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# Environmental Influences on Winter Desiccation of *Picea glauca* Foliage at Treeline, and Implications for Treeline Dynamics in Northern Manitoba

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## Abstract

Winter desiccation and mortality of coniferous foliage are important determinants of carbon balance in trees and thus can influence the location of the subarctic treeline ecotone. The purpose of this study was (i) to assess variation in winter desiccation and viability of first-year conifer needles at several heights and orientations along tree boles across the forest-tundra ecotone near Churchill, Manitoba, from 2008 to 2010, and (ii) determine if there is a noticeable influence of needle health on ongoing treeline advance in the area. Growing season air temperatures around Churchill were significantly cooler in 2009, resulting in the development of significantly shorter needles during 2010. Minimum epidermal conductance ( $g_{\min}$ ) varied little with height on the tree or orientation to the prevailing wind direction. The highest values of  $g_{\min}$  occurred in 2010, when temperatures during the previous June ( $t - 1$ ) were 2.9 °C cooler than normal, and the lowest  $g_{\min}$  occurred during 2009 when June ( $t - 1$ ) was 1.2 °C warmer than normal. There were few correlations between needle viability and water content, and little consistency among years. However, significant correlations occurred during all 3 yr in northwest-facing needles at treeline, which suggests that treeline trees could be the most susceptible to water loss and dieback, relative to forest and tundra stems. Despite the occurrence of some winter desiccation, death of coniferous foliage (<10%) and sapling mortality (4–17%) was low, and rapid height growth of live saplings suggests passage through the wind-blown snow abrasion zone does not significantly impede wood production. Ostensibly winter desiccation and foliage mortality does not significantly influence sapling height growth and treeline dynamics around Churchill.

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## Introduction

Winter desiccation of foliage is believed to contribute to the stress of conifers at treeline. At high altitudes and latitudes, cuticular development can be restricted by a short and cool growing season (Wardle, 1971; Tranquillini, 1979). Increased cuticular transpiration can result in severe winter dehydration, and it has been suggested that winter desiccation resulting in foliage loss is an important determinant of carbon balance for trees and therefore the location of the treeline ecotone (Tranquillini, 1979; Kullman, 2007; Holtmeier and Broll, 2011). Winter desiccation is associated with two processes that can occur simultaneously, though independent of each other: frost drought and abrasion by wind-blown snow grains. Frost drought occurs because soil water is frozen or just cold, and is unavailable to the plant, though transpiration proceeds—even in winter (Michaelis, 1934). Furthermore, increased winter desiccation can occur when the epidermis of needles fails to fully develop as a result of a lack of warmth during the short growing season, and consequently needles are poorly protected against cuticular transpiration during the following winter (Wardle, 1971; Tranquillini, 1979). Strong winds can transport snow grains at high velocities, which abrade the cuticles of needles and damage stomata, leading to increased water losses, particularly at the end of winter (Hadley et al., 1991; van Gardingen et al., 1991). In either case, dehydration would likely be most severe during cold winters

with low precipitation for two reasons: (i) the rooting zone remains frozen longer, during which time the supply of water to the needles is prevented, and (ii) needles that might normally be snow covered and protected from extremely cold temperatures and wind-blown snow abrasion, instead can be exposed to the elements and susceptible to tissue damage and water loss (Grace, 1977; Cairns, 2001).

Climatic changes during the last 20 to 30 yr have resulted in increased scrutiny in marginal environments like the treeline ecotone, as they are most likely to transform with warming (cf. Harsch et al., 2009). A causal linkage has been suggested between temperature and metrics of treeline dynamics (i.e., changes in treeline structure and/or position) such as fecundity, establishment, recruitment, radial and height growth, and treeline advance, among others (Battlori et al., 2009; Holtmeier and Broll, 2010; Kharuk et al., 2010; Mamet and Kershaw, 2013). It seems logical to assume a direct relationship between an environmental factor and a plant performance parameter if the two variables are found to vary concomitantly within an ecotone. However, such co-variation does not necessarily represent a causal mechanism, as indirect effects of an environmental factor (e.g., summer temperature) can have a greater effect on a parameter of interest (e.g., tree growth) through its effects on another factor (e.g., needle maturation). Thus determining how plant performance can be affected by its environment is often quite difficult, and studies can be further complicated by non-linear processes, difficult to predict synergistic interactions, and

fortuitous co-variation between environmental factors and plants (Sveinbjörnsson et al., 2002).

Several studies on coniferous foliage and environmental conditions around Churchill, Manitoba, were completed during the 1980s and 1990s (Scott et al., 1987a, 1987b; Scott and Hansell, 1992, 2002; Scott et al., 1993). Scott et al. (1993) found that wind-blown snow abrasion and needle loss represented a noticeable limitation to height growth above the snowpack, and that treeline trees needed to achieve at least 80 cm in stature over 7 to 8 yr in order to successfully mitigate passage through the abrasion zone. Abrasion was alleviated by tree and branch density, as woodlands (scattered groupings of erect trees) and open forest (>95% full-crowned trees) were virtually free of snow abrasion, and snow load on branches was the dominant winter stress in those treed environments (Scott et al., 1993; Scott and Hansell, 2002). Temperature and moisture extremes in the tundra caused height growth to be reduced in the prostrate trees established there, which meant that the stem of a terminal bud of a tundra “tree” will be forced to spend a substantial number of winters in the abrasion zone, leaving it more vulnerable to damage (Scott et al., 1987a). Thus there is evidence that supports the hypothesis that a synergy of processes operating during the summer (e.g., height growth, needle development) and winter (frost drought and winter desiccation) plays a role in treeline dynamics around Churchill, which also has been suggested by studies from other regions (Baig and Tranquillini, 1980; Hadley and Smith, 1983, 1987; Kayama et al., 2009; Nagano et al., 2009; among others).

Despite the hypothesis that treeline around Churchill would not likely advance with warming, unless there was a disturbance resulting in secondary succession (Scott et al., 1987b), recent evidence suggests that treeline advancement has resumed during the warm period of the last 30 yr (Mamet and Kershaw, 2012). However, several studies suggest the effects of not only summer conditions, but also winter environments cannot be ignored in searching

for regional mechanisms for the treeline phenomenon (Kullman, 2007; Kharuk et al., 2010; Holtmeier and Broll, 2011; Kiryanov et al., 2012). Further, to our knowledge, there have been no studies on winter effects on treeline vegetation in the Churchill area in 20 yr or more, nor have there been comparable studies on finer-scale treelines (<100 m from forest to tundra) in the area. Therefore, the purpose of this study was to compare metrics of needle health within open forest, the forest-tundra ecotone, and tundra, and determine the presence of winter desiccation and its relevance to treeline dynamics in the Churchill region. Specifically, the aim was to answer the following questions—how does needle health vary: (1) within and above the mid-winter snowpack; (2) with orientation to regional wind patterns; (3) in forest-facing and tundra-facing margins of trees; and (4) through time as a function of environmental conditions during needle formation. In addition (5), is there a link between winter desiccation and recent treeline dynamics?

## Materials and Methods

### STUDY AREA

Sampling was completed during mid-winter (late February/early March) of 2008–2010 at four sites east of the Churchill town site (58°45'N, 93°04'W) (Fig. 1; Table 1). Tree populations at the four sites were dominated by *Picea glauca* (Moench) Voss. (white spruce), with scattered *Larix laricina* (Du Roi) K. Koch. (tamarack). *Picea mariana* (Mill.) B.M.P. (black spruce) were very rare at the four sites, though become increasingly prevalent further inland as a thicker layer of peat has accumulated following post-glacial isostatic rebound, making conditions more conducive for *P. mariana* recruitment (Dredge, 1992; Wolf et al., 2006). *Rhododendron groenlandicum* (Oeder) Kron & Judd (Labrador tea) and *Betula glandulosa* Michx. (dwarf birch) dominate the understory in treed environments across the region. Mean January, July, and annual temperatures are  $-26.7$ ,  $12.0$ , and  $-6.9$  °C, respectively

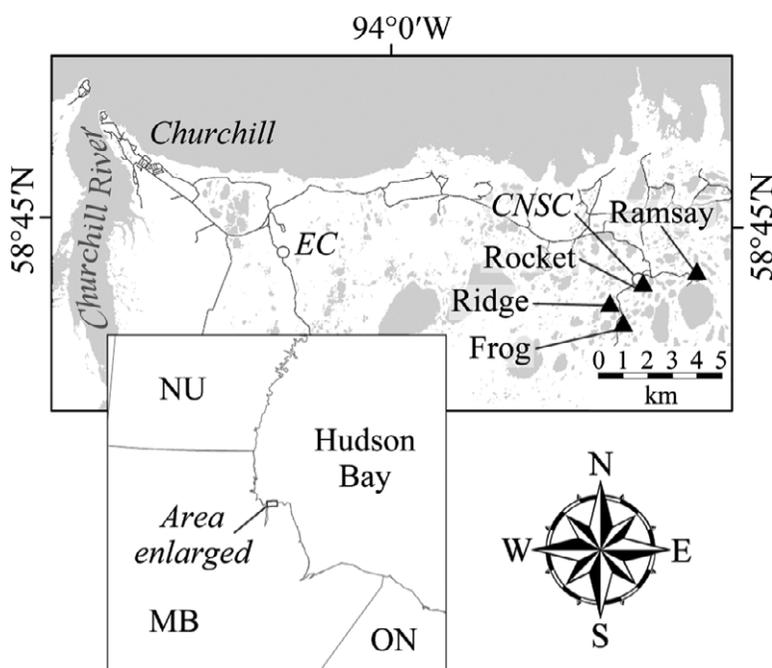


FIGURE 1. Location of the sampling sites southeast of Churchill, Manitoba. The locations of the Environment Canada weather station (EC) and the Churchill Northern Studies Centre (CNSC) are shown by open circles. Site descriptions are given in Table 1.

**TABLE 1**  
**Characteristics of each site from which needles were sampled from 2008 to 2010.**

Site	Abbreviation	Elevation (meters a.s.l.)	Zone <sup>a</sup>	Orientation <sup>b</sup>	Ecotone length (m)	Canopy openness (%) <sup>c</sup>
Frog pond	FRO	16	F	248°	36	91.6 ± 1.6
			E			91.5 ± 1.2
			T			100.0 <sup>d</sup>
Ramsay Lake	RAM	18	F	136°	67	79.6 ± 7.2
			E			81.2 ± 10.5
			T			100.0
Ridge	RID	22	F	38°	49	63.8 ± 8.3
			E			83.6 ± 7.4
			T			100.0
Rocket	ROK	16	F	190°	103	53.2 ± 9.4
			E			83.2 ± 6.3
			T			100.0

<sup>a</sup>F = forest, E = ecotone, T = tundra.

<sup>b</sup>Bearing in which tree density decreases (i.e., forest transitions to tundra).

<sup>c</sup>Determined through analysis of hemispherical photos taken at each site ( $n = 18$  per site) (Frazer et al., 1999).

<sup>d</sup>Canopy openness was assumed to be 100% within the tundra as there was no tree cover.

(1971–2000 normal). An average of 562 mm of precipitation falls annually with 44% as snow (Environment Canada, 2012).

#### NEEDLE COLLECTION

During the winter field season at each of the four sites, the most recent production of needles or “branchlets” formed during the preceding growing season were sampled at several heights and orientations from three randomly selected *P. glauca* trees in each zone: forest, forest-tundra ecotone, and tundra. Using pruning shears, a branchlet was removed from each tree >15 cm depth into the snowpack, within the abrasion zone (0–80 cm above the snow surface), and >1.5 m above the snow surface. This sampling was replicated three times on each tree to represent three cardinal directions: northwest—the dominant wind direction, south—greatest receipt of solar radiation and hence, greatest potential for solar desiccation (cf. Hadley et al., 1991), and east as a control. As the tundra is by definition “treeless” and only stunted individuals were found, samples were only collected from within the snowpack and in the abrasion zone [collected each season:  $n_{P.glauca} = 36$ ,  $n_{branchlets} = 288$  (4 sites × 72 branchlets per site)].

Since not all sites were oriented with the gradient of decreasing tree density into the northwest, in 2010 branchlets were collected from the forest- and tundra-facing aspects of each tree, in addition to the three cardinal directions described previously. However, due to logistical constraints, this double sampling was only completed at one site (Rocket). Following collection in the field, all branchlets were placed in sealed Ziploc<sup>®</sup> bags and kept in the dark at 5 °C or cooler until laboratory processing.

#### SNOWPACK

Mid-winter snowpack sampling was carried out from 28 February to 6 March 2008 and 2009 and included snow pits and snow cores obtained within the three zones at each site using an Adirondack snow sampler (McClung and Schaerer, 2006). Due to time

constraints, no snowpack survey was completed in 2010. Only the snow cores were analyzed for this study. Heat Transfer Coefficient (HTC) was calculated following Kershaw (1991, 2001) in order to compare thermal properties of the snowpack among sites.

#### SOIL TEMPERATURE

To measure soil temperature at 10 cm depth, HOBO microloggers (HOBO H8 Pro, Onset Computer Corporation, Cape Cod, Massachusetts, U.S.A.; with a measuring range of –30 to +50 °C and a resolution of 0.2 °C measured hourly) were deployed within the forest and at treeline. Loggers were initiated 22 June 2008, and data were collected during October and June each year. Due to logistical constraints, loggers were not deployed within the tundra zone at each site.

#### NEEDLE WATER CONTENT AND VIABILITY

Percent water content (WC) was determined from measurements of fresh and dry weights (*f.w.* and *d.w.*) determined using a Scientech<sup>®</sup> SA210 precision weigh balance (Scientech, Inc., Boulder, Colorado, U.S.A.) following Hadley and Smith (1983):

$$WC = \frac{f.w. - d.w.}{d.w.} \times 100 \quad (1)$$

Dry weights were measured after 3 d of drying at 105 °C. Needle viability was determined by computing the percent of needles remaining green (>50% of needle area) after 5 d at room temperature (2008: 18.5 ± 2.3 °C; 2009: 18.3 ± 3.4 °C; 2010: 18.5 ± 1.9 °C) and 9.7–11.3% relative humidity (cf. Hadley and Smith, 1983) as determined at 5-min intervals using a Campbell Scientific<sup>®</sup> HMP45C-L temperature and relative humidity probe (Campbell Scientific Canada Corp., Edmonton, Alberta, Canada).

#### SAPLING HEIGHT GROWTH

During July 2008, at each of the four sites, white spruce saplings (between 0.15 and 2.0 m in height; Hofgaard and Rees,

2008) were destructively sampled in open-ended 30 m plots within the forest and ecotone (for details, see Mamet and Kershaw, 2012). Branch whorls and bud scars were counted and measured on live saplings to determine height growth rates. Any sapling mortality was noted. Mean winter snowpack depth in forest and in the ecotone was determined (see above), and live saplings that extended greater than 80 cm above the mean snow depth were used to assess height growth rates through the abrasion zone (Scott et al., 1993).

### EPIDERMAL CONDUCTANCE

Transpiration rates were determined gravimetrically from the excised branchlets. The cut ends of the each branchlet were sealed with paraffin wax in order to prevent water loss through the cut. Water loss through the stem was assumed to be minimal (Baig and Tranquillini, 1980). Following determination of fresh weight, branchlets were weighed at 24-h intervals for 5 d in a darkened room at ambient conditions before dry weight determination (Baig and Tranquillini, 1980). Determinations of needle surface area (SA) were completed using cross-sectional needle geometries computed for *Picea* by Bond-Lamberty et al. (2003), and the mean needle length ( $l$ ) for each branchlet by:

$$SA = 2l(\sqrt{1.35^2 + 1}) \quad (2)$$

Epidermal conductance was calculated as needle transpiration per unit surface area ( $\text{g m}^{-2} \text{s}^{-1}$ ) divided by the water vapor density ( $\text{g m}^{-3}$ ) gradient between the needle interior and the surrounding environment, assuming 100% relative humidity within the needle and similar needle and air temperatures (Anfodillo et al., 2002). Epidermal conductance was expressed in  $\text{m s}^{-1} 10^{-5}$  as recommended by Kerstiens (1996). Minimum epidermal conductance ( $g_{\min}$ ) was determined by fitting a least-squares regression line to the relationship between epidermal conductance and time since full stomatal closure was assumed to have occurred. It is impossible to determine if all stomata closed, as some could have been damaged or non-functional. Therefore, the term epidermal conductance was used to include both cuticular and any residual stomatal conductance components following closure (van Gardingen et al., 1991). The intercept of the regression line when  $t = 0$  provides an unbiased estimate of  $g_{\min}$  (van Gardingen et al., 1991). Data obtained during the period before full stomatal closure had a curvilinear relationship and were excluded from the regression.

### DATA ANALYSES

Statistical tests were performed using SigmaStat version 3.5 (Systat Software Inc., San Jose, California, U.S.A.). Preliminary analyses of variance (one-way ANOVA) suggested there was little to no difference in each needle metric among zones between sites. Therefore similar zones were combined, and statistical differences in needle metrics among azimuths, heights, and zones were investigated by one-way ANOVA at a regional scale.

## Results

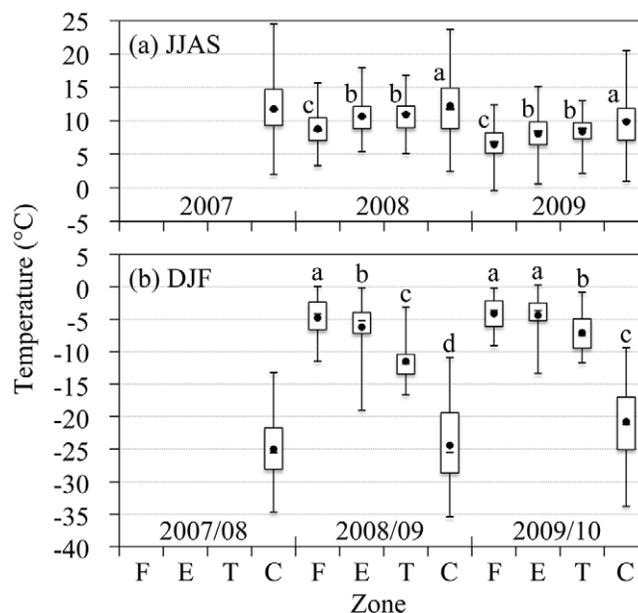
### ENVIRONMENTAL CONDITIONS

Mean daily air temperatures from 22 June to 15 September (growing season as determined by the  $\geq 3.2$  °C soil temperature

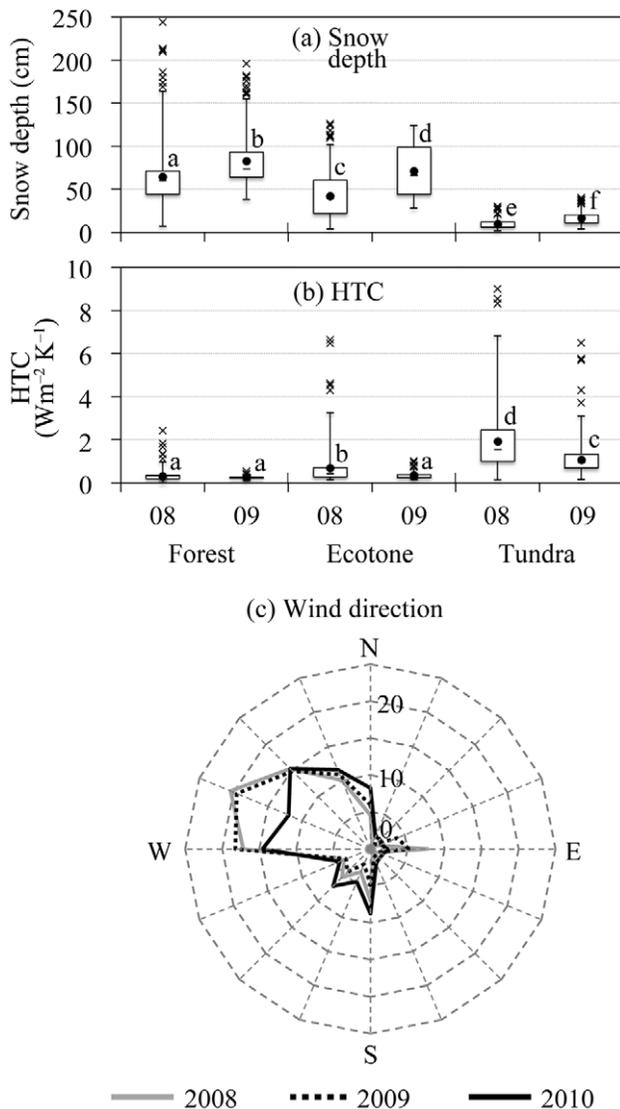
threshold at 10 cm depth; Körner and Paulsen, 2004) were 11.8 °C, 12.3 °C, and 9.8 °C, in 2007, 2008, and 2009, respectively. Air temperatures during 2009 were 1.1 °C cooler than the 1971–2000 normal of 10.9 °C, and significantly cooler than 2007 and 2008 ( $F_{2,254} = 7.087$ ,  $P = 0.001$ ). Air temperatures were also warmer than within the soil, and soil temperatures increased significantly from forest to within the ecotone in both 2008 ( $F_{3,856} = 49.707$ ,  $P < 0.001$ ) and 2009 ( $F_{3,856} = 47.993$ ,  $P < 0.001$ ) (Fig. 2, part a).

Mid-winter air temperatures (December–February) were similar in 2007/2008 (−25.0 °C) and 2008/2009 (−24.4 °C), though significantly warmer during 2009/2010 (−20.7 °C) ( $F_{2,266} = 15.639$ ,  $P < 0.001$ ). Mid-winter of 2009/2010 was also 3.9 °C warmer than normal (−24.8 °C). Mid-winter air temperatures were significantly cooler than soil temperatures (2008/2009:  $F_{3,896} = 723.249$ ,  $P < 0.001$ ; 2009/2010:  $F_{3,894} = 785.992$ ,  $P < 0.001$ ), and soil temperatures decreased from forest to tundra (Fig. 2, part b).

Snow depth ranged from 64 to 82 cm in the forest, 4 to 126 cm in the ecotone, and 9 to 16 cm in the tundra (Fig. 3, part a). Mean snow depth in forest, ecotone, and tundra was 81.6, 58.4, and 13.6 cm, respectively, and was significantly different among zones and years ( $F_{5,731} = 215.314$ ,  $P < 0.001$ ). The thermal conductivity of the snow as indicated by the Heat Transfer Coefficient (HTC) was similar between forest and ecotone (range: 0.28–0.66  $\text{Wm}^{-2} \text{K}^{-1}$ ), but was significantly greater within the tundra



**FIGURE 2.** Temperature of the air and at 10 cm soil depth across the forest-tundra ecotone at hourly intervals. (a) Growing season temperatures from 22 June to 15 September (JJAS) and (b) winter temperatures from 1 December to 28/29 February (DJF). Soil temperature in forest (F), ecotone (E), tundra (T), and Churchill air temperature (C). Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each zone is indicated as a solid circle. Different lowercase letters at the top of each box stand for intra-year differences based on a one-way ANOVA followed by a Holm-Sidak *post hoc* comparison. No soil temperature measurements were available prior to 22 June 2008. Statistical differences are significant at  $P < 0.05$ .



**FIGURE 3.** Mid-winter snowpack characteristics (2008–2009) and wind direction frequency (2008–2010). (a) Snow depth. (b) Heat Transfer Coefficient (HTC). (c) Wind direction frequency (Environment Canada, 2012). Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each zone is indicated as a solid circle. (a, b) Outliers for each year ( $\pm$  two standard deviations) are indicated by the letter “x.” Different lowercase letters at the top of each box stand for differences based on a one-way ANOVA followed by a Holm-Sidak *post hoc* comparison. Statistical differences are significant at  $P < 0.05$ .

( $1.04\text{--}1.90 \text{ Wm}^{-2} \text{ K}^{-1}$ ) ( $F_{5,732} = 119.109, P < 0.001$ ) (Fig. 3, part b).

Mid-winter wind gusts typically originated between west and northwest, with 52.9%, 52.6%, and 41.9% frequency during 2007/2008, 2008/2009, and 2009/2010, respectively (Fig. 3, part c). Mean wind speeds were similar at  $\sim 23 \pm 12 \text{ km h}^{-1}$  between mid-winter of 2007/2008 and 2008/2009, though significantly lower during 2009/2010 ( $20 \pm 13 \text{ km h}^{-1}$ ) ( $F_{2,6485} = 24.146, P < 0.001$ ). Similarly, strong breezes ( $>41 \text{ km h}^{-1}$  according to the

Beaufort Scale) occurred approximately 12% of the time from 2007 to 2009, but with only 9% frequency during 2009–2010.

#### MINIMUM EPIDERMAL CONDUCTANCE

Minimum epidermal conductance ( $g_{\min}$ ) varied little among different azimuths, heights, and zones (Fig. 4). During 2008,  $g_{\min}$  was significantly greater in northwest-facing needles in the tundra compared to east-facing needles ( $F_{2,61} = 3.254, P = 0.045$ ), and  $g_{\min}$  of tundra-northwest needles were significantly greater than values in the forest or ecotone ( $F_{2,75} = 4.556, P = 0.014$ ) (Fig. 4, part a). Though the same patterns were not observed in 2009 (Fig. 4, part b), ecotone needles at a height greater than 0.8 m had greater values of  $g_{\min}$  relative to the abrasion zone and snowpack in 2009 ( $F_{2,92} = 7.854, P < 0.001$ ) (Fig. 4, part d) and 2010 ( $F_{2,45} = 8.474, P < 0.001$ ) (Fig. 5).

There was little difference in  $g_{\min}$  among needles sampled from the forest- and tundra-facing sides of trees (Fig. 5, part a); however, the  $g_{\min}$  of forest-facing needles within the forest zone was significantly lower than that of tundra-facing needles ( $t_{48} = -2.052, P = 0.046$ ). At the same time,  $g_{\min}$  was similar within ecotone and tundra, and significantly lower in the forest ( $F_{2,129} = 7.599, P < 0.001$ ). Needles sampled at a height  $>0.8 \text{ m}$  within the ecotone had a  $g_{\min}$  significantly greater than needles from a similar height within the forest ( $t_{30} = -4.603, P < 0.001$ ) (Fig. 5, part b).

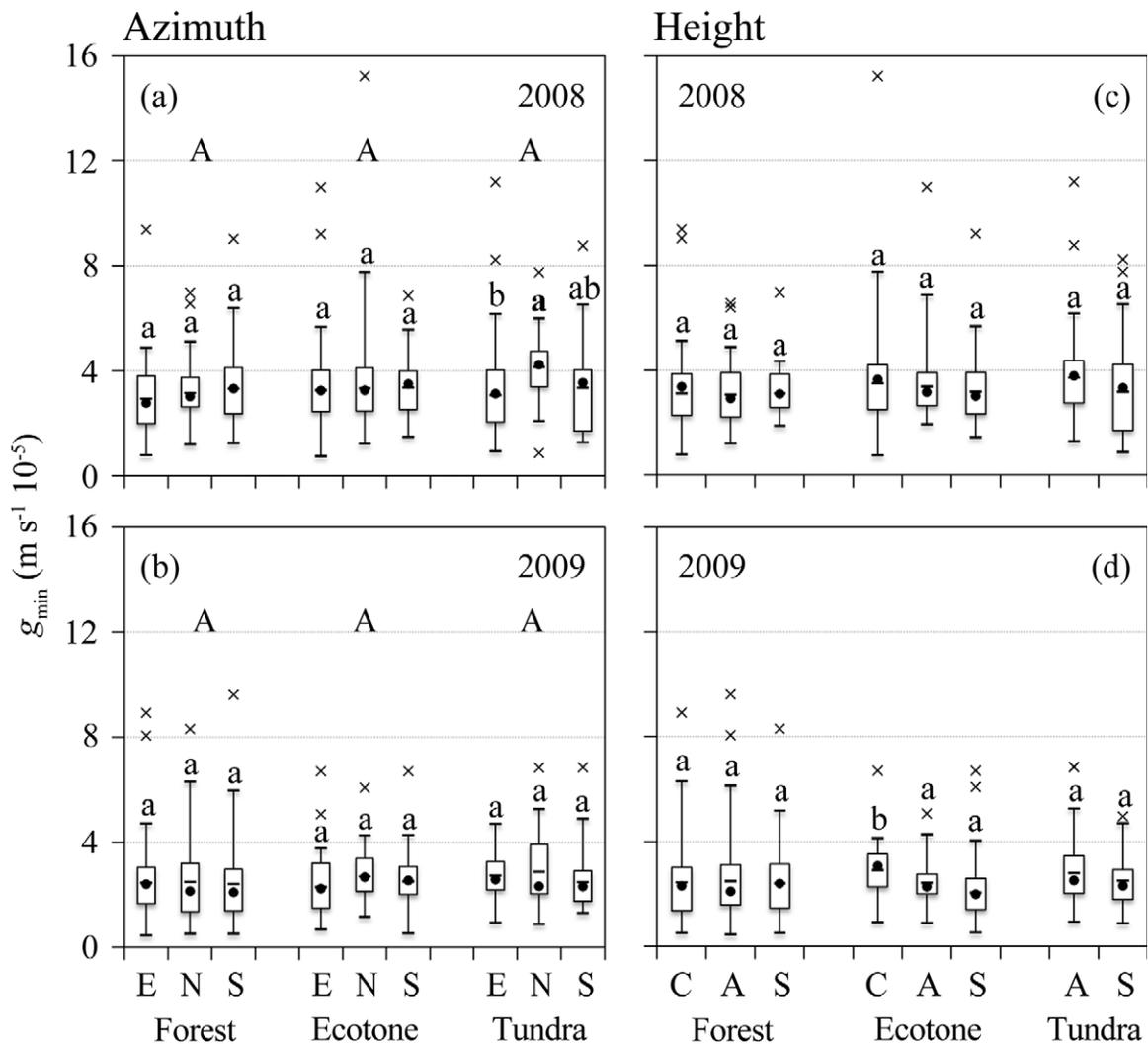
Annual variation in  $g_{\min}$  from 2008 to 2010 was inversely related to temperatures during June of needle formation in the previous year (Fig. 6). Values of  $g_{\min}$  were significantly different among years ( $F_{2,187} = 97.756, P < 0.001$ ), as were June temperatures ( $F_{2,2155} = 127.641, P < 0.001$ ). Most notable perhaps is that the highest values of  $g_{\min}$  ( $4.6 \times 10^{-5} \text{ m s}^{-1}$ ) were observed in 2010, when temperatures during the previous June were  $3.7 \text{ }^{\circ}\text{C}$ , which was  $2.9 \text{ }^{\circ}\text{C}$  cooler than normal. Conversely, the lowest  $g_{\min}$  of  $2.8 \times 10^{-5} \text{ m s}^{-1}$  occurred during 2009 when the previous June was  $7.8 \text{ }^{\circ}\text{C}$ ;  $1.2 \text{ }^{\circ}\text{C}$  warmer than normal.

#### NEEDLE VIABILITY AND WATER CONTENT

Mean length of needles produced during 2009 ( $7.45 \pm 0.04 \text{ mm}$ ; values are  $\pm \text{SE}$ ) was significantly shorter than those originating from 2007 ( $9.42 \pm 0.06 \text{ mm}$ ) and 2008 ( $9.10 \pm 0.04 \text{ mm}$ ) ( $F_{2,3607} = 288.361, P < 0.001$ ). Needle water content and viability across the study sites ranged from 10.5 and 100.0% ( $\sigma = 9.6\%$ ) to 20.2 and 165.1% ( $\sigma = 14.9\%$ ), respectively, though  $>85\%$  of observed water contents exceeded 90%. Indeed, needle water content and viability were consistent among zones, orientations, and years (one-way ANOVAs,  $P > 0.05$ ). There were few correlations between needle viability and water content, and little consistency in correlations from year to year (Table 2). However, significant correlations were observed during all 3 yr in northwestern-facing needles within the ecotone zone.

#### SAPLING HEIGHT GROWTH

Within sampling plots in the forest and ecotone, 23 and 32 live saplings, respectively, were sampled for branch whorl counts and height growth determination. Forest saplings required  $6.6 \pm$



**FIGURE 4.** Minimum epidermal conductance ( $g_{\min}$ ) among different (a, b) azimuths and (c, d) heights from 2008 to 2009. Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each orientation is indicated as a solid circle. Outliers for each orientation ( $\pm$  two standard deviations) are indicated by the letter “x.” Different lowercase letters at the top of each box stand for intra-zone differences based on a one-way ANOVA followed by a Holm-Sidak *post hoc* comparison. Values in bold represent differences among similar orientations between years. Different uppercase letters represent differences among zones. Statistical differences are significant at  $P < 0.05$ . (a, b) E = east, N = northwest, S = south. (c, d) C =  $>0.8$  m and A = 0 to 0.8 m height above the snowpack, S =  $>0.15$  m depth into the snowpack.

2.6 yr (values are  $\pm 1\sigma$ ) to clear the abrasion zone (80 cm above the mean winter snowpack), while ecotone saplings required less time at  $5.6 \pm 3.0$  yr, though there was no significant difference between the two zones (two-tailed  $t$ -test:  $t_{53} = 1.543$ ,  $P = 0.129$ ). Within the forest, 17% of saplings surveyed were dead, compared with 4% in the ecotone.

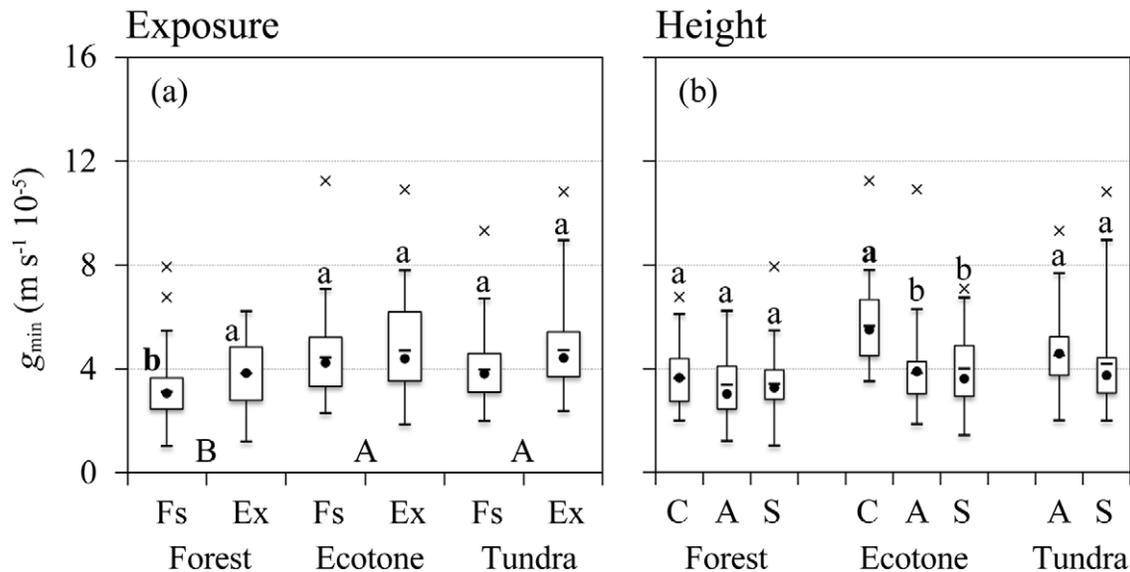
## Discussion

### NEEDLE CHARACTERISTICS AND SAPLING HEIGHT GROWTH

The mean values of  $g_{\min}$  obtained in this study were similar to those obtained by other studies near treeline (Sowell et al., 1982; Heinsoo and Koppel, 1998; Anfodillo et al., 2002), and despite notable inter-tree variability in  $g_{\min}$ , there was very little variation across a gradient of decreasing tree density from 2008 to 2010. However, there was a significant difference in  $g_{\min}$  between years,

and a noticeable correspondence between temporal patterns of  $g_{\min}$  and early growing season temperatures (Fig. 6). This supports the hypothesis of Michaelis (1934) and Wardle (1971) that insufficient maturation of coniferous foliage during the growing season can influence the desiccation resistance of coniferous foliage during the following winter.

There was little variability in  $g_{\min}$ , needle water content, or viability with either sampling height or orientation to the regional wind patterns, though there was some association between viability and water content across the region (Table 2). Based on zone of greatest wind exposure around Churchill and the work of others (Baig and Tranquillini, 1980; Hadley and Smith, 1983; Scott and Hansell, 1992), it was expected that correlations between viability and water content would be greatest within different subsets of the sampling schemes—zone: tundra, azimuth: northwest, and height: abrasion zone. Indeed there were significant correlations observed



**FIGURE 5.** Minimum epidermal conductance ( $g_{\min}$ ) among different (a) exposures and (b) heights during 2010. Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each orientation is indicated as a solid circle. Outliers for each orientation ( $\pm$  two standard deviations) are indicated by the letter “x.” Different lowercase letters at the top of each box stand for intra-zone differences based on a one-way ANOVA followed by a Holm-Sidak *post hoc* comparison. Values in bold represent differences among similar orientations between years. Different uppercase letters represent differences among zones. Statistical differences are significant at  $P < 0.05$ . (a) Fs = forest-facing, Ex = tundra-facing (exposed). (b) C =  $>0.8$  m and A = 0 to 0.8 m height above the snowpack, S =  $>0.15$  m depth into the snowpack.

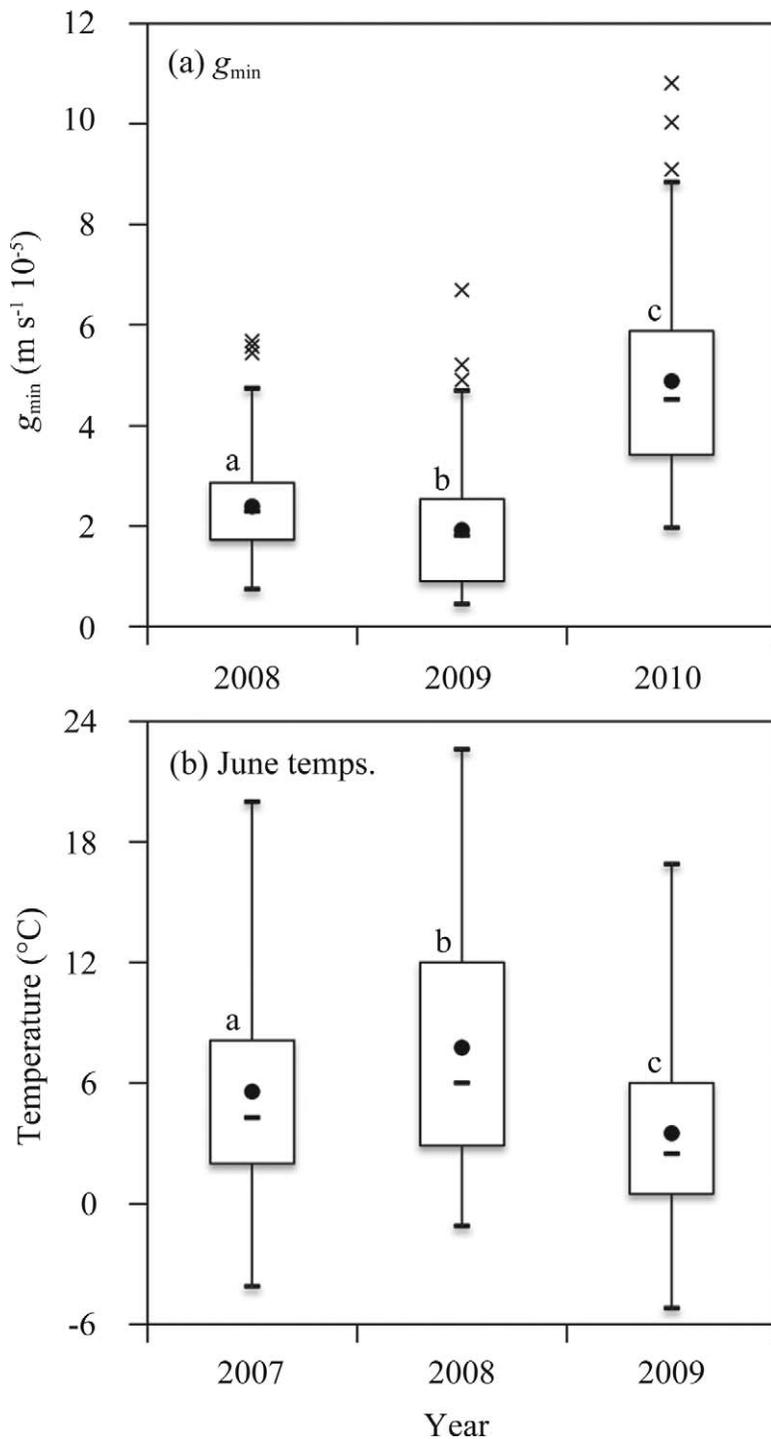
within these sampling units, though the only consistency among years was for northwest-facing branches within the ecotone. These results are exceptional as none of the sampling sites were oriented with the tree density gradient—parallel to the regional wind direction—yet all sites together reflected what could be interpreted as a regional wind signal within the ecotone. While there was a statistically significant relationship between viability and water content, it is beyond the scope of this study to determine if this phenomena is due to increased abrasion from wind blown snow and ice particles, damage to the stomata, the rubbing together of adjacent needles, or the flexing of leaves in the wind (Grace, 1977; van Gardingen et al., 1991). It is likely a combination of two or more of these actions, though the mechanical abrasion by neighboring needles and branches is probably more important for water loss. This is because it would be expected that northwest-facing needles on the more exposed tundra would experience similar—if not more—water loss compared with more sheltered ecotone trees, if snow and ice abrasion was the dominant agent. Further, tundra individuals were very short in stature ( $<0.8$  m) and therefore would not be subject to the same stresses and branch movements as taller trees within the ecotone (cf. Dean et al., 2002). However, further research is necessary to properly evaluate these relationships.

Previous studies around Churchill have suggested that trees must grow 80 cm in 7–8 yr in order to successfully pass through the abrasion zone and achieve tree growth form (Scott et al., 1993). The saplings sampled at the four sites in this study grew through the abrasion zone in less than 7 yr in both the forest and ecotone. Furthermore, sapling mortality was low among the sampling sites (4–17%), which suggests that passage through the abrasion zone does not significantly impede wood production and height growth in forest and ecotone stems.

#### ENVIRONMENTAL CHARACTERISTICS

Some research has suggested a link between winter soil temperatures and winter desiccation (Kullman, 2007). Kullman (2007) found that winter desiccation was a primary limiting factor determining the position of treeline in the Swedish Scandes until the late 1980s, when amelioration of winter temperatures occurred. The limiting factor then shifted from winter temperatures and foliage mortality due to winter desiccation to summer temperatures and their effects on seed viability. Additionally, Cairns (2001) hypothesized that a greater amount of snowfall resulted in late-lying snowpack and longer duration of frozen soils during spring, which limited moisture supply and, consequently, increased winter desiccation at treeline in northern Montana. Stems burdened by heavy snow loads are also vulnerable to physical damage through settling or creeping snow, or infection by various snow fungi (Holtmeier, 2009). Conversely, it has been suggested that a deeper snowpack reduces winter desiccation by burial of exposed stems (Grace, 1977). It is difficult to determine the effects of snowpack and soil temperatures on epidermal conductance around Churchill due to the limited timeframe of this study, and the potential for the aforementioned synergistic effects. Indeed, snowpack was deeper and soil temperatures  $1.5$  °C warmer during 2009 compared with 2008, and the lowest values of  $g_{\min}$  were observed during 2009. Therefore, it is difficult to rule out potential interactions between environmental influences like snowpack, soil, and air temperature. Observations of winter desiccation at a seasonal resolution, or the use of long-term monitoring (*sensu* Kullman, 2007) would be necessary to evaluate synergistic environmental influences beyond conjecture.

Due to the short time frame of this study and the length of the snowfall season (approximately September through May), this study only considered the extent of winter desiccation and water



**FIGURE 6.** (a) Minimum epidermal conductance ( $g_{\min}$ ) at site Rocket and (b) June temperatures (Environment Canada, 2012) from 2007 to 2010. Minimum and maximum values, along with the first, second (median), and third quartiles of each data set are shown as box and whisker plots (Tukey, 1977). The mean of each year is indicated by a solid circle. Outliers for each year ( $\pm$  two standard deviations) are indicated by the letter “x.” Different lowercase letters at the top of each box stand for differences between years based on a one-way ANOVA followed by a Holm-Sidak *post hoc* comparison. Differences are significant at  $P < 0.05$ .

status up to the end of February/beginning of March. It is possible that desiccation as well as premature dehardening and freezing injury could happen during spring (Cannell, 1985). However, amounts of first-year needle death (derived by  $100 - \text{percent viability}$ ) of 1.7–7.0% over the duration of the study were comparable to those found near Churchill during 1989 (~5% in forest and ~6% at treeline; Scott and Hansell, 1992), and at other treelines in North America [e.g., 8.7% in Montana (Cairns, 2001) and 12% in Colorado (Weisberg and Baker, 1995)]. These data, combined with the lack of noticeable spring mortality observed at the sites

sampled in this study, suggest that the possibility of notable spring mortality is likely low at treelines around Churchill. However, substantial winterkill has been observed at tree islands and krummholz stands proximal to the coast, and future sampling could include these sites that might be more susceptible to spring desiccation.

## Conclusion

Winter desiccation is widely believed to be a limitation of treeline position at some locations (Wardle, 1971; Tranquillini,

TABLE 2

Correlations between needle viability and percent water content from *P. glauca* needles collected from various orientations across the forest-tundra transition.

Year	Zone	Orientation	<i>r</i>	<i>n</i>
2008	F	>0.8 m	<b>0.558</b>	33
2008	F	Abrasion	0.434	33
2009	F	Snow	0.408	30
2008	F	Northwest	0.462	28
2008	E	>0.8 m	<b>0.865</b>	35
2008	E	Abrasion	<b>0.716</b>	35
2008	E	Northwest	<b>0.554</b>	33
2009	E	Northwest	<b>0.458</b>	33
2010	E	Northwest	0.806	8
2010	T	Abrasion	0.551	18
2008	T	South	<b>0.609</b>	24

Only values associated with  $P \leq 0.05$  are shown;  $P \leq 0.01$  for bold values. F = forest, E = ecotone, T = tundra.

1979; Sowell et al., 1982; Kullman, 2007), though there is a growing body of evidence that argues against not only the importance of winter desiccation in determination of treeline position, but also the causes of winter desiccation itself (Grace, 1990; Grace, 1993; Anfodillo et al., 2002; Nakamoto et al., 2011). The results of this study suggest that some winter desiccation does occur at diffuse treelines around Churchill and that this desiccation is likely primarily related to needle development, which is controlled by temperature during the early growing season of the previous year—though with synergistic effects among snowpack and winter soil temperatures. Regardless of the origins for winter desiccation around Churchill, death of coniferous foliage appears to be low (<10% of first-year needles), and probably does not significantly influence height growth of trees or fine-scale treeline dynamics in the area (Mamet and Kershaw, 2012)—as indicated by the low sapling mortality and rapid height growth through the abrasion zone among the sampling sites. These results support the assertion that diffuse treelines like those occurring around Churchill might not be constrained by tissue dieback (Harsch and Bader, 2011). However, due to the occurrence of numerous tree islands and krummholz stands in the Churchill area and the presence of substantial winterkill at these locales during the spring, further research should focus on these patches of individuals in order to gain a better understanding of the regional framework for treeline dynamics around Churchill.

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