Structure and Composition of Tree Islands and Krummholz within the Forest-Tundra Ecotone in Central and Eastern Canada

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ABSTRACT. The forest-tundra ecotone is expected to experience some of the initial effects of climate change. At the forefront of this transition zone, we find clonal growth forms of stunted and deformed trees with and without taller erect trees, called tree islands and krummholz, respectively. We sought to assess the potential effects of expansion of these growth forms on tundra plant species at two Canadian locations, one in the Mealy Mountains of Labrador and the other near Churchill, Manitoba. Our objectives were 1) to analyze the structure (height distribution and shape) of these clonal growth forms to determine whether they are expanding; 2) to compare tree cover on the leeward and windward sides of these growth forms and 3) to assess patterns in individual plant species across these growth forms. Cover of trees and other plant species was measured at both locations, while tree stems were mapped near Churchill only. The presence of seedlings and symmetric patterns of tree height suggest that half of the tree islands near Churchill may be expanding. The edges of tree islands and krummholz may harbour safe sites for tundra plant species, as shown by peaks in cover of individual species at these edges. Our results suggest that expansion of tree islands and krummholz would affect the abundance of tundra plant species, which could lead to changes in species composition and biodiversity.

Key words: expansion, forest-tundra ecotone, krummholz, *Picea glauca*, structure, species composition, tree island

RÉSUMÉ. On s'attend à ce que l'écotone de la toundra forestière subisse dans une certaine mesure les premiers effets du changement climatique. À l'avant-plan de cette zone de transition se trouvent des formes de croissance clonales d'arbres rabougris et difformes parfois assortis ou non assortis de plus grands arbres dressés, ce que l'on appelle des îlots boisés et des krummholz, respectivement. Nous avons cherché à évaluer les effets potentiels de l'expansion de ces formes de croissance clonales sur les espèces végétales de la toundra à deux emplacements situés au Canada, un aux monts Mealy du Labrador et l'autre près de Churchill, au Manitoba. Nos objectifs étaient les suivants : 1) analyser la structure (répartition des hauteurs et formes) de ces formes de croissance clonales afin de déterminer si elles prennent de l'expansion; 2) comparer la couverture arborescente en aval et en amont des croissances clonales; et 3) évaluer les modèles se dessinant chez les diverses espèces végétales individuelles au sein de ces formes de croissance. Les couvertures arborescentes et d'autres espèces végétales ont été mesurées aux deux endroits, tandis que les tiges d'arbres n'ont été relevées qu'à l'emplacement de Churchill. La présence de semis et de modèles symétriques en ce qui a trait à la hauteur des arbres suggère que la moitié des îlots boisés près de Churchill pourraient être en expansion. Le bord des îlots boisés et des krummholz pourrait constituer des lieux sûrs pour les espèces végétales de la toundra, comme l'indiquent les crêtes caractérisant la couverture des espèces individuelles situées en bordure. Nos résultats laissent entendre que l'expansion des îlots boisés et des krummholz aurait des incidences sur l'abondance des espèces végétales de la toundra, ce qui pourrait entraîner des changements sur le plan de la composition et de la biodiversité des espèces.

Mots clés : expansion, écotone de la toundra forestière, krummholz, *Picea glauca*, structure, composition des espèces, îlot boisé

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INTRODUCTION

The forest-tundra ecotone (also called the tree line) at the northern limit of the boreal forest is thought to be shaped by cold temperatures, intense winds, and short dry summers, which limit the ability of trees to grow and expand farther north. The forest-tundra ecotone consists of climate-sensitive forests and trees and is a good indicator of the changes occurring in the environment (Payette et al., 2001). As a result, tree-line movement and infilling due to climate

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change have been extensively studied (e.g., Holtmeier and Broll, 2005; Holtmeier, 2009; Mamet and Kershaw, 2012). Although tree-line movement has not been widespread, many studies have found an increase in tree density within the forest-tundra ecotone (Payette and Filion, 1985; Scott et al., 1987; Lavoie and Payette, 1994). Tree-line movement is a long-term process: an initial change in growth of current trees causes reduced wind velocities, increased snow accumulation, more favourable soil conditions, altered vegetation cover (more luxuriant species) and eventually a greater nutrient supply (Holtmeier and Broll, 2010a). This process is likely to lead to an increase in biomass and productivity, allowing regeneration of new individuals beyond the current tree line (Kullman, 2002; Hofgaard et al., 2009; Aune et al., 2011). In the long term, tree-line advance would create more closed forests and thereby reduce the number of tundra species previously found there. A better understanding of tree-line dynamics requires analyses of the growth processes that are occurring within the forest-tundra ecotone.

Tree-line response to climate change depends on its form: krummholz, diffuse, or abrupt (Harsch et al., 2009; Harsch and Bader, 2011). Krummholz tree lines include two defined patch types, tree islands and krummholz. Tree islands are isolated aggregations or patches of stunted and deformed trees (Holtmeier, 1981) with taller stems extending from the shrub layer that can reach several metres (Fig. 1a). Krummholz lacks the presence of taller trees and consists mainly of deformed trees only a few decimetres to 1 m in height (Marr, 1977) (Fig. 1b). These clonal growth forms often originate from seeds during warmer periods or in sheltered areas, and they persist through layering when harsh conditions (e.g., low temperatures, high wind exposure) preclude seed-based regeneration (Holtmeier and Broll, 2010a). The sheltering quality of tree islands and krummholz supplies seedlings with favourable growing conditions (Germino et al., 2002). Sheltered microsites facilitate seedling growth and survival within the tundra by reducing the exposure to wind and radiation, as well as by maintaining soil moisture (Callaway et al., 2002; Maher et al., 2005). These clonal growth forms can facilitate the expansion of tree lines by expanding and increasing tree density into the tundra.

The unique conditions within the forest-tundra ecotone have a strong effect on the structure of these clonal growth forms, creating compact, elongated shapes (Hadley and Smith, 1987; Bekker, 2005; Holtmeier and Broll, 2010b). The growth of these tree islands and krummholz patches depends collectively on many controlling factors such as temperature, precipitation, wind flow, wind and sun exposure, length of growing season, and depth and duration of snow cover, on scales ranging from global to local (Grace et al., 2002; Holtmeier and Broll, 2005; Holtmeier, 2009). Wind intensity in particular has long been considered as a strong driving force in the shaping (height growth, density) of clonal growth forms (Marr, 1977; Hadley and Smith, 1987; Scott et al., 1987; Holtmeier and Broll, 2010b).
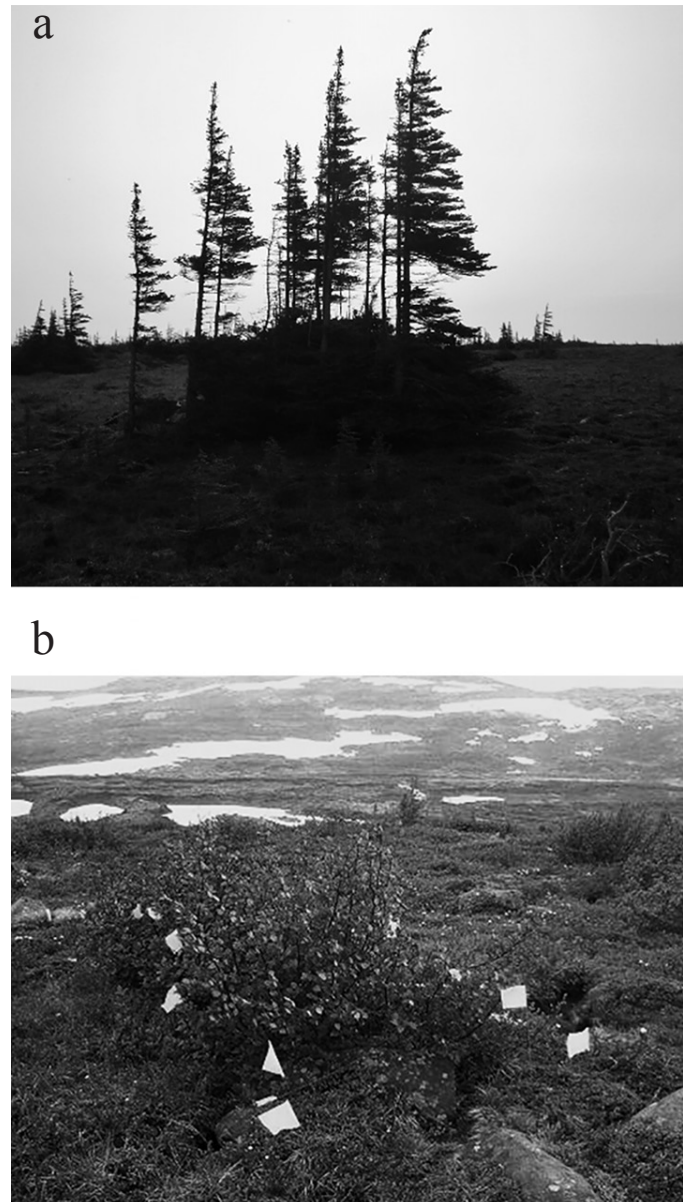
FIG. 1. Photographs of a) tree island no. 2 (*Picea glauca*) near Churchill, Manitoba and b) krummholz no. 12 (*Alnus viridis*) in the Mealy Mountains.

The migration of tree lines is expected to have significant implications for biodiversity of the alpine ecotone (Grace et al., 2002; Hofgaard et al., 2012). Expansion of tree islands could cause changes in plant species composition of the surrounding tundra. A study by Holtmeier and Broll (1992) looked at the tree islands' ability to control microsite conditions within the forest-tundra ecotone and how conditions vary between the interior and the windward and leeward sides. The windward side, which is exposed to wind stressors, has very dry, permeable soil conditions, with vegetation consisting mainly of cushion-like plant species, as well as small patches of grasses, sedges, herbs, dwarfed willows, and lichens. The centre has conditions similar to those found within closed forests with few plant species. The leeward side has more favourable soil conditions (e.g., greater soil moisture, less acidic soils), resulting in

the establishment of more productive vegetation. This vegetation includes grasses, sedges, mosses, herbs, and dwarf shrubs, but excludes plants intolerant to long snow burial. Further study of the patterns of species cover outside the tree islands or krummholz, as well as across them, could improve our knowledge of the consequence of tree island expansion for biodiversity within the forest-tundra ecotone.

The goal of our study was to assess the potential effects of tree island and krummholz expansion on tundra plant species at a local scale. We studied a krummholz zone at the top of a broad forest-tundra ecotone in a valley in the Mealy Mountains of Labrador and scattered tree islands near the coast of Hudson Bay close to Churchill, Manitoba. We had three specific objectives: 1) to look for possible evidence of tree island expansion or stability, 2) to compare tree cover between the leeward and windward sides, and 3) to assess patterns of plant species across the edges of tree islands. To investigate possible tree island expansion, we analyzed tree island structure in terms of height distribution on the leeward side, where growth is expected to occur. Seedlings at the edge of tree islands would indicate expansion, while saplings would indicate expansion that had been occurring over the medium term. For our second objective, we expected a symmetrical height distribution across the tree island or krummholz in response to wind effects if the tree island was expanding rather than the higher tree growth on the leeward side that is typical of stable tree islands. Our third objective was included to predict the effect that expansion might have on the surrounding tundra plant species by comparing cover at different distances from the edges of tree islands or krummholz to cover in nearby tundra.

METHODS

Study Sites

Data were collected near Churchill, Manitoba (58°44′N; 94°04′ W) and in the Mealy Mountains, Labrador (53°62′N; 58°84′ W) (Fig. 2a). Near Churchill, the sampled tree islands were located at the northern edge of the forest-tundra ecotone near the coast of Hudson Bay. The area is in the high Subarctic, in the lowlands ecoregion within the Hudson Plain ecozone, and it is relatively flat, with low elevation. The study site is greatly influenced by Hudson Bay, which brings prominent winds and cold air temperatures from the coast and suppresses evaporation. The average daily temperature (1971–2000) was −26.7°C for January, with an average of 16.9 mm precipitation, and 12.0°C for July, with 56 mm precipitation (Environment Canada, 2013). The summers are short in the lowlands of the Hudson Bay coast: snow cover persists until June (Rouse, 1991) and returns in mid-September (Scott et al., 1993). The dominant tree species are white spruce (*Picea glauca*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*) (Tardif et al., 2008) with patches of green alder (*Alnus viridis*), a tall shrub or short tree that forms krummholz (Holtmeier, 1981).

The Mealy Mountains site is an altitudinal forest-tundra ecotone located within the Mealy Mountains National Park and is described as southern mountainous outliers of the high Subarctic Tundra ecoregion (Meades, 1990). Average temperatures for 2002–08 were −1.6°C (annual), −16.4°C (January), and 13.2°C (July) (Labrador Highlands Research Group, 2007). Annual precipitation is greater than 2000 mm, of which about half falls as snow (Labrador Highlands Research Group, 2007). The dominant tree species are the same as near Churchill with the addition of balsam fir (*Abies balsamiferaea*).

Sampling Design

We sampled 12 patches of krummholz at the Mealy Mountains site in 2007 (Fig. 2b) and 12 tree islands near Churchill in 2008 (Fig. 2c). One transect extended across each island or patch with contiguous quadrats extending 1 m into tundra on either side. In this study, the edge was defined as the limit of continuous tree cover, regardless of tree height. Quadrats were 1 × 1 m in the Mealy Mountains and 0.5 × 1 m (shorter side parallel to the direction of the transect) near Churchill. Three additional quadrats of unforested tundra were sampled along each transect at least 30 m from the tree islands or krummholz on either side. Within the quadrats, we identified all plant species (Johnson, 1998) and visually estimated percent cover in these classes: 0–1%, 1–5%, 5–10%, 10–25%, 25–50%, 50–75%, and 75–100%). Tree cover was also recorded, and near Churchill it was categorized into three height classes (seedlings, < 15 cm; juveniles, 15–200 cm; and trees, > 200 cm). Near Churchill, trees less than 15 cm in height are typically 1–10 years old (S.D. Mamet and G.P. Kershaw, unpubl. data). Only overall canopy cover was recorded in the Mealy Mountains, since only one tree in the krummholz patches was taller than 200 cm (3 m), and only one was under 15 cm (8 cm). Aging of trees at these sites would have helped us to distinguish stunted trees from true seedlings or saplings; however, age determination would have involved destructive sampling and was not considered for this study. Near Churchill, the heights and locations of each tree within the tree islands were determined in 2009. For the taller trees, height was measured with a laser range finder.

Data Analysis

The size and shape of the mapped tree islands near Churchill were assessed by fitting 95% confidence ellipses using PAST version 2.12 freeware (Hammer et al., 2001). Size was estimated using the lengths of the major and minor axes; shape was estimated using the ratio between these measures; and orientation was determined using the angle of the major axis of the ellipse.

The cover of each of the three height categories was compared between the windward and the leeward sides of tree islands near Churchill with paired t-tests, using Minitab
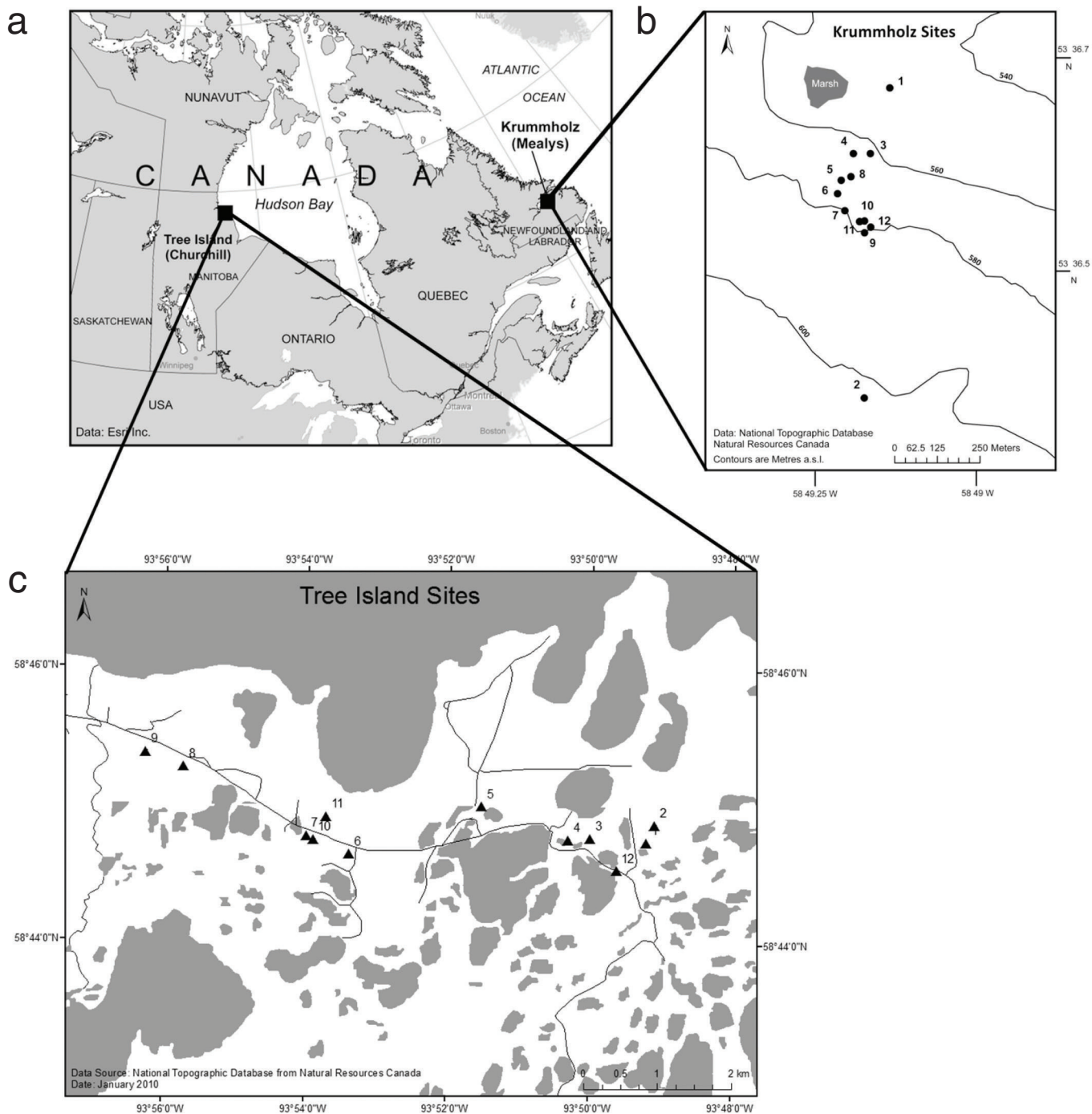
FIG. 2. Locations of a) both study sites, b) 12 krummholz sites in the Mealy Mountains and c) 12 tree island sites near Churchill, Manitoba. In c), grey represents water (Hudson Bay and lakes).

15 (Minitab Inc., 2010). We also used these t-tests for total cover of krummholz patches in the Mealy Mountains that consisted of either *Picea mariana* or *Alnus viridis*, separating these two species to see if the results differed. We matched quadrats at opposite sides of the tree islands with equivalent distances from the edge. For trees on the leeward sides of the tree islands near Churchill, we used height as an indicator of age.

At both sites, we compared the cover of plant species at different distances from the edge of the tree islands to the surrounding tundra using randomization tests, in which data at a specific distance from the edge *d* are randomized with data from surrounding tundra for all transects at a given site (Randomization Test of Edge Influence, RTEI, without blocking for the Mealy Mountains site and with blocking for the Churchill site; Harper and Macdonald, 2011). Separate analyses were conducted at each distance (*d*) from the edge of the tree island on the leeward and windward sides of a transect. Since the shortest transect was 6 m for the Mealy Mountains site and 8 m near Churchill, we

used the three distances (every 1 m for a total of 3 m) closest to the edge for the Mealy Mountains site and the eight distances (every 0.5 m for a total of 4 m) closest to the edge for Churchill. The edge quadrats and not the centre quadrats were used because we were interested in patterns relative to the edge and because tree islands and krummholz patches were different sizes. Tests were conducted using 5000 randomizations and a *p* value of 5%. Species with significant differences at more than 25% of the distances were graphed to assess patterns in cover.

RESULTS

Tree islands near Churchill were composed exclusively of *Picea glauca* (white spruce). Three of these tree islands were small (T6, T8, T11; major axes of 95% confidence ellipses < 4 m), five were elongated (T2, T3, T4, T9, T10; ratio of the major and minor ellipse axes ≥ 2), and two were large and spread out (T1, T5; major axes > 4 m and ratio < 2) (Table 1, Fig. 3). The exception to this classification is tree island T7 with only four trees, which had a large confidence ellipse despite appearing small, as well as a ratio greater than two. Two of the small tree islands were also compact, with tree densities greater than 1 per m² (T6, T11). Only two of the five elongated tree islands (T3 and T4) were elongated in the predominant wind direction from northwest to southeast (approx. 135˚); the orientation of the other three was closer to perpendicular to the dominant winds.

Near Churchill, tall trees (> 200 cm) had greater cover in the centre of the tree islands, with decreasing cover towards the edges (Fig. 4a). The 15–200 cm juvenile trees were present in all tree islands with highly variable cover throughout, as indicated by the wide error bars, and with greater cover on the windward sides (Fig. 4b). The smallest (< 15 cm) trees were found in six of the 12 tree islands. They were located mostly at the edges of the leeward sides, but with a peak on the windward sides (Fig. 4c). The Mealy Mountains site had a similar trend of greater tree cover in the centre of the krummholz, decreasing towards the edges (Fig. 5). The lengths of the krummholz patches varied, with four each at 6, 8, and 10 m. There were no significant differences between the leeward and windward sides for any height category near Churchill (*p*-values = 1 for < 15 cm, 0.061 for 15–200 cm, and 0.236 for > 200 cm) or for the krummholz in Mealy Mountains (*p*-value = 0.689).

Cover of individual plant species varied across the tree islands, and patterns sometimes differed between the two locations. At Churchill, a greater proportion of species showed a pattern of greater or lower cover in the tree islands than in the tundra (8/16 species with > 25% quadrats significantly different, compared to 3/12 species in the krummholz in the Mealy Mountains) (Fig. 6). Near Churchill, lichen, *Rhododendron lapponicum*, and *Dryas integrifolia* had significantly less cover in the tree islands than in the tundra, a pattern that was much stronger on the leeward side for *R. lapponicum* (Fig. 7). Moss, *Vaccinium*

uliginosum, *Andromeda polifolia*, *Salix lanata*, and *Vaccinium vitis-idaea* were more abundant in the tree islands than in the tundra. In the Mealy Mountains, only one species (*Arctostaphylos alpina*) had significantly more cover in the tundra, and two species (lichen and *V. vitis-idaea*) had significantly greater cover in the krummholz. Dominant species in the tree islands and krummholz were moss (mean cover near Churchill = 33%; Mealy Mountains = 38%) and *Vaccinium uliginosum* (mean cover near Churchill = 13%; Mealy Mountains = 17%). Lichen (mean cover = 26%) was also dominant in the Mealy Mountains. The average species richness was lower in the tundra than in either the tree islands or the krummholz (tree islands = 11 ± 2.3 and tundra 8 ± 1.8; krummholz = 9 ± 0.8 and tundra = 5 ± 1.5).

A bimodal distribution with peaks in species cover at the edges of the tree islands was a notable trend near Churchill (Fig. 7). Sometimes in this bimodal distribution the values near the edges were significantly greater than in the reference tundra (moss, *V. uliginosum*, *A. polifolia* near Churchill; lichen in the Mealy Mountains), or values at the centre were significantly lower than in the reference tundra (lichen near Churchill; *A. alpina* in the Mealy Mountains). The distribution was asymmetric for some species, with greater cover on the windward side. This distribution was evident for moss, *D. integrifolia*, and *V. vitis-idaea* near Churchill. The reverse (greater cover on the leeward side) was found for *V. uliginosum* and *S. lanata* near Churchill.

DISCUSSION

Tree island expansion could play a large role in facilitating the process of infilling (increasing tree density within the forest-tundra ecotone) by creating safe sites for tree seedlings to establish and grow. Infilling, along with increased height growth of existing suppressed growth forms, is found to be an early sign of tree-line expansion (Lescop-Sinclair and Payette, 1995; Gamache and Payette, 2005; Holtmeier and Broll, 2010a). Increased tree density aided by the protective properties of tree islands and krummholz is expected to create a positive feedback, causing biomass and productivity to increase over time (Holtmeier and Broll, 2010a). Our results from the Churchill tree islands show that two-thirds of the 12 tree islands had seedlings and saplings and half had seedlings, indicating that expansion is likely occurring for some tree islands in these locations. In very harsh conditions, a gradual increase in height on the windward side occurs, and new trees seek shelter behind the older trees on the leeward side and are able to grow slightly taller each time (Marr, 1977). Therefore, we considered tree islands with a gradual increase in height and tree cover on both the windward and leeward sides to be expanding, as described by Holtmeier and Broll (2010b). The tree cover across tree islands near Churchill and krummholz in the Mealy Mountains did not differ between the leeward and windward sides, suggesting that expansion has been occurring over the medium term (Holtmeier and Broll, 2005). However, there was variation

TABLE 1. Characteristics of selected tree islands in Churchill. We fitted 95% confidence ellipses using PAST freeware (Hammer et al., 2011). Orientation was determined as the angle of the major axis of the ellipse and density as the number of trees per unit area of the ellipse. Juvenile growth is the presence of seedlings or saplings (or both) in the tree island.

| Tree island	Max. height (m)	Length (m)	# trees	Juvenile growth	Major axis (m)	Minor axis (m)	Major: minor	Orientation (degrees)	Density (trees m^{-2})
1	6.5	10	10	–	5.5	3.9	1.4	27	0.15
2	6.8	9.5	5	–	5.6	2.5	2.2	6	0.11
3	4.2	7	6	–	7.9	3	2.6	158	0.08
4	4	5.5	7	Seedling + sapling	5.8	2.2	2.6	178	0.17
5	5	8	20	Sapling	5.3	3.8	1.4	70	0.32
6	3.3	7	30	Seedling	3.2	1.9	1.7	75	1.55
7	4	4	4	Seedling	7.2	2.9	2.5	29	0.06
8	3.5	7.5	12	Seedling + sapling	3.8	2.9	1.3	40	0.35
9	2.9	8	18	Seedling + sapling	4.5	2.3	2	29	0.56
10	6.1	5.5	13	Seedling	6	1.6	3.8	78	0.44
11	4.3	4.5	7	Sapling	1.5	1	1.5	149	1.48
12	5.8	6.5	N/A[1]	–	N/A	N/A	N/A	N/A	N/A

[1] N/A = Data not available.
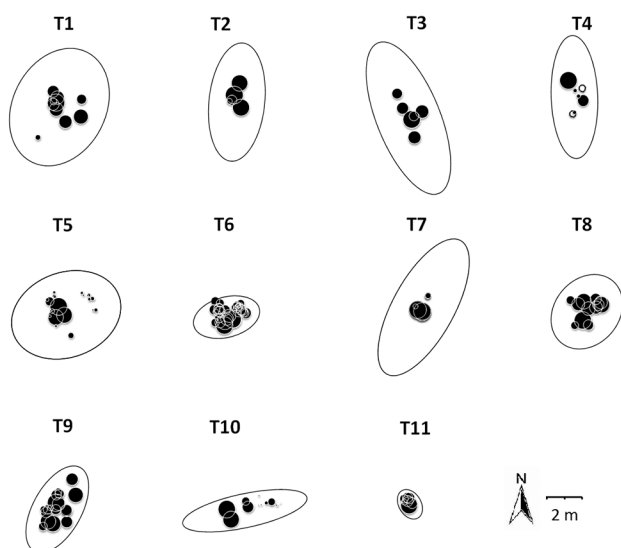
FIG. 3. Mapped trees in tree islands near Churchill. The size of the circle is proportional to the height of each tree. Larger circles around tree islands are the 95% confidence ellipses. The windward side is the northwest side of the islands. T2 has five intermediate trees (15–200 cm height) not indicated on the mapped island due to incomplete location information. T4 was missing height data for two of the plotted data points (indicated as white circles) and T12 had no location data available.

among tree islands, as shown by large error bars and the fact that four tree islands did not have any seedlings or saplings present. This discrepancy could be a response to differences in local environmental conditions within these regions that may be preventing expansion of some tree islands.

Insight into the environmental conditions that might be affecting expansion can be gained through an examination of the shape (elongation, density, size) and the distribution of tree height categories (seedlings, saplings, and trees) within the tree islands near Churchill. Tree islands were either elongated, which indicates the presence of intense winds that limit seedling growth to the leeward side only

(Marr, 1977; Hadley and Smith, 1987), or compact (small and dense), which suggests the need for greater snow accumulation for survival (reflecting harsh growing conditions). Tree growth in tight aggregations can trap snow and accumulate snow more efficiently, creating a protective shell around these tree islands during the harsh winter months (Bekker, 2005; Holtmeier and Broll, 2010b). In contrast, the two tree islands that were spread out and not elongated probably experienced more favourable growing conditions that were independent of snow trapping. However, no seedlings were present at either of these sites, suggesting that conditions were more favourable in the past but recent recruitment has not been successful. One of these tree islands (T1) is located close to three small ponds that provide this site with sufficient moisture during drier periods, and perhaps when dry periods end, an excess of water then limits the establishment of new seedlings.

Expansion of tree islands appeared to be related to their position within the forest-tundra ecotone. Tree islands found close to one another had similar patterns of seedling and sapling distribution: T1, T2, T3, and T12 in the same area had very few seedlings or saplings; adjacent tree islands T8 and T9, which were relatively dense, had both seedlings and saplings; and T6, T7, and T10 had only seedlings and tall trees. Differences in the soil condition (organic matter, nutrients, pH) and moisture resulting from variations in the topography near Churchill could be causing these clumped effects (Holtmeier and Broll, 1992, 2005, 2010b). Differences in wind exposure due to topography may also explain why the tree islands did not always elongate in the predominant wind direction from northwest to southeast. The topography near Churchill is relatively flat, but fine-scale variation in the landscape could cause changes in wind direction or provide shelter from wind and greater snow accumulation. Tree islands could be located in local troughs or valleys, resulting in variation at a scale of only a few metres (Holtmeier and Broll, 2005).
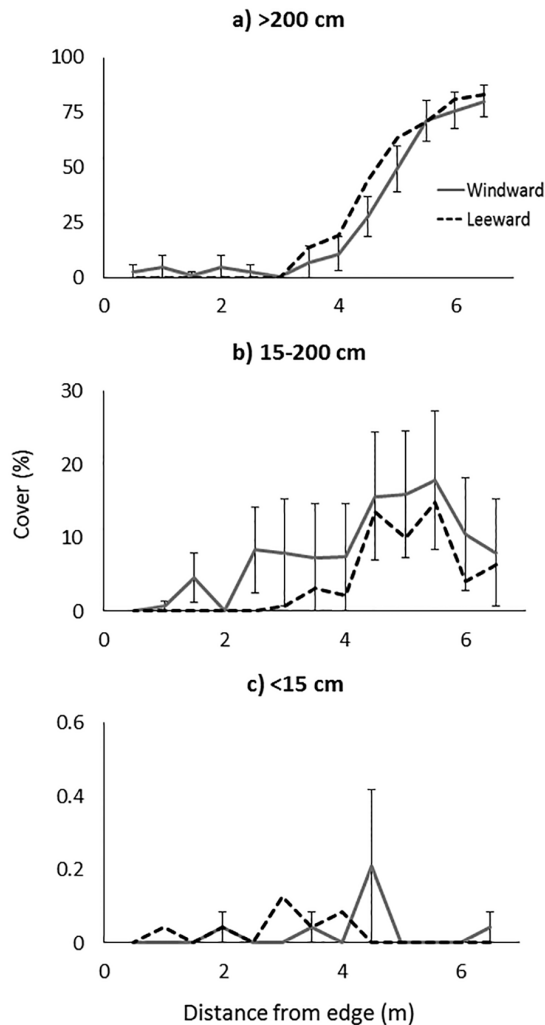
a) >200 cm

b) 15-200 cm

c) <15 cm

FIG. 4. Average percent cover ± 1 SE near Churchill for each distance from the edge on the windward (solid line) and leeward (dashed line) sides of the tree islands for a) trees > 200 cm, b) saplings 15–200 cm and c) seedlings < 15 cm tall. Note the different scales for the y-axis.

Tree islands in turn create microsites that protect against the harsh conditions found in the forest-tundra ecotone (Camarero and Gutiérrez, 2002; Germino et al., 2002; Maher et al., 2005). In this harsh ecotone, the presence of these clonal growth forms has a positive effect on species that require protection from wind desiccation, as well as greater moisture and nutrients, as found on the leeward sides. Our study suggests that tree islands and krummholz are creating safe sites for several plant species: moss, *Vaccinium uliginosum, Andromeda polifolia, Salix lanata*, and *Vaccinium vitis-idaea* near Churchill, and *Vaccinium vitis-idaea* and lichen in the Mealy Mountains. The mean number of species found in the clonal growth forms was also greater than in the tundra for both sites. These growth forms also provide space for cushion-like plants to grow on the dry, permeable soils and wind-exposed areas found on the windward sides (Holtmeier and Broll, 1992; Callaway et al., 2002). The greater cover found in the tundra for *R. lapponicum*, which grows in dry soils with low organic content
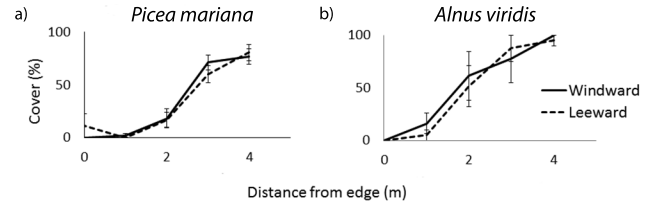

FIG. 5. Average percent cover ± 1 SE in the Mealy Mountains for each distance from the edge on the windward (solid line) and leeward (dashed line) sides of the krummholz patches for a) *Picea mariana* krummholz (K1–K8) and b) *Alnus viridis* krummholz (K9–K12). Results are not differentiated by height since almost all the tree cover was between 15 and 100 cm.
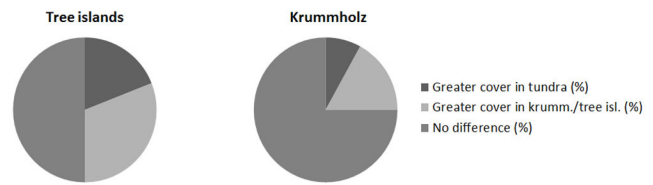

FIG. 6. The proportion of species found more frequently in the tundra, within the tree island or krummholz or equally within both (no difference). Species were considered more frequently found in the tundra or within structures when cover in more than 25% of the distances within the tree island/krummholz was significantly lower or greater, respectively, than in the surrounding tundra.

(Harshberger, 1919), did not differ significantly from that found on the windward side of growth forms, but only from the leeward side. In addition, *V. uliginosum*, a species growing in wet soils (Jacquemart, 1996), had greater cover on the leeward side. This fact supports Holtmeier and Broll (1992) because it illustrates that the conditions on the windward and leeward side differ. We therefore suggest that the expansion of these clonal growth forms could cause shifts in species composition and biodiversity, first by facilitating species that benefit from growing on the edges of clonal growth forms and then by limiting these species as the high tree density starts to form closed forests.

Tree island expansion will therefore cause reduced cover of some tundra species but benefit others. Even though the cover was significantly greater in the tundra or in the clonal growth form, some cover was often present in both habitats, and therefore it is less clear how this shift will affect the overall biodiversity of this ecotone.

The converse pattern of significantly more lichen in the tundra than in the tree islands near Churchill could reflect different species of lichen or trees than are found in the Mealy Mountains or structural differences between tree islands and krummholz that produce different micro-environments and species composition. Similarly, the smaller number of species in the Mealy Mountains with significantly more or less cover in islands or patches than within the tundra may reflect differences in site factors that influence growing conditions, such as topography, elevation, and wind velocity, or it may result from differences between the tree island and krummholz clonal growth forms. Further research on this latter difference would be beneficial because krummholz could become more upright
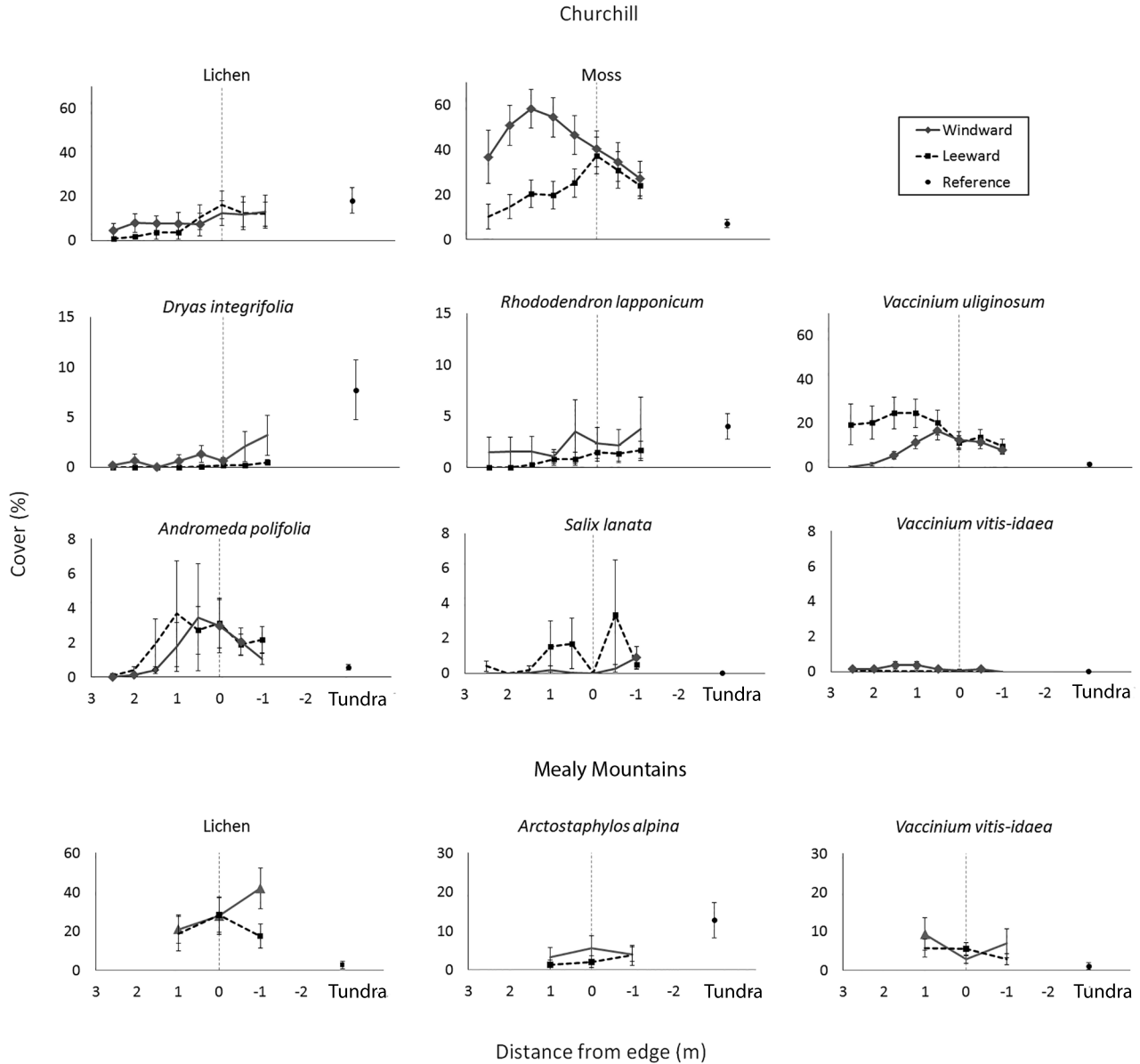
FIG. 7. Average cover ± 1 SE of lichen, moss, and selected plant species across tree islands near Churchill and krummholz in the Mealy Mountains. Solid lines represent the windward sides and dashed lines the leeward sides of the tree islands near Churchill and krummholz in the Mealy Mountains. Symbols indicate significant differences from the surrounding tundra as determined by randomization tests; only species/site combinations with significant patterns are included. The distance of −1 m represents one quadrat into the tundra and adjacent to the tree island or krummholz. Average cover across tree islands and krummholz for all species is given in Appendix 1.

tree forms with climate change (Gamache and Payette, 2004, 2005).

An interesting result near Churchill was the trend in certain plant species toward greater cover closer to the edges of the tree islands than toward the centre. This pattern could be the result of increased wind protection by the branches combined with better access to sunlight than in the centre (Holtmeier and Broll, 1992). Alternatively, increased snow accumulation near the edges might provide more moisture, more stable annual local temperatures, and greater soil stability for the plants (Marr, 1977; Sturm et al., 2001; Germino et al., 2002). This non-monotonic pattern with distance from the edge provides more evidence that edge influence often elicits a more complex response than a

gradual transition zone (Alignier and Deconchat, 2011). For tree islands and krummholz, the transition in the cover of some plant species across the edges may result from interaction of those factors mentioned above, all of which may change with further expansion.

Several factors affect seedling establishment and therefore expansion of these clonal growth forms. Although unexplained variation remains, our results suggest that local conditions, possibly variations in topography, affect recent expansion (in the form of seedling and sapling growth at the edges). Expansion was evident, but conditions within the forest-tundra ecotone vary from year to year, making long-term predictions more difficult (Holtmeier and Broll, 2005). Our results also support the hypothesis that

edges of tree islands and krummholz patches provide conditions for greater growth of both cushion species growing on dry soils and shrub species growing on damp, shaded soils. Despite some evidence supporting the findings of Holtmeier and Broll (1992), for most species we found no strong differences between the leeward and windward sides in plant species cover. Our findings indicate that the initial change in the plant species cover within the forest-tundra ecotone will not be as great for the krummholz, suggesting that montane tundra plant species could be less affected by the increased presence of krummholz than by expanding tree islands, although this conclusion requires further inspection. If the current trend continues, species composition will shift to more productive plant species that prefer reduced wind velocities, increased snow accumulation, and soil with more moisture and nutrients in the intermediate time frame. However, if in the long term the ecotone becomes more dominated by tree species, landscape-level biodiversity will likely be reduced as edges merge and the ecotone converts to closed forest.

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APPENDIX 1

Average percent cover at a given distance from the tree island or krummholz edge for all plant species.

	Windward													Leeward			
Distance from edge (m)	−1	−0.5	edge	0.5	1	1.5	2	2.5	2.5	2	1.5	1	0.5	edge	−0.5	−1	Ref. 30
Churchill:																	
Moss	27.3	34.6	40.4	46.7	54.6	58.3	51.1	36.9	10.3	14.7	20.4	19.9	25.2	37.5	31.1	24.2	7.2
Lichen	13.1	11.8	12.4	7.3	7.6	7.8	8.0	4.5	0.9	1.7	3.6	3.5	10.6	16.2	12.4	12.0	18.2
Dryas integrifolia	3.2	2.1	0.7	1.3	0.6	0.04	0.7	0.2	0.04	0.04	0	0.04	0.1	0.2	0.2	0.5	7.7
Vaccinium uliginosum	8.0	11.7	12.6	16.8	11.5	5.5	1.6	0.4	19.5	20.4	24.8	24.7	20.4	11.2	13.8	9.7	1.8
Arctostaphylos alpina	3.2	4.8	4.9	5.0	6.2	3.2	0.4	1.7	0.04	0.2	4.9	13.0	8.3	6.3	9.4	8.4	4.1
Salix reticulata	4.3	2.7	2.1	1.3	1.4	0.8	0.1	0	0.5	1.4	2.6	4.4	1.5	2.3	2.5	3.4	1.1
Salix planifolia	0.4	4.0	3.6	1.7	1.7	3.1	0.2	0.2	7.3	3.1	0.8	0.3	1.5	1.8	0.7	1.1	0.8
Empetrum nigrum	0.3	0.7	0.2	1.5	6.2	3.6	5.4	1.5	5.5	4.8	6.0	0	0.8	0.7	0.1	0.2	2.2
Ledum decumbens	0	0	0.1	0.3	1.5	0.5	0.8	0.1	0	0	0	0.04	0.04	0	0	0	0.07
Vaccinium vitis-idaea	0	0.2	0.08	0.2	0.4	0.4	0.2	0.2	0.08	0.08	0.04	0.04	0.04	0	0	0	0.04
Andromeda polifolia	1.0	2.0	3.0	3.5	1.8	0.4	0.1	0	0.1	0.4	1.9	3.7	2.7	3.1	1.9	2.2	0.5
Betula glandulosa	1.1	0.9	4.7	4.7	0.7	0.2	0.1	0	0	0.7	1.8	0.4	1.7	2.0	0.9	2.0	1.9
Rhododendron lapponicum	3.8	2.2	2.4	3.5	1.1	1.6	0	1.5	0	0.04	0.3	0.8	0.8	1.5	1.3	1.7	4.0
Salix lanata	0.9	0.3	0	0.04	0.2	0.04	1.5	0	0.4	0	0.2	1.5	1.7	0.04	3.4	0.5	0.03
Myrica gale	2.1	3.8	6.2	1.5	3.1	0.2	0	0	0	0	0.2	3.1	5.2	5.2	3.3	1.7	0.3
Shepherdia Canadensis	0	0	0	0	0.2	0.6	0.04	0	3.2	5.2	5.4	8.4	4.0	4.6	1.7	1.7	0
Mealy Mountains:																	
Lichen	41.9		27.8		21.0							18.8		28.2		17.5	2.7
Moss	15.4		35.4		48.3							47.5		40.8		40.4	36.8
Alnus viridis	3.8		11.2		21.7							25.8		5.4		0	0
Arctostaphylos alpina	4.0		5.5		3.3							1.2		2.1		3.8	12.8
Betula glandulosa	19.2		16.2		18.3							8.3		14.2		18.8	20.4
Empetrum hermaphroditum	11.1		9.6		10.5							6.8		19.5		21.3	14.6
Chamaedaphne calyculata	0.7		1.0		5.0							0.9		0.6		1.2	0
Ledum groenlandicum	10.3		9.5		7.5							6.2		8.7		11.3	3.6
Phyllodoce caerulea	3.3		3.1		0.5							0.9		0.6		0.5	0
Vaccinium uliginosum	19.8		19.0		8.0							10.8		20.0		22.3	11.4
Vaccinium vitis-idaea	7.0		2.9		9.3							5.8		5.5		2.9	1.2
Salix myrtillifolia	0.8		2.1		0							0		0.04		0	0