

LETTER

Shrub expansion at the forest–tundra ecotone: spatial heterogeneity linked to local topography

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Shrub expansion at the forest–tundra ecotone: spatial heterogeneity linked to local topography

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Abstract

Recent densification of shrub cover is now documented in many Arctic regions. However, most studies focus on global scale responses, yielding very little information on the local patterns. This research aims to quantify shrub cover increase at northern treeline (Québec, Canada) in two important types of environment, sandy terraces and hilltops (which cover about 70% of the landscape), and to identify the species involved. The comparison of a mosaic of two aerial photographs from 1957 (137 km²) and one satellite image taken in 2008 (151 km²) revealed that both hilltops and terraces recorded an increase in shrub cover. However, the increase was significantly greater on terraces than on hilltops (21.6% versus 11.6%). According to ground truthing, the shrub cover densification is associated mainly with an increase of *Betula glandulosa* Michx. The numerous seedlings observed during the ground truthing suggest that shrub densification should continue in the future.

Keywords: *Betula glandulosa*, climate change, forest–tundra ecotone, shrub expansion, topography

1. Introduction

Arctic and subarctic regions have been subjected to important changes over the last few decades (IPCC 2007a). Among the rapid changes observed, Myneni *et al* (1997, 1998) were the first to report evidence of the pan-Arctic increase in vegetation cover. By analysing worldwide NDVI trends between 1981 and 1991, they showed that the greatest increase in photosynthetic activity occurred in regions above 50°N. Since then, this phenomenon has been observed for different regions (Alaska: Silapaswan *et al* 2001, Jia *et al* 2003, Verbyla 2008; Russia: Forbes *et al* 2010; Western Canada: Olthof and Pouliot 2010), over a longer time span (≥ 20 y: Jia *et al* 2003, Goetz *et al* 2005, Verbyla 2008, Forbes *et al* 2010, Olthof and Pouliot 2010) and at a better resolution (Jia *et al* 2003, Olthof and Pouliot 2010). Moreover, recent NDVI studies revealed that the increase in photosynthetic activity is more important in regions dominated by erect shrub species (Raynolds *et al*

2006), a result corroborated by the comparison of aerial photographs and satellite images which reported an increase in shrub cover in Alaska (Sturm *et al* 2001, Tape *et al* 2006) and northern Québec (Tremblay 2010).

Changes in shrub cover in Arctic and subarctic regions are however likely to be spatially heterogeneous. In these regions, minor differences in the abiotic environment could translate into important differences in shrub survival, growth and reproduction. Local topography, one of the most influential features at the landscape level (Shaver *et al* 1996), will influence variables such as snow accumulation, duration of the snow cover (Sonesson and Callaghan 1991, Shaver *et al* 1996), nutrient availability (Shaver *et al* 1996), soil moisture (Schimel *et al* 1999) and soil temperature (Romanovsky and Osterkamp 1995), which can all have major impacts on plant growth and recruitment. An increase in shrub cover could then be a function of the different topographic features of the landscape. Such observations have been reported in northern

Alaska (Tape *et al* 2006), where shrub cover increase was more important on hill slopes, in valleys and on south-facing slopes. However, most of the studies used a spatial scale that does not provide insights on the importance of the local topography for shrub densification. Temporal NDVI analyses use NOAA–AVHRR (National Oceanic and Atmospheric Administration–Advanced Very High Resolution Radiometer) satellite images with, at best, a 1 km² resolution (Jia *et al* 2003, Olthof and Pouliot 2010). Furthermore, the NDVI reflects the change in photosynthetic activity without any distinction of the taxa implied. As the shrub cover increases in many Arctic and subarctic regions (ACIA 2005, IPCC 2007b), it becomes necessary to understand how and where the changes occur. A better understanding of the importance of the local topography on the response of shrub communities is therefore important to refine our ability to predict future response of shrub communities to climate change.

The objective of this study was to quantify the change in shrub cover in subarctic western Québec over the last 50 yr, if any. Specific objectives were (1) to determine if shrub cover has increased, (2) to identify the species implied in the cover change, and (3) to determine if the extent of the change varies with the local topography (hilltops and terraces). Based on current knowledge, we hypothesized that there has been a non-uniform increase in shrub cover in the studied area, mostly attributable to *Betula glandulosa* Michx., the main erect shrub species.

2. Methods

2.1. Study area

The study area is located near the Boniface River research station (57°45'N, 76°20'W), 35 km east of Hudson Bay and 10 km south of the treeline in subarctic Québec, Canada (figure 1). The region is located in the shrub subzone of the forest–tundra ecotone (Payette 1983), where black spruce (*Picea mariana* (Mill.) B.S.P.) is the main tree species and dwarf birch (*Betula glandulosa* Michx.) dominates the shrub layer. At the regional scale, shrub–lichen tundra is the dominant community, covering approximately 70% of well-drained sites (Payette *et al* 2008). This vegetation type is found mainly on slopes and exposed hilltops along with spruce–lichen woodlands. The forested stands are confined to more mesic environments, and are remnants of a once more extensive forest (Payette and Morneau 1993). Fires were frequent during the Holocene period (Payette *et al* 2008), but were rather scarce over the last millennium due to cooler and wetter climatic conditions (Filion 1984). More recently, trampling from the Leaf River Caribou Herd (*Rangifer tarandus* L.) exposed mineral soil over substantial areas. Browsing evidence was however mostly observed on *Salix* species.

The nearest weather station (Inukjuag Meteorological Station, 58°28'N, 78°05'W) recorded an annual mean temperature of −7 °C for the 1970–2000 period, with the highest and lowest mean monthly temperatures recorded in July (10.2 °C) and February (−25.2 °C), respectively (Environment Canada 2010). Over this period, annual precipitation

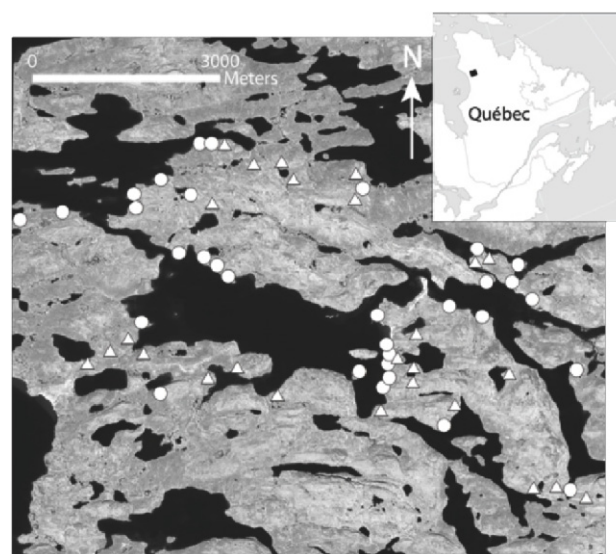


Figure 1. Satellite image of the Boniface River region at the forest–tundra ecotone in subarctic Québec. The terraces (circles, 33) and hilltops (triangles, 26) used in this study are identified on the map. The study region is located at the forest–tundra ecotone, about 10 km south of the treeline.

averaged 460 mm, of which 44% fell as snow (Environment Canada 2010). The temperature trend in the region has changed considerably over the last 50 years. Between 1969 and 1993, the region experienced a cooling trend at a rate of −0.03 °C yr^{−1} while a warming trend (+0.09 °C yr^{−1}) was observed afterwards. This rapid change in temperature was also recorded for most of northern Québec (Chouinard *et al* 2007).

2.2. Ortho-photo analyses

Change in shrub cover was evaluated through the comparison of two aerial photographs and a satellite image taken in July 1957 and 2008, respectively (figure 2). The 2008 image is a WorldView-1 Standard Ortho-Ready panchromatic satellite image taken on 15th July and covers 151 km². The 1957 photos are two adjacent 9" × 9" aerial photos produced from high quality negatives stored at the National Air Photo Library of Canada and covering an area of 137 km² (taken on 29th July, 1:40 000). Aerial photos were scanned at 1200 dpi for further analysis.

Aerial photographs and the WorldView image were orthorectified in order to remove topographic distortions. The WorldView image was first reprojected into UTM 18 N, NAD 1983 and orthorectified using PCI Geomatics V.10.3 software, resulting in a 0.5 m ortho-photo. The 1957 image was then rigorously matched to the 2008 image. A 15 m resolution digital elevation model (DEM) of the study region generated by Natural Resources Canada was used as an elevation input. These manipulations were performed with the ALTA Photogrammetry Suite 7 software and resulted in a 1 m resolution 1957 ortho-photo. The spatial lag between the two ortho-photos is <1 m. From here on, the satellite image and aerial photos are both referred to as ortho-photos.

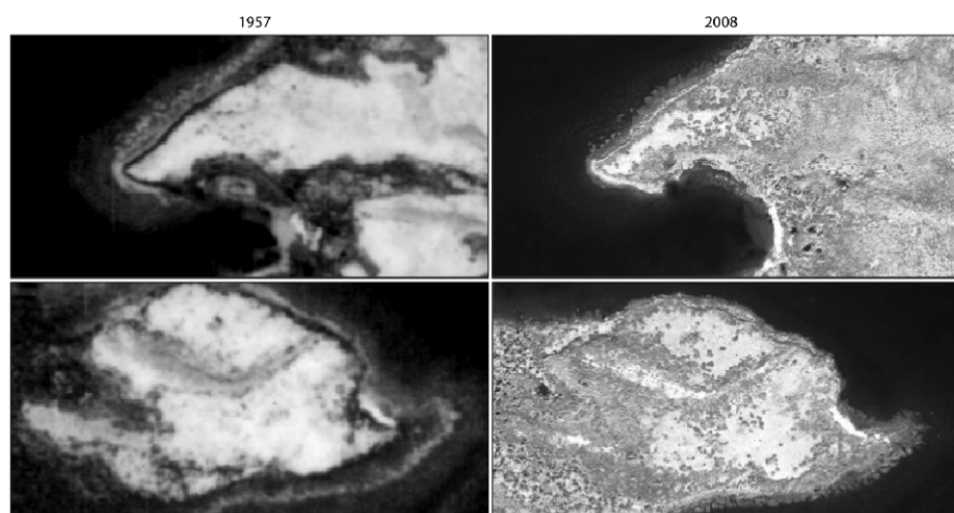


Figure 2. Portions of the aerial photos (1957) and WorldView-1 satellite image (2008) used to evaluate shrub cover in the study area.

In general, erect shrub species were easily detected by their darker shade and the roundish aspect of each individual (figure 3), while trees were recognized by the triangular shape of their projected shade. Pale areas were mostly characterized by lichen and graminoid vegetation. Therefore, shrub cover identification was based on both the pixel colour and the texture of the ortho-photo. Preliminary observations of both ortho-photos suggested that the analyses should be restricted to non-forested, well-drained sites, because shrub cover was difficult to accurately evaluate between trees and in wetlands, riparian ecosystems and snowbeds. These well-drained, non-forested sites, which cover about 70% of the landscape, are characterized by hilltops and sandy terraces. Hilltops are characterized by the presence of Arctic–alpine species and exposed mineral soil. Sandy terraces, located on the river’s margin, are low altitude sites dominated by shrub, lichen and herbaceous species. Prior to the field season, the 113 km² overlapping zones of the two ortho-photos were scrutinized to identify potential sites belonging to either hilltop or terrace. Once in the field, 59 of the 106 pre-identified sites were selected to evaluate shrub cover change from 1957 to 2008 (26 hilltops and 33 terraces, table 1). Sites were excluded when they did not correspond with the given definition of one of the two environments and/or were not easily accessible by foot from the river. On average, exposed hilltops and terraces covered 1.2 ha and 1.1 ha, respectively. The 59 sites covered a total area of 671.7 ha (13.8% of the total well-drained non-forested area of the study area).

In the laboratory, the transects used for the ground truthing (see section 2.3) were located on the ortho-photos for each of the 59 study sites. Subsequently, the analysed area for each site, ranging from 0.4 to 2.1 ha, was delimited with ArcGIS 9.3 (by ESRI; figure 4) in order to encompass the transects but to exclude areas not relevant for shrub cover photo-interpretation (water bodies, forested area, etc). A grid consisting of a series of 16 m²-cells (4 m × 4 m) was then overlaid on both ortho-photos. Inside the analysed area, shrub

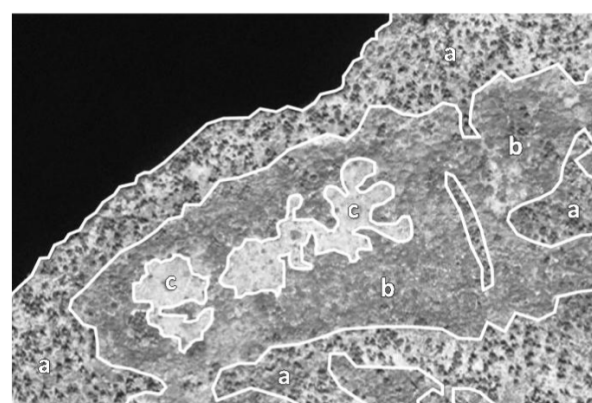


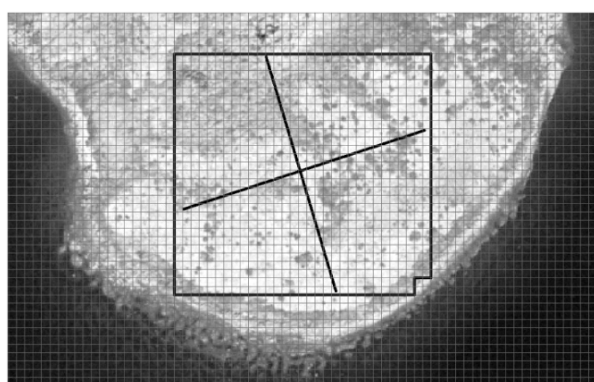
Figure 3. Detail of the 2008 ortho-photo showing (a) tree-covered areas, (b) shrub-covered areas, and (c) open areas mostly colonized by lichens, herbaceous species and some shrubs.

cover was estimated within each cell (see table 1 for additional information on the number of cells per site) and assigned to one of the following cover classes: (1) 0%, (2) 1–25%, (3) 26–50%, (4) 51–75%, and (5) 76–100%. Total shrub cover for each site was calculated for both ortho-photos by averaging the median value of the cover class assigned to each cell. Shrub cover change over the last 50 yr was then calculated as the difference in shrub cover between 2008 and 1957. Moreover, the delta value was calculated for each cell as the difference between the cover class assigned in 2008 and 1957. The evaluation of shrub cover was carried out by the same observer for every site and was recorded in Excel tables with respect to the spatial position of each cell.

Rather than degrading the 2008 ortho-photos to match the resolution of the 1957 ortho-photo, we decided to conduct the analyses at the finest resolution for each ortho-photo (1 m and 0.5 m for 1957 and 2008, respectively) in order to retain as much information as possible. However, to evaluate if different resolutions could influence shrub cover evaluation, we conducted a supplemental analysis for ten sites after having degraded the 2008 ortho-photo to a 1.0 m resolution

Table 1. Description of the 59 sites studied. The transects correspond to the total length of the linear surveys in the field (sum of the four transects).

Site	Terraces						Site	Hilltops					
	Altitude (m a.s.l.)	Length (m) ^a	Width (m) ^a	Area (ha)	Number of cells ^b	Transects (m) ^c		Altitude (m a.s.l.)	Length (m) ^a	Width (m) ^a	Area (ha)	Number of cells ^b	Transects (m) ^c
1	118.6	124	116	1.4	895	240	11	125.8	120	116	1.3	840	240
2	120.2	104	100	1.0	650	240	28	129.8	120	132	1.5	907	235
3	119.6	172	128	2.1	1302	240	29	135.7	112	108	1.2	732	240
4	118.9	108	100	0.9	554	240	30	134.7	108	100	1.0	673	240
5	115.1	112	92	0.9	588	220	31	128.7	112	92	0.9	583	240
6	113.0	124	108	1.0	646	239	32	139.5	120	116	1.4	847	240
7	115.9	100	104	1.0	595	240	34	123.5	112	112	1.0	632	240
8	122.0	116	112	1.3	804	240	36	122.9	116	112	1.2	720	240
9	116.1	120	92	0.8	525	210	38	126.9	120	116	1.4	870	240
10	116.0	84	100	0.7	432	205	42	151.8	108	112	0.9	579	240
12	115.8	124	72	0.8	518	190	43	131.0	120	116	1.2	725	240
13	114.2	124	92	1.0	628	240	45	121.8	112	68	0.5	282	185
14	121.0	124	100	1.1	713	240	48	123.0	116	116	0.9	555	240
15	118.6	120	136	1.6	1002	240	52	140.7	68	108	0.6	369	230
17	118.4	120	112	1.2	767	240	55	140.0	116	120	1.3	828	240
33	135.6	120	120	1.2	764	240	56	132.5	116	120	1.2	740	240
37	117.0	112	116	1.2	774	240	59	147.6	112	112	1.1	678	240
41	132.4	96	100	1.0	600	240	88	120.9	116	136	1.5	942	240
46	114.1	120	104	1.0	649	223	90	129.6	120	100	1.1	716	221
47	115.9	124	104	1.2	737	230	97	142.8	120	112	1.3	840	240
49	119.5	128	116	1.2	750	240	98	137.2	120	112	1.3	830	240
50	121.9	124	112	1.3	805	240	99	135.1	116	116	1.3	787	240
51	122.9	120	116	1.2	741	240	100	142.7	116	116	1.3	813	240
58	125.2	96	80	0.6	378	197	102	142.3	120	120	1.4	819	240
86	125.4	112	120	1.3	801	225	103	135.8	112	112	1.3	784	240
87	118.5	120	120	1.2	764	240	106	137.0	120	112	1.3	840	240
89	115.7	116	52	0.4	274	166							
91	122.2	128	104	1.3	808	240							
94	127.6	112	112	1.2	775	240							
95	116.0	112	104	1.1	665	240							
96	120.2	108	96	0.9	585	240							
101	122.9	116	104	1.1	672	225							
105	124.7	116	116	1.2	774	240							

^a Maximal length and width of the site.^b Number of cells analysed on the ortho-photos.^c Total length of the linear surveys in the field (sum of four transects).**Figure 4.** Satellite image of a sandy terrace (site 1) over which a 16 m²-cell grid was overlaid. The two perpendicular lines represent transects along which linear surveys were conducted. Outer black line shows the site's perimeter.

(Aggregate tool in ArcGIS, which uses cubic convolution resampling). Shrub cover evaluations for both the degraded and non-degraded 2008 ortho-photos were compared.

2.3. Ground truthing

An extensive ground truthing was carried out in order to identify which species were implicated in the shrub cover change, if any, and to evaluate our accuracy in evaluating shrub cover on the 2008 ortho-photo. At each site, four 60 m transects were delimited, when possible, from the centre of the site and extended respectively towards the four cardinal points (N, E, S, W; figure 4). For 17 sites however, some transects were shorter due to the smaller size of the site (see table 1). The position of each transect was determined with a high-precision GPS (Leica, Model GS20, ± 30 cm). Tree and shrub species were recorded at every centimetre along the transects. Each species cover could then be calculated for each site by dividing the number of centimetres on which it was recorded by the total number of centimetres surveyed.

To determine our accuracy in evaluating shrub cover on the 2008 ortho-photo, we conducted an additional photo-interpretation analysis. We overlaid a 1 m²-cell grid over the 2008 ortho-photo (at 5 hilltop sites and 5 terrace

Table 2. Shrub cover change results for terraces (33 sites) and hilltops (26 sites).

Terraces				Hilltops			
Site	Shrub cover 1957 (%)	Shrub cover 2008 (%)	Change (%)	Site	Shrub cover 1957 (%)	Shrub cover 2008 (%)	Change (%)
1	16.0	32.1	16.1	11	20.8	44.7	23.9
2	12.5	27.8	15.3	28	22.5	46.0	23.5
3	10.0	38.2	28.2	29	33.0	40.5	7.4
4	8.2	55.6	47.4	30	35.6	44.3	8.7
5	24.6	45.7	21.2	31	36.0	47.0	11.0
6	11.3	49.6	38.3	32	31.5	34.9	3.4
7	29.7	50.1	20.4	34	39.1	59.2	20.1
8	25.6	60.5	34.9	36	38.4	45.2	6.8
9	26.6	43.7	17.1	38	41.6	44.8	3.2
10	30.0	46.8	16.8	42	50.4	46.1	−4.3
12	43.0	62.7	19.8	43	43.6	52.9	9.3
13	40.8	57.2	16.4	45	45.8	57.3	11.4
14	27.3	48.8	21.5	48	42.6	41.6	−1.1
15	38.9	57.6	18.7	52	46.7	47.8	1.1
17	25.2	50.7	25.5	55	48.8	47.6	−1.2
33	27.4	63.5	36.1	56	40.8	49.5	8.8
37	41.4	35.5	−5.9	59	39.3	49.3	10.0
41	51.9	44.9	−7.0	88	31.5	40.1	8.6
46	42.9	64.2	21.3	90	33.7	51.6	17.8
47	19.1	49.7	30.6	97	28.6	44.8	16.1
49	25.0	45.4	20.4	98	22.5	49.4	26.9
50	27.4	49.0	21.6	99	30.9	50.2	19.3
51	48.2	56.9	8.7	100	31.5	49.6	18.1
58	45.0	58.4	13.4	102	29.7	45.1	15.4
86	39.9	50.2	10.3	103	19.9	48.6	28.7
87	44.1	55.4	11.4	106	33.2	42.3	9.1
89	33.9	57.4	23.5				
91	31.6	50.0	18.4				
94	14.8	52.7	37.8				
95	11.2	51.4	40.2				
96	16.7	56.6	39.9				
101	30.5	47.3	16.8				
105	23.0	40.6	17.6				
Mean	28.6	50.2	21.6		35.3	46.9	11.6

sites) and we evaluated the shrub cover in every single cell touching the linear transects surveyed in the field. We used 1 m² cells to optimize the comparison with the results from the ground truthing exercise, as larger cell size would include more variability.

2.4. Statistical analysis

Differences in shrub cover between 1957 and 2008 in terraces and hilltops, as well as dwarf birch cover from ground truthing data were tested using one-sample *t*-tests. Changes in shrub cover from 1957 to 2008 in both environments and between the different validation procedures (resolution and field and ortho-photo results) were evaluated using paired *t*-tests. The frequency distribution of delta values in terraces and hilltops were compared using a Kolmogorov–Smirnov test.

3. Results

3.1. Shrub cover change

In 1957, hilltops had a greater shrub cover than terraces (35.3% versus 28.6%; $t(57) = -2.39$, $P < 0.05$; figure 5,

table 2). From 1957 to 2008, shrub cover increased in most of the studied sites (31/33 terraces, 23/26 hilltops), with a substantial increase (>15%) in 27 terraces and 10 hilltops. This increase resulted in a significant difference in shrub cover between 1957 and 2008 in both environments (terraces: 28.6% versus 50.2%; $t(32) = -10.27$, $P < 0.01$; hilltops: 35.3% versus 46.9%; $t(25) = -6.67$, $P < 0.01$). Terraces showed a greater increase than hilltops (21.6% versus 11.6%; $t(57) = -3.52$, $P < 0.05$). As a result, shrub cover in 2008 did not significantly differ between hilltops and terraces (46.9% versus 50.2%; $t(57) = 1.68$, $P = 0.10$; figure 5). There was no significant difference between the delta frequency distribution of terraces and hilltops (Kolmogorov–Smirnov test: $P = 0.96$). However, terraces tended to have a higher proportion of cells showing a large increase in shrub cover (delta = 2–4; figure 6).

Differential resolution between the 2008 and 1957 ortho-photos did not have a major impact on shrub cover evaluation, as revealed by the comparison of the degraded and non-degraded 2008 ortho-photos. On hilltops, 68.2% of the cells were assigned to the correct cover class, while 14.3% and 17.1% were assigned to the cover classes directly above

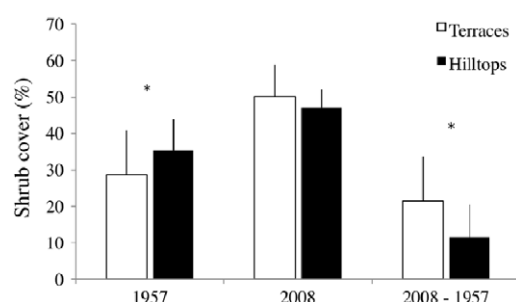


Figure 5. Shrub cover on terraces and hilltops in 1957, in 2008 and the increase from 1957 to 2008 as evaluated on the two ortho-photos. Mean $\pm$ 1 st. dev. Significant differences ($P < 0.05$) are marked by an asterisk.

Table 3. Comparison of shrub cover evaluated using the non-degraded (0.5 m resolution) and the degraded (1 m resolution) 2008 ortho-photos for 10 sites.

Terraces				Hilltops			
Site	2008 (%)	2008 deg. (%)	Diff. (%)	Site	2008 (%)	2008 deg. (%)	Diff. (%)
10	46.8	42.0	4.8	36	45.2	49.3	-4.1
12	62.7	58.0	4.7	43	52.9	53.2	-0.3
14	48.8	44.1	4.7	56	49.5	48.0	1.5
91	50.0	53.3	-3.3	98	49.4	45.7	3.7
95	51.4	48.9	2.5	106	42.3	46.3	-4.0

and below. On terraces, 62.5% of the cells were assigned to the correct cover class, while 22.2% and 14.4% were respectively assigned to the cover classes above and below. The remaining cells (<1%) were assigned to more distant cover classes (2 or more cover classes). Overall, the observed differences in shrub cover at the site scale ranged from -4.8% to 4.1% (table 3), shrub cover being under-evaluated for 6 sites and over-evaluated for 4 sites. Differences in shrub cover were not statistically significant between the degraded and non-degraded 2008 ortho-photos ($t(9) = 0.89$, $P = 0.39$).

3.2. Species implicated

Dwarf birch was the major shrub species recorded during ground truthing. On average, dwarf birch covered 36.7% of the surveyed area. The cover of this species ranged from 13.2% to 58.6% and was significantly higher on terraces than on hilltops (40.1% versus 32.5%; $t(57) = 2.48$, $P < 0.05$). Dwarf birch was the only species found at every site. Moreover, several dwarf birch seedlings not detected on the ortho-photos were found in open areas in both terraces and hilltops. The other most abundant species on terraces were *Rhododendron tomentosum* Harmaja, *Empetrum nigrum* L., and *R. groenlandicum* Oeder, with a cover of 7.0%, 6.3% and 4.9%, respectively. On hilltops, *R. tomentosum*, *E. nigrum*, and *Vaccinium uliginosum* L. were the other most abundant species, with a cover of 10.0%, 8.7% and 2.5%, respectively. *Salix planifolia* Pursh, *S. glauca* L., *S. uva-ursi* Pursh, *Alnus viridis* ssp. *crispa* (Ait.) Turrill, *Diapensia lapponica* L., *Kalmia procumbens* L., *Arctous* sp., and *Rubus chamaemorus*

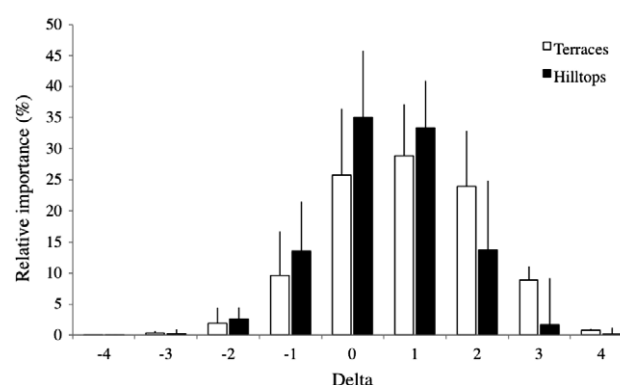


Figure 6. Frequency distribution of shrub cover change between 1957 and 2008 for terraces and hilltops (from 33 terraces and 26 hilltops, respectively). Delta represents the difference in the cover class assigned in 2008 and in 1957. A positive delta indicates cells for which shrub cover increased from 1957 to 2008, while a negative delta indicates a decrease of the shrub cover.

L. were also recorded in the vegetation surveys on both terraces and hilltops, but covered less than 2.1% of the surveyed area.

Shrub cover evaluation inside the 1 m² cell touching the transects used for ground truthing closely matched the dwarf birch cover evaluated in the field (differences ranging from -5.5% to 5.5%, $t(9) = 0.71$, $P = 0.49$). However, it was lower than the total shrub cover recorded in the field for 9 of the 10 sites (table 4; $t(9) = 5.16$, $P < 0.01$). Such results strongly suggest that the perceived shrub cover on the ortho-photos corresponds to the dwarf birch cover and not to the total shrub cover.

4. Discussion

Our results indicate an increase in shrub cover over the past 50 yr at the northern limit of the forest-tundra ecotone in subarctic Québec. This finding corroborates other studies using a similar method conducted in different regions of the Arctic (Alaska: Sturm *et al* 2001, Tape *et al* 2006; northern Québec: Tremblay 2010; Russia: Forbes *et al* 2010) and studies which revealed a major increase of the NDVI over the last few decades (Jia *et al* 2003, Verbyla 2008).

4.1. *Betula glandulosa*, a key species for shrub expansion

The observed increase in shrub cover is mainly attributable to dwarf birch, a species previously identified as one of the key species in pan-Arctic shrub densification (Tape *et al* 2006). Dwarf birch was found at all sites and was the dominant shrub species at 56 out of 59 sites.

Dwarf birch's fast response to environmental change could be linked to its growth plasticity, clonal growth and reproduction potential. As shown by Bret-Harte *et al* (2001), dwarf birch generates numerous leaf-producing long shoots, which allows it to rapidly take advantage of experimental fertilization and warming treatments. It can also reproduce asexually via clonal growth, with stems producing

Table 4. Comparison of the shrub cover evaluated from the 2008 ortho-photo (1 m² cell) and the ground truthing results (total shrub cover and dwarf birch cover).

Type of environment	Site	Cover estimated with 2008 ortho-photo 1 m ² cell (%)	Cover estimated from linear relevés (%)			
			Total shrub cover (%)	Dwarf birch cover (%)	Cover ortho-photo-total cover (%)	Cover ortho-photo-birch cover (%)
Terraces	10	21.2	43.9	22.8	−22.7	−1.6
	12	48.9	64.4	45.6	−15.5	3.3
	14	34.7	42.5	33.0	−7.8	1.7
	91	48.7	85.5	53.6	−36.8	−4.9
	95	30.2	28.3	27.6	1.9	2.6
Hilltops	36	44.4	90.4	44.3	−46.0	0.1
	43	31.6	53.6	33.2	−22.0	−1.6
	56	47.5	65.7	47.7	−18.2	−0.2
	98	29.2	53.8	23.7	−24.6	5.5
	106	28.0	49.8	33.5	−21.8	−5.5

adventitious roots when over-grown by adjacent vegetation (Shaver and Cutler 1979). It also produces an abundant seed rain (>13 000 seeds m^{−2}; Weis and Hermanutz 1988), and seed germination is higher under experimental warming (Vaartaja 1959). In fact, several seedlings were observed in the field, which suggest that the densification should continue in the upcoming years.

4.2. Potential causes of shrub expansion: climate change, fire or caribou?

The recent increase in temperature is the most likely factor explaining the shrub expansion in the Boniface River region. To the best of our knowledge, climate warming is the only large-scale phenomenon observed in the region over the last few decades that could promote a regional response of such intensity. The warming trend observed since the 1990s has already triggered an increase in black spruce seed viability in the region (Dufour-Tremblay and Boudreau 2011) and preliminary dendrochronological analyses revealed an important increase in radial growth since the mid-1990s. Many studies have demonstrated a similar growth increase for other shrub species under extensive warming (*Hippophae rhamnoides* L.: Xiao *et al* 2007, *Empetrum nigrum* ssp. *hermaphroditum* Hagerup: Bär *et al* 2008, *Artemisia tridentata* Nutt.: Poore *et al* 2009, *Salix lanata* L.: Forbes *et al* 2010, *Juniperus nana* Willd.: Hallinger *et al* 2010).

Besides improving radial and vertical growth, climate warming has many indirect effects that can be beneficial for shrub species. For example, an increase in temperature is known to enhance decomposition rate and nutrient cycling (Chapin and Shaver 1996, Hobbie 1996, Bret-Harte *et al* 2001, 2002, Wahren *et al* 2005). Combined with the capacity of birch litter to promote nitrogen availability (Buckneridge *et al* 2010), shrub growth can be largely enhanced (Jonasson *et al* 1999, Gordon *et al* 2001, Sturm *et al* 2005). Winter events could also play a major role in the observed pan-Arctic shrub densification. The abrasive effect of windblown ice particles may limit the vertical growth of erect species (Sonesson and Callaghan 1991). Thicker snow cover under large shrub patches enhances decomposition during winter

because of its insulating effect (Liston *et al* 2002) and may also result in greater water availability at the beginning of the growing season. In fact, differential snow accumulation, one of the most important environmental factors for plant growth in subarctic regions (Payette *et al* 1973), could at least partially explain why shrub cover increased significantly more on terraces than on hilltops. As they are more exposed to wind, hilltops have thinner snow cover, which could result in greater winter damage to aboveground biomass because of mechanical breakage of exposed tissues (Marchand and Chabot 1978) and winter desiccation (Sonesson and Callaghan 1991). On the other hand, individuals established on terraces are protected by a thicker snow cover and the reduced importance of wind is believed to allow dwarf birch individuals to grow rapidly and to expand.

Fire and large herbivores are among other disturbances that could be considered to explain this shrub densification. The Boniface River area has experienced massive deforestation in the last few millennia because of the combined effects of fire and climate. However, fires are unlikely to have triggered the recent shrub densification, as few fires occurred over the last millennium in the study region (Payette *et al* 2008). In fact, some of the study sites have not burned for at least 1300 yr.

On a shorter timescale, the role of large herbivores in shrub expansion might also be given some consideration. Caribou (*Rangifer tarandus* L.) activity in the study area was high from the mid-1990s to the mid-2000s. Although caribou browsing can inhibit shrub performance, caribou trampling creates suitable seedbeds for dwarf birch by exposing the mineral soil, on which numerous *B. glandulosa* seedlings were observed. However, because dwarf birch expansion was observed on sites with or without caribou activity evidence, it strongly suggests that caribou activity did not trigger shrub expansion.

5. Conclusion

This research shows an increase in shrub cover in the last 50 yr for the studied region. Exhaustive ground truthing allowed us to identify dwarf birch as the main species implicated in this phenomenon. We also demonstrated that the shrubification is

non-uniform across the landscape, with terraces promoting a higher shrub densification during the last decades. Further studies are now warranted to understand the processes at play in subarctic shrub densification. Does expansion rely mainly on clonal growth or on sexual reproduction? What is the spatial pattern of shrub expansion? Our ability to predict changes at the landscape level depends on our ability to understand the ecological processes underlying the observed changes.

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