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Climatology of the Forest-Tundra Ecotone at a Maritime Subarctic-Alpine Site, Mealy Mountains, Labrador

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ABSTRACT. Climatological investigations were conducted from 2001 to 2009 in the central Mealy Mountains, Labrador (53.6˚ N), as part of interdisciplinary research on tree line ecology and climate change. The aim was to describe local climatic and edaphic variables along an altitudinal gradient from the closed forest edge to the alpine tundra and to relate recent changes in regional climate to potential changes in the forest tundra ecotone. Results show relatively warm, moist summers and cool winters, with abundant precipitation and moderate to gale-force winds. At ca. 600 m a.s.l., the tree line was characterized by 694 ± 85 growing degree-days and a mean July air temperature of 12.9 ± 0.8˚C. Growing season soil temperatures of ca. 8˚C were similar across the forest-tundra ecotone, but their seasonal regimes differed among subzones. Soil nutrient fluxes showed some variation but no consistent pattern that would suggest nutrients as a limiting factor. Snow depth in the forest-tundra subzone was more variable than in the forest, indicating that microtopography is an important factor for tree survival there in winter. Comparisons of the field data with long-term regional climatic and hydrographic records show that conditions have become warmer and drier in the most recent decade compared with the previous half-century or more. Concurrent vegetation studies indicate that changes expected with a warming climate are already occurring.

Key words: Labrador, subarctic-alpine climate, forest-tundra ecotone, growing degree-days, soil temperature, nutrient flux, water balance, climate warming

RÉSUMÉ. De 2001 à 2009, des études climatologiques ont été effectuées dans les monts centraux Mealy, au Labrador (53,6˚ N) dans le cadre d'une recherche interdisciplinaire sur l'écologie de la limite forestière et le changement climatique. Ces études avaient pour but de décrire les variables climatiques et édaphiques locales le long d'une pente altitudinale allant de la lisière de la forêt dense jusqu'à la toundra alpine. Elles avaient également pour but de faire le lien entre les récents changements enregistrés dans le climat régional et les changements susceptibles de se produire dans l'écotone de la toundra forestière. Les résultats montrent des étés humides et relativement chauds ainsi que des hivers frais, avec des précipitations abondantes et des vents allant de modérés à coups de vent. À environ 600 m ASL, la limite forestière était caractérisée par 694 ± 85 degrés-jours de croissance et une température de l'air moyenne de 12,9 ± 0,8 ˚C en juillet. En saison de croissance, les températures du sol d'environ 8 ˚C étaient semblables à la grandeur de l'écotone de la forêt-toundra, bien que les régimes saisonniers différaient d'une sous-zone à l'autre. Les flux de nutriments du sol affichaient une certaine variation, mais il n'existait aucun modèle uniforme laissant entrevoir que les nutriments pouvaient être un facteur limitant. L'épaisseur de la neige dans la sous-zone forêt-toundra variait plus que dans la forêt, ce qui indique que la microtopographie est un facteur important pour la survie des arbres dans cet endroit-là l'hiver. La comparaison des données obtenues sur le terrain aux données climatiques et hydrographiques régionales à long terme laisse entrevoir que les conditions se sont réchauffées et asséchées au cours de la toute dernière décennie comparativement au demi-siècle précédent ou plus. Les études concurrentes sur la végétation indiquent que les changements qui étaient escomptés de même que le réchauffement du climat se manifestent déjà.

Mots clés : Labrador, climat alpin subarctique, écotone forêt-toundra, degrés-jours de croissance, température du sol, flux des nutriments, équilibre hydrique, réchauffement du climat

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INTRODUCTION

Studies have shown that a simple model of poleward and upslope movement of the forest limit under a warming climate is inadequate to explain the complexity of boreal forest ecotone responses to a changing climate (Körner, 1998; Sveinbjornsson et al., 2002; Gamache and Payette, 2005; Holtmeier and Broll, 2005, 2010; Harsch et al., 2009).

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The measure of growing degree-days (GDD), calculated using the mean daily surface air temperature (T_A) threshold of 5˚C, is frequently used in bioclimatic studies, including those of high-altitude black spruce (Sirois et al., 1999; Sirois, 2000). Meunier et al. (2007) analyzed the thermal requirements for black spruce (*Picea mariana*), the dominant tree line species in the eastern Canadian boreal region, in relation to GDD. They found a threshold for seed viability of approximately 800 GDD and mapped this bioclimatic threshold for the Canadian boreal region in terms of recent and projected future climates. On the basis of the observations that root-zone temperature is strongly correlated to tree canopy temperatures and that both are important physiological criteria for trees, Körner and Paulsen (2004) analyzed 10 cm soil temperatures at 46 alpine tree line sites between latitude 68˚ N and 42˚ S. They found growing season temperatures averaged 6.7 ± 0.8˚C overall and concluded that soil temperature was a better predictor of tree line on a global scale than either growing season length or GDD. Although their study included only three subarctic or boreal sites, it offers a global indicator of tree line climate for more intensive testing at the regional and local levels. Thawing degree-days (TDD), the cumulative number of daily heat units above 0˚C, is a bioclimatic measure used in relation to vegetation zonation and climate change impacts on vegetation in Arctic tundra (Edlund and Alt, 1989; Walker, 2000; Hollister et al., 2005), the boreal forest-tundra transition zone (Rouse, 1991), and subarctic alpine regions (Callaghan et al., 2010). TDD can be a useful indicator of the thermal potential for forest species expansion into tundra areas (Sundqvist et al., 2008).

Along with growing season conditions, winter climate can also constrain tree line expansion through damage to shoots and seedlings by wind abrasion and desiccation (Kullman, 1998; Cairns, 2001), and the krummholz form of tree line is generally associated with such winter stresses (e.g., Harsch et al., 2009). No single climatic variable adequately captures winter severity, although mean winter T_A is normally used as such a measure. Freezing degree-days (FDD), the cumulative degree-days below 0˚C, provide a winter counterpart to GDD that has some explanatory value in relation to tree line environments (Gamache and Payette, 2004; Palmer et al., 2012). The fact that snow provides protection to seedlings and shoots in winter but may also cause damage by excessive weight and delay growth in spring (Lavoie and Payette, 1992; Gamache and Payette, 2004) suggests that snow cover should be considered in assessing tree line climates.

Hare (1951) first argued that snowfall in central Labrador was primarily the result of tropospheric flow from the south and west, with surface convergence in migrating low-pressure systems, even though surface winds into these lows at the Labrador Sea were easterly. Regionally, large precipitation amounts over the Labrador plateau were subsequently confirmed through analysis of runoff from major rivers in the region (Hare, 1980). A recent review of temperate and boreal rainforests in eastern Canada (Clayden et al., 2011) identified areas south of the Mealy Mountains as "perhumid" boreal forest, i.e., forest with annual precipitation greatly exceeding evapotranspiration, and noted that adjacent montane areas below the resolution of their analysis might have even higher precipitation amounts.

Soil development is a reflection of climate and may be expected to vary across a climatic gradient. Conifer species require soil macronutrients, particularly nitrogen (N), phosphorous (P), and potassium (K), in relatively large amounts, as well as small amounts of certain micronutrients, (Brady and Weil, 1996; Grossnickle, 2000), and differences across the ecotone may indicate a limiting nutrient factor in tree growth.

Research on tree line and tundra ecology has been conducted since 2001 in the Mealy Mountains, a subarctic-alpine location in south-central Labrador (Fig. 1). This work included obtaining baseline biophysical data to test hypotheses regarding tree line dynamics. The most recent regional climate records indicated that a warming trend was in progress (EC, 2013a); therefore, the research context was ecosystem change in a warming climate. Initial results demonstrated that transplanted conifer seedlings can survive in the Mealy Mountains above the altitude at which trees now occur, pointing to the possibility of future upward expansion of the forest limit (Munier et al., 2010). In 2007 – 09, this research was intensified and coordinated with that of other research groups in an International Polar Year project focusing on the circumpolar forest-tundra ecotone (Hofgaard and Harper, 2011). These studies have further elucidated the nature of the forest-tundra ecotone, both in the study area (Trindade et al., 2011; Wheeler et al., 2011; Trant et al., 2011; Jameson, 2012; Trant, 2013) and more generally in relation to local topography (and implicitly, microclimate) at this and other locations (Harper et al., 2011). Dendrochronological analysis (Trindade et al., 2011) showed that growth of conifer species is not limited by precipitation, supporting the case for abundant precipitation in the Mealy Mountains region.

Here we apply results from investigations of the climate of the Mealy Mountains (Chan, 2010) toward understanding the constraints on forest-tundra ecotone change. The forest-tundra ecotone is defined here as "the transition zone between forest and tundra at high elevation or latitude" (Harper et al., 2011:480). We examine relevant abiotic factors, including air and soil temperature and moisture, precipitation, and soil nutrients (Timoney, 1995; Grace et al., 2002), and compare the results with biogeographic generalizations regarding tree line climate (e.g., Körner and Paulsen, 2004; Meunier et al., 2007). The overall objectives are 1) to provide a quantitative description of the local climate in the context of the long-term regional climate and climate change, 2) to assess the spatial variability of specific climatic and edaphic variables along an altitudinal gradient from the closed forest edge to the alpine tundra as factors determining tree line character, and 3) to relate observed changes in climate to reported and potential changes in the forest-tundra ecotone.

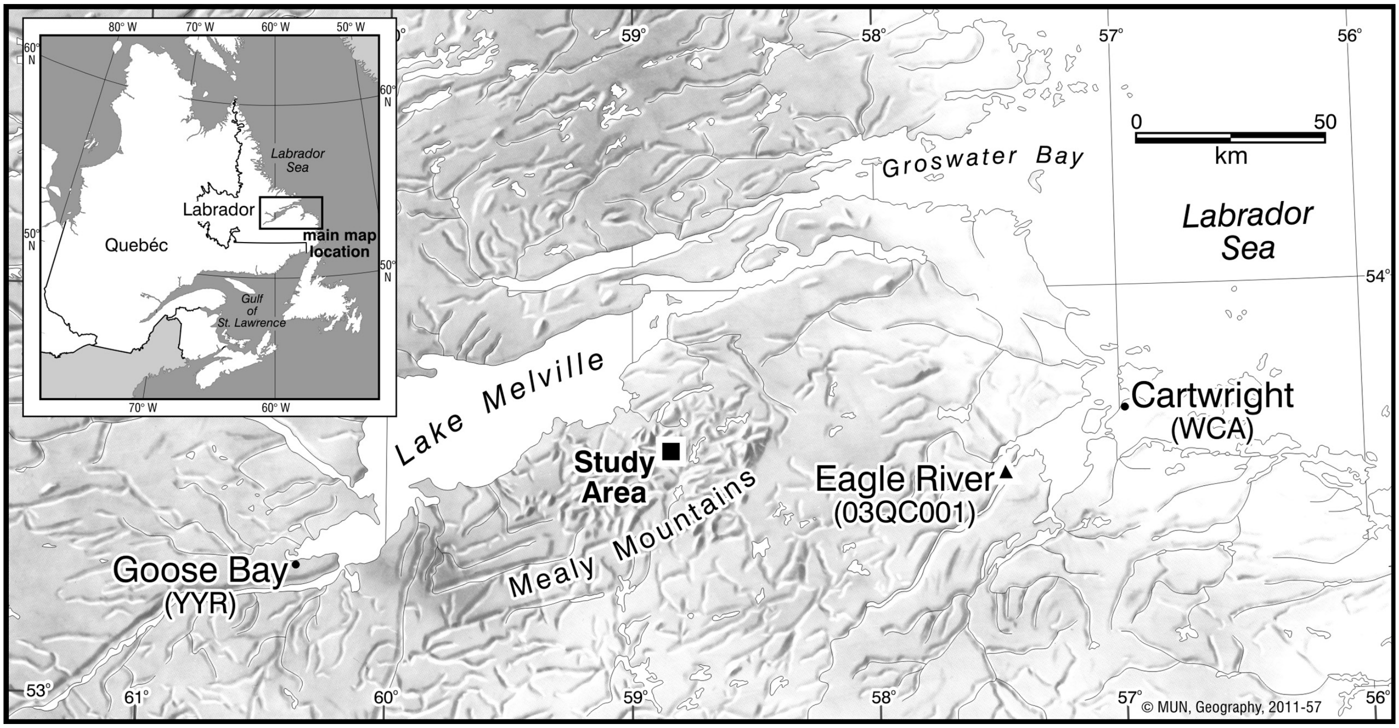

FIG. 1. Central Labrador, showing location of the Mealy Mountains study area and meteorological (●) and hydrometric (▲) stations referred to in the text.

STUDY AREA

Central Labrador is characterized by a broad glaciated plateau that rises westward from the Labrador Sea coast to elevations of more than 500 m above sea level (a.s.l.). The coast is incised by many narrow inlets, the most prominent being Lake Melville, a saltwater body that extends some 170 km inland from the Labrador Sea. The Mealy Mountains rise abruptly from a narrow coastal plain south of Lake Melville (Fig. 1). The local bedrock geology consists mainly of granite and anorthosite (Wardle et al., 1997). With summit elevations approaching 1100 m a.s.l., these highly glaciated mountains have a different climatic regime compared with the Labrador Sea coast and the interior lowlands adjacent to Lake Melville.

The bioclimatic zones of Labrador can be represented in terms of tundra, forest-tundra, open woodland, and closed forest (Hare and Ritchie, 1972). The northernmost limits of scattered, coniferous trees, predominantly black spruce and white spruce (*Picea glauca*), define the boundary between tundra and forest-tundra on the regional scale. In northern Quebec and Labrador, this limit dips southward from ca. 58.5˚ N at Ungava Bay to about 55˚ N over the northern Labrador Plateau before returning northward to ca. 58˚ N at the Labrador Sea (Hare and Ritchie, 1972; Elliott and Short, 1979; Payette, 2007).

According to Meades (2007), the central Mealy Mountains are the most southerly outlier of the High Subarctic Tundra ecoregion, fringed by elements of the High Boreal Forest ecoregion and abutted to the south by extensive peatlands of the Eagle River Plateau. Altitude results in a local bioclimatic gradient that encompasses a range of vegetation zones, from isolated patches of closed forest to alpine tundra. At latitude 53.6˚ N, the Mealy Mountains are more than 100 km south of the present latitudinal tree limit, but 200 km north of the 800 GDD isoline mapped by Meunier et al. (2007) as the northern limit of black spruce seedling viability.

The study area (53.6˚ N, 58.8˚ W) is centered in an eastward-trending valley below an unnamed 1057 m a.s.l. summit, and it extends from alpine tundra at 1000 m a.s.l. to forest east of a chain of headwater lakes at ca. 500 m a.s.l. (Fig. 1). A complex glacial history is evident in the surface features and geomorphology of the valley (Fig. 2), where extensive glacial and glaciofluvial deposits, glacial erratics, and ground moraine overlay bedrock. On the basis of regional temperatures, this area is considered to be in the zone of sporadic discontinuous permafrost (Smith and Riseborough, 2002).

The forest in this area is mainly open lichen woodland made up of four boreal conifer species: black spruce, white spruce, balsam fir (*Abies balsamea*), and eastern larch (*Larix laricina*). Surveys in the study area (Trant, 2013) found black spruce to be dominant in the closed forest and krummholz, while in the transition between those zones eastern larch is dominant, followed by balsam fir. Patches of shrub birch (*Betula* spp.) and mountain alder (*Alnus crispa*) occur in open areas, becoming dense in riparian floodplains. Locally, the forest-tundra ecotone extends from the highest open woodland patches at ca. 550 m a.s.l. to the limit of tree species in krummholz form near 750 m a.s.l. (Trant et al., 2011). Above that level, where

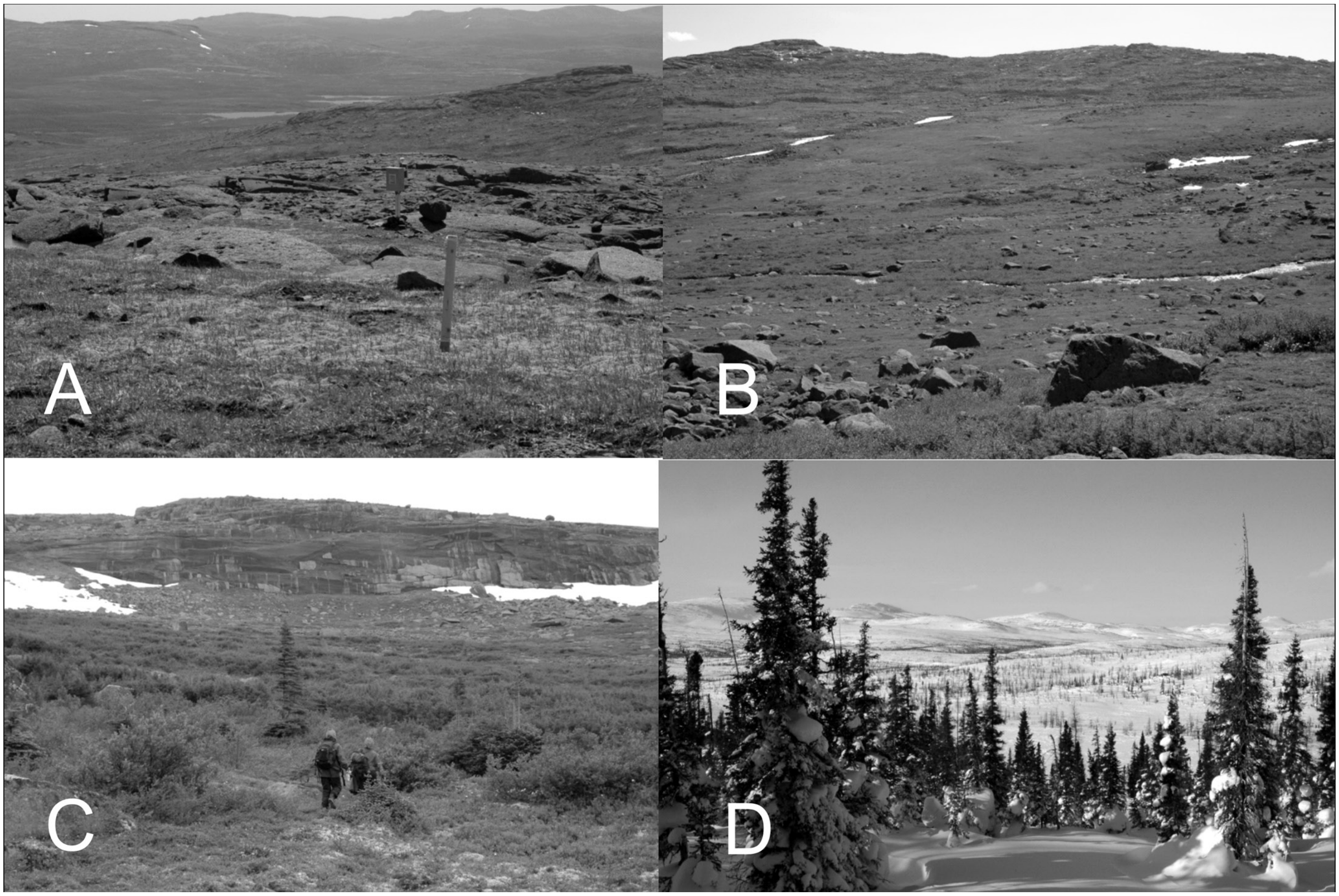

FIG. 2. Landscape views representative of ecotone subzones: A) tundra (T) site with prostrate shrubs, grass, sedge and lichens (1000 m a.s.l.), looking down the study transect; B) mixed shrub tundra and coniferous krummholz landscape (FT) at ca. 700 m a.s.l.; C) dense krummholz and isolated erect conifers within the forest-tundra transition (FT) zone at 600 m a.s.l.; and D) closed forest (F) site at lower end of the transect (ca. 500 m a.s.l.).

soils and substrate permit, the vegetation consists of typical Arctic-alpine low shrubs, herbaceous plants, moss and lichen (Munier et al., 2010). Summits are predominately bare bedrock and boulder fields. Soils are observed to be generally shallow and include cryogenic mineral soils, poorly developed podzols, and some hygric organic soils. Except in well-drained tills and gravels, soils are assumed to be near saturation for most of the year, as is the case over much of northern and central Labrador (Hare, 1980).

Although there are a few earlier records, the regional instrumental record of climate in central Labrador begins ca. 1940 with meteorological stations established at Cartwright in 1936 and Goose Bay in 1941 (Fig. 1). Warming over much of the Arctic in the mid-to-late 20th century (ACIA, 2004) did not initially include the eastern Canadian Arctic and Labrador. From the mid-1970s through the early 1990s, a pronounced winter cooling occurred over northeastern Canada, including Labrador (Banfield and Jacobs, 1998; Feldstein, 2002; Chouinard et al., 2007); however, by 2000 a warming trend in all seasons was underway in this region (Vose et al., 2005). As is generally the case around the North Atlantic, Labrador temperature records show decadal-scale variability that is strongly associated with the North Atlantic Oscillation and Arctic Oscillation (NAO/AO) (D'Arrigo et al., 1993, 2003). Over the 20th century, a significant increase in annual precipitation in Labrador was accompanied by an increase in the rain-to-snow ratio, particularly in the spring (Zhang et al., 2000).

Climate variability is also reflected in the regional hydrology. The Eagle River has a drainage area of 10 900 km^2 and flows south and eastward from the Mealy Mountains to the Labrador Sea (Fig. 1). Gauges near its mouth have produced a mostly uninterrupted record from 1969 to the present of the combined runoff from the Mealy Mountains and the adjacent Eagle River plateau. In Whitfield and Cannon's (2000) analysis of hydrologic records across Canada, the Eagle River fell into the class of stations characteristic of the boreal forest zone, with low winter flow, a snowmelt-driven spring flood, and a relatively high sustained summer flow diminishing into fall. Comparison of differences in flow between the decades 1976–85 and 1986–95 showed the Eagle River to be in a group that experienced lower winter temperatures, slight decreases in precipitation, and decreased flow in the latter period (Whitfield and Cannon, 2000). Our investigations provide an opportunity to extend the analysis of the Eagle River record, while providing new information on the hydroclimatology of the Mealy Mountains.

METHODS

Field studies were carried out from July 2001 through September 2009, and in 2008 and 2009, surveys and measurements were standardized according to IPY-PPSA protocols (Hofgaard and Rees, 2008; Harper et al., 2011). For purposes of this analysis, the ecotone is divided into three subzones: F, the continuous forest below 550 m a.s.l.; FT, a subzone with isolated erect trees (stem height > 2 m) and dense krummholz transitioning upslope increasingly into krummholz and shrub; and T, the alpine tundra above the uppermost limit of tree species, observed to be ca. 750 m a.s.l. (Trant et al., 2011). Examples of vegetation in these subzones are shown in Figure 2.

Automatic climate stations (Campbell Scientific, 2014) were installed in 2001 near the lower margin of the forest-tundra ecotone (“Lower”) at 570 m a.s.l. and at a tundra site near the summit (“Upper”) at 995 m a.s.l. These stations recorded the following variables at hourly intervals: air temperature (T_A) and relative humidity (RH) at 1.5 m above the ground, solar irradiance ($K\downarrow$), and ground temperature (T_G) at the mineral soil – bedrock interface (1.0 m at Upper and 0.7 m at Lower). At both sites, a storage type of precipitation collector, charged with antifreeze and mineral oil to inhibit freezing and evaporation, was used to measure annual total precipitation (P). In 2005, a third station (“Base”) was set up at the base campsite at 600 m a.s.l. to record wind speed and direction, T_A, RH, and vapor pressure deficit (VPD), as well as soil temperature at 10, 30, and 60 cm depths. During summer periods when the camp was occupied, rainfall (R) was measured daily at Base using a manual gauge.

Short-term and seasonal data, including air temperature and humidity, soil temperature, and soil moisture, were collected along the altitudinal transect. Portable T_A and RH sensors (Onset Hobo ProV2™, Onset Computer Corp., 2012) mounted in solar radiation shields on posts at 1.5 m height served for these temporary installations. Soil temperature at 10 cm depth (T_{10}) was recorded with buried miniature temperature loggers (Onset Tidbit™ and Onset Pendant™), supplemented by manual measurements using a digital thermometer. Soil moisture was sampled initially using gypsum block sensors, which proved to be relatively insensitive in this near-saturated environment, and subsequently with a Delta-T™ radio frequency soil moisture probe (Delta-T, 2005).

Soils were sampled for chemistry initially in 2005 (Yurich, 2007) and more intensively along the transect in 2007 and 2008. Soil pits were dug for bulk samples and to determine the depth of the organic layer (defined as the layer between the base of loose litter and the humus-mineral interface). To provide a standard measure of availability of the principal and minor nutrients (Hofgaard and Rees, 2008), fluxes of major ions were sampled during the growing seasons of 2007 and 2008 using ion exchange membranes buried to a depth of 10 cm. The membranes were of a commercial type (PRS™) obtained from and analyzed by Western Ag Innovations Inc. (2006).

Snow surveys were conducted in late March in 2008, 2009, and 2010 (Leblanc et al., 2010). On each occasion, pits were dug at seven sites from forest to tundra to determine depth, density, and structure of the snowpack. Snow depth was further sampled at 1 m intervals over a radius of 10 m around each snow pit. Digital photography was used to document the late-winter landscape.

Annual thawing degree-days (TDD) were calculated using cumulative daily mean T_A above 0˚C; growing degree-days (GDD), using T_A above 5˚C; and freezing degree-days (FDD), using T_A below 0˚C. Soil temperature at 10 cm depth (T_{10}) was analyzed with respect to two soil temperature thresholds: 0˚C as indicating root-zone freeze and thaw and 3.2˚C to define growing season length, following Körner and Paulsen (2004).

Climatological measurements provide the data for estimating evaporation and transpiration (evapotranspiration, ET) when combined with hydrologic data. Discharge from the Eagle River (Fig. 1) is a response to hydroclimatic conditions within its drainage basin, which includes the study area. Basin runoff, Ro, is given by the water balance equation, $Ro = P - ET \pm \Delta S$, where P is precipitation, ET is evapotranspiration, and ΔS is the change in storage. For annual Ro, and given a sufficiently long record, it can be assumed to a first approximation that $\Delta S = 0$ (Hare, 1980). Discharge data for the Eagle River were obtained from the Water Survey of Canada (EC, 2013b).

To understand the results in a regional context, we compared climate data from Goose Bay and Cartwright with data from the field site, which is located midway between them. Homogenized and adjusted surface air temperature and precipitation datasets of the Canadian Climate Program (Mekis and Vincent, 2011; Vincent et al., 2012; EC, 2013c) were used in this analysis. To estimate long-term climate series for the Mealy Mountains, midpoint series were interpolated using arithmetic means of Goose Bay and Cartwright data (monthly and seasonal T_A and annual P, GDD, TDD, and FDD). Further adjustments to series for T_A, TDD, GDD, and FDD were made using linear regression between data from the study area (dependent) and the interpolated midpoint values for the eight years of observations. ANOVA was applied to test the significance of the results, with the Durbin-Watson statistic used to check for autocorrelation effects (Bowerman and O’Connell, 1993). Regional temperature anomalies were analyzed using gridded NCAR/NCEP reanalysis data (Kalnay et al., 1996) obtained from the interactive mapping site of the National Oceanic and Atmospheric Administration (NOAA, 2012a). Statistical and graphical analyses were done using Microsoft Excel and IBM SPSS Statistics Version 19 (IBM, 2012). Wind frequency plots were constructed using Rose Works (UAI Environmental, 2003).

TABLE 1. Summary of observational annual and seasonal climatic data for the Mealy Mountains study site (2001–09), by ecotone subzone. For comparison, Cartwright (WCA) and Goose Bay (YYR) data for the same period are also shown. T_G = ground temperature (˚C), T_A = surface air temperature (˚C), GDD = growing degree-days, TDD = thawing degree-days, FDD = freezing degree-days, P = precipitation (mm), R = rainfall (mm), and K↓ = solar irradiance (MJ $m^{-2}d^{-1}$). "n.d." means no data.

Ecotone subzone variable	F	FT	T	WCA	YYR
Elevation (m)	500	600	995	14	48
T_G (Annual)	n.d.	−0.1 ± 0.7	−1.9 ± 0.9	n.d.	n.d.
T_A (Annual)	(−1.2 ± 0.8)[1]	−1.9 ± 0.8	−4.3 ± 0.8	1.1 ± 0.8	0.9 ± 0.8
T_A (June–September)	(11.0 ± 0.6)	10.1 ± 0.6	7.7 ± 0.7	11.8 ± 0.7	14.0 ± 0.7
T_A (December–February)	(−14.8 ± 1.5)	−15.2 ± 1.6	−16.7 ± 1.5	−10.7 ± 1.8	−14.2 ± 1.5
T_A (July)	(13.6 ± 0.9)	12.9 ± 0.8	10.5 ± 0.8	13.8 ± 1.7	16.7 ± 1.6
Days $T_A > 0$	(119 ± 13)	113 ± 12	90 ± 10	179 ± 5	180 ± 5
Days $T_A > 5$	(71 ± 9)	65 ± 7	42 ± 6	83 ± 12	104 ± 10
GDD (Annual)	(764 ± 93)	694 ± 85	455 ± 62	922 ± 108	1227 ± 121
TDD (Annual)	(1502 ± 157)	1399 ± 149	1029 ± 119	1806 ± 176	2133 ± 175
FDD (October–May)	(−1968 ± 227)	−2059 ± 231	−2393 ± 234	−1386 ± 229	−1816 ± 202
P (Annual)	n.d	3265 ± 853	1682 ± 521	1055 ± 117	917 ± 67
R (July–August)	n.d.	329 ± 161	n.d.	186 ± 48	226 ± 39
K↓ (Annual)	n.d.	11.8 ± 6.9	10.6 ± 6.9	n.d.	n.d.
K↓ (June–September)	n.d.	15.8 ± 4.3	15.2 ± 4.3	n.d.	n.d.

[1] Values in parentheses were estimated by extrapolation.

RESULTS

Tables 1 and 2 summarize climatic and soil data, respectively, obtained at each ecotone subzone in our study area in the Mealy Mountains during the period 2001 to 2009, as well as data from Cartwright and Goose Bay from the same period for comparison. Table 3 shows the statistics of the regression analysis used to estimate long-term climate series for our tree line site, and Table 4 shows the results.

Solar Irradiance

K↓ was consistently higher (11% annually) at Lower station than at Upper (Table 1). This difference was greater than the maximum ± 5% difference in hourly fluxes found in a post-field comparison of the instruments and the ± 3% maximum instrumental error specified by the manufacturer. Lower K↓ near the summit can be attributed to more frequent cloud cover there, as was often observed during the field season, but possibly also to rime in colder periods. During the June–September growing season, K↓ at Lower station was only 4% higher than at the summit, i.e., within the range of instrumental uncertainty.

Wind

The prevailing winds were westerly, with wind speed most frequently between 5 and 10 m s^{-1}. Seasonal plots (Fig. 3) indicate a wind shift to northwest from winter to spring, with a slight increase in the frequency of northerly through northeasterly winds. Wind speeds are consistently lower in the summer months (by about 5 m s^{-1}) and increase in the fall. Peak daily winds averaged more than 12 m s^{-1} from December through March, with an hourly maximum of 28 m s^{-1} recorded in January 2008.

Temperature

Monthly and seasonal means of T_A, TDD, GDD, and FDD were calculated from eight years of daily values (sample size from 224 to 248 days for each month). Growing season (June–September) T_A averaged 11˚C at the forest edge (500 m), 10˚C within the transition, and 8˚C at the upper tundra site (995 m), with corresponding GDD of 764, 694, and 455, respectively (Table 1). Mean annual T_A was below freezing at all sites, as was T_G at 1 m depth at the Tundra site, indicating the presence of permafrost at higher elevations in the area. The altitudinal gradient of T_A between the Lower and Upper stations averaged −0.6 ± 0.2˚C/100 m annually, −0.4 ± 0.1˚C/100 m in winter (December–February), and −0.8 ± 0.1˚C/100 m in the June–September growing period. Nighttime and winter hourly data for these gradients were positively skewed, indicating more frequent temperature inversions at those times.

Precipitation

Annual precipitation at Lower station (3265 mm) was nearly twice that at Upper (1682 mm). Both gauges were of the same design with wind shields to reduce blow-by and were on locally elevated sites where little snow accumulated on the ground. However, the summit ridge location of Upper station was more exposed to prevailing westerly winds than sites lower in the valley, and it is likely that these winds further reduced snow and rain catch in that gauge relative to the catch at the valley site. Snow blowing from the ridge tops and summit may have added to the catch in the gauge lower in the valley. Given that these sites were unmonitored for most of the year, the measurements reported here can only be taken as approximate. A conservative estimate of the annual precipitation is between 2000 and 3000 mm, compared with about 1000 mm at the two

TABLE 2. Soil variables by ecotone subzone. Values are spatial averages and standard deviations from observations at multiple (n) sample sites. Comparisons used one-way ANOVA with post hoc tests. Differences between subzones are considered significant when $p \leq 0.01$.

Ecotone subzone Soil variable	Forest F	Transition FT	Tundra T	ANOVA Sig. (p)
Soil temperature at 10 cm	n = 8	n = 10	n = 6	
Annual[1]	3.0 ± 0.2*	2.1 ± 0.7*	1.4 ± 5.9*	< 0.01
Jun–Nov	6.2 ± 0.4	6.2 ± 0.9	5.9 ± 0.6	0.66
Dec–May	−0.2 ± 0.4*	−1.9 ± 1.4*	−3.2 ± 1.3*	< 0.01
Growing season[2]	8.2 ± 0.6	7.9 ± 1.5	8.0 ± 1.2	0.90
Days T_{10} > 3.2˚C	111	115	106	n.d.
Days T_{10} > 0˚C	220	193	179	n.d.
Soil moisture % volumetric capacity[3]	n = 26	n = 131	n = 33	
	77.2 ± 17.0*	42.2 ± 21.2	55.2 ± 24.5	< 0.01
Soil humic layer thickness (cm)	n = 40	n = 64	n = 40	
	1.5 ± 1.6*	6.9 ± 4.7	5.6 ± 4.5	< 0.01
Soil nutrient flux[4]	n = 66	n = 113	n = 42	
Total N	19.1 ± 8.4	17.8 ± 9.2	18.0 ± 12.0	0.68
$N\text{-}NO_3$	2.40 ± 2.88	3.24 ± 2.79	4.69 ± 4.52*	< 0.01
$NH_4\text{-}N$	16.7 ± 8.4	14.6 ± 9.5	13.3 ±10.5	0.16
Ca	379 ± 329*	455 ± 292*	177 ± 58*	< 0.01
Mg	90.1 ± 75.6	96.9 ± 61.0	35.6 ± 18.7*	< 0.01
K	137.9 ± 116.9*	76.7 ± 47.7*	49.2 ± 22.0*	< 0.01
P	1.55 ± 1.62	1.67 ± 2.78	1.03 ± 0.55	0.27
S	17.4 ± 14.8	19.2 ± 15.6	23.6 ± 16.0	0.13
Mn	5.00 ± 5.82	3.00 ± 6.16	0.94 ± 1.04*	< 0.01
Zn	1.89 ± 1.67	1.72 ± 1.24	0.71 ± 0.44*	< 0.01
B	0.97 ± 0.45	1.00 ± 0.53	0.86 ± 0.38	0.25
Fe	4.29 ± 5.37	34.0 ±188	17.8 ± 87.2	0.38
Al	34.0 ± 20.4	39.6 ± 23.5	43.4 ± 12.8	0.06

* Post-hoc test shows value differs significantly from those in other subzones at $p < 0.01$.

[1] Soil temperatures based on daily means over two years at multiple sites.

[2] Based on a threshold of 3.2˚C (Körner and Paulsen, 2004).

[3] Non-parametric test used on soil moisture.

[4] Units are µg/10 cm^2 – four weeks.

permanent stations (Table 1), indicating a strong local orographic enhancement of precipitation in the central Mealy Mountains. This enhancement was also seen in rainfall observations during the summer field season (total of 229 field-days from 2001 to 2009) at Base Camp, where July-August totals averaged 329 mm, or 1.5 times the amounts recorded in the same summer periods at Goose Bay and Cartwright. March snow survey data for 2008–10 show large variation in depth within subzones and between years (Fig. 4). Snowpack density for the study area ranged from 400 to 450 kg m^{-3}, resulting in a late-March snow water equivalent (SWE) of 0.65 m.

Humidity

RH was recorded hourly at all climate stations, while Base station also recorded vapor pressure (VP) and vapor pressure deficit (VPD) derived from RH and T_A. Average RH increased with elevation (from 75% at Lower to 78% at Base and 88% at Upper station), as would be expected with decreasing temperature. At Upper station, RH exceeded 80% during 90% of the hourly observations. Hourly VPD was 0.52 ± 0.45 kPa at Base station (600 m a.s.l.) during the summer months (June–August) between 0800 and 2200 local time.

TABLE 3. Statistics of regression models for predicting T_A, GDD, TDD, and FDD in the Mealy Mountains study area from midpoint averages of data from Goose Bay and Cartwright. N = 8 years. R^2 is the coefficient of determination, F is the ANOVA F-statistic for the regression, p is the significance level of F, and d is the Durbin-Watson statistic, which for all the variables significantly exceeded the critical value for positive autocorrelation ($p < 0.01$).

Variable	R^2	SE est.	F	p	d
T_A (Annual)	0.92	0.28	53.5	0.001	2.3
T_A (January)	0.97	0.62	190.5	< 0.001	1.5
T_A (Dec–Feb)	0.98	0.22	352.7	< 0.001	2.7
T_A (July)	0.94	0.24	87.3	< 0.001	2.6
T_A (Jun–Sep)	0.77	0.36	19.7	0.004	3.2
GDD	0.88	33.6	43.9	0.001	1.9
TDD	0.83	70.2	18.8	0.004	1.7
FDD	0.91	75.6	36.1	0.001	1.3

Analysis across the Forest-Tundra Ecotone

Climate and soil data were analyzed according to ecotone subzone (Tables 1 and 2). Upper station was taken to represent conditions in the T subzone, while the data for Base and Lower stations were averaged to provide a single estimate for the FT subzone. There was no climate station within the continuous forest, but soil temperature was

TABLE 4. Climate and water balance variables during three different periods for the Mealy Mountains tree line at 600 m a.s.l, calculated from regression on Goose Bay and Cartwright data. ET is estimated from midpoint P and Eagle annual Ro, all in mm. All temperatures are °C. Values marked by an asterisk (*) were significantly greater in the most recent decade than in the previous intervals (Student's t, $p < 0.01$), and "n.d." indicates no data.

Variable\Period	1942–2000	1971–2000	2001–10
T_A (Annual)	−2.6 ± 0.9	−2.8 ± 1.0	−1.3 ± 1.0*
T_A (January)	−17.2 ± 3.5	−17.9 ± 3.0	−16.1 ± 3.5*
T_A (Dec–Feb)	−16.2 ± 2.5	−16.9 ± 1.9	−14.8 ± 2.3*
T_A (July)	12.4 ± 0.8	12.3 ± 1.0	13.2 ± 1.1*
T_A (Jun–Sep)	9.0 ± 0.8	9.2 ± 0.8	10.5 ± 0.6*
GDD	591 ± 67	600 ± 68	724 ± 76*
TDD	1110 ± 137	1132 ± 140	1350 ± 137*
FDD	−2285 ± 298	−2360 ± 333	−2053 ± 330
P	1128 ± 172	1201 ± 139	1181 ± 103
Ro	n.d.	752 ± 136	694 ± 82
ET	n.d.	450 ± 113	487 ± 58

measured there. Air temperatures and degree-day variables were estimated by extrapolation to 500 m in the F subzone using seasonal altitudinal gradients observed between Lower and Upper stations.

To provide further detail on the spatial variability of T_A, a temporary station in the upper FT subzone at 700 m was operated for 10 days in the summer of 2009. The full array of stations provided a sample of 240 hourly measurements at 570, 600, 700, and 995 m a.s.l. The comparison showed the altitudinal gradient of T_A during typical midsummer days to be non-linear, falling initially at about 1°C/100 m between Lower and Base stations, then less steeply at about 0.3°C/100 m to the upper part of the FT zone at 700 m. Between 700 m and the tundra site at 995 m, the gradient was about 0.9°C/100 m. Post-field comparisons found differences between sensors to be less than 0.3°C. This analysis shows that there is a non-linear relationship between T_A and altitude within the FT subzone, with similar growing season temperatures over a relatively broad ecotone area.

Late-March snow depths were taken over three consecutive years (Fig. 4). Aggregated over the three years, mean depths (m) by subzone were 1.98 ± 0.30 at F, 1.42 ± 0.58 at FT, and 1.28 ± 0.51 at T. Differences in depth between F and FT and between F and T were significant (Independent Samples Median Test with Multiple Comparisons, N = 748, $p < 0.01$), but those between FT and T were not ($p = 0.08$). Spatial variability was least in the F subzone.

Analysis of two years of measurements found soil temperature T_{10} to be significantly different between subzones in winter, but not in summer and fall (Table 2). The annual cycle of T_{10} differed between subzones (Fig. 5): no deep freezing occurred at the F sites because of their more uniformly deep snow cover (Fig. 4) and because soil moisture was greater in the forest. The period with T_{10} above 0°C was nearly a month longer at F sites than at the FT and T sites (Table 2). Growing season length, based on T_{10} above 3.2°C (sensu Körner and Paulsen, 2004), was similar, and growing season T_{10} means of 7.9° to 8.2°C did not differ significantly between subzones across an altitudinal range of nearly 500 m.

Soil moisture was greater at F sites than at FT and T sites, while the latter two did not differ significantly (Table 2). Humic layer thickness was significantly less at F sites than at FT or T. The macronutrients total N, NH_4-N, P, and S were not significantly different ($p > 0.01$), but significant differences were found for N-NO_3, Ca, Mg, and K and the micronutrients Mn and Zn ($p < 0.01$). Overall, there was no consistent pattern to indicate a more favorable nutrient environment at the forest edge than in the other subzones.

Regional Water Balance

An estimate of basin runoff (Ro) was obtained from long-term (1967–2010) discharge records for the Eagle River. The total annual discharge near the river mouth was divided by the drainage basin area to get the annual Ro. Annual P for the basin was estimated by the arithmetic mean of the annual total P reported at Goose Bay and Cartwright. Over the 44-year record, Eagle River Ro correlated significantly ($p < 0.001$) with P at Goose Bay (r = 0.62) and Cartwright (r = 0.52), and more strongly (r = 0.66) with P interpolated at their midpoint. The estimated annual basin P (1967–2010) was 1187 ± 133 mm, and the observed Ro was 734 ± 124 mm, giving an estimated basin ET of 452 ± 106 mm. The actual value for ET is likely larger, considering that locally enhanced precipitation effects were not considered in this estimate.

Representativeness of Study Period Conditions in Relation to the Long-Term Climate

Monthly averages of T_A, TDD, GDD, FDD, and P were highly correlated between Goose Bay and Cartwright over the 1942–2010 period of record. No significant trend was found in those variables over that period (N = 68, $p > 0.05$). For the period 2001 to 2009, monthly averages of T_A, GDD, TDD, and FDD in the study area were highly correlated with those at Goose Bay and Cartwright (R^2 from 0.57 to 0.90, $p < 0.01$). Differences between stations are attributed to altitude and distance from the Labrador Sea. Eight years of observations is a relatively small sample for climatological estimates. However, comparisons of mean monthly and seasonal values among stations are strengthened by the fact that the data derive from daily values.

As noted in the preceding section, annual P interpolated between the two permanent stations was taken as an estimate for the Mealy Mountains region, without further adjustment for orographic effects. For T_A, TDD, GDD, and FDD, linear regression was applied between the midpoint series and the study area data for 2001–09, and the resulting equations were used to provide long-term estimates for the study area at tree line elevation. All regression models showed a high degree of explanation of the estimated variables (Table 3). Effects of autocorrelation were ruled out at the $\alpha = 0.01$ significance level using the Durbin-Watson

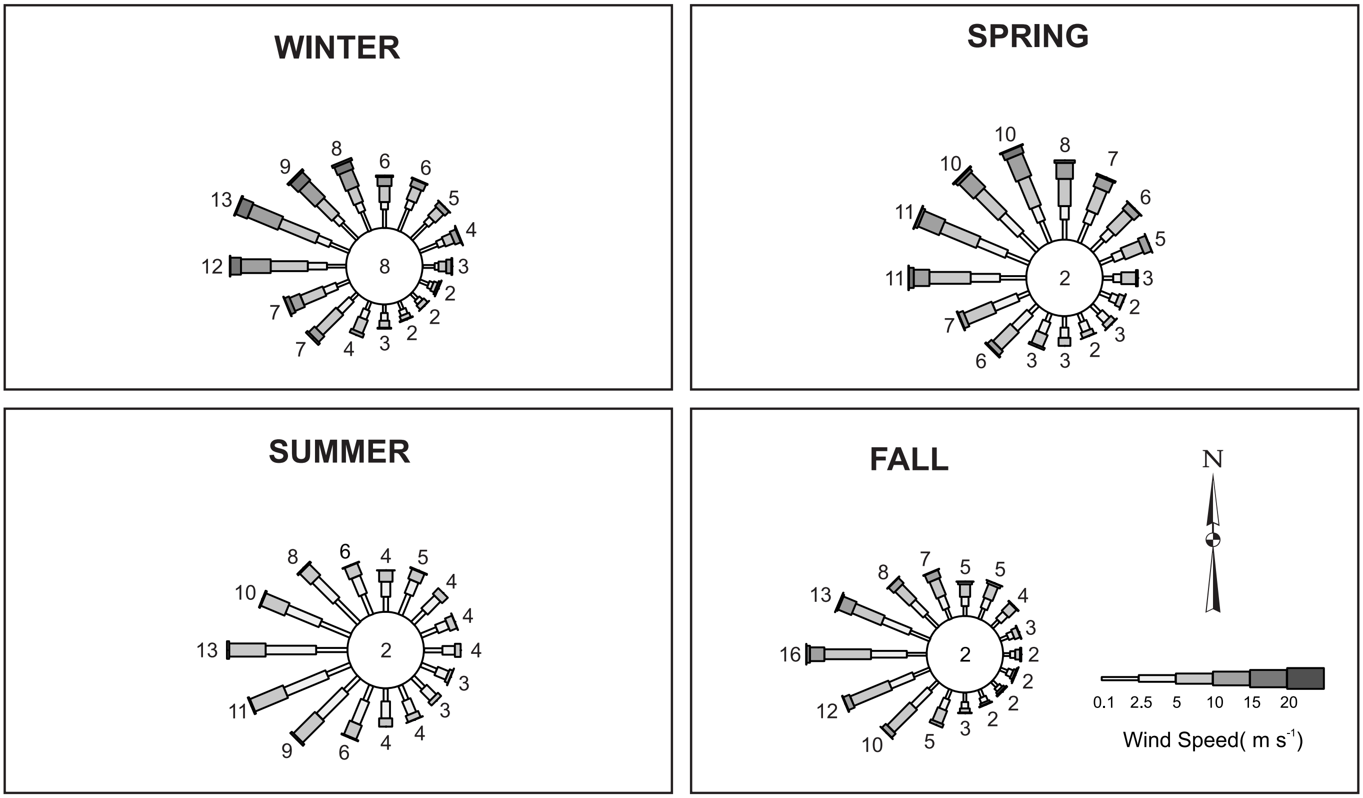

FIG. 3. Summary of hourly winds, Mealy Mountains Base station, for the period 2005–09. Seasons are Winter (December–February), Spring (March and April), Summer (June–August), and Fall (September–November). Winds are *from* the direction indicated by rays. Lengths of ray segments represent frequencies (%) by speed class and direction. Values at ends are total frequencies for that direction. Thickness and shading indicate wind speed class, as shown in the legend. The value in the centre of each plot indicates frequency of calms.

statistic for small samples (Bowerman and O'Connell, 1993).

The estimated long-term climatic series for the Mealy Mountains study area are shown in Figure 6. There was no significant trend in growing season T_A or GDD until the late 1990s, when the current regional warming started. The water balance terms show a positive trend in P at an average rate of 3.3 mm y^{-1} ($R^2 = 0.16$, $F = 13.1$, and $p = 0.001$), a slight decrease in Ro (not significant), and a corresponding increase in ET. Table 4 shows comparative summary statistics from those series for the periods 1942–2000, 1971–2000, and 2001–10. The most recent decade was the warmest over the 68 years of record, with significantly higher temperatures in all seasons and higher TDD and GDD. In contrast, differences in P, Ro, and ET were not statistically significant. Winter temperatures and FDD, indicators of winter severity, were less negative in the most recent period than during the colder 1971–2000 period. Gridded NCEP/NCAR reanalysis data for the same periods confirmed an increase in growing season T_A of approximately 1˚C in the Mealy Mountains area relative to the preceding tri-decade (Fig. 7), while annual P over the region increased by about 6%. These interpolated gridded data have a relatively coarse resolution of 2.5˚ latitude by 2.5˚ longitude (Kalnay et al., 1996; NOAA, 2012a) and therefore do not show anomalies on the scale of the Mealy Mountains. Concurrently, during most of 2001–10, sea surface temperatures in the adjacent Labrador Sea were 1˚ to 3˚C above their 1971–2000 averages (NOAA, 2012b).

DISCUSSION AND CONCLUSIONS

This study has examined climatic and soil factors relevant to vegetation growth across an altitudinal range of ca. 500 m, where outliers of closed-canopy boreal forest transition through open woodland and krummholz forms into alpine tundra. Several factors can be ruled out as constraining forest advance. Observations of solar irradiance agreed with climatological estimates for this region (Gullett, 1987) and did not differ significantly across the ecotone during the growing season. Annual precipitation, summer rainfall, and soil moisture were sufficient for tree growth at all levels, and the availability of most soil nutrients did not differ significantly from forest to tundra. Growing season climate and winter severity are very likely the controlling factors. Additionally, some vegetation changes might also be associated with the regional warming that has been shown to be underway.

Mean T_A in the FT subzone for the warmest month (July) was 13˚C, which is well above 10˚C, the value often associated with the northern latitudinal limit of erect trees (Sveinbjörnsson, 1992), but within the range for altitudinal tree lines reviewed by Körner (1998). An estimated 764 GDD

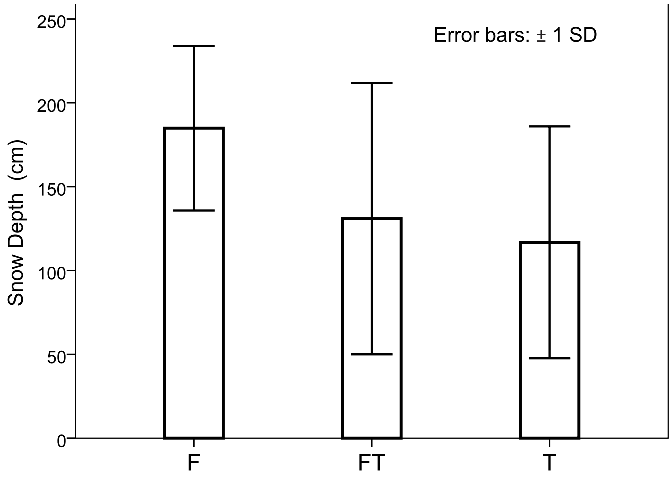

FIG. 4. Late March snow depth at the Mealy Mountains study area over three years of surveys (2008–10), by subzone. Vertical bars are ± 1 standard deviation calculated from all measurements, with N = 748.

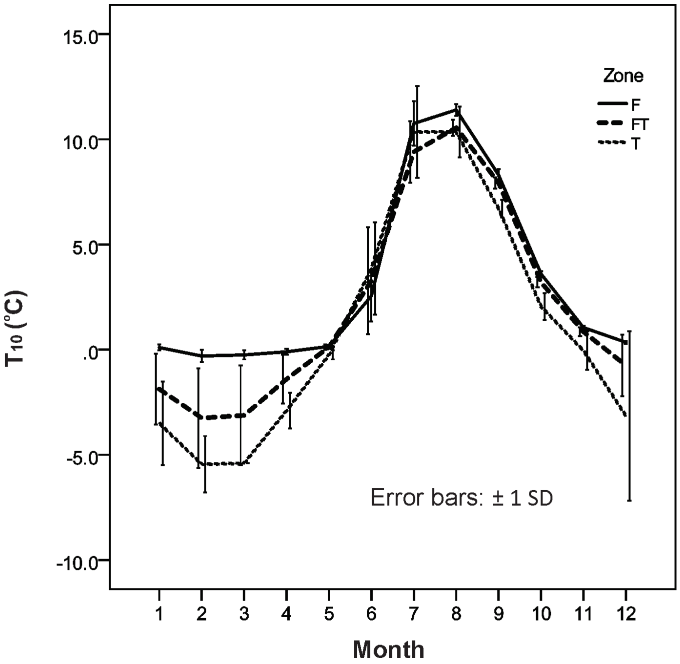

FIG. 5. Monthly means and standard deviations of 10 cm soil temperatures, by subzone, based on observations from July 2008 to July 2009 at 17 sites.

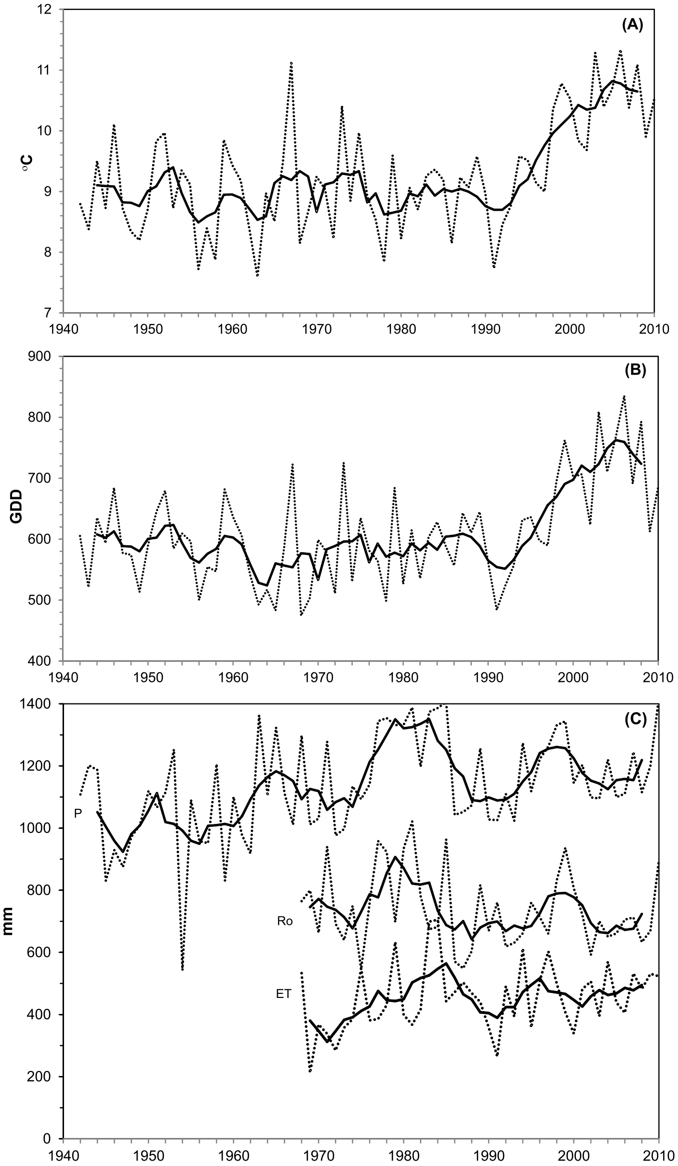

FIG. 6. Estimated 1942–2010 climate series for the Mealy Mountain tree line study area. (A) T_A (June–September) and (B) GDD estimated by regression on Goose Bay and Cartwright data. (C) Water balance terms for the Eagle River watershed: P, interpolated from Goose Bay and Cartwright to the study area, Ro calculated from discharge recorded at the river mouth, and ET calculated as the difference of P and Ro. Dotted lines represent annual values, and heavy solid lines show five-year moving averages.

for the F subzone (Table 1) was near the thermal limit for black spruce seed viability of 800 to 940 GDD found by Meunier et al. (2007). The value within the FT zone was only 694 GDD; however, eastern larch seedlings were found there (Trant, 2013), indicating that viable seeds were being produced for that species. For winter conditions in the FT subzone, the 2001–09 average of −2059 FDD is well below the value of −1816 FDD reported for the same period at Goose Bay (Table 1). However, continuous boreal forest at Goose Bay (Meades, 2007) is a response to the longer-term climate and is better represented by the 1971–2000 normals value of −2025 FDD (EC, 2013a). Therefore, winter severity based on FDD could explain the absence of continuous coniferous forest above 600 m a.s.l. in the Mealy Mountains, only if long-term FDD were much lower than present, as was the case for most of the 20th century (Table 4) and probably longer.

From the forest edge through the ecotone to the tundra site, 10 cm soil temperatures for the growing season were about 2°C above the average value reported by Körner and Paulsen (2004) in their global survey. Our observations took place in an anomalously warm decade, but the tree line we observed was largely a response to the climate of the previous several decades, when air and soil temperatures were 1° to 2°C cooler than at present (Fig. 6), but still within

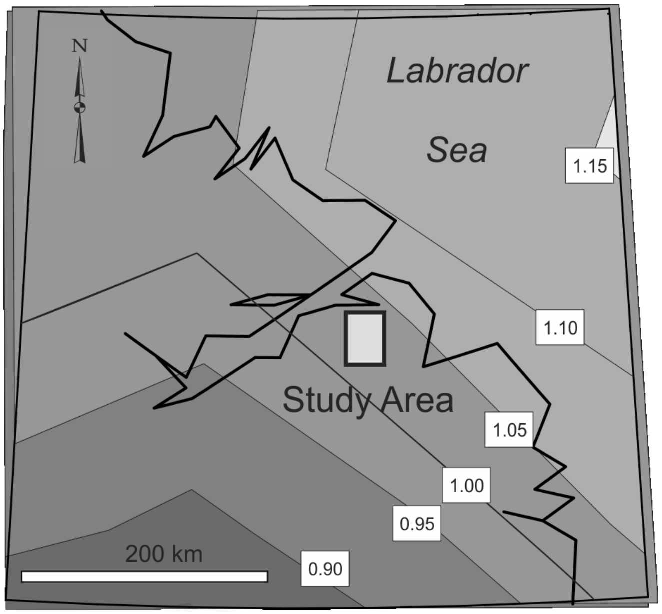

FIG. 7. South-central Labrador, showing the mean June through September surface air temperature (˚C) for the period 2001 to 2010 minus the mean for 1971 to 2000. The shaded contour interval is 0.05˚C. Image created using gridded NCEP/NCAR Reanalysis data on the interactive web site of NOAA/ESRL Physical Sciences Division, Boulder, Colorado (http://www.esrl.noaa.gov/psd/).

the 6˚ to 7˚C range. Therefore, long-term growing season soil temperature does not contraindicate the presence of trees in the FT subzone, a conclusion supported by the presence there of isolated erect conifers in some sheltered areas.

VPD, coupled with temperature, is a predictor for leaf stomatal water vapor conductance and net photosynthesis. Stomatal conductance and CO_2 assimilation decrease when VPD increases (Oke, 1987; Aber and Federer, 1992), i.e., with higher VPD, a tree is more water-stressed and photosynthesis is slowed. Judging by the relatively low summer daytime VPD observed in the FT subzone, drought or moisture stress do not seem to be significant factors constraining tree growth, although more detailed observations would be needed to confirm this.

Our observations have confirmed an orographic enhancement of P and particularly snowfall in the Mealy Mountains, as shown by Hare (1951, 1980) at a larger scale for central Labrador. Snowfall makes up more than half of annual P, while rainfall is substantial in summer and is likely significant in late spring and early fall. The snow pit stratigraphy (Leblanc et al., 2010) showed evidence of midwinter freezing rain events. Such icing conditions are a major factor inhibiting the survival of arboreal vegetation (e.g., Carlson et al., 2011), and they are likely to become more frequent in a warming climate.

There was large spatial variability in late-winter snow depth in the ecotone compared with sites inside the forest edge (Fig. 4). Prevailing westerly winds, persistent and sometimes gale-force in winter (Fig. 3), resulted in redistribution of snow in exposed areas, giving protection to vegetation in the lee of obstacles, but exposing unsheltered vegetation to abrasion and desiccation. This kind of severe winter environment cannot be captured in the FDD measure, but is well recognized as limiting growth and survival of seedlings and saplings and inhibiting the formation of erect stems in krummholz (Harsch et al., 2009; Holtmeier and Broll, 2010). In the Mealy Mountains, a glaciated landscape with a variety of surficial deposits, spatial differences in snow accumulation, and shelter from or exposure to winter winds, as well as localized summer heating facilitated by microtopography, all contribute to an extended and heterogeneous forest-tundra ecotone.

In the absence of other limiting factors, our analysis indicates that the regional warming of the most recent decade, which is projected to continue (Meehl et al, 2007; Meunier et al., 2007), is sufficient to cause an upslope expansion of forest in the Mealy Mountains. But will it be the same perhumid forest, or will it become drier? The 1942–2010 series for P interpolated from Goose Bay and Cartwright to the study area (Fig. 6) had a positive trend of 3.3 mm y^{-1}, in agreement with a regional analysis by Zhang et al. (2000). However, our analysis for 2001–10 shows that while P, T_A, and ET increased, annual Ro in the Eagle River basin decreased by 8% relative to the 1971–2000 average (Fig. 6), continuing a decrease observed in the mid-1990s (Whitfield and Cannon, 2000). The decrease in Ro was most pronounced in the spring, which is likely a reflection of less winter snowfall. For the same period, snowfall as a proportion of total P at both Goose Bay and Cartwright decreased from 48% to 40% (EC, 2013a). Decreased snowfall means less soil moisture stored into the growing season. Our conclusion is that although precipitation in the area is increasing, the growing season climate is becoming drier as a consequence of increased evapotranspiration driven by climate warming. If sustained, this trend will result in significant changes to forest growth patterns and feedbacks to climate (Meunier et al., 2007).

Warmer, drier summers increase the likelihood of disturbance due to insect herbivory and wildfires (Allen et al., 2010; Peng et al., 2011). Cone collections in the study area during the warm summer of 2008 revealed a high proportion of insect damage to seeds (Jameson, 2012). Foster (1983) investigated wildfire patterns in southeastern Labrador using dendrochronology to date the fire history of areas burned between ca. 1870 and 1979. The central plateau area bordered by the south slopes of the Mealy Mountains was found to have very infrequent small fires, with a fire interval estimated to be over 500 years. The perhumid climate was identified as the dominant factor in this regime. Ignition was attributed almost exclusively to lightning, while the tendency for fires to burn upslope was inhibited by the patchy nature of the glaciated terrain, with its many natural firebreaks. Although wildfires were associated with summer drought, fire did not occur in many years of below-average summer precipitation, possibly for lack of ignition (Foster, 1983). During the 2001–09 field seasons, occasional thunderstorms with lightning were observed in the Mealy Mountains, although no near strikes were observed.

Our observations of summer rainfall and soil moisture do not support the conclusion that a shift to a more frequent fire regime has yet occurred in the Mealy Mountains.

It is expected that the warming climate will produce a response in the vegetation. In northern Quebec, where warming is also occurring, Gamache and Payette (2004) found a positive correlation at a number of sites between stem elongation in black spruce krummholz and regional GDD. In the Mealy Mountains FT subzone, conifer species appeared mostly in krummholz form, and reproduction was by layering. However, erect stems were observed emerging from black spruce krummholz, and true seedlings of eastern larch were found (Trant et al., 2011; Trant, 2013). Mealy Mountains GDD for 2001 – 10 were 20% higher than in the climatological baseline or "normal" period 1971 – 2000 and 22% higher than the average for the longer-term record (Table 4). This means that during the previous half-century, and almost certainly longer, the climate of this tree line zone was less favorable than at present for seedling germination and survival and for tree growth generally. Winter severity, as measured by lower T_A and FDD, was significantly greater in the preceding periods, particularly during the 1971 – 2000 tri-decade. Long-term studies elsewhere (e.g., Kullman, 2007; Payette, 2007; Harsch et al., 2009; Harper et al., 2011; Tremblay and Boudreau, 2011) indicate that boreal forest ecosystems may take several decades to adjust to a change in climate. Our results show that local climate warming is well underway in the tree line ecotone in the Mealy Mountains, and according to concurrent vegetation surveys (Trant et al., 2011; Trant, 2013), that change is first becoming evident in the krummholz.

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