Dendroclimatic response of a coastal alpine treeline ecotone: a multispecies perspective from Labrador[1]

M. Trindade, T. Bell, C.P. Laroque, J.D. Jacobs, and L. Hermanutz

Abstract: Coastal alpine forests are highly vulnerable to oceanic climate trends, yet these diverse environmental interactions remain poorly understood. We used a multispecies perspective to try to better assess the radial growth response of alpine treeline species within the Northeast Atlantic region of North America to climate variables using bootstrapped correlation analysis. The four species present, black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and eastern larch (*Larix laricina* (Du Roi) K. Koch) were sampled in an effort to capture tree–climate sensitivity that is representative of this entire alpine treeline. The climate–growth relationships of spruce trees were comparable with those reported in other Labrador studies, but spring drought sensitivity as reported for coastal northern white spruce trees was not observed. Rather, high levels of precipitation suggest that drought did not limit the radial growth of any of the four species. The relatively small number of statistically significant correlations between monthly climate variables and fir and larch trees suggests that factors other than climate limit their radial growth. The multispecies approach better highlighted the range of species-specific relationships between alpine treeline forests and maritime climates (monthly temperature and precipitation) found at the treeline ecotone.

Résumé : Les forêts alpines côtières sont très vulnérables aux tendances climatiques océaniques bien que ces diverses interactions environnementales demeurent peu comprises. À l'aide d'une analyse de corrélation par la méthode bootstrap, nous avons utilisé une perspective multispécifique pour tenter d'améliorer l'estimation de la réaction en croissance radiale d'espèces aux variables climatiques, à la limite alpine des arbres, dans la région du nord-est de l'Atlantique en Amérique du Nord. Les quatre espèces présentes, l'épinette noire (*Picea mariana* (Mill.) B.S.P.), l'épinette blanche (*Picea glauca* (Moench) Voss), le sapin baumier (*Abies balsamea* (L.) Mill.) et le mélèze laricin (*Larix laricina* (Du Roi) K. Koch), ont été échantillonnées de façon à détecter une sensibilité entre l'arbre et le climat qui soit représentative de l'ensemble de la limite alpine des arbres. La relation entre le climat et la croissance des épinettes était comparable à celle rapportée par d'autres études réalisées au Labrador, mais la sensibilité à la sécheresse printanière rapportée pour l'épinette blanche côtière nordique n'a pas été observée. Au contraire, de fortes précipitations indiquent que la sécheresse n'a limité la croissance radiale d'aucune des quatre espèces. Le nombre relativement faible de corrélations statistiquement significatives entre les variables climatiques mensuelles et la croissance radiale du sapin et du mélèze indiquent que des facteurs autres que le climat limitent leur croissance radiale. L'approche multispécifique a permis de mieux faire ressortir la gamme des relations propres à chaque espèce entre les forêts de la limite alpine des arbres et le climat maritime (température et précipitation mensuelles) de l'écotone de la limite des arbres.

[Traduit par la Rédaction]

Introduction

The climate of most coastal forests is regulated by the proximity of the ocean, which imparts a maritime climate to the region through a complex suite of forcing mechanisms (Hanawa 1995). There is a growing recognition that the climates of such regions are not static and that shifts between climate states (e.g., the Pacific Decadal Oscillation, the North Atlantic Oscillation, and the Arctic Oscillation) have occurred not only repeatedly, but often abruptly, within the last millennium (Hare 1996; Charles 1998; Gedalof and Smith 2001). This behaviour is largely a response related to interdecadal climate variability driven by oceanic forces (Zhang et al. 1997; D'Arrigo et al. 2003*a*). Given the potential for even greater climate fluctuations over the next century (Flato and Boer 2001), there is growing concern that these ocean–forest interactions could have a profound impact on the long-term productivity and sustainability of

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coastal forests worldwide and in particular at the alpine forest ecotone in coastal locations (Wiles et al. 1996).

If future climate changes mirror or enhance maritime conditions in coastal locations, then it is likely that these changes will have the greatest impact at treeline, where climate is known to play an important role in limiting tree growth (e.g., Laroque and Smith 2003; McKenney et al. 2007). Meaningful evaluations of these impacts rely on developing a comprehensive understanding of the consequences of past climate changes on forest diversity, composition, and productivity. The approach to better understand these relationships is to employ a methodological framework that uses annual tree rings and dendroclimatological techniques to construct a database suitable for assessing the potential impacts of climate change (Fritts 1976). These techniques have been used in areas where radial growth – climate relationships are direct and a single or a seasonal parameter is almost exclusively limiting to growth (e.g., dry locations (Watson and Luckman 2001); treeline locations (MacDonald et al. 1998)). However, these strong overriding associations usually break down when the radial growth – climate relationships are assessed in coastal tree-ring series (e.g., Laroque and Smith 1999; Case and Peterson 2005).

In locations with a strong oceanic influence, trees usually exhibit a wider ecological amplitude, and in doing so, the range of annual inputs that can go into making an average annual increment can also be as wide. The radial growth – climate relationships begin to be more complex in these environment types, and methodological shifts such as response surfaces are used when a simple two-dimensional relationship between a climate parameter and radial growth is taken to a third dimension (e.g., Graumlich and Brubaker 1986; Smith and Laroque 1998). Beyond three dimensions, eigenvector analyses (e.g., Pederson et al. 2004) and neural networks (e.g., Woodhouse 1999; Helama et al. 2009) have been employed to try to understand the wider ranges of climatological scenarios that can go into making up the annual increment of a ring.

An alternative strategy to coastal forest research that has had little previous investigation in these complex situations is to switch the focus from an intensely studied single species to multiple species studied in comparison (Laroque 2002; Frank and Esper 2005; Büntgen et al. 2007). The multispecies approach investigates the interactions between an oceanic climatological effect and the wider ecology of a mixed forest, rather than the more focused climate – tree growth relationship of a key species within a coastal forest. Although the change in methodological framework is slight, the power of investigating multiple species and comparing how each would react to the same climatological inputs has as great a benefit to the researcher as understanding how a single species works in great detail (Tardif et al. 2001; Nishimura and Laroque 2011).

Another area of research that has had scant investigation is high-elevation forested areas that are proximal to the ocean (Laroque and Smith 1999). Many of these sites have climate influences that are perhaps more relevant to high-elevation climate stations from farther afield, rather than a close station, but at a dramatic elevation change. These kinds of scenarios are common as long-term climate stations tend to be found at low-elevation coastal sites, yet the dramatic changes in growing environments experienced by the trees at upper elevations adjacent to the existing long-term station are often poorly represented by the historical records.

In this paper, a collection of increment cores from an upland treeline site in a near-coastal Labrador location was used to assess the radial growth response of black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and eastern larch (*Larix laricina* (Du Roi) K. Koch) trees located at the alpine tundra ecotone within the Northeast Atlantic region of North America. Although previous studies had established that white spruce in this region was climatically sensitive (e.g., Schweingruber et al. 1993; D'Arrigo et al. 1996, 2003*a*, 2003*b*), there is very limited appreciation of the dendroclimatological characteristics of all of the various tree species that co-habit these near-coastal sites. This paper focused on describing the tree-ring characteristics of the four coniferous trees species that are commonly found growing across Labrador. Most of these species have proven their ability to retain a climate signal in other studies in North America (e.g., Tardif et al. 2001; Nishimura and Laroque 2011), but they have never been looked at as a group to help understand the entire forest and the potential changes that might occur to the high-elevation forest in this coastal region.

Methods

Study area

The study area was in the Mealy Mountains (53.61°N, 58.84°W) of east-central Labrador, within the High Subarctic Tundra Ecoregion, approximately 115 km from the Labrador Sea and 20 km south of the marine inlet of Lake Melville (Fig. 1). Local summits reached 1092 m above sea level (a.s.l.). Lower slopes and valleys were predominantly covered by boreal forest. Vegetation density decreased from the local altitudinal limit of erect tree growth (approximately 600 m a.s.l.) into a deciduous shrub, krummholz, and heath subzone, culminating in patchy tundra vegetation between bedrock exposures on summits. The treeline is composed of four species, black spruce, white spruce, balsam fir, and eastern larch, but white spruce was slightly more frequent at the higher elevations. Soils are generally thin acidic podzols, especially on exposed summits (Yurich 2006). An unnamed, eastward-trending valley has been the focus of interdisciplinary research on climate, treeline, and tundra ecosystems by the Labrador Highlands Research Group (LHRG), hosted by Memorial University of Newfoundland, since July 2001 (http://www.mun.ca/geog/lhrg/).

Regional climate

Labrador generally experiences relatively mild, snowy winters and cool summers. The climate is a result of both continental and maritime influences; prevailing westerly and southwesterly winds carry relatively cool, dry air into the region in the winter and warmer, moist air in the summer. The cold Labrador Current brings Arctic-origin water and sea ice southward along the Labrador coast. As a result, coastal locations have summer (June–August) temperatures that average about 3 °C cooler than interior locations at about the

Fig. 1. Map of Labrador showing locations of Goose Bay, Lake Melville, Cartwright, and Mealy Mountains, as mentioned in the text. The two Environment Canada climate stations from which data are used in this study are indicated by solid squares.

same latitude but are warmer by about the same amount in winter (December–February). Mean monthly temperatures are above 0 °C between May and October (Environment Canada 2009*a*).

Following the end of the Little Ice Age (ca. 1850), northeastern Canada saw an increase in both temperature and precipitation (Lamb 1985). This is consistent with the general warming trend now recognized to be across the circumpolar northern region (Kaufman et al. 2009). Central Labrador became cooler in the latter half of the 20th century with no significant change in precipitation (Banfield and Jacobs 1998); however, a warming trend in the region has resumed, with mean May–October temperatures increasing by about 1 °C since the 1990s (Lines 2008).

Climate data sources

Monthly temperature and precipitation data from the Adjusted and Homogenized Canadian Climate Data (AHCCD) archive (Vincent et al. 2002; Environment Canada 2009*b*) were used in this study. Records were obtained for the two nearest stations: Goose Bay Airport (Station ID 8501900), located 106 km west of the study area at 49 m a.s.l., and Cartwright (Station ID 8501100), located 120 km to the east, at 14 m a.s.l. on the Labrador Sea coast. The variables used were the monthly averages of daily surface air temperature and monthly totals of daily precipitation. The period used in the tree-ring analysis was from 1942 (start of the Goose Bay record) to 2004.

To evaluate the climate of the central Mealy Mountains in relation to that of the region represented by Goose Bay and Cartwright, use was made of records from automated climate stations (Campbell Scientific Inc.) set up in the study area in 2001. The temperature data were monthly averages of daily average surface air temperature from a station near the upper limit of the open canopy forest (around 570 m a.s.l.). Precipitation was measured annually using a bulk collector (charged with antifreeze to inhibit freezing and mineral oil to reduce evaporation), supplemented with rain gauges deployed during the summer field season. Statistical analysis of the climate data consisted of descriptive statistics and multivariate linear regression and was done using the SPSS statistical package (IBM Corporation 2006).

Tree-ring sampling

In an effort to capture an overall climate signal in trees that was devoid of microsite effects, tree sampling was performed in a spatially extensive fashion, both within the main study valley of the LHRG and in adjacent valleys. Sampled trees were typically located within the open canopy (>10 m between trees) and sometimes were clumped together in sheltered locations. Tree selection was based on two primary criteria: (*i*) good visible health — those trees with visible signs of stress (e.g., scarring due to fire or animals) were overlooked in favour of samples with the best chance to capture any climate sensitivity; and (*ii*) size — only trees more than 10 cm in diameter were sampled. Sites were located between 500 and 600 m a.s.l., on slopes between 0° and 16°, and within 5 km of the local climate station.

Every effort was made to base the master tree-ring width chronologies on 60 tree cores from each species (two cores at right angles to each other per tree, 30 trees per species) at breast height (~1.3 m) using a 5.1 mm increment borer (Table 1). However, some samples were discovered to be unusable once in the lab because of damage and were removed from the analysis (Table 1). The great majority of damaged cores had rot in their centers, which resulted in cores with only a few visible growth rings; others suffered irreversible damage during transportation out of the field. It was also discovered during cross-dating that the smallest trees, which were typically located close to their elevational limit of growth, did not correlate well with samples from lower elevations and so did not contribute to the master chronology for their species. This was the case for the balsam fir species in particular (Table 1). Tree cross sections were also collected at breast height from coarse woody debris (CWD) to extend the length of each chronology using cross-dating techniques. The number of CWD series represented in each master chronology ranged from 33% to 56%.

All cores were mounted onto boards for processing following standard dendrochronological techniques (Stokes and Smiley 1968). All samples were sanded to expose the tree rings and measured using WINDENDRO, a semi-automated imaging software that measures the tree-ring widths with 0.001 mm precision (Guay et al. 1992). Two radii were also measured for each CWD disk. CWD samples were identified at the species level using cellular techniques, primarily the presence (spruce) or absence (fir) of resin ducts (Robichaud et al. 2007). Larch species were visually distinguished based on their distinct earlywood–latewood transitions.

Table 1. Statistical characteristics of tree-ring width chronologies, as per COFECHA output. The total number of segments measured to produce each master chronology is shown along with the number of coarse woody debris (CWD) samples used (in parentheses). In addition, the year when the expressed population signal (EPS) value is above 0.85 is given.

Species	No. of series*	Period	$r^{\dagger}$	SD‡	MS§	AC$^{\|}$	EPS > 0.85
Black spruce	32 (14)	1825–2003	0.509	0.335	0.267	0.718	1847
White spruce	45 (11)	1758–2004	0.581	0.376	0.252	0.658	1805
Balsam fir	23 (10)	1826–2004	0.509	0.348	0.275	0.567	1913
Eastern larch	52 (27)	1717–2004	0.470	0.379	0.345	0.631	1829

Note: Black spruce, *Picea mariana*; white spruce, *Picea glauca*; balsam fir, *Abies balsamea*; eastern larch, *Larix laricina*.

*Number of measured segments (series) in the final chronology, including live and CWD samples.

†Mean interseries correlation values (using 50-year segments) averaged over the chronology.

‡Standard deviation of the mean tree ring measurements.

§Mean sensitivity value.

$^{\|}$Unfiltered autocorrelation value.

Chronology development

Cross-dating is a process in which the tree-ring width pattern of an undated sample is matched to that of a master (i.e., a dated chronology). The quality and accuracy of the tree-ring chronology measurements were first assessed visually and then statistically using COFECHA software (http://www.ncdc.noaa.gov/paleo/treering/cofecha/cofecha.html) for each of the four species (Holmes 1983). In addition, CWD was cross-dated into the master chronologies using a similar correlation approach. As it was not possible to distinguish between the two spruce species using visual analysis, the unidentified spruce disks were fit into that master spruce chronology where they correlated most strongly. This method appeared to readily distinguish the two species.

Standardization was accomplished using ARSTAN software (Cook 1985). In this study, either a relatively conservative single-detrending negative exponential procedure or a linear regression procedure was applied, given the open canopy nature of the alpine treeline forest in the Mealy Mountains and the unlikely occurrence of density-dependent effects on tree growth. This method retains a large amount of the low- and high-frequency variability present in the tree-ring chronologies, thereby exposing long-term patterns in the data (Helama et al. 2004). Autocorrelation effects were not removed from the chronologies in an effort to retain the connection between current year's growth and the growth that occurred in the previous growth year. The expressed population signal (EPS) was also used as a measure of the statistical quality of the tree-ring chronology, based on the sample size; a value above 0.85 is generally deemed statistically acceptable for the purpose of climate reconstruction (Wigley et al. 1984; Briffa and Jones 1990) and so was used to establish a threshold of reliability in the data.

Species response to climate

The computer program DENDROCLIM was used to assess the relationship between radial tree growth and monthly averages for daily air temperature and total precipitation (Biondi and Waikul 2004). This program computes Pearson's correlation coefficients between climate variables and radial growth with a 95% confidence interval using bootstrapping (1000 simulations) techniques. Each master chronology was correlated to the Goose Bay and Cartwright records of mean monthly air temperature and precipitation for a period of 18 months, including the spring and summer months of the year prior to ring formation.

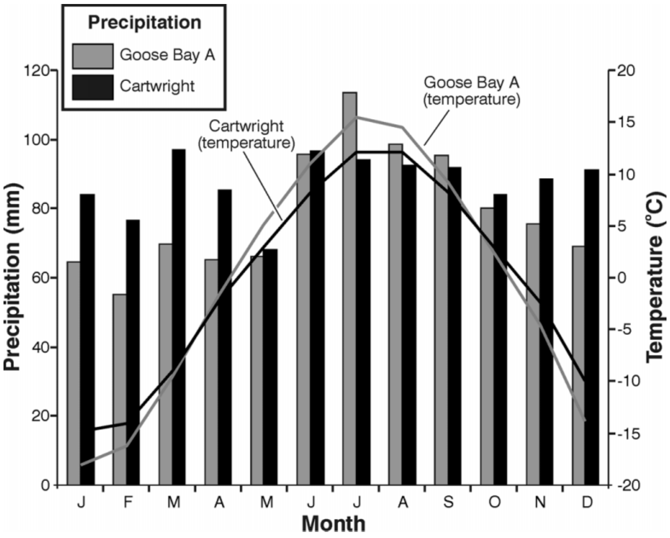
Results

Regional and local climate

Climate normals (1971–2000) from the nearby Goose Bay and Cartwright stations indicate that although mean annual temperatures were similar (–0.5 °C), winters were nearly 3 °C colder and summers 3 °C warmer at Goose Bay compared with Cartwright (Fig. 2). Average annual rainfall (573 mm in Cartwright and 560 mm in Goose Bay) and snowfall amounts (488 cm in Cartwright and 459 cm in Goose Bay) were similar, although there was a more pronounced summer rainfall maximum at Goose Bay. Monthly temperatures were found to be significantly correlated between the two stations for the 1942–2009 period of record, with r^2 values of around 0.9 in winter and 0.7 in summer, indicating strong regional coherence of surface temperatures, although somewhat weaker in the summer period. For the same period, precipitation was only weakly correlated between the two stations, with $r^2 = 0.11$ for annual totals and $r^2 < 0.30$ for monthly and seasonal totals. Temperatures in the mountains were generally lower, reflecting the higher elevation, whereas the annual amplitude of 27 °C was intermediate between those of the two lowland stations (Table 2).

Linear regression was carried out on monthly temperatures for 2001–2009 between the Mealy Mountains study site (dependent variable) and Goose Bay and Cartwright (predictors). Application of the Durbin–Watson test (Bowerman and O'Connell 1993) indicated no temporal autocorrelation in the 12 sets of monthly time series. Despite the small sample size (n = 8 years), the regression model showed significant correlations in all months ($p < 0.01$). The variance in monthly values explained by the multiple regression (r^2) ranged from 57% to over 90%, with no clear seasonal pattern. Based on these results, monthly averages of daily temperatures at the Mealy Mountain study site can be estimated from Goose Bay and Cartwright with a stand-

Fig. 2. Long-term averages (1971–2000 normals) of monthly temperature and precipitation for Goose Bay Airport (Goose Bay A) and Cartwright, Labrador (Source: Environment Canada 2009*a*).



ard error ranging from 0.2 to 1.4 °C, depending on the month.

Annual precipitation collected in the bulk gauge at 570 m a.s.l. averaged 3260 mm (SD = 852) for 2001–2009, far exceeding the averages at Goose Bay and Cartwright of 1041 mm and 1263 mm, respectively, over the same period. Summer (June–August) field days with rainfall observations totalled 209 days between July 2001 and July 2009, with an average rainfall intensity of 5.3 mm/day (SD = 2.6). The brevity of the Mealy Mountain rainfall record permits only an approximate comparison with the other stations. However, July–August rainfall rates (= total rainfall amount / number of days of observation) for the same years averaged 3.9 and 3.2 mm/day for Goose Bay and Cartwright, respectively. This suggests a 40% to 70% greater summer rainfall in the Mealy Mountain study area than at the two long-term stations. Allowing for uncertainties of measurement and in the absence of direct observation for much of the year, a conservative estimate would be that the annual amount of rainfall plus snowfall at the Mealy Mountains site is at least twice that at the two Environment Canada stations (i.e., greater than 2000 mm).

Chronology statistics

The standardized master tree-ring chronologies for the four species spanned an age range of 178–287 years, the longest chronology belonging to eastern larch (1717–2004; Table 1). Considering only the portion of the chronologies where the EPS value is greater than 0.85, then the tree-ring width record spanned from 91 (balsam fir) to 199 years (white spruce). The interseries correlation value was highest for white spruce and lowest for larch. Descriptive statistical values (standard deviation, mean sensitivity, and autocorrelation) were similar between all species with the exception of the above-average mean sensitivity value for larch (Table 1).

Correlation analysis between the chronologies illustrates that the two spruce chronologies were significantly similar and, to a lesser extent, so were the black spruce and larch chronologies (Table 3). The two spruce chronologies shared very similar growth patterns from the mid-1800s to the present, including decade-long periods of below-average growth in the 1850s, 1910s, early 1960s, and late 1970s, the latter two periods of lesser growth being common to all four species (Fig. 3). Between 1920 and 1950, black spruce rings widened, whereas white spruce rings narrowed slightly and followed a pattern that is more similar to that of fir. The larch chronology is characterized by high interannual variability and periods of growth suppression that irregularly occurred every 20–30 years and lasted between 5 and 20 years. Since the 1990s, all species except larch have experienced reduced variability in ring width.

Table 2. Comparison of seasonal temperatures between the Mealy Mountain study site and Environment Canada stations (including elevations (metres above sea level (m a.s.l.)) for the period 2001–2009.

	Mealy Mountains (570 m a.s.l.)	Goose Bay Airport (49 m a.s.l.)	Cartwright (14 m a.s.l.)
Winter	–15.0	–14.4	–10.9
Spring	–4.2	–1.4	–1.7
Summer	11.7	14.9	12.4
Fall	1.1	–1.7	4.7
Annual	–1.6	0.9	1.1

Note: Winter, December–February; spring, March–May; summer, June–August; fall, September–November.

Table 3. Interchronology correlations: matrix of Pearson's correlation coefficient values between four master tree-ring chronologies.

	White spruce	Balsam fir	Eastern larch
Black spruce	**0.67 (0.00)**	0.09 (0.97)	**0.21 (0.03)**
White spruce		0.08 (0.97)	0.03 (1.00)
Balsam fir			–0.04 (1.00)

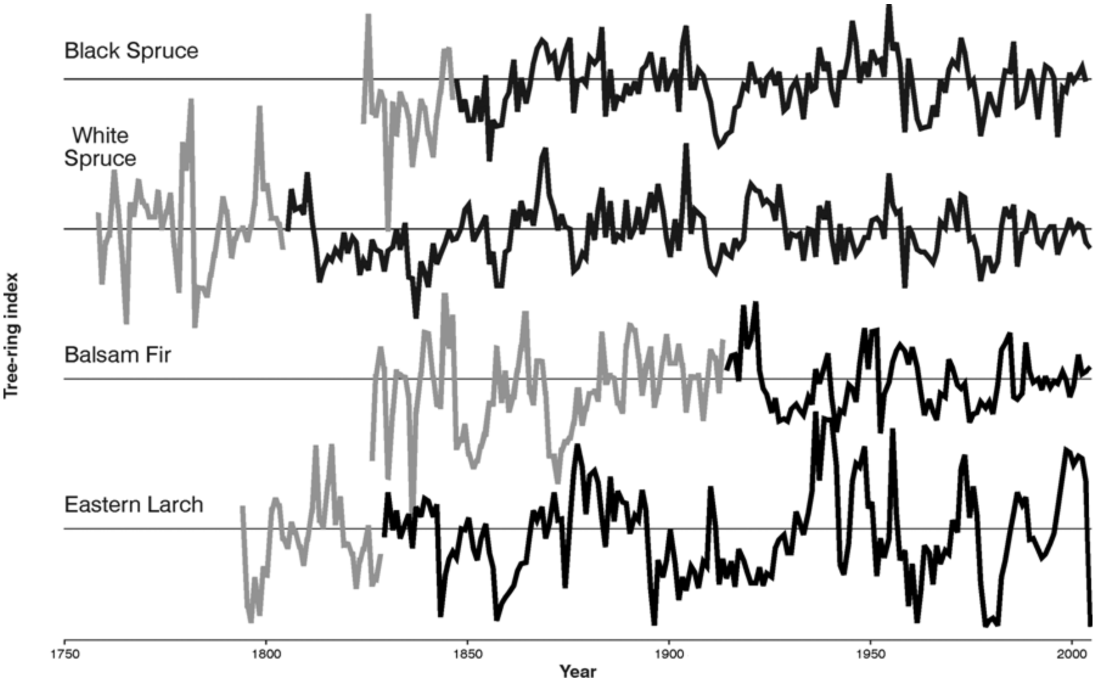
Note: Black spruce, *Picea mariana*; white spruce, *Picea glauca*; balsam fir, *Abies balsamea*; eastern larch, *Larix laricina*. Correlation values are based on the common time period (1826–2003, $n = 177$); p values are shown in parentheses; significant correlations ($p < 0.05$) are bolded.

Species response to climate

The radial growth records of black and white spruce were positively correlated to temperature during June–July and negatively correlated to February temperatures (Fig. 4). Fir and larch were positively correlated with September temperatures during the growth year for fir and during the previous year for larch.

The radial growth of all four tree species was negatively correlated to precipitation in part or all of the growing season (June–August), an association that continued for black spruce and fir trees from the previous year (Fig. 5). White spruce radial growth was positively correlated to November, December, and March precipitation (Fig. 5). With the exception of black spruce, significant correlations between radial tree growth and precipitation typically occurred in only one month of the growing season and never in July.

Fig. 3. Time series of standardized tree-ring width chronologies for the four treeline study species (black spruce, *Picea mariana*; white spruce, *Picea glauca*; balsam fir, *Abies balsamea*; eastern larch, *Larix laricina*). Sections of each chronology where the expressed population signal falls below 0.85 appear as a grey line. The standardization process divides the mean annual ring measurement by an idealized curve, resulting in a unitless index of tree-ring growth.



Discussion

This study presented the first dendroclimatic assessment of multiple tree species at the coastal treeline of northeastern North America. The interseries correlations and mean sensitivity values suggested that all four species are appropriate for dendrochronological analysis, but that white spruce may preserve the strongest climate signal. The magnitude of the interseries correlation values were consistent with those from dendrochronological studies elsewhere in Labrador and western Quebec, particularly for black and white spruce and balsam fir, but less so for eastern larch (white spruce (Schweingruber et al. 1993; Briffa et al. 1996); seven boreal species (Tardif et al. 2001); black and white spruce, fir, and larch (Nishimura and Laroque 2011)). The mean sensitivity values for each of the master chronologies were higher than those reported for western Labrador (Nishimura and Laroque 2011), with a strongly elevated value for eastern larch, which indicated a particular tendency for inter- and intra-annual fluctuations in radial growth.

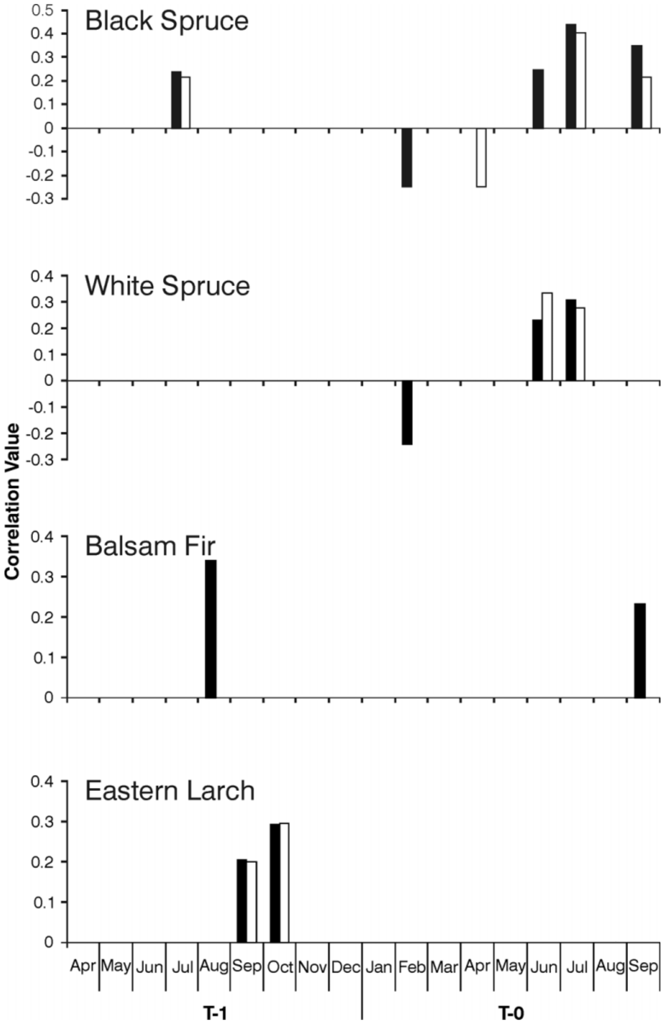
Although the length of the Mealy Mountain climate record is relatively short, analysis illustrated that temperatures in the central Mealy Mountains were significantly correlated with those at the nearest long-term climate stations, Goose Bay Airport and Cartwright. Precipitation, including annual total rain plus snowfall, summer rainfall, and midwinter snowfall in the mountains, exceeded that at the lowland stations. In terms of both temperature and precipitation, the climate of the mountains can be said to be distinctive, reflecting effects of both altitude and intermediate location with respect to the Labrador Sea coast.

Species response to climate

Our dendroclimatological analysis suggests that both precipitation and growing-season temperature were significant contributors to the radial growth of trees in the Mealy Mountains. Specifically, the two spruce species were positively correlated to temperature during the growing season, a pattern that is similar to that seen in western Labrador (Nishimura and Laroque 2011). Although previous studies from farther north along coastal Labrador have shown that white spruce trees experience drought-related stress in the spring, as expressed through decreased temperature sensitivity (D'Arrigo et al. 2003*a*), this phenomenon was not observed for white spruce in the Mealy Mountains. This may reflect our findings that about twice as much moisture was available through the growing year in the Mealy Mountains than at lower elevations and would also support our field records of adequate soil moisture in spring and early summer for all trees in the study area. Another study in northern Labrador reported that the radial growth of white spruce trees was not found to be limited by precipitation (Payette 2007). Because our southern site has much more precipitation than those more northern stations, a "wet" year may mean excessive moisture and may be associated with other factors that negatively affect ring width but do not show up in our analysis.

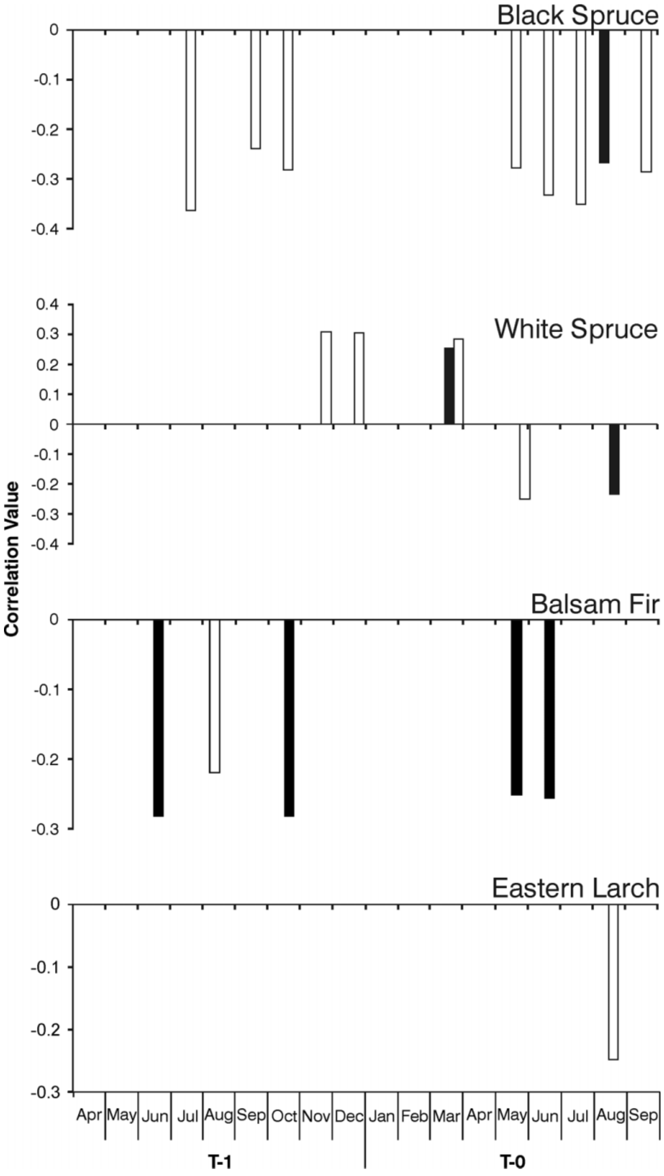
White spruce showed strong positive relationships between radial growth and snowfall in November, December, and March. High snowfall accumulation (snow surveys in the study area near the forest limit in early March 2008 and 2009 showed average snow depths (and water equivalents (w.e.)) of 1.8 m (0.68 m w.e.) and 2.2 m (0.92 m w.e.), re-

Fig. 4. Sensitivity of four alpine treeline species (black spruce, *Picea mariana*; white spruce, *Picea glauca*; balsam fir, *Abies balsamea*; eastern larch, *Larix laricina*) to Environment Canada temperature data. Solid and open bars represent statistically significant (95th percentile) correlations to mean monthly temperature at Cartwright and Goose Bay Airport, respectively. T–0 represents the year of tree-ring growth; T–1 is the year prior to tree-ring growth. See text for discussion.



spectively (P. LeBlanc, unpublished data), likely benefits white spruce trees by providing some protection from frequent, strong winter winds, while field observations of multiple and damaged leaders, as well as flagging on white spruce where they occupy the most exposed sites at the elevational treeline, demonstrated their vulnerability to winter winds. Icy winds damage needles and other tissues on exposed trees, necessitating the tree to allocate resources for healing in the spring (e.g., Hadley and Smith 1983; Scott et al. 1993). Significant correlations between radial tree growth and snowfall are common in coastal western Canada where both winter snowfall amount and persistence of the snow pack into the summer months may be important determinants of the position of alpine treeline (e.g., Scott et al. 1993).

Fig. 5. Sensitivity of four alpine treeline species (black spruce, *Picea mariana*; white spruce, *Picea glauca*; balsam fir, *Abies balsamea*; eastern larch, *Larix laricina*) to Environment Canada precipitation data. Solid and open bars represent statistically significant (95th percentile) correlations to mean monthly precipitation for Cartwright and Goose Bay Airport, respectively. T–0 represents the year of tree-ring growth; T–1 is the year prior to tree-ring growth. See text for discussion.



The limited climate sensitivity observed in balsam fir and larch trees (seven and five significant monthly correlations, respectively, versus 17 and 11 for black and white spruce, respectively) may be indicative of frequent insect infestations in the Mealy Mountains. Defoliating insects can cause trees to allocate resources to needle regeneration at the expense of radial growth, resulting in narrow tree rings and a reduction or loss in climate sensitivity (e.g., Boulanger and Arsenault 2004). In the study area, balsam fir trees are the primary hosts for the spruce budworm (*Choristoneura fumiferana* (Clemens)) and larch trees are vulnerable to the larch sawfly (*Pristiphora erichsonii* (Hartig)). Evidence for episodic spruce budworm infestations exists in tree-ring records from nearby neighbouring Quebec (e.g., Boulanger and Arsenault 2004), and larch sawfly impacts have also been reported from trees in western Labrador (Nishimura and Laroque 2010). Given that the characteristic pattern of insect infestations in radial tree growth — rapidly narrowing tree rings followed by gradual widening over a number of years — was apparent in both the balsam fir and larch tree-ring series in this study, it is tentatively concluded that past insect defoliations may have played a role in the radial growth sensitivity to climate here as well.

Conclusion

Single-species studies would not have adequately characterized the complex climate – radial growth relationships occurring in the Mealy Mountains. For example, if only balsam fir was studied, precipitation would be interpreted to be the primary factor affecting tree-ring growth, and if only white spruce was studied, growing-season temperature would be solely used to explain tree-ring growth variation. It is only from a multispecies perspective that a broader understanding of the climate sensitivity of this coastal forest ecotone is gained. Any changes to the multiple climate drivers of the high-elevation forest would then have repercussions in other aspects of the forest ecology of the area, e.g., upper treeline migration and frequency and magnitude of disturbance agents.

By looking at all four species at one site through an extended temporal frame, it is interesting to see that these co-existing species' radial growth sequences are able to illustrate the variations in the different sets of optimum climatic conditions. In some cases, one species is growing well, while another tree species is neutral or not growing well at all. Through the multispecies methodology we utilized in this study, we can finally better understand the wide array of varying ocean-influenced climatic conditions that allows each species a short window when it can outcompete the other species in the same forest. It will be interesting to see during some of the dramatic changes forecasted to occur in Labrador's climate in the future, if one species will be able to establish a dominance across the alpine treeline, where four species currently co-exist.

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