments. Growth of *B. glandulosa* has been shown to be associated with the thermal sum received during the growing season (Boudreau and Villeneuve-Simard 2012) and to increase in response to experimental warming in a birch hummock tundra community in the Northwest Territories (Grogan 2008). Similar response to simulated climate warming was observed for a closely related birch species, *Betula nana* L. (arctic dwarf birch), in Iceland and Alaska (Jonsdottir *et al* 2005, Wahren *et al* 2005). The growth response of *B. nana* appears to be linked to its ability to produce both long and short shoots and to its developmental plasticity in secondary growth (Bret-Harte *et al* 2001).

The contribution of other shrub species to the increase in shrub cover in the study area was low. Most *Salix planifolia* and *Salix argyrocarpa* Anderss. (Labrador willow) stands were observed in the field inside polygons located on lowland peaty soil and alluvium for which shrub cover appear to have increased only slightly over the last decades. Unlike in Alaska where it played an important role in shrub expansion (Sturm *et al* 2001b, Tape *et al* 2006), *Alnus viridis* (Chaix) DC. *sensu lato* (green alder) was mainly restricted to favourably exposed slopes along the George River where some thickets have expanded and seedlings were observed.

The high number of *L. laricina* seedlings and saplings, which might lead to a treeline shift in a near future, contrasts with previous report of low *L. laricina* density above treeline along the Leaf River, on the west side of the Ungava Bay (Morin and Payette 1984). In 1984, the authors concluded that climate warming since the end of the Little Ice Age had probably resulted in the consolidation of pre-existing tree populations rather than in altitudinal expansion. Considering the accelerated warming of many arctic areas in recent years, the situation might have changed and *L. laricina* could be increasing in abundance in this region.

4.2. Processes underlying shrubification: climate change, caribou and anthropogenic disturbances

Although not spatially uniform, the observed expansion of erect woody vegetation was detected in all landscape types, suggesting that the environmental change which triggered the densification or colonization of new sites by shrub and tree species, was at least regional in scale. No evidence of anthropogenic disturbances that could explain such expansion was observed during the ground-truthing exercise. It is most likely that warmer temperatures since the beginning of the 1990s (figure 2), probably accompanied by a lengthening of the growing season, is the dominant factor explaining the expansion of erect woody vegetation in the study area. Repeated ground photos (1988 and 2008) taken in the vicinity of the village suggest that shrub expansion occurred mainly over the last two decades (figure 7), the period of the greatest climate warming (figure 2).

Aside from climate, caribou disturbance at the landscape scale could have triggered or inhibited erect woody vegetation increase. The study area is located in the summer range of the George River Caribou Herd (GRCH) which occupies the eastern half of Nunavik (Couturier *et al* 2004). Decreased ground cover and leaf biomass of *B. glandulosa* in grazed stands has been shown in calving grounds on either side of the George River (Manseau *et al* 1996). Although erect shrub growth and expansion can be constrained to some extent during periods of high caribou abundance, grazing pressure release after the sudden demographic downfall of the GRCH in the 1990s (Boudreau *et al* 2003) cannot solely explain the observed shrubification in this region. The GRCH population estimates were higher in 2001 (385 000 ± 28.0%; Couturier *et al* 2004) than in 1964 (about 62 000; Messier *et al* 1988) when the aerial vertical photos used in this study were taken. On the other hand, the partial or complete destruction of the lichen cover observed in the GRCH summer range (Manseau *et al* 1996, Morneau and Payette 1998, Boudreau and Payette 2004a, 2004b, Théau and Duguay 2004) might have favoured *B. glandulosa* recruitment. Our field work around Kangiqsualujjuaq has shown that *B. glandulosa* seedlings are more abundant on mineral or organic bare soil. We cannot separate the influences of climate warming and changing caribou disturbance, and it is likely that both these factors are related to the observed woody vegetation increase in the Kangiqsualujjuaq region.

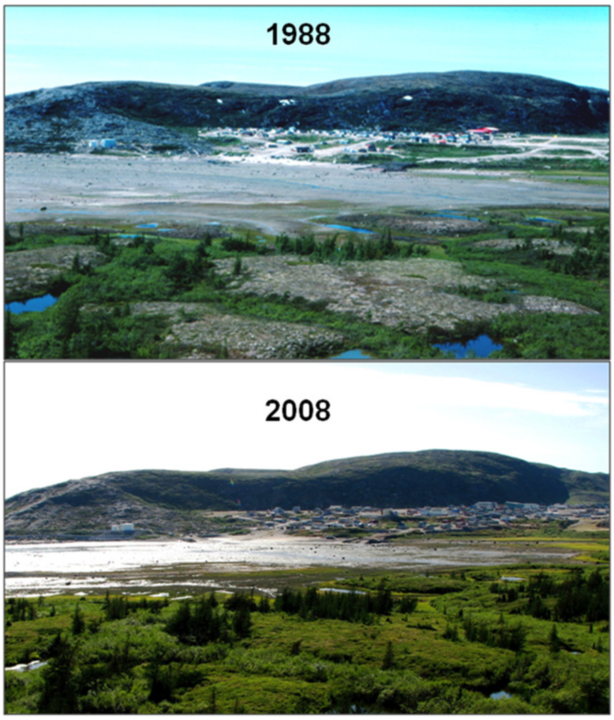

Figure 7. Repeat ground photography of a landscape near Kangiqsualujjuaq. View is from the east side of Akilasakallak Bay and shows substantial colonization of palsa summits by erect shrubs and trees in only 20 years. The 1988 photo was provided by Marcel Blondeau and was taken at the end of July. The 2008 photo was taken 7th August.

5. Conclusions

We observed a substantial erect woody vegetation increase in the vicinity of Kangiqsualujjuaq for the period 1964 to 2003. Sites previously devoid of erect woody vegetation underwent colonization by erect shrubs and/or trees and pre-existing erect shrub or tree stands underwent partial or total infilling. The shrub *B. glandulosa* was the most abundant woody species in the areas undergoing vegetation change. The high frequency of erect shrub seedlings and *L. laricina* saplings observed in the field suggests that colonization and infilling are ongoing processes. Further expansion is therefore expected, especially of *B. glandulosa*, if favourable climatic conditions persist. How climate warming, caribou disturbance and other ecological processes interact to determine woody vegetation changes across the landscape remain uncertain. Identifying the determinants of the observed land cover change, including shrub and tree recruitment and growth will improve estimates of feedbacks to climate warming and future vegetation change in subarctic terrestrial ecosystems.

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Appendix

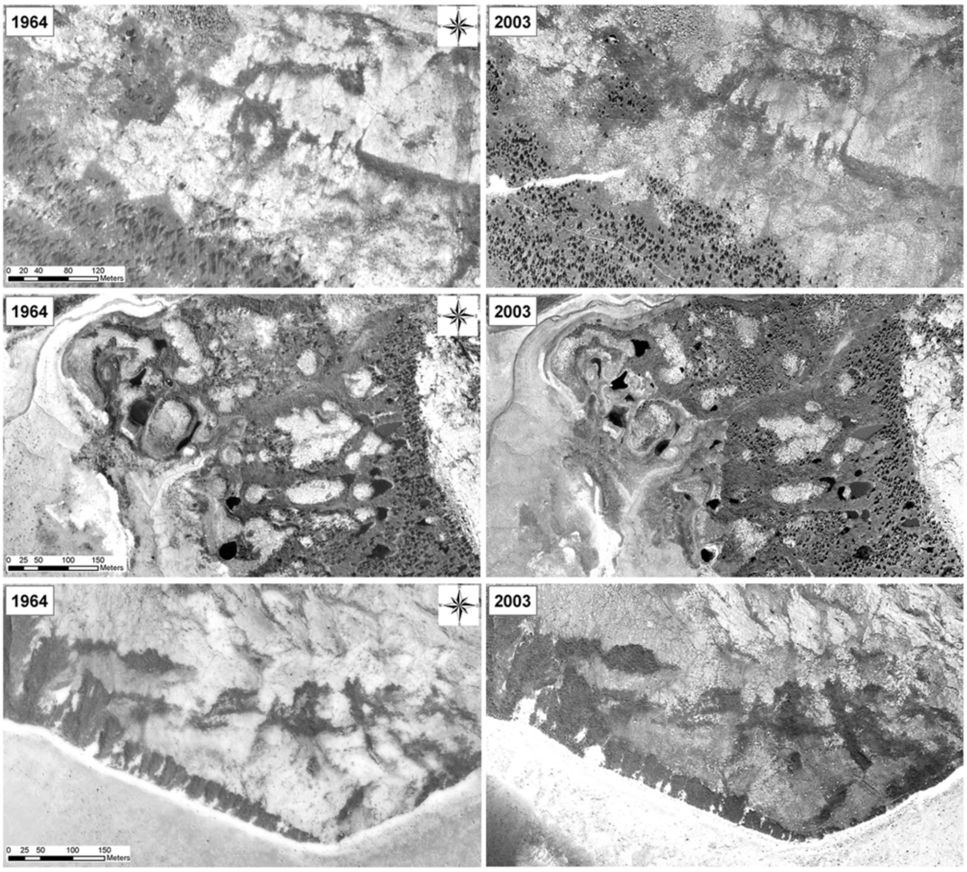

Figure A.1. Portions of the aerial photos (1964 and 2003) used to evaluate erect woody vegetation cover change in the study area, near Kangiqsualujjuak (Nunavik, Québec). Erect shrub and/or tree cover increase can be clearly seen in each 2003 photo compared with its associated 1964 photo. Left panels reprinted with permission from Natural Resources Canada 2012, courtesy of the National Air Photo Library (A18324-11, 13, 19 (1964-08-06)). Right panels reprinted with the permission of Géoboutique Québec, Ministère des Ressources naturelles et de la Faune (24I12-1502, 1603 and 1604 (2003-07-23); © Government of Québec).

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