CHANGING TREELINES: HOW VARIABILITY IN SCALE AND APPROACH IMPROVE OUR UNDERSTANDING

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Abstract

With treeline position expected to expand northward, and upward, with climate change, there is increased attention towards understanding the mechanisms that control these patterns. Using a regional and broad scale approach, treeline dynamics, disturbance and response to recent climate warming were explored along an altitudinal gradient in the Mealy Mountains, Labrador (Canada), and across the circumpolar subarctic. To complement the western science approach to understanding climate change, a critique of modules taught to the Innu Guardians will be presented. At a regional scale in the Mealy Mountains, treeline dynamics over the past few centuries showed species-specific differences in when treeline was established and the relative rates of subsequent infilling and mortality. All tree species showed increased variability in recruitment correlations to climate across the treeline ecotone with black spruce (*Picea mariana*) showing consistently positive correlations, while larch (*Larix laricina*) shifted from strongly positive to negative and white spruce (*Picea glauca*) showing consistently negative correlations. Long-lived black spruce krummholz also showed significant recent increases in radial growth. Disturbance at treeline resulted in characteristic gap dynamics with low-levels of tree mortality attributed to porcupine (*Erethizon dorsatum*) herbivory and small-scale outbreaks of spruce budworm (*Choristoneura fumiferana*) and larch sawfly (*Pristiphora erichsonii*). These outbreaks occurred at lower magnitudes than observed in other parts of the boreal forest due to decreased tree density, supporting the Resource Concentration Hypothesis. Canopy gaps associated with windthrow did not have significantly different canopy structures but seedling densities of larch and black spruce, were significantly higher in exposed soil associated with windthrow disturbance. At broader spatial scales across circumpolar treeline, growth form and advancement were not significantly related to the extent of site warming but rather treeline advancement was predicted by diffuse, or 'gradual' treelines and closeness to the ocean. At the regional scale, it was expected that larch and black spruce would capitalize on warming temperatures, since these species are already exhibiting early signs of response. The frequency and magnitude of insect outbreaks is expected to increase with climate change and these data suggest that larch, and to a lesser extent, black spruce, will have enhanced regeneration dynamics. At broad spatial scales, ecological factors will continue to be significant drivers of treeline change until temperatures warm past a point where regeneration limitations, such as seed viability and establishment, are removed. Teaching and communicating climate change science illustrated the best results when taught in field conditions, while some difficulties were encountered in differentiating between short-term versus long-term change. Working with the Innu Environmental Guardians to develop a framework for detecting change in northern forests, helped to contextualize the western science approach to treeline research.

To EJU and SJT, for sustenance

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List of Abbreviations and Symbols

Symbol/Abbreviation	Meaning
°C	Degrees Celsius
Δ	Change in
±	Plus or minus
%	Percentage
=	Equal
<	Less than
>	Greater than
α	Alpha
Adj. R^2	Adjusted coefficient of determination
c.f.	Confer or see
CI	Confidence Interval
cm	Centimetre
CRU-T3	Climate Research Unit temperature data
D	D-statistic
df	Degrees of freedom
e.g.	For example
F	F-statistic
ha	Hectare
i.e.	Which means
JJA	June, July, August
km	Kilometre
L_e	Effective leaf area index
m	Metre
m a.s.l.	Metres above sea level
m^2	Metre squared
Max.	Maximum
Min.	Minimum
mm	Millimetre
n	Sample size
P	Probability
r	Pearson's correlation value
R^2	Coefficient of determination
SD	Standard deviation
SE	Standard error
sp.	Unknown species
spp.	More than one species
T	T-statistic
US	United States

Chapter 1: General introduction

1.1 Introduction

Species range limits have long fascinated ecologists as competition, dispersal barriers and environment gradients partition the landscape (Gaston 2009). In the case of environmental gradients, when these conditions shift, as they have been with recent climate change, the ranges of those species constrained by environmental factors are expected to reposition accordingly. This repositioning, or synchronizing of range limits to climate is complex as the area beyond the current range limit is most often occupied by other species that too are experiencing range shifts (Parmesan et al. 2005).

The forest-tundra ecotone, or 'treeline', is an excellent system to explore range dynamics since trees are obvious, in terms of their physical structure, making range shifts detectable at multiple scales (Danby 2011). Also, since trees are a valued resource to permanent and seasonal human residents, there is often local knowledge on past treeline position and great interest in future scenarios of treeline change. In arctic and alpine ecosystems, treeline migration occurs at the expense of tundra habitat, giving rise to concerns that if current vegetation models are accurate, tundra habitat and associated wildlife will decrease significantly (Kaplan and New 2006).

While northern latitude treelines are technically part of the boreal forest region, they are classified as being in the low-arctic ecoclimatic region (Scott 1995), suggesting that ecological processes and mechanisms of change at treeline are significantly different. Perhaps the most important example is disturbance, that structures plant communities at large spatial scales in much of the boreal forest (Weber and Flannigan 1997). Fire and insect outbreaks often result in high levels of tree mortality in affected areas and are responsible for initiating stand-level regeneration (Greene et al. 2007). At treeline, the role of disturbance is less well understood and, while fire is important for controlling the position of treeline in the Western Canadian subarctic (Brown and Johnstone 2012), in eastern Canada the frequency and magnitude of disturbance events are not well-documented (Caccianiga et al. 2008). The lack of large-scale disturbance events suggests that patterns of regeneration and persistence may be driven by small-scale disturbance events. When disturbance events are less frequent and of lower magnitude, the death of a single tree, or a small patch, drives what is referred to as 'gap dynamics' (McCarthy 2001).

Treelines also differ from contiguous boreal forests in that climatic factors may limit reproduction and survivorship of earlier life history stages (Sirois 2000). These climatic limitations can restrict treeline position until these limitations are ameliorated. Referred to as a 'positive response', we expect recent climate warming to initiate a northward and upward movement of treeline position (e.g., Kullman 2002, Danby and Hik 2007). However, over the past century, the circumpolar response of treeline has been highly variable (Harsch et al. 2009). Reasons for this variability in observed treeline response identifies the importance of considering ecological factors, including disturbance, and the interaction with climate, that manifests in treeline change.

1.2 Thesis Outline

The overall objective of this dissertation is to explore ecological processes at multiple spatial and temporal scales, to generate an understanding of treeline dynamics from a historic and contemporary context. This research offers a novel contribution to the existing literature by incorporating multispecies perspective that occurs at treeline in our study site in Labrador. With four co-dominant treeline species, differences in dynamics and susceptibility to disturbance can be evaluated by species-specific traits and life history attributes. Following the regional investigation of treeline dynamics, a synthesis of circumpolar treeline dynamics addresses ecological patterns and process across broad spatial scales. Another objective of this dissertation is to explore the successes and shortcomings of teaching forest ecosystem and climate change to a group of Innu participants from Labrador. In its entirety, this dissertation offers important insight into the fate of treeline and tundra ecosystems.

To begin, treeline dynamics over the past 200 years were reconstructed in Chapter 2, *Four treeline species, four different responses: a multispecies approach to treeline dynamics in subarctic alpine Labrador*. This chapter combines ecological and age structure data, patterns of growth form, stand densities and recruitment analyses from a multispecies perspective, with an emphasis on climate change. While providing an in-depth understanding of treeline dynamics in the Mealy Mountains, ecological processes that influence dynamics, such as persistence (Chapter 3) and disturbance (Chapter 4), are introduced for subsequent exploration. In Chapter 5, I address many questions about what is happening with treeline dynamics at the circumpolar scale by synthesizing data from multiple treeline sites.

With the discovery of an extremely old and physically unimpressive black spruce (*Picea mariana*) krummholz at treeline, Chapter 3, *Persistence at the treeline: old trees as opportunists*, explores the idea of persistence being an integral part of treeline dynamics. At treeline, persistence of individuals through vegetative reproduction and tolerance to inhospitable climatic conditions enhances individuals' response potential. This chapter was published in *Arctic* (Trant et al. 2011).

In Chapter 4, *Is small-scale disturbance important at treeline?*, the role of disturbance at treeline is quantified using a variety of observational techniques and reconstructed insect herbivory outbreaks. Exploring patterns of disturbance along an elevation gradient, the importance and ecological significance of small-scale disturbance at treeline is explored within the context of gap dynamics and climate change. In this chapter, the Resource Concentration Hypothesis (Root 1973) is tested to look at how the frequency and magnitude of insect outbreaks changes across treeline.

In Chapter 5, *Ecological factors, not climate warming, explain variability in treeline patterns*, a synthesis of data contributed by co-authors from circumpolar treeline sites is presented to address the issue of treeline dynamics and change, at broader spatial scales. Growth form and treeline response, including data from all life history stages, are explored while considering the extent of warming and ecological factors at each site. Such a life history approach has not been attempted across such a large scale to date.

Lastly, the questions and methods involved in this treeline research were integrated into an alternative approach for understanding climate change. An overview and discussion from a series of field-based modules for Innu Environmental Guardians is presented in Chapter 6, *Teaching and learning about climate change with Innu Environmental Guardians,* and published in *Polar Geography* (Trant et al. 2012). Differing from the ecological chapters that constitute the rest of this dissertation, this chapter bridges the gap between science and education, incorporating different knowledge systems. Integrating methods for detecting change at treeline, and northern forests in general, this chapter discusses the successes and difficulties associated with communicating and teaching climate science initiatives in northern communities. Communicating and teaching this science also provides an excellent opportunity for learning.

1.3 Co-authorship Statement

This research was conducted independently under the supervision of Dr. Luise Hermanutz. For Chapters 2, 3 and 4, I was responsible for the experimental design, collection of data, processing of samples and statistical analysis but data collection in the field was assisted by Ryan Jameson, Grant Sampson, Leslie Rich, Daniel Myers, Megan Andrews, Julia Wheeler, Brittany Cranston, Brian Starzomski, Keith Lewis, Peter Koncz, Danielle De Fields, and Luise Hermanutz. A subset of tree ring samples used in chapters three and five were processed by Amanda Young and Colin Laroque at the Mount Allison Dendrochronology Laboratory in Sackville, NB. For Chapter 5, I was responsible for experimental design, collection of data and processing of samples for the data from the Mealy Mountains, Labrador. As a synthesis chapter, other co-authors contributed data from different geographical locations. For this chapter, I was responsible for the data collation, building of datasets, analysis and writing of the manuscript. For Chapter 6, John Jacobs and I were responsible for designing and teaching the climate change modules that would become the basis for this chapter. I wrote the original drafts for all of the manuscripts that make up the chapters of this thesis. Chapters 2 and 3 are co-authored by Luise Hermanutz. Chapter 4 was co-authored by Ryan Jameson and Luise Hermanutz. Chapter 5 was co-authored by Carissa Brown, Stephen Mamet, Ingrid Mathisen, Geneviève Dufour Tremblay, Jayme Viglas, Xanthe Walker, Stéphane Boudreau, David Cairns, Ryan Danby, Greg Henry, Luise Hermanutz, David Hik, Annika Hofgaard, Jill Johnstone, Colin Laroque, Andrea Lloyd, Peter Kershaw, Jackie Weir and Martin Wilmking. Chapter 6 was co-authored by John Jacobs and Trudy Sable. Financial support for the research conducted in Chapters 2, 3 and 4 was provided by Luise Hermanutz. Financial support for Chapter 5 was in part provided by Luise Hermanutz, with other funding from co-authors, which was needed to collect data needed to contribute to this synthesis manuscript. Financial support for Chapter 6 was provided by a SSHRC grant to Trudy Sable.

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Chapter 6 Trant, A. J., Jacobs, J. D. and T. Sable. 2012. Teaching and learning about climate change with Innu Environmental Guardians. Polar Geography: 10.1080/1088937X.1082012.1682229.

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Chapter 2: Four treeline species, four responses: a multispecies approach to treeline dynamics in subarctic alpine Labrador

Abstract

Comparing how different species respond to the same change in climatic conditions offers insight into key life history traits and growth preferences that are not possible in a single-species system. Forest-tundra ecotones, or ‘treelines’, are generally thought to be climate-sensitive, making treeline position responsive to climate warming. Using four tree species, we examined recent treeline dynamics using ecological and age structure data to explore elements of species responses through growth form relationships and periods of establishment, mortality and recruitment. With the exception of white spruce (*Picea glauca*), variability in growth form, explained by height and diameter relationships, increased across treeline. Differences in growth form varied among species with larch (*Larix laricina*) having the least amount of plasticity across treeline. Seedlings (height<0.15 m) were uncommon across treeline with the exception of larch, while sapling (height between 0.15 and 2.0 m) density increased across treeline, especially for black spruce (*Picea mariana*). Age structure of trees (height>2.0 m) showed that larch and balsam fir (*Abies balsamea*) were more recently established at treeline and, based on reconstructed stand densities, illustrated higher rates of infilling. Mortality was detected in all species except balsam fir. Variability in recruitment increased across

treeline with larch recruitment switching from strongly positive to negative correlations to mean summer temperature, while black spruce recruitment remained positively correlated to mean summer temperature across treeline. This multispecies approach provides evidence that species are responding differentially to climate. With the exception of larch, regeneration patterns are largely dependent on vegetative reproduction, such as layering. As climate changes, we expect a dramatic shift in treeline composition with larch and black spruce being the first to benefit from warming temperatures but responding to change with very different strategies.

2.1 Introduction

Multiple species exposed to the same changing climatic conditions allow for important comparisons of species-specific life history traits that are not possible in a single-species system. Forest-tundra ecotones, or 'treelines', are generally thought to be climate-sensitive making treeline position responsive to climate warming (e.g., Holtmeier and Broll 2005). At broad spatial scales, treeline position correlates well with certain climate parameters such as mean annual soil temperature (Körner and Paulsen 2004). However at finer spatial scales, the site-specific relationship between treeline position and climate is highly variable (Harsch et al. 2009). This variability may reflect the ecological lag-time needed for treeline species to respond to shifts in climate or more likely, that factors controlling treeline processes are multifaceted and species-specific (Hofgaard et al. 2012). A multispecies approach will enable comparisons to climate, as well as ecological factors that regulate species distribution and population size, which can be used to predict how treelines will respond to future climate change.

Changes in range limits, tree density, regeneration dynamics, recruitment, and growth patterns have all been used to quantify recent treeline dynamics of northern forests. At many sites, treeline expansion has been reported (e.g., Lescop-Sinclair and Payette 1995, Lloyd et al. 2002, Danby and Hik 2007), although stable and retreating treelines have also been documented (e.g., Szeicz and MacDonald 1995). Reconstructed stand densities have been used for understanding range dynamics by interpreting patterns of treeline establishment (e.g., Lloyd and Fastie 2003). Individual trees at the northern range edge show higher levels of responsiveness to temperature increases compared to those from the main part of the range (Huang et al. 2010, Ettinger et al. 2011). While trees in some regions are showing enhanced vertical and radial growth with increased temperature (Tremblay et al. 2012), many illustrate variability in these responses, suggesting complex spatial and temporal interactions between growth, temperature and precipitation (Wilmking et al. 2004, D'Arrigo et al. 2007, Messaoud and Chen 2011). In a multispecies treeline, ecological and biogeographical factors can be compared and will ultimately improve our understanding of observed treeline changes and ability to predict future responses. Furthermore, less commonly studied multispecies treelines offer the possibility of understanding differential responses among species and potential interspecific interactions.

Adopting a life history approach, treeline response to climate warming is dependent upon the success of many processes – each with its own climate vulnerability and uncertainty. Seed production and viability requires a minimum number of growing degree-days, which is marginally supported at treeline (Sirois 2000). Dispersal and establishment of seeds requires appropriate safe sites, which are species-specific and, at treeline, may be less abundant than in a contiguous boreal forest site (Germino et al. 2002). Upon establishment, an individual's ability to persist requires a positive carbon balance (assimilation>respiration), which often depends on growing season length (Hoch and Körner 2003). Species response potential is also influenced by their reproductive strategy, giving the advantage to those individuals that are capable of reproducing asexually (e.g., layering) when conditions for sexual reproduction may not be available (Trant et al. 2011). These species-specific life history characteristics are crucial for explaining the variability in responses observed in treeline environments.

With substantial warming being observed in most subarctic and alpine regions (IPCC 2007), there is interest in understanding treeline dynamics as a means of predicting future changes that would influence carbon balance (Cairns and Malanson 1998), albedo effects (Chapin et al. 2005), and the potential displacement of arctic and alpine ecosystems (Kaplan and New 2006). Using a multispecies approach at treeline, the objectives of this study were to: (1) explore differences in tree growth form among species and zones; (2) identify and compare temporal patterns of establishment; (3) reconstruct stand densities to compare rates of infilling and mortality and; (4) explore linkages among climate, recruitment and mortality at treeline. We expect treeline dynamics to vary substantially among species due to species-specific reproductive tendencies and ecological plasticity in response to climate.

2.2 Materials and Methods

2.2.1 STUDY AREA

The dynamics of a multispecies treeline was studied in the north-central Mealy Mountains, Labrador, within the boundary of the proposed (Akamiuapishk^{u}) Mealy Mountains National Park Reserve (N 53°36'6", W 58°49'0"; Fig. 2.1). This area is ideal for treeline research because the treeline ecotone occurs along an elevation gradient of approximately 600 m. Treeline was divided into three zones based on growth form and structural attributes of trees along an elevation gradient: 1) 'forest zone' is dominated by trees with erect growth forms and represents the most closed canopy stands at treeline, though with lower stem densities and less canopy structure than found in contiguous boreal or taiga forests (Scott 1995); 2) 'transition zone' is composed of trees with primarily erect growth forms with some prostrate, or krummholz, growth forms, less canopy structure than the forest zones and represents the tree limit (height>2.0 m) and; 3) 'krummholz zone' is dominated by shrub species with occasional krummholz and or isolated tree islands. Beyond the krummholz zone, the 'tundra zone' is beyond the species limit for trees and is dominated by shrubs such as arctic dwarf birch (*Betula glandulosa* Michx.) and other alpine tundra plants. The Mealy Mountains treeline is composed of four co-dominant tree species: balsam fir [*Abies balsamea* (L.) Mill.], larch [*Larix laricina* (Du Roi) K. Koch], black spruce [*Picea mariana* (Mill.) Britton, Sterns & Poggenb.] and white spruce [*Picea glauca* (Moench) Voss] (Table 2.1). The majority of soils across treeline are slightly acidic loamy sand (Sutton 2008).

The local climate was recorded at three elevations using Campbell Scientific Inc® automated climate stations and will henceforth be referred to as transition (570 m a.s.l.), krummholz (600 m a.s.l.) and tundra (995 m a.s.l.) climate stations. The average number of growing degree days (>5°C) was 732.7 for the transition climate station (2002 to 2006), 719.9 for the krummholz climate station (2006 to 2008) and 454.8 for the tundra climate station (2002 to 2008). The average of monthly temperature lapse rates between the tundra and transition climate stations between 2004 and 2009 was -0.51°C/100 m (Chan 2012). While Central Labrador has not experienced significant warming over the 20th century (Banfield and Jacobs 2008), summer temperatures for the first decade of the 21st century have increased by almost 1°C, compared to the period from 1970 to 2000 (Environment Canada 2011). This warming trend in central Labrador is predicted to continue resulting in temperature increases of 3 to 4°C in the winter and 2 to 3°C in the summer by 2050 (Lemmen et al. 2008).

In the Mealy Mountains, there is a long-standing tradition of seasonal land-use by Labrador Innu with the majority of sustenance resource extraction being restricted to areas lower in elevation than where this study was conducted (P.

Armitage pers. comm. 2012). Therefore, in the absence of human influence, differences in stand history and current patterns can be attributed to climate, site characteristics and ecological processes, such as disturbance and not human-mediated changes.

2.2.2 FIELD METHODS

All sampling was conducted in 2007 and 2008 at three treed zones (forest, transition and krummholz) with a total of 7 sites (Table 2.2). Due to high levels of heterogeneity (e.g., forested, open water and exposed bedrock), sites in the forest and transition zone were non-randomly selected to best represent the typical forest structure. In forest and transition zones, forest structure and stem density were measured using fixed-area plots with dimensions that varied between zones, reflecting the size and variability (Table 2.2). For the krummholz zone, the starting point for each 4 m wide transect was randomly selected and established perpendicular to the elevation gradient. Site data for each zone [forest (n=2), transition (n=3) and krummholz (n=2)] were combined for analysis to better reflect the variability captured in each zone and for simplification when comparing between zones. In the forest and transition zones, all living and dead trees (height>2 m) were sampled using a 4.3 or 5.15 mm increment borer as close to the root collar as possible to ensure an accurate stem age. To obtain the best possible age estimate in the krummholz zone, increment cores were taken where stem diameter was the largest and, presumably, the oldest. Cores were air dried in straws until processed in the laboratory. In the forest and transition zones, regeneration was divided into seedlings (height<0.15 m) and saplings (height between 0.15 and 2.0 m) and measured using five systematically located 2 x 2 m subplots for each site (for details see: Hofgaard and Rees 2008). Within each subplot, a basal cross-section from each sapling and seedling was removed for age determination, while trees were sampled as described in the fixed area plots. For saplings and seedlings, two radii per cross-section were counted. When seedlings were too small to remove a cross-section, a thin section (using a scalpel blade) was removed and counted.

For each tree, individuals were measured for height, diameter at breast height (DBH=1.4 m), physical signs of damage (e.g., frost cracks, insect damage, porcupine scars), and whether individuals originated from seed or asexual layering. Individuals were considered to have arisen from layering if stems had the diagnostic J-shape at the litter/soil interface (Hofgaard and Rees 2008).

2.2.3 LABORATORY METHODS

Cores were glued into pre-grooved boards, sanded and polished to increase the visibility of annual radial growth rings (Stokes and Smiley 1996). All samples were counted using a Velmex® sliding stage micrometre (precision 0.005 mm) under a binocular microscope at 40X with a digital encoder. When the pith was missing from a sample, an adjustment was made to the reflect this by estimating the age of the missing section based on the curvature of the inner most ring (Szeicz and MacDonald 1995). Corrections were needed for 67% of samples, with the majority of corrections being less than 10 years. Missing and false rings are uncommon at this study site (A. Trant unpublished data).

2.2.4 DATA ANALYSIS

Growth form

To assess growth form, relationships between tree height and diameter were explored among species and zones using linear regression. For the forest and transition zones, trees over 2 m in height were included, while for the krummholz zone, all individuals sampled were included since most individuals grew prostrate and were less than 2 m in height. For the forest and transition zone, the diameter corresponds to DBH but for the krummholz zone, individuals do not always obtain heights over 1.4 m so the diameter was taken where the stem was the largest, often at the base.

Age structure and establishment

For the forest and transition zones, seedling, sapling and tree age were used to obtain age structure. For the krummholz zone, all stems sampled were considered to be trees, irrespective of their height, since most individuals had a prostrate growth form and were <2 m in height. Stand dynamics were examined using static age structures of living trees, saplings and seedlings, compiled by species, using decadal age class frequency distributions to reduce error associated with age determination (Wong and Lertzman 2001). For regeneration, data from subplots were scaled so that the survey area matched those of trees (Table 2.2). Saplings were compared among zones using two approaches: (1) the ratio of the number of saplings per tree and (2) the median age of saplings using a non-parametric Mann-Whitney test (M-W test). Age structures were compared among the forest, transition and krummholz zones using three statistics (Danby and Hik 2007): (1) age class distributions were compared using a non-parametric Kolmogorov-Smirnov test (K-S test); (2) median age of individuals were compared using a non-parametric Mann-Whitney test (M-W test); and (3) establishment date was inferred using the 5 oldest individuals and compared using a M-W test. Frequency histograms of establishment dates were visually assessed to examine trends across species and zones.

Density reconstructions

Another approach to examine stand dynamics involved reconstructing stand density and recruitment over time for each species and zone. This approach incorporates establishment and mortality data to look at the density of living trees at the decadal-scale. From these data, the period at which stands reached 50 stems per hectare was used to approximate commonly observed treeline densities (Danby and Hik 2007). Using this approach, transitions zones that established after the forest zones can be used to infer treeline advance. Also, comparing the relative patterns of reconstructed densities among zones, it is possible to infer rates of infilling and mortality (i.e., increases in local density), with positive slopes corresponding to faster rates of infilling and/or lower rates of mortality (e.g., Mamet and Kershaw 2012).

Recruitment and climate

The final method used to understand recent treeline dynamics was to explore relationships between recruitment, mortality and climate. For long-lived species, such as trees, it is expected that fewer individuals will survive to the older age classes and therefore decrease in abundance moving away from the present. Negative exponential function models are best suited for age structures with constant mortality rates and may be more suitable for clonal trees (Legere and Payette 1981), while power function models are more appropriate for age structures that exhibit high mortality in younger age classes with survivorship increasing with age (Hett and Loucks 1976). Interpretation of recruitment periods and mortality were carefully examined so as to not overlook asymmetrical contributions of different cohorts through time that are not explained by environmental conditions (Johnson et al. 1994). Model selection of either negative exponential or power functions was based on significant *P*-values and by the function with the largest R^2 value. Significant models represent static age structures that follow expected distribution while non-significant models are either the result of limited sample size or patterns that are not representative of naturally regenerated stands. The residuals from these models, calculated as the difference between the theoretical and observed values, provide valuable information about recruitment peaks (high levels of establishment and/or low levels of mortality) and recruitment troughs (low levels of establishment and/or high levels of mortality) over time (e.g., Daniels and Veblen 2004, Danby and Hik 2007, Mamet and Kershaw 2012).

The nearest instrumental climate record (N 53°19’12”, W 60°25’12”; Goose Bay, Labrador) includes monthly climate data from 1942 to 2010. To increase the length of the climate record used in these analyses, CRU TS 3.1 reconstructed data were used, providing data coverage from 1901 to 2009 (University of East Anglia Climatic Research Unit 2008). Pearson’s correlation between the instrumental record and the reconstructed temperature data were determined to assess the appropriateness of using reconstructed data for these analyses. The residuals from negative exponential and power models at the decadal scale were correlated with decadal mean summer monthly temperatures (June, July, August). Since recruitment can be influenced by climate at various temporal scales, decadal recruitment was correlated to multi-decadal windows of forward means - 10, 20, 30, 40, and 50 years following establishment (Szeicz and MacDonald 1995, Danby and Hik 2007, Mamet and Kershaw 2012). Despite the limitations of using multi-decadal windows of forward means past 1950 (e.g., only 40 years of climate data are available for the decade of 1960), using this approach allows for exploration of post-establishment influences of climate throughout the early life history stages of the trees. All statistical analyses were performed in R (v. 2.14; R Development Core Team 2006).

2.3 Results

Growth form

Height on diameter relationships were significant for all species and zones (Fig. 2.2). With the exception of white spruce, linear models show that the amount of variability explained by the height and diameter relationship tended to decrease with increasing elevation, suggesting a shift in growth form across treeline. For all species, the pattern of taller and upright trees were observed in the forest zone, compared to the transition zone (i.e., largest slopes from linear models were observed in the forest zone). Visually comparing the slopes within species, balsam fir showed the largest difference between the forest and transition zones with larch showing the most similar slopes. This result suggests that growth plasticity may be most pronounced in balsam fir, while larch shows a similar growth form among zones.

Age structure and establishment

The number of seedlings varied substantially across species and zones. Larch had the highest density of seedlings in the forest zone (8750 seedlings/ha) while black spruce was the only species to produce seedlings in the transition zone (1333 seedlings/ha)(Fig. 2.3). Of all the seedlings reported, only larch was observed to be reproducing sexually via seed, while balsam fir and black spruce seedlings regeneration was from layering stems.

Sapling density increased across treeline, with the exception of larch that lacked saplings in the transition zone. Black spruce had an order of magnitude higher increase in the number of saplings per tree in the transition zone (1204.0 stems/ha), followed by white spruce (95.1 stems/ha) and balsam fir (6.0 stems/ha) (Table 2.3). The median age of balsam fir saplings was significantly older in the transition zone (71.5 years) compared to the forest zone (11.0 years)(Table 2.3). All of tree sampled (n=367), the only six tree were dead giving a mortality rate of 2.0%. For trees, age class distributions were significantly different in balsam fir and larch between the forest zone and the transition zone (Table 2.4A). Based on median ages, all tree species were older in the transition zone (85.0 years) compared to the forest zone (70.5 years) and while not significant, trees in the krummholz zone (99 years) were older than those in the transition zone (Table 2.4B). Based on the oldest five trees per zone, establishment date of balsam fir, though non-significant, showed the transition zone (1888) established before the forest zone (1905) and the krummholz zone (1907). White and black spruce in the forest zone (1826 and 1796, respectively) established before the transition zone (1885 and 1883, respectively) and for black spruce, the krummholz zone (1753) established before the transition zone (Table 2.4C). Establishment dates among species show an interesting pattern of black and white spruce establishing before larch, with balsam fir being the most recent colonist (Fig. 2.4).

Density reconstructions

Balsam fir and larch reached 50 stems per hectare around 1930 in the forest zone and the transition zone, while neither species has reached 50 stems per hectare in the krummholz zone (Fig. 2.5). Larch shows infilling of the transition zone occurring more gradually than the forest zone (i.e., lower slope). In the forest zone, white spruce reached 50 stems per hectare around 1850, while the transition zone and the krummholz zone remain below this value. Black spruce in the forest zone reached 50 stems per hectare around 1820 with increasing rates of infilling in the early 1900s, while densities in the transition zone and the krummholz zone remained below 50 stems per hectare with little change in the transition zone since the early 1900s. Comparing all species, the forest zone reached 50 stems per hectare around 1800, the transition zone around 1890 and the krummholz zone remains below this value (Fig. 2.6). Rates of infilling were similar in the forest zone and the transition zone when all species were combined.

Recruitment and climate

For the forest zone, age structure models were significant for all species, while only larch and black spruce were significant for the transition zone and black spruce significant for the krummholz zone (Fig. 2.7). Significant static age structure models in the forest zone suggest that all species are exhibiting the expected patterns of establishment and mortality, with no obvious deviations. In the transition zone, balsam fir ages were over-represented in certain decadal frequencies that contributed to a non-significant age structure model. Age structure models for white spruce in the transition zone and balsam fir in the krummholz zone were likely non-significant due to small sample sizes.

Mean summer temperatures from the instrumental climate record from Goose Bay (Labrador), were strongly correlated with the CRU-T3 reconstructed climate data ($r=0.826$, $P=0.022$), justifying the use of the reconstructed data for subsequent analyses. For the period of 1901 to 2009, recruitment residuals show high variability in correlations to mean summer temperature in both direction and significance, with only significant correlations using residuals from significant age structure models reported here (Table 2.5). Balsam fir, larch and black spruce recruitment in the forest zone was positively correlated with mean summer temperature, with white spruce showing a negative correlation. In the transition zone, black spruce recruitment was positively correlated to mean summer temperature, while larch recruitment was negatively correlated. Positive correlations to mean summer temperature are interpreted as species having more successful recruitment in warmer summers while negative correlations suggest more successful recruitment in cooler summers.

With the exception of white spruce, all species in the forest zone had higher recruitment that coincides with recent increases in mean summer temperature observed over the past 30 years, and was most pronounced in larch (Fig. 2.8). Across the transition zone and the krummholz zone, the recruitment response was more variable. No one decadal window of forward means was best correlated with recruitment, suggesting that the effects of summer temperature on recruitment are species-specific and that these relationships change across treeline. Observed variability at treeline may be a result of the long-lived status of these tree species, where individuals can persist for many centuries; therefore 10 decades of recruitment data may be insufficient to track changes.

2.4 Discussion

Differences in how species respond to recent climate warming offers important insight into past and future change at treeline. This multispecies approach enables us to envision future treelines that reflect species-specific responses and changes associated with climate warming. With this research, we illustrate differences in growth form among species across treeline, with the more recently established larch having the least amount of variation in growth form. In using a life history approach, we were able to identify species-specific treeline response that may have been muted if examined together. Though we do not report an upward migration of trees, there is strong evidence to suggest that larch and black spruce are responding to recent climate warming as seen by strong correlations to mean summer temperatures. Our results show that past treeline advance is species-specific suggesting that climate warming over the past few decades may initiate a similar response and continue to be species-specific.

Growth form

This multispecies approach allows for discussion on the role of species-specific life history traits as a means of explaining growth form differences encountered at treeline. For all species, trees in the transition zone were more stunted than those in the forest zone but growth forms varied among species. Larch showed the least variable growth form, with trees being the most similar in growth form across treeline as evidenced by similarity of slopes from regression analyses between zones. From a species-traits perspective, this may be best explained by the flexibility of larch stems and their ability to tolerate more extreme conditions without stem damage or breaks (Sakai and Weiser 1973).

Another interesting pattern to emerge by looking at tree growth form is that, with the exception of white spruce, that was limited by sample size, the relationship between height and diameter appears less pronounced in the transition zone and the krummholz zone with less of the variability explained by height on diameter models, suggesting an enhanced influence of climate on growth form across treeline.

Age structure

We interpreted treeline to be advancing if the transition zone was younger than the forest zone. One of the main assumptions when using this approach is that age estimates represent the actual age of individuals and can be used as a proxy for establishment. Overall, we found that treeline did not appear to be advancing since the mean and median age was older in the transition zone and the krummholz zone compared to the forest zone for all species. In most cases, our data suggest that the transition zone or the krummholz zone established before the forest zone; however we believe this pattern reflects the persistence of trees in the transition zone, such that they have lower growth and turnover rates, than trees in the forest zone. Once established, survivorship of these individuals is very high as they are able to persist for centuries through layering.

Regeneration patterns, examined by density of saplings and seedlings, hold little evidence to support an advancing treeline. The number of saplings per tree was substantially higher in the transition zone for black spruce, less pronounced for white spruce and balsam fir, with no larch saplings observed. While this initially suggests enhanced regeneration, characteristic of an advancing treeline, the life history of these species suggests a different explanation. Many studies have identified increases in vegetative reproduction in northern, compared to southern, environments (e.g., Black and Bliss 1980, Szeicz and MacDonald 1995, Pereg and Payette 1998) with Laberge et al. (2000) showing that, for black spruce, the number of layers increases with patch age. Therefore, combining the observed sapling densities with expected reproductive strategies at treeline, we conclude that infilling is largely the result of stems layering rather than establishment from seed.

Reinforcing our hypothesis that layering is driving regeneration patterns for black spruce, white spruce and balsam fir, there was a pronounced underrepresentation of seedlings in the transition and the krummholz zones. Our classification of 'seedlings' is based on height and not origin (i.e., from seed or layering stems), and therefore, it is important to consider origin in the context of species response potential. In our plots, the only true seedlings arising from seed were larch in the forest zone. All of the seedlings from all other species presented here were the result of layering. Previous findings from this location show that trees are producing viable seed into the krummholz zone (Jameson 2012) and that when planted as seedlings or seeds, black and white spruce will establish and grow beyond current treeline and do not seem to be limited by seedbed (Munier et al. 2010, Wheeler et al. 2011). However, treeline advance or stasis may require a substantial quantity of seeds, typical of masting events (Danby and Hik 2007, Holtmeier 2009), a phenomenon that has not been observed at our study site between 2002 to 2010 (L. Hermanutz pers. comm. 2012).

Density reconstructions

Differences in reconstructed densities among species suggest that balsam fir and larch have more recently established treeline and have experienced higher levels of infilling than black and white spruce. Despite establishing in the forest 150-200 years ago, neither spruce species has reached 50 stems per hectare in the transition zone. Spruce species have been shown to be very persistent at treeline (Trant et al. 2011), which is further supported by low densities of spruce establishment in the transition zone with little infilling. An alternative explanation for the variation in reconstructed stand densities is that the turnover rates among species are different. However, we found very low levels of tree mortality across treeline (2%), which would suggest that no species exhibited substantially higher turnover rates.

Recruitment and climate

For all species but white spruce, age structure data in the forest zone were best described by negative exponential functions, which assume constant mortality rates and dynamics that are governed by regeneration, not mortality, and are usually characteristic of stands that reproduce asexually via layering (Legere and Payette 1981). For the forest zone, constant mortality rates (i.e., age independent) may be partially explained by small-scale disturbance that drives mortality patterns. Once specific conditions for establishment and recruitment are satisfied (e.g., mineral soil exposed following windthrow), mortality rates are low at 2% of trees sampled. Whereas in the transition zone, where the dominance of asexual reproduction is often assumed to result in constant mortality rates (e.g., Legere and Payette 1981), we found that power models, which represent age-dependent mortality rates, best describe the observed age structure. Age-dependent mortality rates in the transition zone may be the result of climate severity, which acts differentially on trees of different ages and sizes. For example, snow cover offers protection from ice abrasion, which is pervasive in the transition zone (e.g., Scott et al. 1993), resulting in disturbance thresholds as tree height exceeds winter snow depth.

Tree establishment in the forest zone appear to be positively related to climate for all species but white spruce, suggesting that climate change will likely result in the advance of treeline for balsam fir, larch and black spruce. For white spruce recruitment, the negative correlation to mean summer temperature suggests that observed climate warming may not yet be strong enough to promote white spruce regeneration (Payette 2007) or that white spruce may be more susceptible to summer moisture deficits that can manifest in warmer summers (Barber et al. 2000). Our results are supported by Payette (2007), who reported inland white spruce as showing a negative response to climate warming in northern Labrador, compared to coastal sites, which are showing a positive response. If future climatic conditions become favourable for white spruce, we expect that the other species will have already experienced a range expansion, making it more difficult for white spruce to advance, due to competition (Price and Kirkpatrick 2009).

Recruitment of black spruce has steadily increased over the past century with a gradual decrease over the past 30 years. Our results are similar to those of Mamet and Kershaw (2012) who report a gradual decrease of black spruce recruitment at treeline near Churchill, Manitoba. Also, while black spruce in northern Quebec has shown patterns of increase height over the past 20 years (Gamache and Payette 2004), there has not been an observed increase in recruitment (Dufour-Tremblay et al. 2012). While black spruce recruitment decreases, larch, and to a less extent balsam fir, show a pulse in recruitment over the past 30 years.

Across circumpolar treeline, there has been a recent surge in larch (*Larix* spp.) recruitment (Devi et al. 2008, MacDonald et al. 2008, Mamet and Kershaw 2012, Tremblay et al. 2012), a pattern that we observed in Labrador, perhaps to a lesser extent. The combination of high stem flexibility and the deciduous habit of larch, make it an ideal species to thrive through more winters in environments where stochastic icing events are expected to be more common (Sakai and Weiser 1973). Also, larch has an additional advantage over the conifer treeline species as shedding needles decreases the chance of experiencing winter drought (Berg and Chapin 1994).

2.4.1 CONCLUSION

The Mealy Mountains treeline is showing multifaceted dynamics with little evidence of upward treeline migration but is experiencing species-specific differences in establishment, infilling and sensitivity of recruitment to climate over the past century. Our results suggest a possible surge of recruitment and upward migration of larch, as it is the only species observed to have substantial seedling regeneration, climate-sensitive recruitment and physical characteristics well-suited for the predicted future climate. However, summer moisture deficits, which are likely to become more common with warmer summers (ACIA 2005), may limit the response anticipated from larch. Balsam fir, despite the relatively strong climate sensitive recruitment, was depauperate in regeneration from seed and stem fragility may limit tree height, which could ultimately detract from dispersal potential. We also expect black spruce to continue with gradual increases in density, and given its high persistence value, it may fare as well as larch in a warming climate. In conclusion, we expect treeline position and composition to change dramatically as temperatures continue to rise, with priority given to those species that are first to initiate a climate-warming advance and to those species, like black spruce and larch, that can tolerate increased environmental stochasticity.

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Table 2.1 Life history profile of dominant treeline species.

Species	**Soil conditions**	**Adult conditions**	**Seed/Wing size (mm)**	**Seedling conditions**	**Vegetative Reproduction**
Balsam fir	Variable	Shade tolerant	3-6/10-15	Very shade tolerant	Layering/Seed
Larch	Wet to moist organic, often nutrient poor	Shade intolerant	3/6	Warm, moist mineral or organic soil, shade intolerant	Layering uncommon/ Seed
White spruce	Well-drained	Shade tolerant	2-4/4-9	Mineral soil or shallow organic, full sun	Layering/Seed
Black spruce	Moist organic, wet	Moderately shade tolerant	2/2-4	Feather moss or mineral soil , shade tolerant	Layering/Seed

*Information from US Forest Service plant database: www.fs.fed.us/database/feis/plants/tree/

Table 2.2 Stand characteristics in the Mealy Mountains (Canada), separated by zone and species and includes data from living (n=361) and dead (n=6) trees.

Zone	**Area (ha)**	**Species**	**Density (stems/ha)**	**Mean Age (years) ± SE**	**Oldest tree (years)**
Forest	0.10	Balsam Fir	199	62.5 ± 5.5	130
		Larch	340	57.0 ± 5.2	140
		White spruce	256	118.2 ± 19.1	340
		Black spruce	1250	78.3 ± 3.4	280
Transition	0.10	Balsam fir	171	79.1 ± 3.0	130
		Larch	239	107.9 ± 8.8	250
		White spruce	27	138.8 ± 17.1	210
		Black spruce	91	101.0 ± 12.1	180
Krummholz	9.43	Balsam fir	3	80.3 ± 8.8	150
		Black spruce	6	144.0 ± 14.2	370

Table 2.3 Comparison of sapling age structure in the Mealy Mountains (Canada), shown by the change in density between the forest and transition zones and difference in median age between forest and transition zones using a Mann-Whitney test for significant differences. Note: Positive changes in sapling density correspond to more saplings in the transition zone, compared to the forest zone. Larch was excluded as no saplings were recorded in the transition zone.

Species	**Zone Comparison**	**Δ Sapling Density (stems/ha)**	**Median Age**
Balsam fir	Forest/Transition	6.0	**W=10, P<0.001^{T}**
White spruce	Forest/Transition	95.1	*Insufficient data*
Black spruce	Forest/Transition	1204.1	W=2395, P=0.367^{F}

^{F,T} Denotes zone with older median age
Bolded values are significant (P<0.05)

Table 2.4 Tree age structure in the Mealy Mountains (Canada), shown by: (A) age class distribution using a Kolmogorov-Smirnov test; (B) median age using a Mann-Whitney (M-W) test; and (C) establishment date using the five oldest individuals and a M-W test.

Species	Zone Comparison	A) Age Class Distribution	B) Median Age	C) Establishment Date
Balsam fir	Forest/Transition	**D=0.342, P=0.050**	**W=334, P=0.004^{T}**	W=5, P=0.130^{T}
	Transition/Krummholz	D=0.153, P=0.977	W=308, P=0.893^{K}	W=20, P=0.107^{T}
Larch	Forest/Transition	**D=0.518, P<0.001**	**W=184, P<0.001^{T}**	W=5, P=0.151^{T}
White spruce	Forest/Transition	D=0.588, P=0.138	W=26, P=0.209^{T}	W=22, P=0.056^{*F}
Black spruce	Forest/Transition	D=0.349, P=0.166	**W=506, P=0.034^{T}**	**W=25, P=0.012^{F}**
	Transition/Krummholz	D=0.334, P=0.324	W=123, P=0.173^{K}	**W=3, P=0.046^{K}**

^{F,T,K} Denotes zone with older median age or established earlier
Bolded values are significant (P<0.05)
* Moderately significant (P<0.1)

Table 2.5 Pearson correlation values between recruitment residuals in the Mealy Mountains (Canada), for tree species in forest and transition sites and reconstructed mean summer temperature data from 1901 to 2009 (CRU TS 3.1; University of East Anglia Climatic Research Unit 2008). The years in parenthesis correspond to the multi-decadal window of forward summer temperature means that best correlated to recruitment/survival residuals.

Species	**Forest**	**Transition**	**Krummholz**
Balsam fir	**0.783 (40 years)**	0.220 (10 years)^	**-0.743 (30 years)^**
Larch	**0.725 (10 years)**	**-0.647 (30 years)**	
White spruce	-0.651 (30 years)*	-0.649 (20 years)^*	
Black spruce	0.555 (20 years)*	**0.862 (40 years)**	-0.456 (40 years)

Bolded values are significant (*P*<0.05)
* Moderately significant (*P*<0.1)
^Model generating residuals was not significant

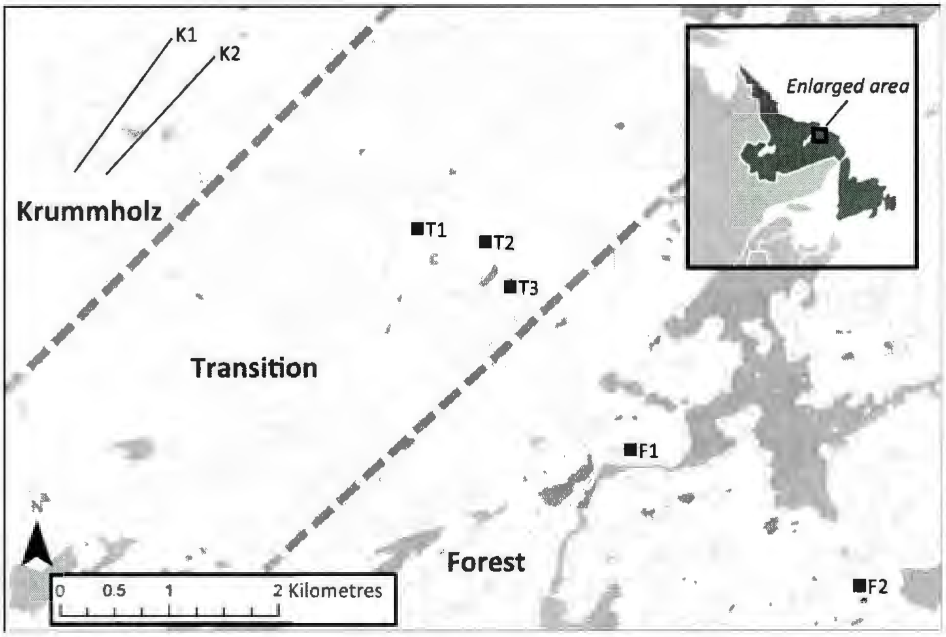


Fig. 2.1 Map of Eastern Canada with Newfoundland Labrador shaded in darker grey and location of field site in the Mealy Mountains, Labrador (N 53°36'6", W 58°49'0"; enlarged area). The enlarged area shows sites within the forest zone (F1 and F2), transition zone (T1 and T2) and transects within the krummholz zone (K1 and K2). Grey dashed lines approximate zone delineation. Bodies of water and contour lines at 20 m intervals are shown in grey.

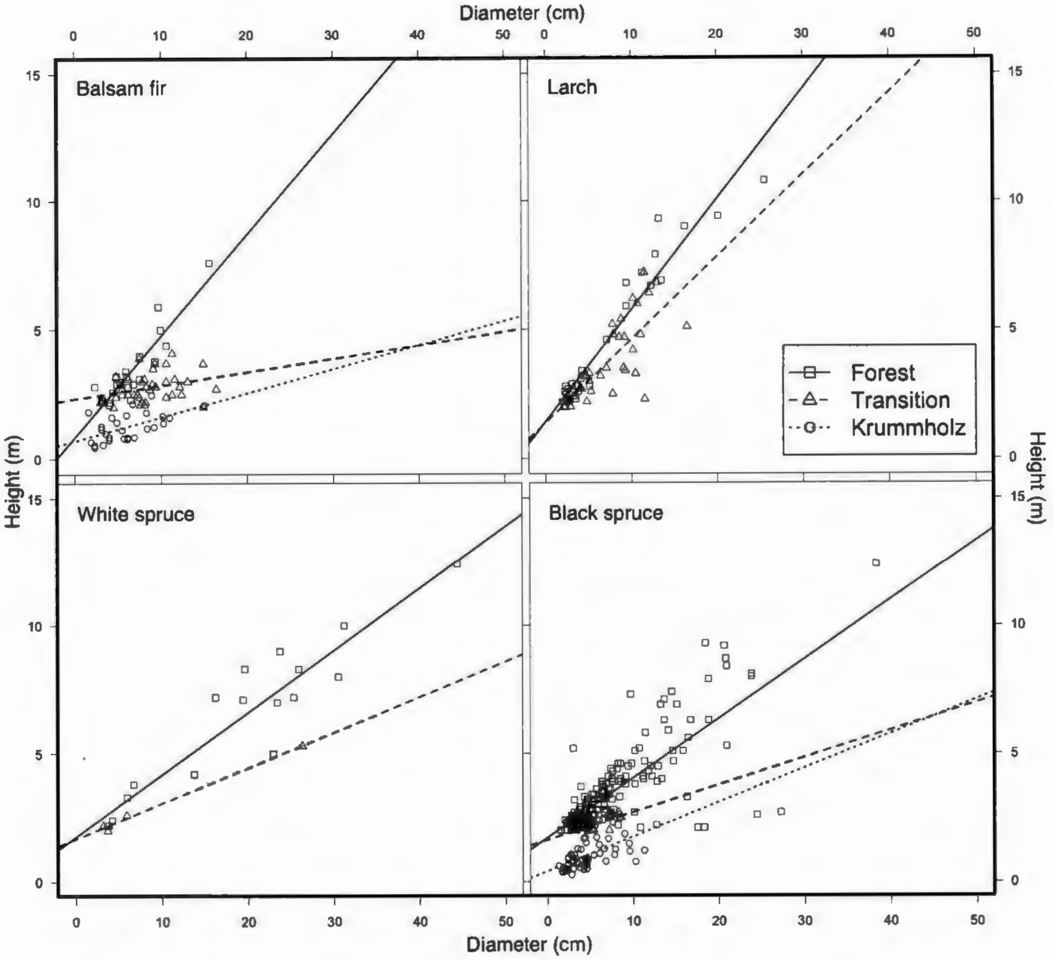


Fig. 2.2 Tree growth form relationship of height by diameter in the Mealy Mountains (Canada), from linear regression analyses for balsam fir: Adj $R^2_F=0.818$, $P<0.001$, Adj $R^2_T=0.064$, $P=0.068$, Adj $R^2_K=0.289$, $P=0.002$; larch: Adj $R^2_F=0.931$, $P<0.001$, Adj $R^2_T=0.552$, $P<0.001$; white spruce: Adj $R^2_F=0.868$, $P<0.001$, Adj $R^2_T=0.990$, $P=0.004$; and black spruce: Adj $R^2_F=0.591$, $P<0.001$, Adj $R^2_T=0.521$, $P=0.011$, Adj $R^2_K=0.326$, $P<0.001$. Subscripts F, T and K correspond to forest, transition and krummholz.

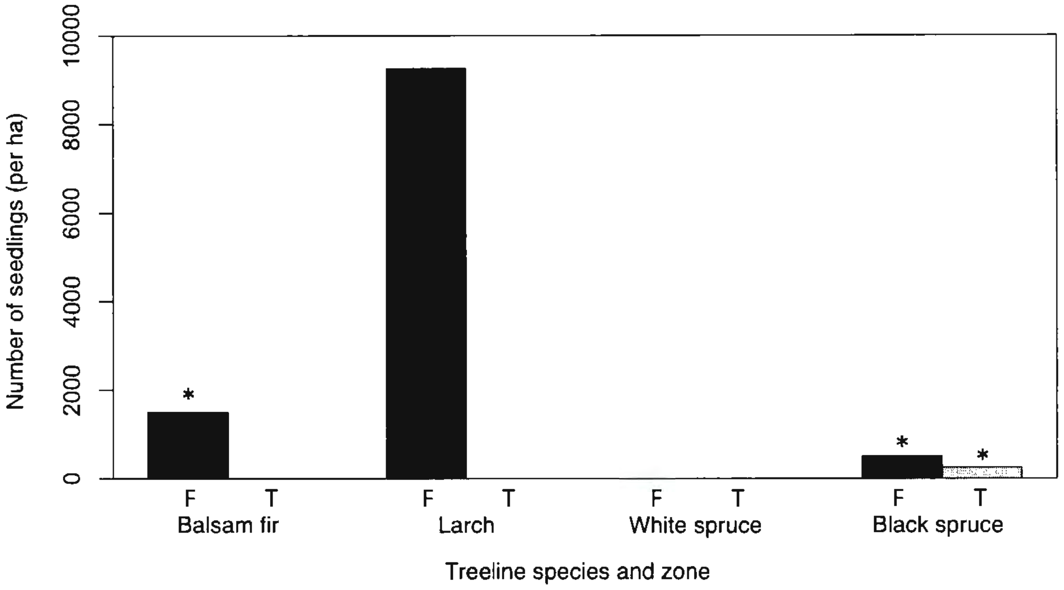


Fig. 2.3 Seedling densities per hectare in the Mealy Mountains (Canada), across zones, separated by species. Zone codes are: F=forest (dark grey) and T=transition (light grey). *Seedlings most likely from vegetative layering and not from seed.

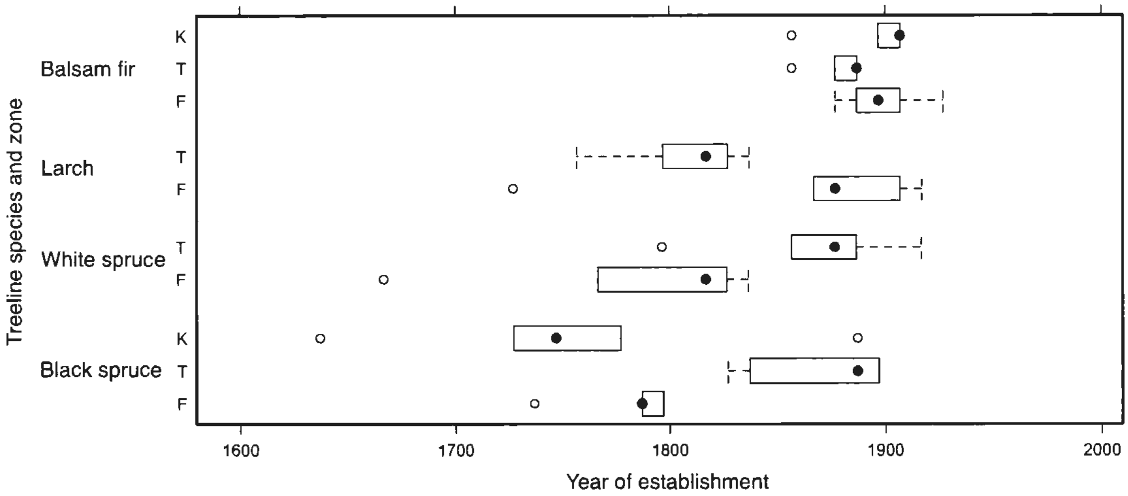
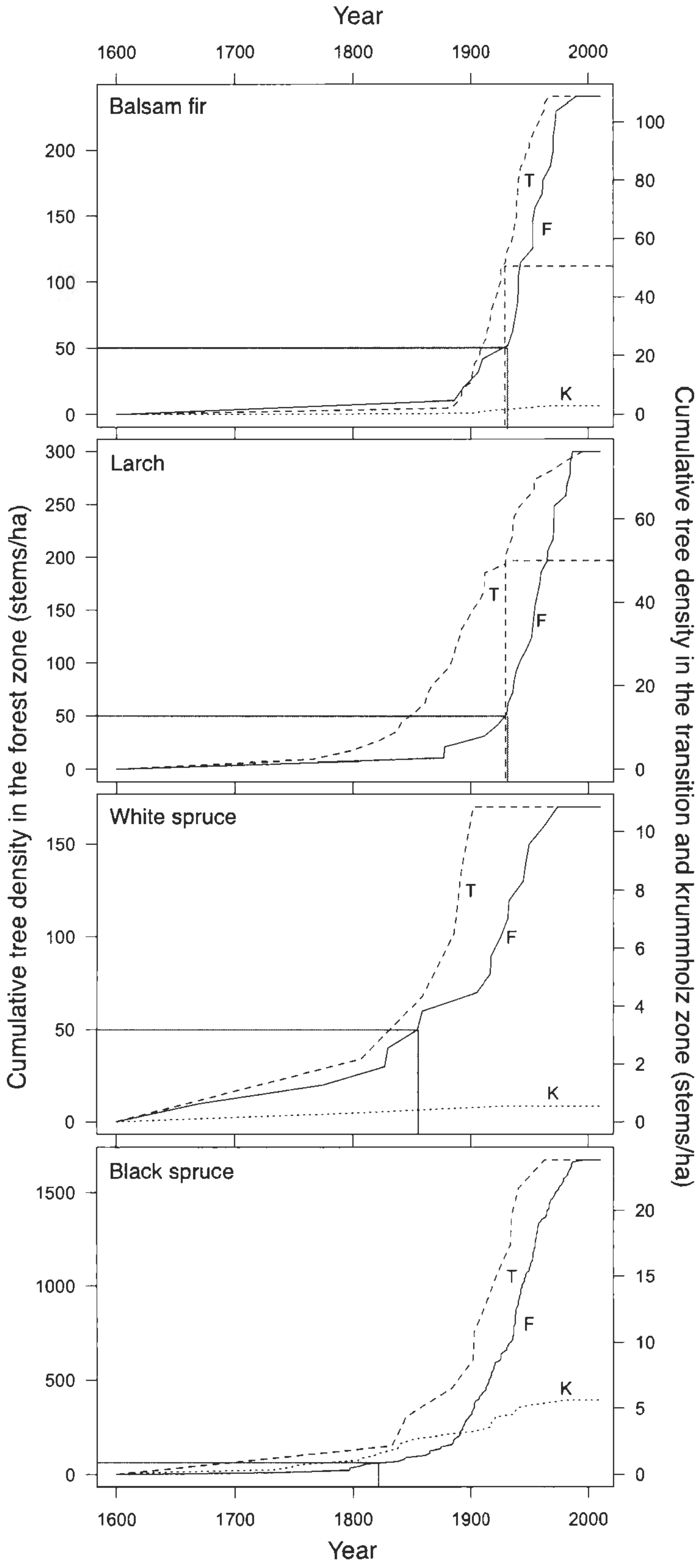


Fig. 2.4 Box and whisker plots showing establishment of trees in the Mealy Mountains (Canada), based on the establishment dates of the five oldest individuals by zone and species. Filled circles are median values and open circles are data points that are beyond 1.5 times the size of the box (3rd quartile to 1st quartile). Zone codes are: F=forest and T=transition and K=krummholz.



Year
1600
1700
1800
1900
2000
Balsam fir
Larch
White spruce
Black spruce
T
F
K
Cumulative tree density in the forest zone (stems/ha)
Cumulative tree density in the transition and krummholz zone (stems/ha)
Year

Fig. 2.5 Reconstructed densities of living and dead trees in the Mealy Mountains (Canada), for the forest (F: solid lines), transition zones (T: large dashed lines) and krummholz zones (K: small dashed lines), separated by species. The year in which 50 stems per hectare was reached is indicated by red lines (solid line for the forest zone and a large dashed line for the transition zone). Note: scale on y-axis changes between species.

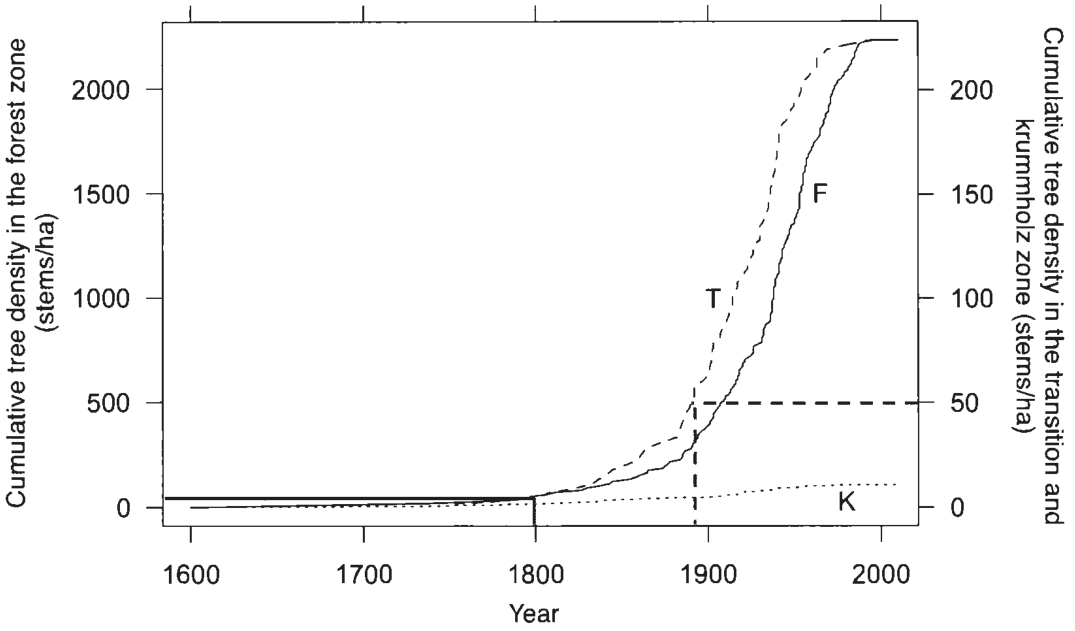
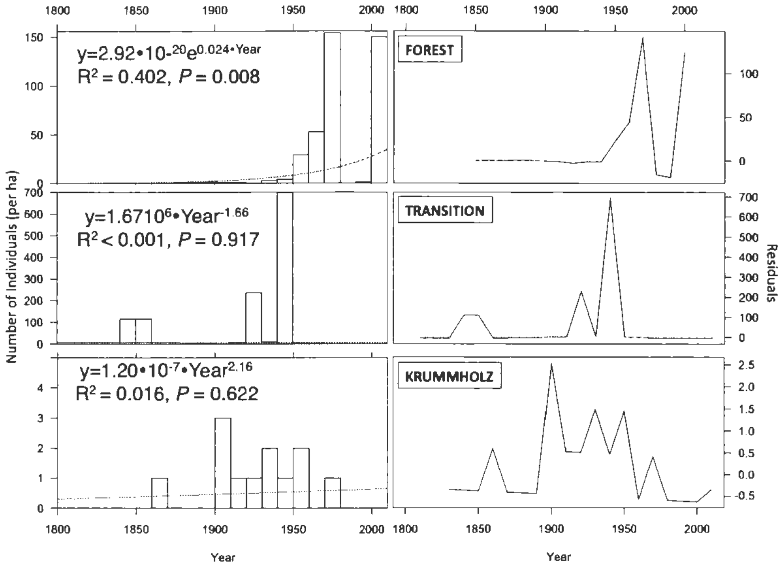
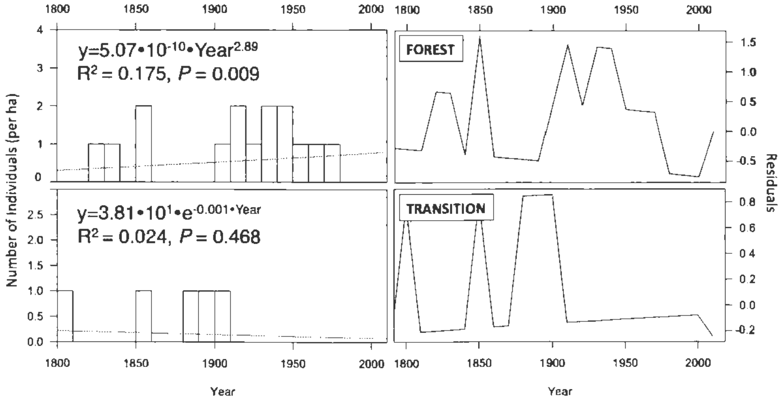


Fig. 2.6 Reconstructed densities of living and dead trees in the Mealy Mountains (Canada), for the forest (F: solid line), transition zones (T: large dashed line) and krummholz zones (K: fine dashed lines), combined for all species. The year in which the stand reached 50 stems per hectare, is indicated by red lines (solid line for the forest zone and a large dashed line for the transition zone).

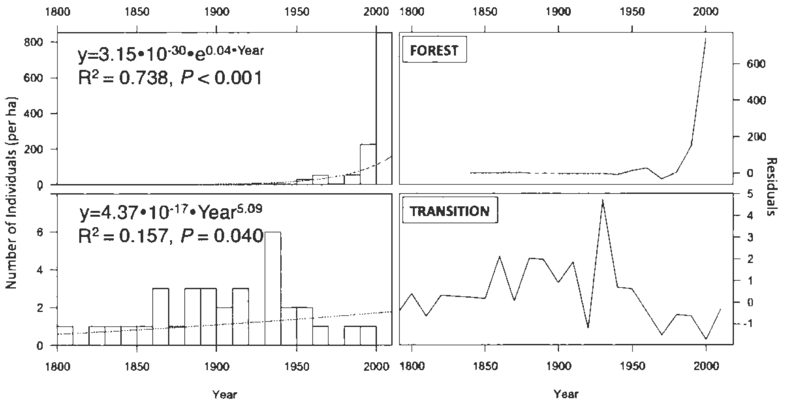
Balsam fir



White spruce



Larch



Black spruce

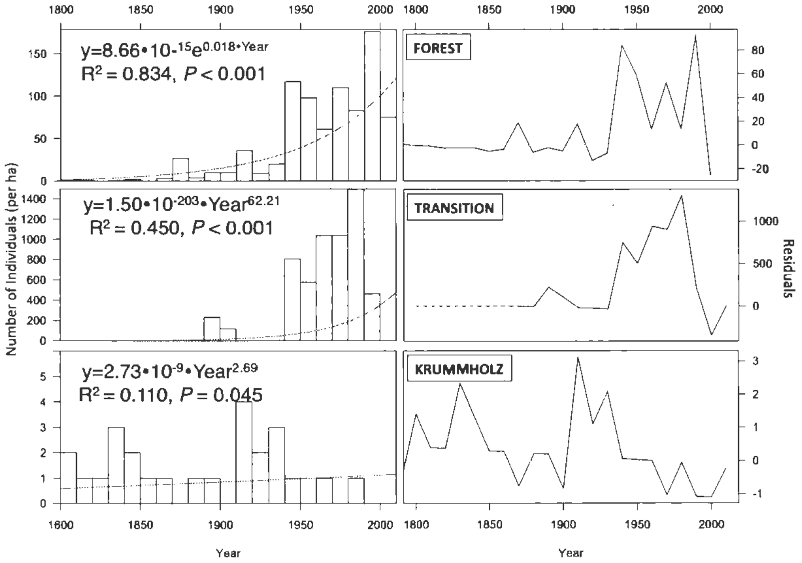


Fig. 2.7 Age structure and residual plots for treeline in the Mealy Mountains (Canada), grouped into 10-year age classes and separated by zone. Red lines represent either negative exponential or power models, depending on which model had the highest R^2 value.

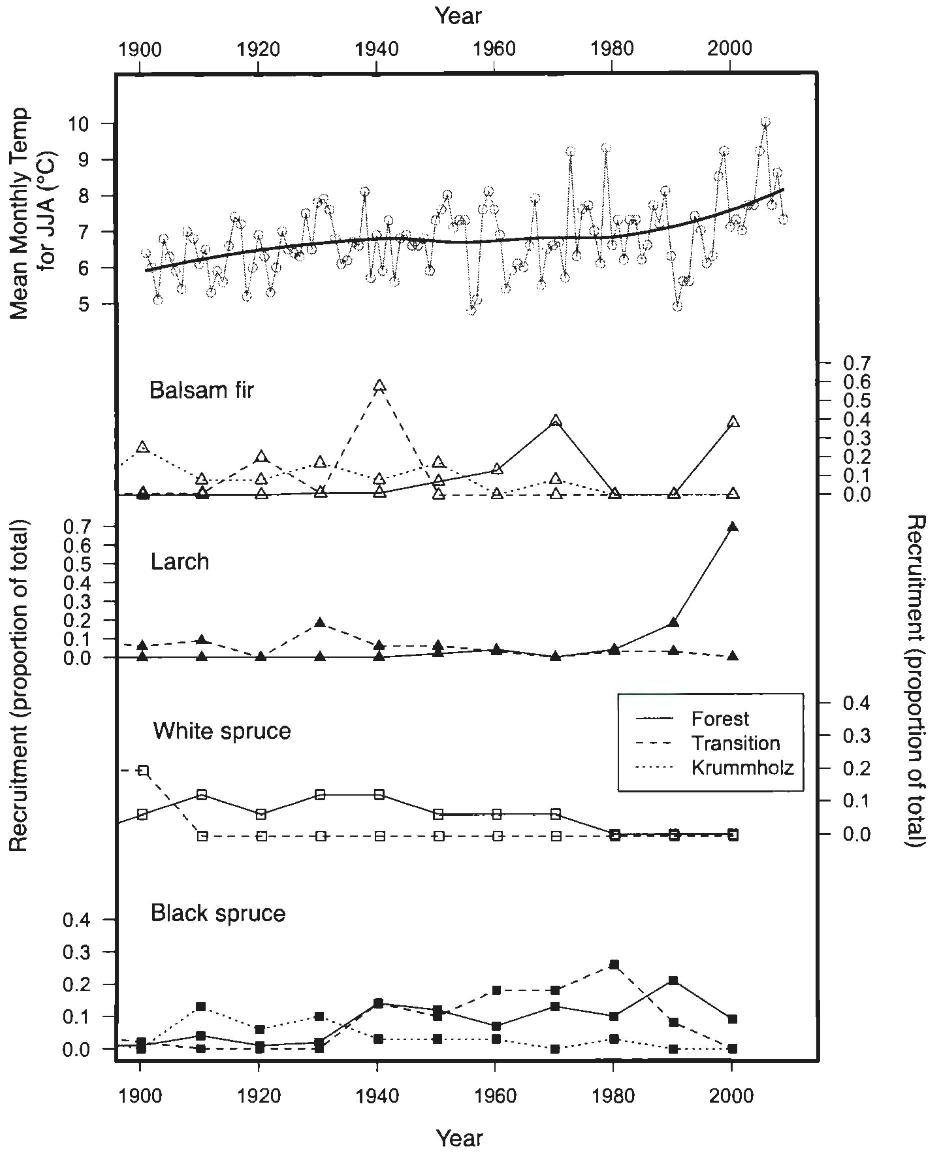


Fig. 2.8 Relationship between treeline dynamics and mean summer (June, July and August) temperatures (CRU-T3 data) in the Mealy Mountains (Canada). For temperature data, the black line represents locally weighted scatterplot smoothing line (LOESS). For each treeline species, the portion of individuals that established per decade is shown for forest (solid line), transition (large dashed line) and krummholz zones (fine dashed line).

Chapter 3: Persistence at treeline: old trees as opportunists

Abstract

While old trees have long been of interest, the significance of old trees at northern treelines has been overlooked with respect to their role in responding to climate change. Long-lived black spruce (*Picea mariana*) at treeline in Labrador show a synchronous response in radial growth to recent climate warming. The ability of individuals to persist with suppressed radial growth rates during adverse growing conditions may have significant implications on the rate at which these trees are able to respond when conditions become favorable.

Despite the recent attention given to treeline advance resulting from climate warming (e.g. Harsch et al. 2009) the significance of old trees at treeline as the 'frontline' of expansion has not been adequately explored. While the persistence of long-lived trees has been reported from other climatically harsh environments (e.g. Larson et al. 2000), northern treelines (e.g. Vallee and Payette 2004, Asselin and Payette 2006) and some altitudinal treelines (LaMarche Jr and Mooney 1972), the importance of a persistence-mediated response to climate change deserves more attention. Long-lived clonal patches at treeline have been used to reconstruct post-glacial migration patterns (e.g. Kullman 2006) but discussion on the importance of ramets has been largely overlooked. In North America, black spruce [*Picea mariana* (Mill.) Britton, Sterns & Poggenb.] are widely distributed and are the dominant species forming these clonal patches (Pereg and Payette 1998), making them ideal for exploring ideas of persistence.

On July 19, 2007, a cone-bearing, shrub-like krummholz black spruce was sampled at ground-level using an increment borer in the Mealy Mountains, Labrador (53°36'N, 58°51'W; Fig. 3.1A). This black spruce found at 748 m elevation (~130 m above the forest limit; *sensu* Scott 1995), was sampled as part of a larger survey effort exploring patterns of age structure and reproductive potential at the alpine treeline ecotone (for details see ppsarctic.nina.no). Using a Velmex® micrometre (precision 0.005 mm) under a binocular microscope at 40X to count annual rings, it was determined the individual's oldest living stem was at least 370 years old. According to the CanDendro database (www.mta.ca/candendro) and a literature review, this is the oldest known living black spruce in Atlantic Canada and at alpine treeline across Canada. The black spruce krummholz measured 4.8 m by 3.1 m with an average stem height of 0.7 m. The tallest of the 14 clonal stems was 1.85 m with a diameter of <3 cm at breast height with no evidence of older dead stems. Three stems produced mature pollen and seed cones in the 2007 and 2008 growing seasons, and although viability was not tested for this individual, viable black spruce pollen and seeds were documented within a distance of 585 m (Jameson 2012).

The mechanisms by which treelines are able to respond to climate warming may depend on how long individual trees can persist once established, commonly in suboptimal conditions. Climatic conditions directly affect all stages of sexual reproduction in boreal tree species (Zasada et al. 1992, Farmer 1996) and can limit viable seed production and the successful recruitment of new individuals, particularly toward the edge of their respective ranges (e.g. Elliott 1979, Henttonen et al. 1986, Sirois 2000). Growing degree day requirements are less for vegetative growth than reproductive growth suggesting reproductive growth does not occur when radial growth is suppressed (Woodward 1987). In the long term, the ability of black spruce to grow and regenerate vegetatively allows long-lived individuals to endure unfavorable climates and resume sexual reproduction under ameliorating conditions.

Krummholz are the dominant tree form in many treelines. Resulting from winter wind desiccation and ice-crystal abrasion, these low-lying trees rarely grow higher than the average snow depth (Scott 1995). Nurse-effects by deciduous shrubs, microtopography, and glacial erratics may play a significant role in establishment and persistence of krummholz in otherwise inhospitable environments by protection from increased snow drifting and through shelter in snow-free periods (see Fig. 3.1: Daley 2009, Cranston 2010). With growing conditions at these higher elevations often being sub-optimal, the amount of radial annual wood put down by krummholz is minimal compared to forest trees of the same species (e.g. mean ring size for forest trees in the study area is 0.45 mm compared to 0.17 mm for krummholz).

Despite the old age and harsh growing conditions, the black spruce reported here has exhibited a dramatic increase in annual radial growth, as evidenced in the basal sample, that matches the observed pattern from recent climate records (Fig. 3.2A: Bell et al. 2008). The greater part of the last century shows larger ring width values than the series mean that continue to increase from the more recent Little Ice Age minima (Fig. 3.2: around years 1770 and 1850) towards present day. The running mean (Fig. 3.2A: grey line) uses a 50-year window in order to visualize this pattern, excluding some of the interannual variation. At a larger scale, a chronology for 22 radii from 20 stems of black spruce krummholz in the Mealy Mountains shows similar patterns of significant suppression of radial growth for the majority of the available record with dramatic recent increases that correspond to increases in growing season temperature (Fig. 3.2B: Bell et al. 2008). This chronology was detrended using a modified negative exponential model that removes biological growth trends thus presenting standardized ring width indices.

These old krummholz may persist for centuries until conditions become more favorable, at which time they may increase radial growth rates and initiate sexual reproduction (Jameson 2012). Older trees are likely to have greater below-ground biomass and access to resources essential to these processes. Once viable seeds are produced, expansion of treeline could occur rapidly as strong winds disperse seeds from the 'frontline' of old tree islands. Light black spruce seeds, disseminated from semi-serotinous cones throughout the year, have the potential to travel great distances atop hard snow and ice layers during the winter. In slow-growing environments such as treeline, the advantage may be given to those individuals who have been waiting.

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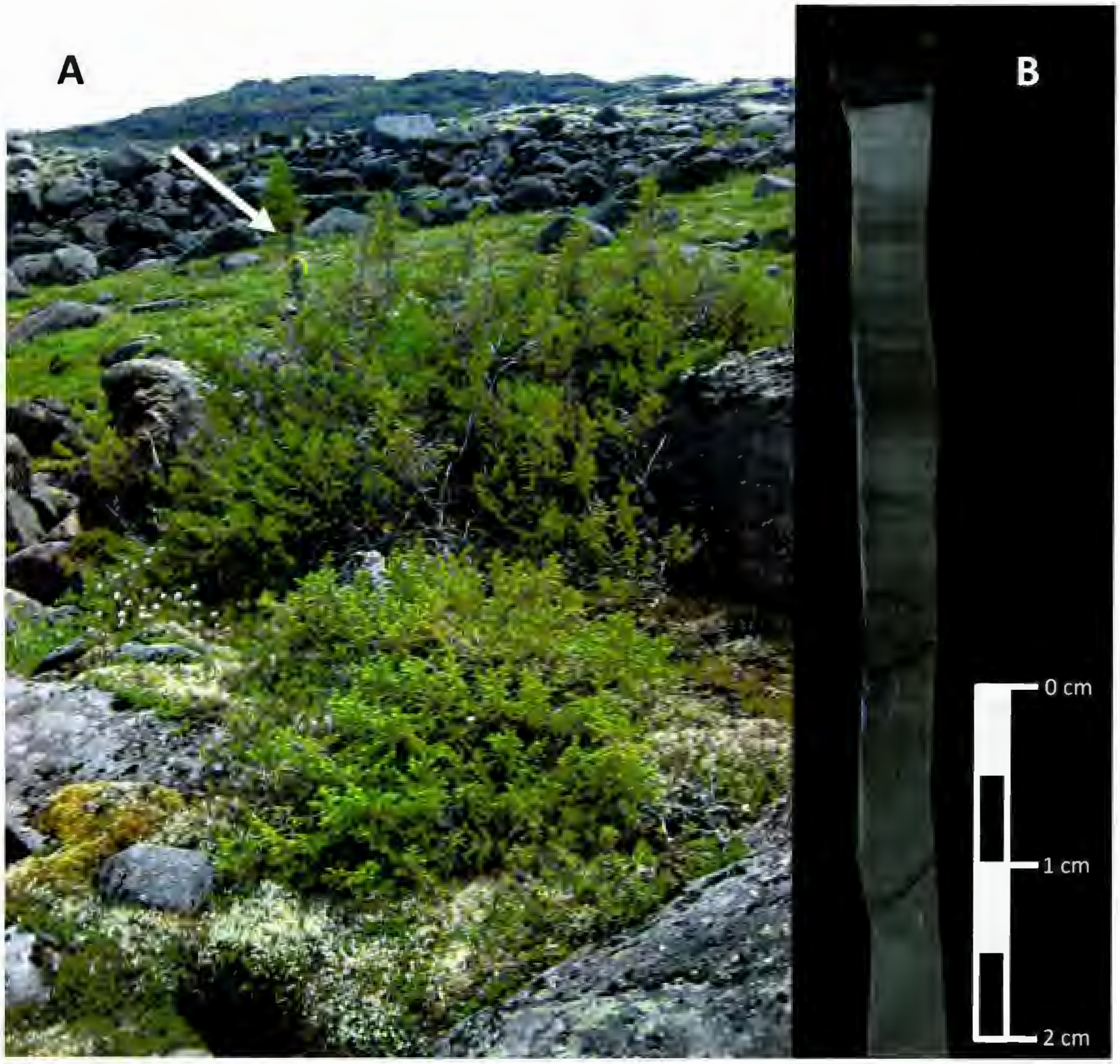

Fig. 3.1 Black spruce (*P. mariana*) krummholz at 748 m a.s.l., near the species limit in the Mealy Mountains (Canada), with A) arrow indicating tallest leader of krummholz (1.85 m) and B) basal increment core used for age determination.

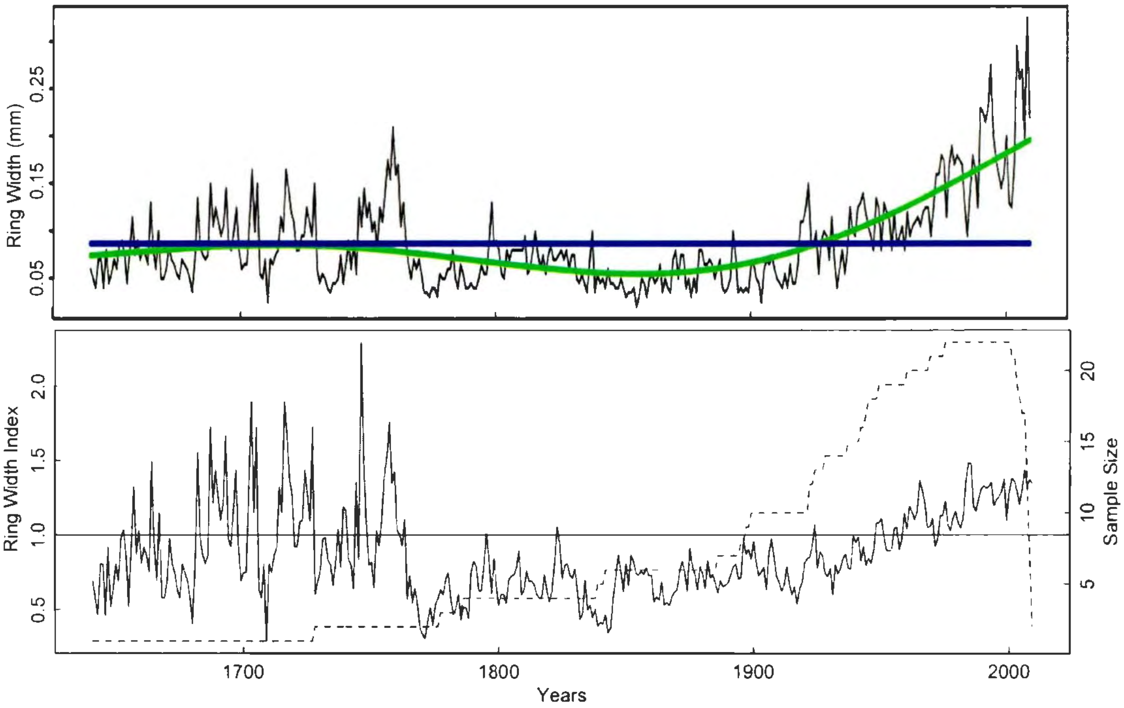

Fig. 3.2 A) Raw ring widths for the old black spruce krummholz individual with overall mean (blue line) and running mean with a 50-year window (green line) and B) Standardized Ring Width Index chronology of black spruce krummholz for the Mealy Mountains (Canada), with the average Ring Width Index of 1 (black line) and sample size (broken line).

Chapter 4: Is small-scale disturbance important at treeline?

Abstract

Disturbance in the boreal forest plays a significant role in driving forest dynamics. At the forest-tundra ecotone, or 'treeline', the role of disturbance is less pronounced and poorly understood. Using a multispecies approach, we investigated the extent and role of disturbance as a mechanism for understanding treeline change, which is expected with climate change. Combining forest composition and dendrochronological data, disturbance events were quantified across treeline to address their contributions to regeneration dynamics and tree mortality. Lastly, the importance of forest gaps was investigated by examining the role of windthrow in promoting coniferous tree regeneration. Porcupines (*Erethizon dorsatum*) herbivory was most pronounced at intermediate stand densities on larch (*Larix laricina*) and black spruce (*Picea mariana*), but resulted in limited tree mortality. Reconstructed forest insect dynamics for spruce budworm (*Choristoneura fumiferana*) and larch sawfly (*Pristiphora erichsonii*) across treeline showed lower magnitude outbreaks compared to nearby contiguous boreal forests but still an ecological meaningful cause of tree mortality. For all tree species, the magnitude of outbreaks across treeline was best explained by tree density and not the environmental stress gradient. Gaps caused by windthrow did not result in significantly different canopy structure but these gaps had significantly more seedlings than randomly chosen

sites. Overall, tree species were differentially affected by disturbance with larch (*Larix laricina*) and black spruce (*Picea mariana*) showing higher levels of disturbance and recruitment than balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*). In contrast to much of the boreal forest, disturbance at treeline includes more infrequent and lower magnitude events that are important for creating conditions required for forest regeneration, especially seedling recruitment rather than layering. With disturbance closely linked to climate, we expect that disturbance at treeline will become more frequent and of greater magnitude under the influence of predicted climate change, similar to the closed canopy eastern boreal forest (Roberts et al. 2006), potentially facilitating the upward migration of larch and black spruce.

4.1 Introduction

Forest dynamics are driven by disturbance through the mobilization of sequestered resources and alteration of the physical environment (Pickett and White 1985). In turn, this disrupts population, community or ecosystem structure, providing opportunity for new individuals to establish. Disturbance plays a key ecological role throughout much of the boreal forest though the importance of disturbance at northern range edges is poorly understood (Scott 1995). In the forest-tundra ecotone, or 'treeline', conditions are often suboptimal for tree growth and reproduction (Paulsen et al. 2000), making trees more susceptible to shifts in climate and disturbance (Körner 1998, Malanson et al. 2011). The scale of disturbance events, referring to the frequency and magnitude (c.f. Pickett and White 1985), are increasing with climate warming because many types of disturbance have a significant climate forcing mechanism within their structure (Turner 2010). Given the profound influence disturbance events have on forest dynamics, understanding past and present conditions is critical for anticipating future change (Dale et al. 2001).

Treeline position is strongly influenced by disturbance. Ecological control of treeline position has been seen through herbivory by mammals (Cairns and Moen 2004, Hofgaard et al. 2009, Herrero et al. 2011), outbreak insects (Girardin et al. 2005) and non-outbreak insects (Dulamsuren et al. 2008). Disturbance may be a prerequisite for treeline to advance, as is the case with fire (Hattenschwiler and Korner 1995, Brown and Johnstone 2012), but can also cause retrogression (Payette 1992). Gap-forming disturbances that arise from windthrow or winter damage may also be a prerequisite for treelines to advance (Veblen et al. 1981, Cullen et al. 2001). Despite being one of the dominant disturbance factors of the boreal forest (Fleming 2000), little is known about insect outbreak cycles at treeline (Eckstein et al. 1991, Sonia et al. 2011) and how climate warming will affect these patterns (Bonan 2008).

In systems where large-scale disturbances are not present or infrequent, the role of small-scale disturbance becomes increasingly important (Lorimer 1989, Romme et al. 1998). The death of single trees, or an isolated patch, has been documented to release sufficient resources to drive gap-dynamics, such as increased light availability and modification of microsite conditions (McCarthy 2001). Thus, small-scale disturbance can arise naturally, from age-related tree mortality or from a disturbance event that either kills or compromises the tree's health, ultimately resulting in the formation of a forest gap (Kneeshaw and Bergeron 1998). In forests with low tree density, such as treeline, disturbance functions to enhance seedbed quality (Brown and Johnstone 2012) and reduce competition for seedlings (Johnstone and Chapin III 2006). Since much of the boreal forest is driven by large-scale disturbance patterns, such as fire, little attention has been given to the role of small-scale disturbance in stand dynamics (McCarthy 2001), especially from the perspective of climate induced range change.

In the North American boreal forest, fire, herbivory and associated pathogens constitute the natural disturbance regime. In the eastern Canadian boreal forest, the dominant herbivores are eastern spruce budworm [*Choristoneura fumiferana* (Clem.)], larch sawfly [*Pristiphora erichsonii* (Hartig)], eastern hemlock looper [*Lambdina fiscellaria* (Gueneé)] and porcupine (*Erethizon dorsatum* L.). Distinguishing between epidemic and endemic levels is important for understanding detection and impact of insect-related disturbance. Endemic refers to insects that occur at low-densities and seldom cause significant damage to plants, while epidemic refers to insects that are exhibiting outbreak dynamics, resulting in significant plant damage and commonly mortality (Wallner 1987). Porcupine feeding damage varies with stand composition (Tenneson and Oring 1985). In the Mealy Mountains of central Labrador, high levels of precipitation limit fire (Foster 1983), while pathogens do not appear to cause significant tree mortality (Trindade

2009). We therefore hypothesize that insect herbivores play a key role in driving treeline dynamics, along with other small-scale disturbances, such as windthrow.

Understanding how forest structure and density influence patterns of disturbance is important for predicting climate-influenced changes to these patterns. Introduced by Root (1973), the Resource Concentration Hypothesis (RCH) predicts that herbivores will preferentially select areas of higher resource density or those in nearly pure stands. This hypothesis can be extended to treelines where the density of host-species decreases towards the range edge thus predicting that herbivore density would also decrease towards the range edge. At treeline, where climatic gradients may limit tree growth (Paulsen et al. 2000, Ettinger et al. 2011), we expect that the climatic conditions that limit the density of host trees may also limit the diversity and abundance of herbivores, strengthening the observation that would support the RCH.

At a multispecies treeline in the Mealy Mountains, Labrador (Canada), our main objectives are: (1) to determine the frequency, magnitude and host species preference of porcupine herbivory across treeline; (2) using a novel approach, reconstruct insect outbreaks across the treeline ecotone and test the RCH that herbivory densities will decrease with stand density; (3) examine the importance of windthrow as a process driving forest regeneration; and (4) assess the implications of disturbance on past and future treeline dynamics. Our overall hypothesis is that the scale of disturbance will decrease across treeline, responding to a decrease in tree density and increased abiotic stress. From a multispecies perspective, we expect different regeneration dynamics based on the feeding preference of herbivore species, which may interact with climate change and the host species response potential to climate warming. Ultimately, this interaction between climate change and disturbance will determine future treeline structure and function.

4.2 Materials and Methods

4.2.1 STUDY AREA

We conducted this study in the north-central Mealy Mountains, Labrador, within the boundary of the proposed (Akamiuapishk^{u}) Mealy Mountains National Park Reserve (N 53°36'6", W 58°49'0"; Fig. 4.1). The study area was selected because of the presence of a multispecies treeline that occurs along a relatively compressed topographic gradient of approximately 600 m a.s.l. into a southern outlier of high subarctic tundra (Meades 1989). The Mealy Mountains continue to have a tradition of seasonal land-use by Labrador Innu with the majority of sustenance resource extraction being restricted to areas lower in elevation, such that the study area was free of anthropogenic impacts (P. Armitage pers. comm. 2012). Therefore, with a paucity of human influence, differences in forest structure between zones can be attributed to climate, site characteristics and ecological processes, such as disturbance.

Based on growth form and structural attributes along an elevation gradient, treeline was classified into three zones: 1) 'forest zone' is comprised of trees with predominantly erect growth forms and has the most closed canopy at treeline; 2) 'transition zone' is composed of trees with both erect and prostrate, or 'krummholz' growth forms growth forms and represents the tree limit (height>2.0 m) and; 3) 'krummholz zone' is dominated by shrub species with occasional trees with krummholz growth forms. Beyond the krummholz zone, the 'tundra zone' is treeless and is dominated by shrubs such as arctic dwarf birch (*Betula glandulosa* Michx.) and other alpine tundra plants. The Mealy Mountains treeline is composed of four co-dominant tree species: balsam fir (*Abies balsamea*), larch (*Larix laricina*), black spruce (*Picea mariana*) and white spruce (*Picea glauca*)(Table 2.1). The forest zone occurs from approximately 500 to 575 m a.s.l., the transition zone from 575 to 680 m a.s.l. and the krummholz zone from 680 m a.s.l. to the species limit measured to be 690 m a.s.l. for larch, 795 m a.s.l. for balsam fir, 805 m a.s.l. for black spruce and 855 m a.s.l. for white spruce. The majority of soils across treeline are slightly acidic loamy sand (Sutton 2008).

Growing degree days (GDD; >5°C) were calculated from local climate data collected using Campbell Scientific Inc® automated climate stations in the transition zone (732.7 GDD from 2002 to 2006; 570 m a.s.l.), krummholz zone (719.9 GDD from 2006 to 2008; 600 m a.s.l.) and tundra zone (454.8 GDD from 2002 to 2008; 995 m a.s.l.). Average monthly temperature lapse rates between the tundra and transition zones from 2004 and 2009 was -0.51°C/100 m (Chan 2012). Over the 20th century, Central Labrador has not experienced significant warming (Banfield and Jacobs 2008) but from 2000 to 2010, summer temperatures have increased by almost 1°C (Environment Canada 2011).

The main forest insect herbivores in this region are spruce budworm and larch sawfly. Eastern hemlock looper has exhibited outbreak dynamics in more low-lying regions of central Labrador in recent years, but there are no records of it occurring at our study site. A comparison of host-preferences and life histories is summarized in Table 4.1.

4.2.2 FIELD METHODS

At treeline, all tree species were sampled in 2007 and 2008 at five sites (two forest and three transition) and along two transects through a higher-elevation krummholz area (Fig. 4.1). Locations of these sites and transects were selected based on tree growth forms and representative stand attributes (e.g., forest sites were established in areas with the greatest extent of canopy closure and krummholz transects were situated in areas dominated by trees exhibiting prostrate growth forms. For each site and belt transect, forest structure including visible signs of disturbance, notably debarking by porcupines, and stem density was measured using fixed-area plots with dimensions that varied between zones (Table 4.3). At each site with trees greater than 2 m, hemispherical photography (Nikkor® 10-5 mm fisheye lens) was used to determine canopy cover and effective leaf area index (L_e) approximations. Past dendrochronology research in the area by Trindade (2009) found a single occurrence of fire scars in living and dead trees which was thought to be from lightening. To confirm this assumption of no recent history of large-scale fires at our study site, we excavated soil profiles (forest: n=20, transition: n=40) to look for evidence of charcoal (e.g., Talon et al. 2005)

To reconstruct past insect outbreaks fusing dendrochronology, all tree species were sampled using an increment borer (4.35 mm or 5.1 mm) with two cores taken from every tree to improve the strength of the radial growth signal. Trees growing vertically on flat ground were cored at perpendicular angles while leaning trees or those growing on slopes, had cores sampled parallel to each other from opposite sides. Trees with erect growth forms were sampled at breast height (1.4 m above ground-level) to reduce irregular growth that is common around root buttresses. When tree forms were prostrate (i.e. krummholz), cores were taken where stem diameter was largest. Cores were air dried in straws until processed in the laboratory. Samples from dead trees (n=156) collected during previous study at the same location were obtained to examine tree mortality (Trindade 2009). The species and location of these dead trees represent the entire study area, as exact sample locations were unknown, so differentiating mortality rates between the forest zone and the transitions zone was not possible.

The importance of windthrow as a disturbance event promoting regeneration was determined by opportunistically sampling downed trees in the forest and transition zones. For each downed tree, circular plots with a radius of 1 m (plot area=3.1 m^2) were established in the exposed mineral soil to survey tree seedlings and saplings. Randomly selected plots of 3.1 m^2 adjacent to the windthrow were also surveyed for seedlings and saplings. Hemispherical images were taken at each site to quantify gap attributes and canopy closure. For purposes of standardization, efforts were made to record hemispherical images on cloudless days.

4.2.3 LABORATORY METHODS

Cores were glued into pre-grooved boards, sanded using 100-800 grit and then polished to increase the visibility of annual radial growth rings (Stokes and Smiley 1996). All samples were counted and measured using a Velmex® sliding stage micrometre (precision 0.005 mm) under a binocular microscope at 40X with a digital encoder. For each tree, two radii were measured and cross-dated visually using narrow marker years (Fritts 2001). In some cases, individual radii were removed from the analysis if the samples were damaged or if they had large amounts of reaction wood. Statistical verification of crossdating was accomplished using the program COFECHA (Holmes 1983, Grissino-Mayer 2001). To account for relative differences in magnitude, ring-width values for each radius were standardized using the mean ring-width value. The two radii were then averaged into a single series, which minimizes the effect of growth asymmetry within individual trees. Tree-ring series were then detrended using a modified negative exponential function using R (package dplR; R Development Core Team 2006, Bunn 2008), that removes biological age trends while preserving low-frequency trends, such as insect herbivory.

4.2.4 DATA ANALYSIS

Visible disturbance and stand characteristics

Physical signs of damage were compiled for the site and zone levels showing the proportion of trees affected by porcupine herbivory and for fire history, the presence or absence of charcoal was noted. Hemispheric images were processed using Gap Light Analyzer (Frazer et al. 1999), to calculate percent site openness and effective leaf area index over zenith angles of 0 to 75° (Welles and Norman 1991).

Insect outbreaks

Traditional approaches to detecting insect outbreaks were attempted before statistical approaches were implemented. For larch sawfly, visual inspection of rings was performed to look for the presence of light rings, ring suppression and increase incidence of missing or incomplete rings (e.g. Harper 1913, Case and MacDonald 2003, Nishimura and Laroque 2010). The program OUTBREAK (Holmes and Swetnam 1996) is commonly used to quantify the outbreak patterns of insect herbivore outbreaks, typically by comparing the radial growth patterns of host tree species to non-host tree species. Program OUTBREAK has been successful at identifying epidemic outbreak patterns occurring at large spatial scales (e.g. Sonia et al. 2011) but is potentially limited for epidemic outbreaks patterns occurring at smaller spatial scales and where tree growth is strongly site-specific, making traditional host and non-host designations unreliable.

Building on the work of Holmes and Swetnam (1996), we developed a program that scans each series and identifies annual growth rings as being disturbed or not disturbed by insect herbivory. At epidemic levels, insect herbivory defoliates trees causing a reduction in photosynthetic capacity, and hence reduced radial growth rates. Criteria for making this designation of disturbed or non-disturbed are species specific, based on consecutive years of radial growth suppression below a predefined threshold value. For spruce budworm, the radial suppression signature is at least five consecutive years below the mean ring width for the entire series with one of these five rings being smaller than 1.28 standard deviations from the mean (c.f., Sonia et al. 2011). For larch sawfly, the radial suppression signature is at least four consecutive years below the mean ring width for the entire series with one of these four rings being smaller than 1.3 standard deviations from the mean (c.f., Nishimura and Laroque 2010). In both cases, the outbreak period is preceded by a period of growth reduction and followed by a period of growth recovery (Swetnam et al. 1985, Swetnam et al. 1995). The program starts with the first year of growth (first ring) and looks at the subsequent number of years specified by the radial suppression signature. If the criteria are met, the ring is identified as disturbed and the program then moves to the second year of growth (second ring). Once each series is processed, the disturbed and non-disturbed rings are pooled separately. A master chronology for each species and each zone is computed for the disturbed and non-disturbed ring width values by taking the mean value for each year available. For most years, there is a mean value for both disturbed and not disturbed rings. For each chronology, the proportion of unique trees for every year that exhibits a disturbed ring is calculated to examine outbreak dynamics.

Insect outbreaks were reconstructed for each of the four co-dominant species in the forest, transition and krummholz zones. To maximize sample sizes and because our *a priori* hypotheses were that similar processes are occurring among zones, analyses were conducted at the zone level. Based on the proportion of trees affected each year, the cyclic outbreak dynamics for spruce budworm and larch sawfly were identified visually from the maximum proportion of trees affected. To explore the RCH, the effects of host tree density and herbivory were examined by comparing the differences in the proportion of trees affected between forest and transition sites. Maximum herbivory, calculated as the mean proportion of trees affected during peak outbreak years, was compared among zones using a two-tailed *t*-test and in relation to stem density for each species using a linear regression.

To understand the contribution of insect outbreaks to tree mortality, 161 dead trees were crossdated using COFECHA to determine the year of death by comparing the radial growth patterns of the dead samples of unknown locations to living tree chronologies for each tree species. To account for the loss of years due to weathering, which is typically approximated at one ring per decade (Szeicz and MacDonald 1995, Danby and Hik 2007), we used 5-year age class frequency distributions.

When reconstructing insect outbreaks, it is difficult to accurately differentiate between insect species since different species can be present and feeding simultaneously. This is the case for larch, which is the primary host of larch sawfly but can also be defoliated by spruce budworm, making it difficult to assign evidence of past insect herbivory to one but not the other species. Therefore identification of insect herbivores is assigned based on feeding preference though it is possible that the disturbance signature we are detecting is the result of multiple species defoliation.

Windthrow

To determine if canopy structure in gaps formed from windthrow was significantly different from random sites, a non-parametric Kolmogorov-Smirnov test was performed on the percent-canopy openness between gaps and random sites for the forest and transition zones. The krummholz zone was excluded from these and later analyses since no windthrow was identified.

The role of windthrow was determined by modeling the number of seedlings found in gap versus randomly chosen sites in the forest and transition zones, using Generalized Linear Models (GLM) with Poisson error structure typical of count data and presented using the odds ratios (with 95% confidence intervals). The number of seedlings was modeled by zone (forest or transition), plot type (gap or random), effective leaf area index and percent canopy openness, as possible explanatory variables. Due to low numbers of seedlings found, seedlings of all species were pooled for these analyses. All analyses were performed in R (v. 2.14; R Development Core Team 2006) unless otherwise noted.

4.3 Results

Visible disturbance and stand characteristics

With the total area surveyed in the forest zone of 0.16 ha and 0.57 ha in the transition zone, the proportion of trees showing visible signs of debarking from porcupines varied greatly among species and zones (Table 4.2). In the forest zone, all species showed evidence of debarking with black spruce often having the highest proportion of trees affected with the balsam fir, larch and white spruce exhibiting less consistent patterns but high values in individual plots (e.g., larch 27%, white spruce 15%). In the transition zone, debarking was 2% more prevalent than the forest zone with the percent of affected balsam fir reaching 23% across all sites and as high as 65% at one site (T-3). White and black spruce also had high levels of debarking in the transition zone (22% and 17%, respectively), while larch was affected less often (3%). Overall, the percentage of trees affected in the transition zone (13%) was slightly greater than in the forest zone (11%). No porcupine damage was observed in the krummholz zone. To result in top dieback or tree death, the debarking must ring the entire circumference of the tree, either in single or multiple events. Of all trees affected by debarking, two trees died in the forest zone, one larch and one black spruce, and one balsam fir in the transition zone died although many of the debarked trees showed evidence of top dieback, which would compromise growth rather than contribute to tree mortality.

We did not detect any charcoal in the soil profiles of the forest or transition zones, confirming our hypothesis that this area does not have a history of stand-level fires. Small fires that burn individual trees, such as those arising from lightening strikes, may have gone undetected, but appear to be very rare across all zones at our study site.

Canopy openness increased and effective leaf area index decreased with increasing elevation from the forest zone to the transition zone (Table 4.3). Mean percent canopy openness values for the forest zone were 86.10 ± 7.7% SE and for the transition zone were 97.45 ± 3.6% SE. Mean effective leaf area index values in the forest zone were 0.13 ± 0.1 SE and 0.02 ± 0.0 SE in the transition zone. The prostrate growth form and diffuse distribution of trees in the krummholz zone prevented comparable canopy cover and effective leaf area index measurements, although individuals do form a low-lying, closed canopy among branches within the patch.

Insect outbreaks

Insect outbreaks were reconstructed across treeline for spruce budworm and larch sawfly to understand if these insects are meaningful, from an ecological perspective, for influencing stand dynamics. For balsam fir, the forest and transition zones had similar outbreak magnitudes (50%), though unexpectedly, there were more frequent outbreaks in the transition zone (Fig. 4.2, Table 4.4Ai). Looking at balsam fir across treeline, the transition zone shows relatively more trees affected compared to the forest zone (Fig. 4.2). White spruce in the forest and transition zones have many synchronous suppressions with the highest magnitude seen in the early 1960s with 44% of trees in the transition zone and 65% of trees in the forest zone affected (Fig. 4.3, Table 4.4Aii). During synchronous outbreaks, the proportion of trees affected was always greater in the forest zone, compared to the transition zone (Fig. 4.4). Black spruce also shows a similar pattern of synchronous outbreaks between the forest and transition zone, often with a greater number of trees affected in the forest zone than the transition zone (Fig. 4.4, Table 4.4Aiii). The patterns of outbreaks in the krummholz zone are less clear perhaps due to the poor series correlation values (Table 4.4Aiii).

The magnitude of outbreaks were greater for larch sawfly on larch than those of spruce budworm on the other co-dominant tree species (Table 4.4B). The outbreak with the greatest magnitude was detected around 1981, which showed over 90% of the larch affected in the forest zone and the transition zone (Fig. 4.5, Table 4.4B). Interestingly, a high magnitude outbreak in the forest zone was detected around 1958 but was not seen in the transition zone.

To examine whether herbivore activity decreased across treeline, as predicted by RCH, maximum herbivory was compared among zones and in relation to stem density. In all cases, maximum herbivory decreases across treeline, though only moderately significant between the forest and transition zones for blacks spruce ($P<0.10$, Fig. 4.6). With the exception of black spruce in the forest zone, there was a significant linear relationship between the maximum proportion of trees affected and stem density (Adj. $R^2=0.691$, $P=0.01$; Fig. 4.7). The high density of black spruce in the forest zone is attributed to extensive vegetative reproduction via layering. Lower than expected values of maximum herbivory on black spruce in the forest zone could suggest a nonlinear response, meaning that above certain host densities, there is a lessened response by the herbivore.

Using COFECHA with 50-year overlapping segments, 82 of 156 dead tree samples were successfully crossdated with 61 samples having correlations to local chronologies over 0.20 and 21 samples with correlations over 0.30 (Fig. 4.8). Patterns of tree mortality show higher values for the early 1980s, 1970s and early 1950s. Looking by species, the majority of white spruce died between 1980-1985, 1970-1975 and 1960-1965. The period of 1960-1965 coincides with the highest magnitude outbreak detected in white spruce in the forest zone and the transition zone around 1962-1964. Black spruce mortality was highest in the early 1980s, which follows with outbreaks detected in the mid to late 1970s. The peak mortality identified for larch was in the early 1950s, 1970s and 1980s. No mortality was detected for balsam fir.

Windthrow

Canopy openness was not significantly different at gaps versus randomly chosen locations in the forest zone ($D=0.46$, $P=0.38$; Fig. 4.9) or the transition zone

(*D*=0.28, *P*=0.81; Fig. 4.9) suggesting that within each zone, canopy gaps caused by windthrow are small-scale, by not contributing significantly more light to regeneration than non-gaps. This pattern was consistent when looking at leaf area index. Combining the windthrow and randomly chosen sites, percent canopy openness was significantly different between forest and transition zones (*D*=0.58, *P*=0.006; Fig. 4.10) with higher canopy openness in the transition zone. This finding is consistent with measures of stand density that decrease with elevation (Table 4.3).

The majority of seedlings found at the base of windthrown trees were larch, with lower numbers of black spruce, and to a lesser extent, balsam fir (Table 4.5). While gaps were not significant in increasing the amount of light available for regeneration, the chances of finding seedlings at the base of windthrown trees were 3.0 times greater than at random sites and this is 2.3 more likely in the forest than the transition zone (Table 4.6). These results suggest that windthrows may play a significant role in providing appropriate microsite conditions (e.g., exposed mineral soil) required by some species (e.g., black spruce), especially in the forest zone.

4.4 Discussion

Compared to most closed canopy boreal forest (Fleming 2000), disturbance at treeline in the Mealy Mountains is occurring less frequently, at lower magnitudes and at smaller spatial scales. Feeding damage by porcupines increased slightly across treeline, despite the decrease in host tree density. We detected species-specific host tree response to insect infestation that results in non-linear impacts across treeline, with some species having comparable (larch) or higher (balsam fir) levels in transition compared to forest zone. Larch and black spruce seedlings were the most abundant species and had a greater chance of being found in exposed mineral soil associated with windthrows, especially in the forest zone. Across a treeline in the Mealy Mountains spanning a few kilometres, patterns of disturbance show variability in frequency and magnitude. This variability may be explained by changes in tree density and/or environmental stress across treeline.

Visible disturbance and stand characteristics

Feeding damage by porcupines was common but patchy across the forest and transition zone but absent in the krummholz zone. Though variable across the species range, northern populations of porcupine have winter home ranges around 1 to 2 km^2, which greater exceeds more southern winter home ranges of around 0.001 km^2 in scrub desert of Idaho and 0.015 km^2 in second growth western hemlock forest of British Columbia (Coltrane and Sinnott 2012). At the northern range edge of porcupines, larger winter home ranges would manifest in similar levels of feeding damage in the forest and transition zone. The absence of feeding damage in the krummholz zone is probably due to the prostrate nature of these trees that are under snowpack for much of the winter and have short trunks, thus resulting in the trees being inaccessible for porcupines. Deteriorating winter conditions associated with reduced food quality can result in a shift to higher risk feeding behavior in juvenile but not in adult porcupines (Sweitzer and Berger 1992). Open areas also have more severe wind and icing events in the higher elevations, making the krummholz zone less hospitable to porcupines than either the transition or forest zone, where shelter from snow-exposed vegetation is more abundant. Overall, porcupine herbivory contributes to small-scale disturbance at treeline in the Mealy Mountains. While tree mortality associated with feeding damage is uncommon, the implications of this mortality are still important.

Despite the prevalence of porcupine herbivory at treeline, the associated level of tree mortality was low with only three trees dying from what we suspect to be the result of debarking by porcupine. If the porcupine does not completely girdle the tree, the debarked area will scar (similar to a fire scar) but the remaining bark will persist. If the tree is completely girdled, the portion above the debarking will die. Many trees showed evidence of top dieback but did not result in mortality. Given that porcupines are feeding on tree cambium primarily during the winter, the lower portion of the trees appear to be debarked less often, explaining the low levels of tree mortality. Future changes to the timing and amount of snow could significantly influence the rates of mortality caused by porcupines if more of the trees would be exposed and available for herbivory. In Northern Quebec, Payette (1987) documented a range expansion of porcupine that coincided with recent 20th century expansion of white spruce and we thereby expect that increases in tree density and tree range expansion will be accompanied by increased porcupine feeding damage.

Insect outbreaks

Reconstructing insect herbivory dynamics links to potential of treeline movement as the frequency and magnitude of outbreaks determine the magnitude of treeline regeneration. Spruce budworm dynamics were characterized by epidemic outbreaks with fewer trees affected than in reconstructions from nearby continuous boreal forests (<100 km, balsam fir: 60-75% affected, black spruce: 55-75% affected; Dumaresq 2011) and continuous boreal forests further from the Mealy Mountains (~1100 km, spruce: ~80%; Sonia et al. 2011). Larch sawfly dynamics in the Mealy Mountains, on the other hand, are comparable to the closest known reconstructions (<300 km, 50-100% affected; Nishimura and Laroque 2010). Nearby spruce budworm reconstructions identify peak outbreaks around 1985, 1970 and 1945 for balsam fir and 2000, 1975 and 1950 for black spruce (Dumaresq 2011). From eastern and southern Quebec, spruce budworm outbreaks have been reconstructed in spruce (*Picea* spp.) for 1980, 1950 and more extending back 400 years (Boulanger and Arseneault 2004, Boulanger et al. 2012). Compared to the nearby reconstructions by Dumaresq (2011), we detected synchronous, though slightly delayed, outbreaks in white spruce, black spruce and early balsam fir. Following the outbreak in the early 1960s, balsam fir shows asynchronous outbreaks compared to other species at the site level and also when compared to other nearby reconstructions by Dumaresq (2011).

Outbreak asynchrony combined with the small number of dead balsam fir detected in the Mealy Mountains was an unexpected result. Mismatched shifts in phenology could have long-reaching effects on spruce budworm dynamics in a system with multiple hosts (van Asch and Visser 2007). Interspecific differences in bud-break could shift the host-feeding preference for budworm as larvae emerge. Balsam fir is often considered the host target for spruce budworm but, if newly emerged buds are more abundant on less palatable host species, this could manifest in a host shift. The small number of dead balsam fir in our study area is perplexing and may be underestimated in our results due to errors associated with crossdating samples and the assigning species designation. Although this finding could possibly be related to the complex dynamics of a multi-host system in which the density of balsam fir is too low, compared to the black spruce, to host an epidemic level outbreak event. Also, with black spruce being a suitable overwintering host for spruce budworm, shifts in the phenology of budburst could result in shifts in host preference for black spruce (Cooke et al. 2007).

For larch sawfly, the closest outbreak reconstructions are from Nishimura and Laroque (2010) in western Labrador that show evidence of outbreaks peaking around 1985, 1940 and 1900. Our reconstructions also show a major outbreak in the early 1980s but are not consistent with the other outbreaks identified by Nishimura and Laroque (2010). Patterns showing lower proportion of trees affected during outbreaks at treeline, compared to closed canopy boreal forest was also seen at treeline in Churchill, Manitoba, in which seldom more than 25% of trees were affected during larch sawfly outbreaks (Girardin et al. 2005). Thus at treeline, insect herbivory may be more frequent but of equal (larch sawfly) or lower (spruce budworm) magnitude than other parts of the boreal forest, confirming insect herbivory as an important disturbance.

One of the unexpected results was the amount of local variability in insect herbivory outside of peak outbreak years. We demonstrate that localized and patchy epidemic levels of herbivory occur in greater frequency than previously reported. Where mass outbreaks are spreading across the landscape (i.e., insect herbivores are 'transient' and not 'residents'), we would expect little evidence of outbreaks in the dendrochronological record outside of peak outbreak periods. However, in almost all periods reconstructed outside of peak outbreaks, we detected low-magnitude outbreak activity ranging from ~1-40% of trees being affected. It is still expected that during mass outbreak periods, 'transient' insect herbivores move into these areas but we are highlighting the importance of 'resident' insect herbivores that persist in relatively high abundance. Low-magnitude epidemic levels outside of peak outbreak periods, as we detected in the dendrochronological record, provides valuable insight into the sustained contributions of insect herbivory to tree mortality and related implications for treeline change and regeneration.

Between the forest and transition zones, differences in the frequency and magnitude of outbreaks were detected. Though all species showed a decrease in maximum herbivory across treeline, balsam fir and larch show maximum outbreak values equivalent or higher in the transition zone. In the context of the RCH (Root 1973), this interspecific variability decreases as there is a strong linear relationship between maximum herbivory and stem density. With treeline occurring along an environmental stress gradient, attributing the decrease in herbivory to the decrease in resources, rather than increased environmental severity, is difficult. However, the example of larch and balsam fir having similar or higher values in the transition zone provides evidence that climate severity alone does not explain decreases in insect herbivory.

Windthrow

The incomplete canopy closure and high level of variability in stand structure across treeline results in the canopy openings caused by downed trees to be no less open than randomly located sites. Despite the comparable canopy openness at windthrow and random sites, it does not rule out the importance for regeneration of light reaching the forest floor. In high latitude forests, the low angle of the sun may require larger gaps that those resulting from downed single trees, in order for light to penetrate the forest floor (St-Denis et al. 2009). However, we did document higher levels of seedling establishment associated with windthrown trees, suggesting that light may not be the limiting factor for regeneration at treeline.

The importance of windthrow for seedling establishment may therefore be in providing microsite conditions of exposed mineral soil and shelter from the upturned root mass. The contributions of windthrow to gap-dynamics in continuous boreal forests is well-understood (e.g., Ulanova 2000), though little work has focused on treeline and possible implications for range expansion. Veblen et al. (1981) suggest *Nothofagus*-dominated treelines in Chile are driven by gap-inducing disturbances, such as windthrow. In our field site, windthrow appears to be important for seedling establishment of black spruce and especially larch seedling establishment in the forest and transition zones. As stand density decreases into the krummholz zone, windthrow is less common due to the compact architecture of the trees (i.e., reduced surface area; Rich et al. 2007), well-developed root systems and multiple 'anchoring' locations from extensive layering by adaptive reiteration as the result of growing axis dedifferentiation (Laberge et al. 2001). As canopy openness approaches 100%, the exposed mineral soil would be subject to rapid moisture loss, reducing the suitability for seedling establishment. At our study site, Wheeler et al. (2011) found that in open transition/krummholz areas, black spruce seedlings had higher survivorship on feathermoss than on small patches of exposed mineral soil. Although exposed mineral soil may play a key role in maintaining established treeline forests, range expansion or infilling of open areas seems less likely to be driven by exposed mineral soil.

How important is small-scale disturbance at treeline?

Unlike the closed-canopy boreal forest, which is often driven by stand-replacing disturbances, at treeline a variety of small-scale gap replacement disturbances drive change and turnover. With climate change expected to result in increased stem density and mean annual temperatures more conducive to insect overwinter success, we expect the magnitude of disturbances, especially insect herbivory and fire, to increase and manifest in higher levels of tree mortality (Volney and Fleming 2000, Bonan 2008, Candau and Fleming 2011, Wolken et al. 2011). The role of small-scale disturbance at treeline is important for causing tree stress and mortality, which ultimately results in microsite conditions needed for seedling establishment and potentially recruitment.

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Table 4.1 Comparison of feeding preferences and life history of forest herbivores in the Mealy Mountains (Canada).

Insect Species	Host Preference	Life History	Dendrochronological Signature
Porcupine	-Variable and dependent on stand composition[1] -Unknown in the Mealy Mountains	-nocturnal -range varies across species range (0.001-2.0 km^2)[2] -feeds on leaves and fruit in summer and cambial layer and conifer needles in winter[3]	-cambial layer removed -scars can be dated
Spruce Budworm[4]	1. Fir 2. White spruce 3. Black spruce 4. Larch	-Spans 1 year -Overwinters at 2nd instar -Feeds on pollen flowers, buds and needles until 6th or last instar (April –June) -Adult lays eggs in late summer	-5 years with at least 1 year -1.28 SD below the mean -8 to12 year period of growth reduction and recovery
Larch Sawfly[4]	Larch	-Not native -Spans 1 year Overwinters in soil as prepupa -Adults emerge in late spring and lay eggs in elongating shoots -Larva feeds on needles throughout the summer	-4 years with at least 1 year -1.3 SD below the mean -8 to12 year period of growth reduction and recovery

[1] Tenneson and Oring (1985)
[2] Payette (1987)
[3] Coltrane and Sinnott (2012)
[4] Information on feeding preference and life history from: http://www.na.fs.fed.us/

Table 4.2 Summary of porcupine feeding damage in the Mealy Mountains (Canada), by zone and species with the number of individuals affected and the proportion of trees in parentheses. Bolded values represent the averages of plots by zone. Zone codes are F=forest, T=transition and K=krummholz.

Zone		**Porcupine**				
	Plot	**Balsam fir**	**Larch**	**White spruce**	**Black spruce**	**All species**
F		**1 (0.03)**	**4 (0.08)**	**2 (0.05)**	**27 (0.14)**	**34 (0.11)**
	1	1 (0.05)	3 (0.27)	2 (0.15)	7 (0.11)	13 (0.12)
	2	0 (0.00)	0 (0.00)	0 (0.00)	15 (0.13)	15 (0.11)
	3	0 (0.00)	1 (0.04)	0 (0.00)	5 (0.21)	6 (0.08)
T		**23 (0.23)**	**4 (0.03)**	**5 (0.22)**	**9 (0.17)**	**41 (0.13)**
	1	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
	2	0 (0.05)	0 (0.00)	0 (0.00)	1 (0.09)	1 (0.01)
	3	13 (0.65)	1 (0.01)	3 (0.23)	6 (0.33)	23 (0.20)
	4	10 (0.37)	3 (0.08)	2 (0.09)	2 (0.09)	17 (0.16)
K		**0 (0.00)**	**0 (0.00)**	**0 (0.00)**	**0 (0.00)**	**0 (0.00)**
	1	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
	2	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)

Table 4.3 Site characteristics in the Mealy Mountains (Canada), with stand density (stems/ha) and percent canopy openness and effective leaf area index (L_e) with standard error (SE). Zone codes are F=forest, T=transition and K=krummholz.

		Density (stems/ha)						
Zone Plot	Area (ha)	Balsam Fir	Larch	White spruce	Black spruce	All species	% Canopy Openness ± SE	Effective Leaf Area Index (L_e) ± SE
F	**0.16**	**198.7**	**339.7**	**256.4**	**1250.0**	**2044.9**	**86.10±7.8**	**0.13±0.1**
1	0.05	400.0	220.0	260.0	1280.0	2160.0	81.54±3.2	0.19±0.0
2	0.05	80.0	400.0	100.0	2140.0	2720.0	88.26±2.4	0.10±0.0
3	0.06	125.0	392.9	392.9	428.6	1339.3	88.51±2.1	0.11±0.0
T	**0.57**	**171.4**	**239.6**	**71.7**	**90.9**	**573.6**	**97.45±3.6**	**0.02±0.0**
1	0.25	52.0	4.0	4.0	4.0	64.0	99.98±0.01	0.00±0.0
2	0.21	181.0	161.9	19.0	47.6	409.5	98.78±1.0	0.01±0.0
3	0.06	351.5	1159.9	228.5	316.3	2056.2	94.54±1.5	0.06±0.0
4	0.05	491.8	655.7	418.9	418.9	1985.4	96.49±1.0	0.02±0.0
K	**9.43**	**2.9**	**0.1**	**0.5**	**5.8**	**9.3**	**N/A**	**N/A**
1	6.34	0.2	0.0	0.5	2.8	3.5	N/A	N/A
2	3.01	8.6	0.3	0.7	12.0	21.6	N/A	N/A

Table 4.4 Reconstructed outbreak history for (A) spruce budworm and (B) larch sawfly for the Mealy Mountains (Canada), by treeline species and zone. "Corr." refers to series correlations from COFECHA using 50-year overlapping segments. Zone codes are F=forest, T=transition and K=krummholz. Bolded values in table represent the year with the highest proportion of trees affected for each species and zone.

A. SPRUCE BUDWORM

Host Species	Site	Corr.	Cores	Min. Year	Max. Year	Peak outbreak years (proportion of trees affected)
i. Balsam fir	T	0.358	31	1879	2007	2003 (0.21), 1995 (0.46), 1977 (0.25), **1962 (0.50)**, 1943 (0.13)
	F	0.359	41	1921	2007	**1994 (0.50)**, 1969 (0.25)
ii. White spruce	T	0.437	54	1830	2006	2000 (0.40), 1988 (0.22), 1977 (0.37), **1964 (0.44)**, 1953 (0.22), 1939 (0.31), 1930 (0.25), 1911 (0.16)
	F	0.455	57	1802	2007	2004 (0.12), 1993 (0.44), 1977 (0.50), **1962 (0.65)**, 1949 (0.26), 1931 (0.29), 1911 (0.21), 1900 (0.29)
iii. Black spruce	K	0.158	24	1641	2009	**1970 (0.41)**, 1953 (0.32), 1943 (0.23), 1931 (0.18), 1915 (0.23)
	T	0.374	18	1920	2006	**1989 (0.43)**, 1975 (0.36), 1960 (0.36), 1951 (0.36)
	F	0.412	71	1818	2007	2004 (0.28), 1987 (0.40), **1975 (0.50)**, 1962 (0.48), 1947 (0.20), 1932 (0.32), 1923 (0.27), 1914 (0.23), 1899 (0.22)

B. LARCH SAWFLY

Host Species	Site	Corr.	Cores	Min. Year	Max. Year	Peak outbreak years (proportion of trees affected)
Larch	T	0.471	101	1796	2006	1992 (0.48), **1981 (0.92)**, 1966 (0.46), 1942 (0.16)
	F	0.413	36	1830	2007	**1981 (0.91)**, 1958 (0.90), 1863 (0.14)

Table 4.5 Summary of seedlings numbers found at (A) the base of windthrows and (B) random sites in the Mealy Mountains (Canada).

Zone	Balsam fir	Larch	White spruce	Black spruce	All species
A. WINDTHROW					
Forest	1	10	0	6	17
Transition	0	9	0	0	9
Total	**1**	**19**	**0**	**6**	**26**
B. RANDOM					
Forest	0	4	0	0	4
Transition	0	4	0	0	4
Total	**0**	**8**	**0**	**0**	**8**

Table 4.6 Influence of ecological and site factors on seedling occurrence across treeline in the Mealy Mountains (Canada), using generalized linear models (GLM) with Poisson distribution with significantly more seedlings found in the forest zone (*P*=0.012) and associated with windthrows (*P*=0.007).

	Odds ratio [95% CI]	**df**	**Z**	***P***
Number of seedlings				**0.003**
Zone (Transition/Forest)	2.30 [1.16, 4.70]	34	2.35	0.012
Site (Random/Windthrow)	3.00 [1.42, 7.01]	34	2.71	0.007

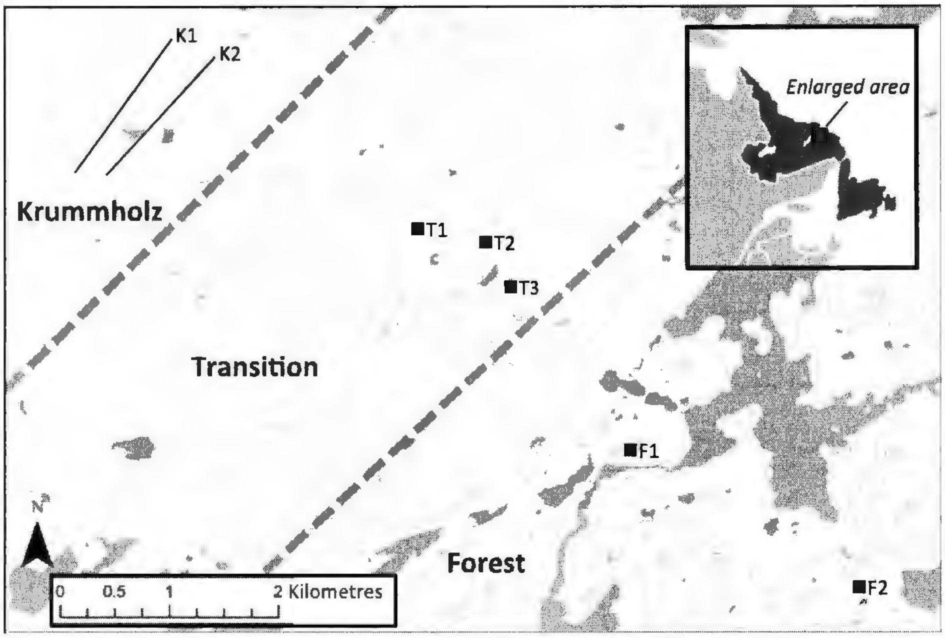


Fig. 4.1 Map of Eastern Canada with Newfoundland and Labrador shaded in darker grey and location of field site located in the Mealy Mountains (N 53°36'6", W 58°49'0"; enlarged area). The enlarged area shows sites within the forest zone (F1 and F2), transition zone (T1, T2 and T3) and transects within the krummholz zone (K1 and K2). Grey dashed lines approximate zone delineation. Bodies of water and contour lines at 20 m intervals are shown in grey.

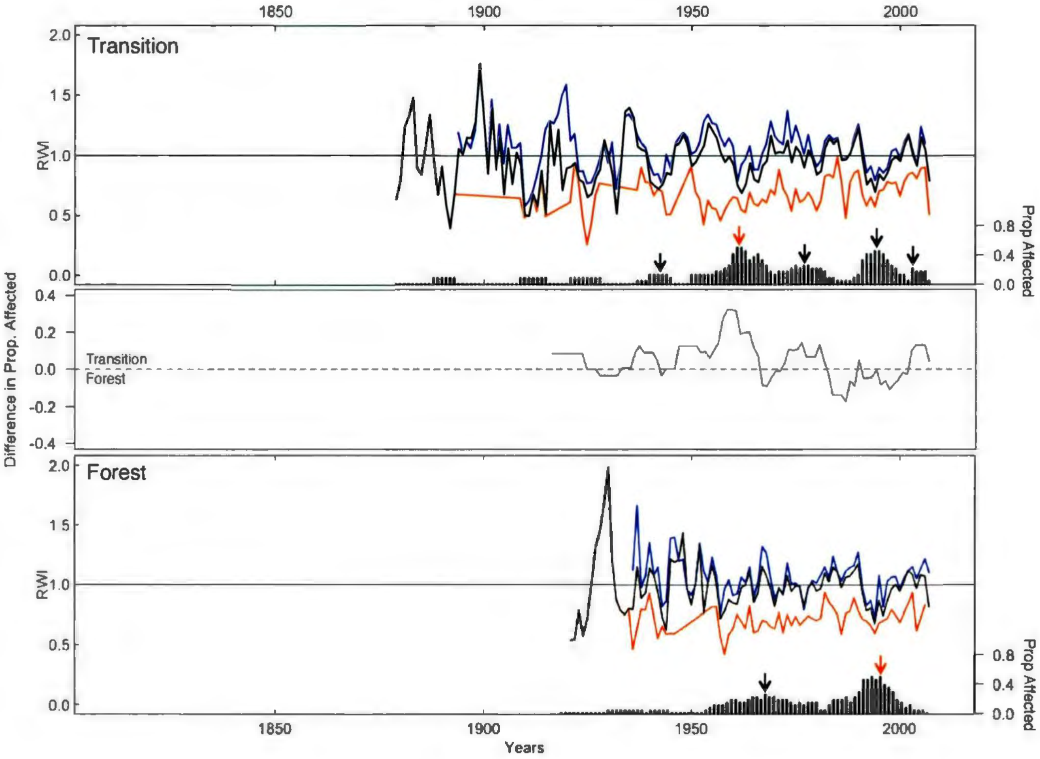


Fig. 4.2 Outbreak reconstructions for spruce budworm on balsam fir in the Mealy Mountains (Canada), for the transition and forest zones with the difference between the proportions of trees affected. Shown here is the main chronology (black line), the chronology with insect disturbance removed (blue line) and the chronology composed of the disturbance sections (red line). Black arrows identify outbreak years and the red arrow represents the maximum value for each zone.

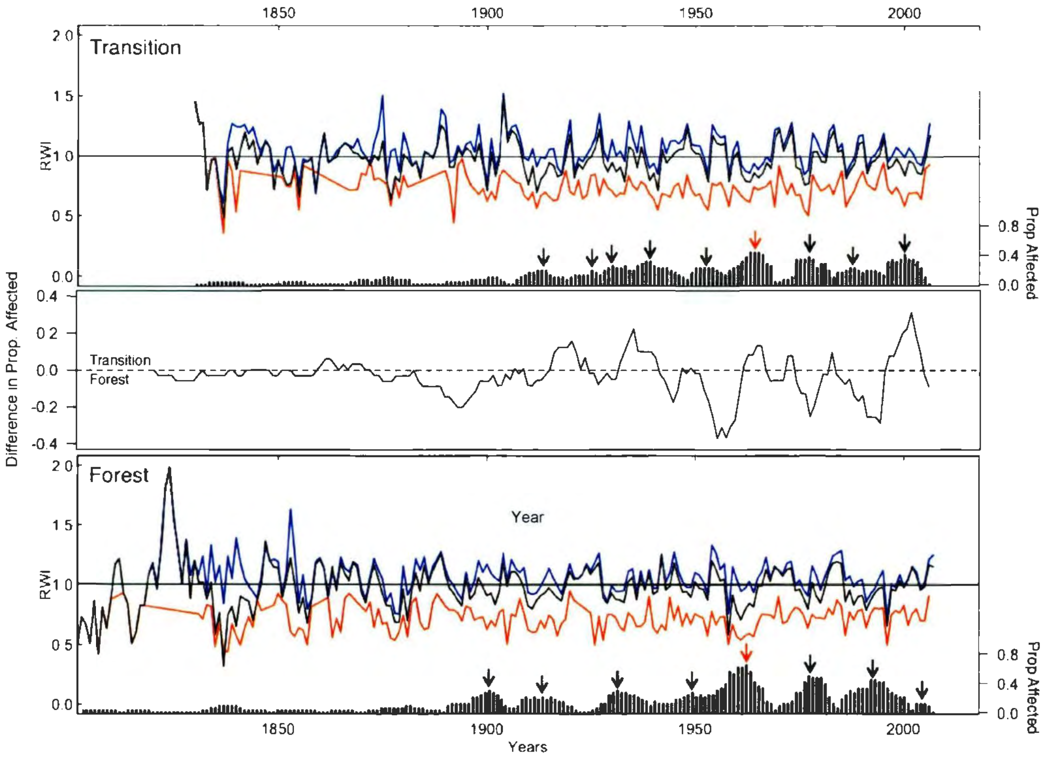
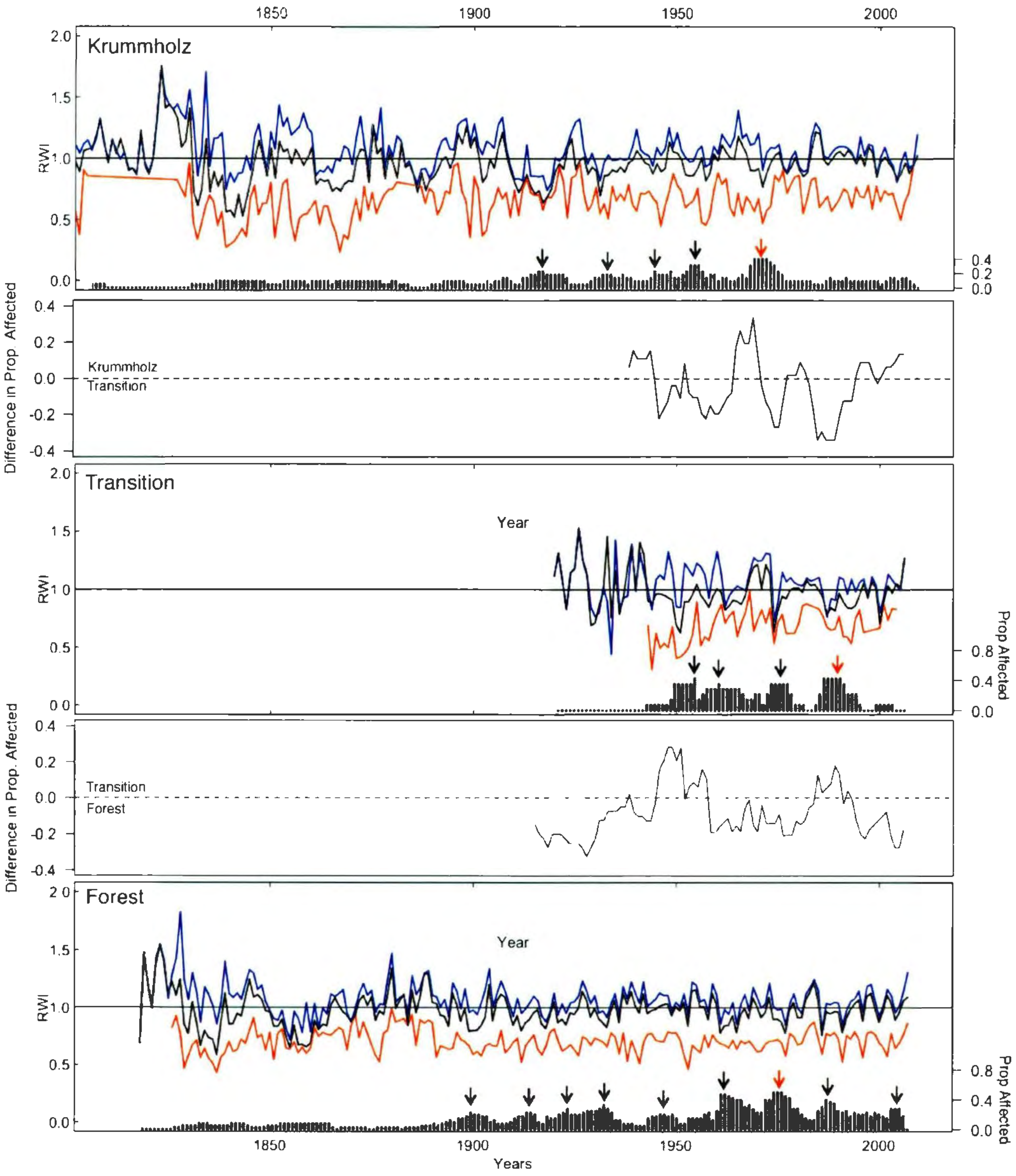


Fig. 4.3 Outbreak reconstructions for spruce budworm on white spruce in the Mealy Mountains (Canada), for the transition and forest zones with the difference between the proportions of trees affected. Shown here is the main chronology (black line), the chronology with insect disturbance removed (blue line) and the chronology composed of the disturbance sections (red line). Black arrows identify outbreak years and the red arrow represents the maximum value for each zone.



1850
1900
1950
2000
Krummholz
RWI
2.0
1.5
1.0
0.5
0.0
0.4
0.2
0.0
Difference in Prop. Affected
0.4
0.2
0.0
-0.2
-0.4
Krummholz
Transition
Transition
Year
Prop Affected
0.8
0.4
0.0
Difference in Prop. Affected
Transition
Forest
Forest
Year
Years

Fig. 4.4 Outbreak reconstructions for spruce budworm on black spruce in the Mealy Mountains (Canada), for the krummholz, transition and forest zones and staggered by the differences between the proportion of trees affected between the krummholz/transition and the transition/forest. Shown here is the main chronology (black line), the chronology with insect disturbance removed (blue line) and the chronology composed of the disturbance sections (red line). Black arrows identify outbreak years and the red arrow represents the maximum value for each zone.

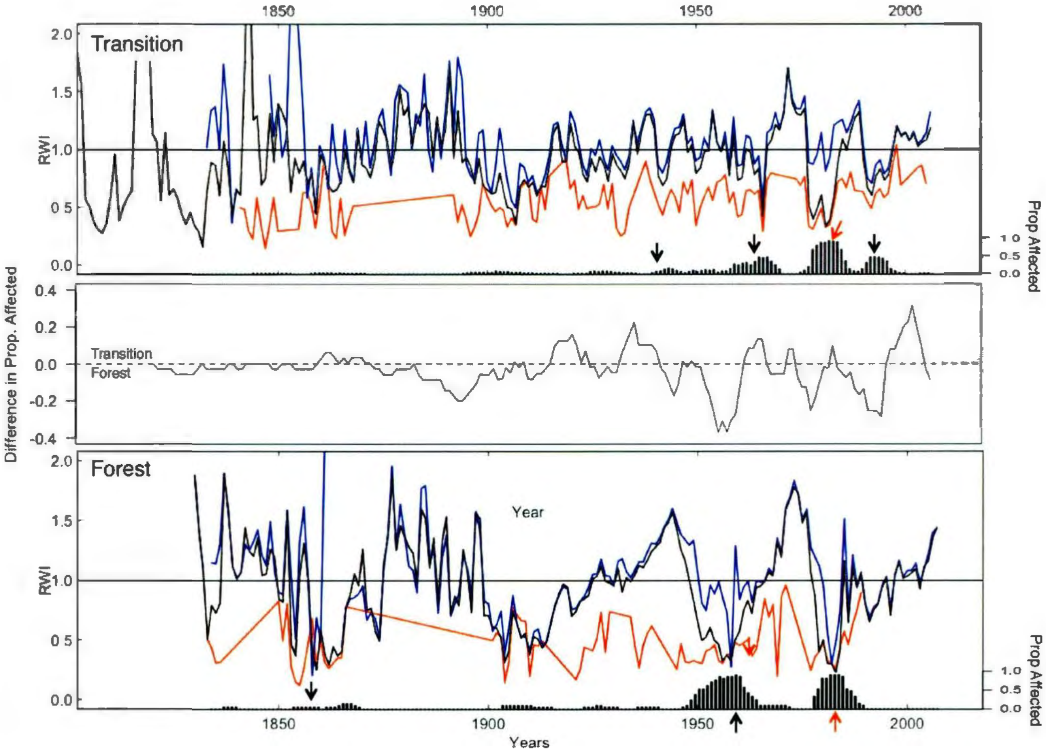


Fig. 4.5 Outbreak reconstructions for larch sawfly on larch in the Mealy Mountains (Canada), for the transition and forest zones with the difference between the proportions of trees affected. Shown here is the main chronology (black line), the chronology with insect disturbance removed (blue line) and the chronology composed of the disturbance sections (red line). Black arrows identify outbreak years and the red arrow represents the maximum value for each zone.

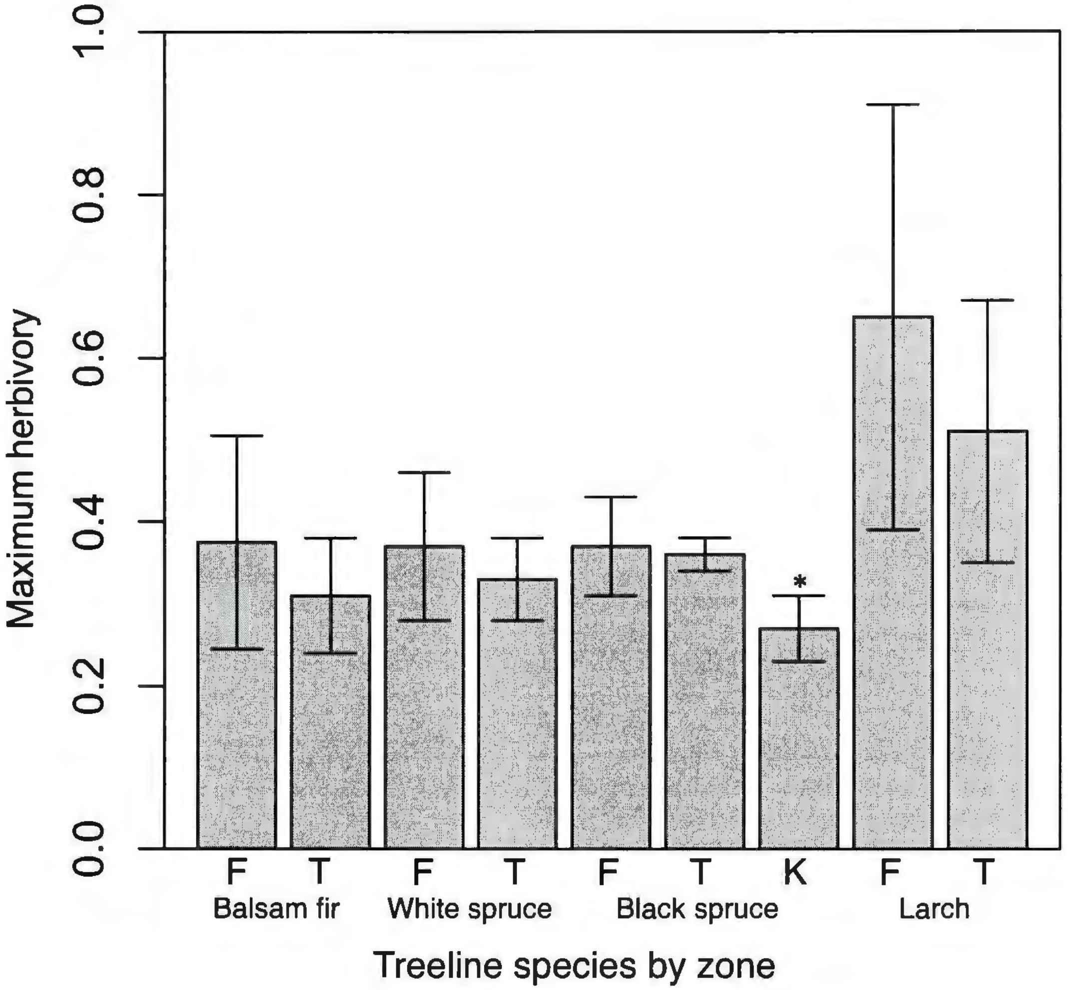


Fig. 4.6 Relationship between the maximum herbivory across treeline. Zone codes are: F=forest, T=transition and K=krummholz. Error bars show standard error. *Moderately significantly different (*P*<0.10) between the krummholz zone and the transition zone for black spruce.

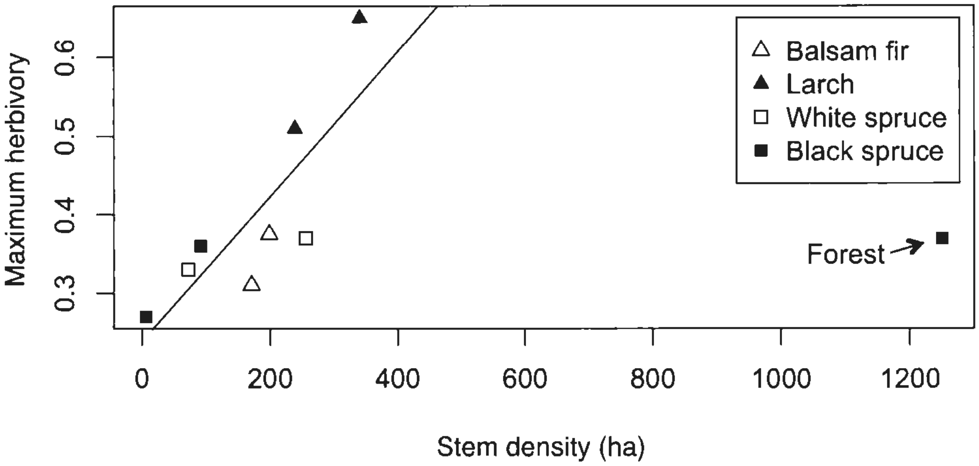


Fig. 4.7 Relationship between the maximum herbivory and the corresponding stem density (per ha) across treeline. Line represents significant linear regression (*F*=12.18, Adj. R^2 =0.615, *P*=0.01) calculated without black spruce in the forest zone.

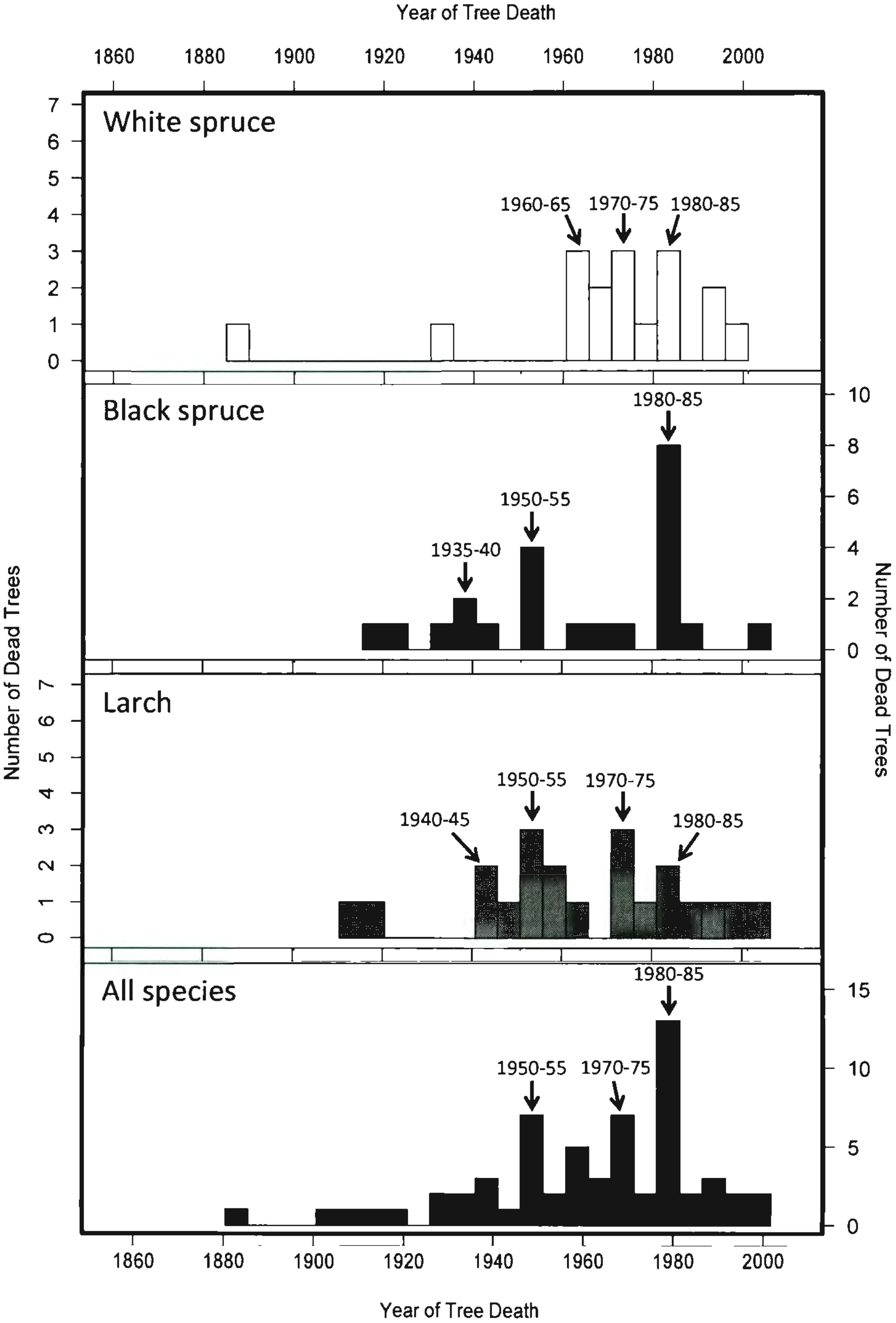


Fig. 4.8 Histograms of 5-year age class frequency distributions of tree mortality in the Mealy Mountains (Canada), reconstructed from crossdated dead individuals. The three peak yeas are identified by black arrows.

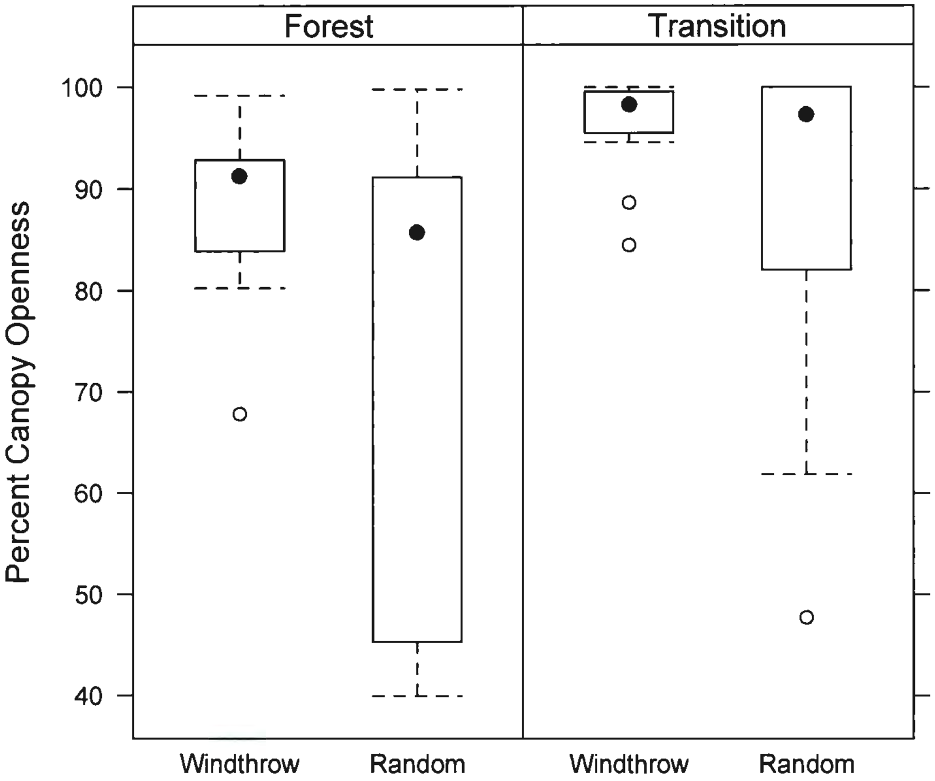


Fig. 4.9 Differences in percent canopy openness between gaps created by windthrow and randomly selected adjacent locations in the Mealy Mountains (Canada), between forest and transition zones. Solid circles correspond to median values with empty circles correspond to outlying data points that are beyond 1.5 times the size of the box (3rd quartile – 1st quartile). Data were not significant in the forest zone (*P*=0.38) or the transition zone (*P*=0.81).

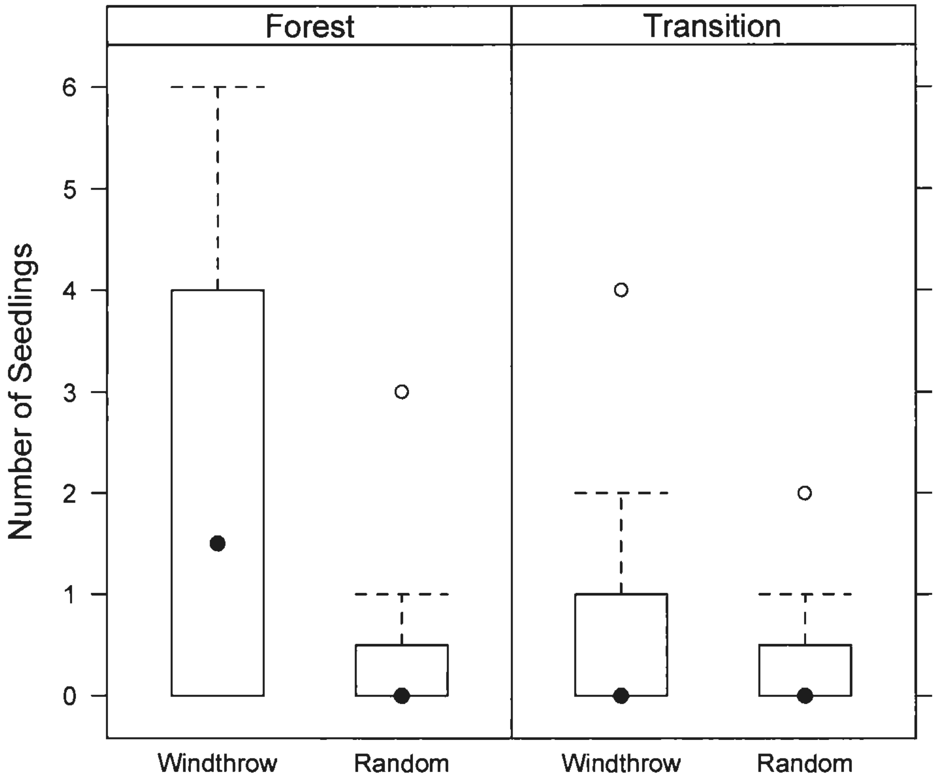


Fig. 4.10 Differences in number of seedlings (n=34) found between gaps created by windthrow and randomly selected adjacent locations in the Mealy Mountains (Canada), between forest and transition zones with a total survey area of 114.7 m^2. For both zones, significantly more seedlings were found associated with windthrows than at randomly chosen sites (*P*=0.006), with the majority of them being larch and black spruce. Solid circles correspond to median values and empty circles correspond to outlying data points that are beyond 1.5 times the size of the box (3rd quartile – 1st quartile).

Chapter 5: Ecological factors, not climate warming, explain variability in treeline patterns

Abstract

Current vegetation models predict that as climate warms, forests will replace large areas of tundra. However, observed treeline response to climate warming has been highly variable across the subarctic. Using a life history approach, we synthesized 25 datasets from 10 regions across circumpolar treeline to determine what ecological and climate factors are good predictors of treeline growth form and change. Growth form relationships for trees could not be explained by the extent of treeline warming, although shifts in growth form across treeline were detected. Using Generalized Linear Mixed Models (GLMM), we showed that ecological factors were better at predicting treeline advance and responses to these factors depended on the life history stage (seedling, sapling or adult trees) of the tree species. We found that the best predictor of whether a treeline would respond positively was treeline form (diffuse or persistent) and how close the treeline was to the ocean. Our findings also suggest that treelines with a propensity for vegetative reproduction were more likely to respond positively. However, direct estimates of climate warming (summer and winter mean temperature, growing degree-days) were not significant in predicting treeline response. Despite the assertion that treeline position is controlled by temperature, ecological factors play a significant role in

predicting treeline patterns. Our results show that ecological factors, in the context of climate change, best explain treeline patterns though continued climate warming will play a significant role in treeline migration.

5.1 Introduction

Current model projections suggest tundra vegetation is at risk of being transformed by expanding forests that are taking advantage of warmer climates (Kaplan and New 2006). The position of the ecotone between the forest and tundra, or 'treeline', is often cited as being temperature limited (e.g., Körner and Paulsen 2004) either directly (e.g., stem damage resulting from harsh growing conditions; Scott et al. 1993) or indirectly (e.g., insufficient heat accumulation needed to produce viable seeds; Sirois 2000). However, ecological factors such as fire (Brown and Johnstone 2012), herbivory (Cairns and Moen 2004, Speed et al. 2010), species-specific life history (Laberge et al. 2001), persistence (Trant et al. 2011) and facilitation (Wheeler et al. 2011) may also play a significant role in driving treeline patterns and processes. It therefore comes as no surprise that there is tremendous variability globally in treeline dynamics among and within geographic regions.

The treeline response to climate warming that is given the most attention in the literature and by the media is the poleward or upward advance (e.g., Holtmeier and Broll 2007, Berdanier 2010). However, Harsch et al. (2009) report in a meta-analysis of recent treeline studies that only just over half of the 166 sites examined show evidence of treeline advance. Furthermore, Harper et al. (2011) identified significant variability in spatial structure across the Canadian treeline emphasizing the importance of biogeographical and ecological constraints. While all treelines demarcate a physical boundary of occurrence, Harsch and Bader (2011) suggest that treeline form is important for understanding mechanisms controlling treeline position with diffuse treelines, rather than abrupt treelines, being more responsive to climate warming. The high level of variability in how treelines are structured and responding to climate warming requires further comparison of treeline responses at each life history stage (rather than just using the adult stage) to identify which stages control the rate of change. To date, this has not been done at a global scale.

Dieback related to moisture-stress and increased magnitude of disturbance has matched or exceeded climate-warming predictions in many northern forests (Soja et al. 2007). However, why has a uniform response across circumpolar treeline not been detected? Perhaps the response (i.e., treeline advance) that many studies aimed to detect has resulted in an underrepresentation of the actual treeline responses, based on the distribution of adult trees, rather than seedlings or saplings. By looking at each life history stage, it is possible to detect positive treeline responses in seedling and sapling data as evidenced by increases in density (i.e., infilling and mortality), rather than looking at all stages combined, which may not give an accurate reflection of the mechanisms driving treeline change. The term treeline advance will be reserved for the discussion of trees that are responding to recent climate warming by extending their previous range. Examining life history stages separately provides greater resolution for determining if treelines are responding and what the possible impediments may be, even in situations when they are not yet expanding or advancing.

Synthesizing 25 treeline datasets from 10 circumpolar regions, the strength of this analysis is the detailed life history data that can be examined at multiple spatial and temporal scales to determine the extent of treeline response needed to untangle whether climatic or ecological mechanisms are driving the observed patterns. This is accomplished by examining treeline response separately for seedlings, saplings and adult trees with each life history stage being compared to the appropriate length climate record and ecological factors. The objectives of this synthesis were to: (1) examine the influence of climatic factors driving differences in tree growth forms across treeline with the hypothesis that regions that have experienced more warming would have more similar growth forms between zones; (2) compare seedling and sapling densities across treeline with the hypothesis that higher levels of regeneration in the forest-tundra transition compared to forest zones would be found in regions experiencing the largest increases in recent warming; and (3) compare patterns of age structure for saplings and adult trees across treeline to identify which climatic and ecological factors are important for predicting treeline response with the hypothesis that treelines will respond positively to increases in temperature but that ecological factors, such as the propensity for vegetative reproduction, may explain the variability in how treelines are responding; and (4) combine all life history stages to determine how treelines are responding based on which climatic and ecological factors are important for predicting treeline response at any scale (seedling, sapling or adult tree) with the hypothesis that treeline response will be best predicted by climatic and not ecological factors.

5.2 Materials and Methods

5.2.1 STUDY AREAS

Data presented in this synthesis were collected between 1996 and 2009 across the circumpolar treeline including representation from the United States (Alaska), Canada, Norway, and Russia (Table A.1, Fig. 5.1). The majority of these data were collected between 2007 and 2009 as part of an international effort to document changes occurring at treeline (http://ppsarctic.nina.no/). Within Canada, treeline sites are in the Yukon (Printer's Pass and along the Dempster Highway), Northwest Territories (Inuvik), Manitoba (Churchill), Quebec (Kangiqsualujjuaq, Nunavik) and Newfoundland and Labrador (Mealy Mountains). Alaska is represented by sites in the White Mountains and the Alaska Range. Eurasian sites include Khibiny in northern Norway, the Kola Peninsula plus four additional sites in northwestern Russia (Khoseda, Rogovaya I, Rogovaya II, Seida). Site specific data have been published from Alaska (Lloyd and Fastie 2003), Churchill (Mamet and Kershaw 2012) and NW Russia (Wilmking et al. 2012) and are in preparation from sites in Inuvik, Nunavik, Mealy Mountains, Norway and Kola Peninsula.

All sites were positioned within the forest-tundra ecotone, or 'treeline', which can be subdivided into forest, forest-tundra transition, or 'transition', and tundra zones (Scott 1995). Forest zones are dominated by stems exhibiting erect growth form with varying amounts of canopy closure, depending on the region and species. Transition zones have less canopy structure and trees typically exhibit both erect and prostrate growth forms. The transition zones most often delineate the true treeline, representing the limit of individual trees growing above 2 m in height. For the purpose of these syntheses of tree physical and age structure, we exclude the tundra zone from further analyses as, by definition, it is treeless. Treeline zones were positioned along a stress gradient and captured representative forest structure and variability (Table 5.1). In most cases, the local species limit were not included in transition zones because even at abrupt treelines, individuals are often found scattered beyond treeline at low densities, commonly due to microsite topographic features (Resler 2006). Treeline form was considered: (1) 'abrupt' if stem density did not decrease gradually across treeline; (2) 'diffuse' if stem density decreased gradually across treeline; and (3) 'persistent' if tree islands or krummholz were present at treeline.

5.2.2 FIELD METHODS

All treeline sites included in this synthesis are composed of paired sites in the forest zone and the transition zone. While many of these data were collected using similar protocols (Hofgaard and Rees 2008), a summary of methods used and time periods sampled is available in Table A.1. A total of 18 treeline sites from 10 regions were included in this synthesis. The majority of sites used fixed area plots, with plotless point-centered quarters (PCQ; Cottam and Curtis 1956) used at three sites. In both cases, it was possible to quantify the area surveyed for comparison between sites.

At each site, the dominant tree species was sampled, which ranged from a single species for eight sites to a maximum of four species for one site (Mealy Mountains). Within each fixed area plot, all adult trees (height>2.0 m) were sampled for height, diameter at breast height (DBH=1.4 m) and age was determined by extracting a core from the base of each tree using an increment borer, as close to the root collar as possible. When the tree diameter was too small to use an increment borer (species-specific but generally between 3.5 – 5.0 cm), the individual was harvested and a cross-section above the root collar was obtained for aging.

At most treelines, seedlings (height<0.15 m) and saplings (height between 0.15 and 1.99 m) were sampled at the same spatial scale as the adult trees with the exception of Churchill and Mealy Mountains sites that used subplots for seedling and sapling data that were later standardized to match the other sites. Height classifications were agreed upon *a priori* to field sampling (Hofgaard and Rees 2008). For Yukon sites using PCQ, the Dempster site obtained sapling densities separately from adult trees while the Printer's Pass site measured to the closest individual, regardless of size class, which prevented the calculation of separate density values for adult trees and saplings.

5.2.3 LABORATORY METHODS

Increment cores and sections were air dried prior to processing. Increment cores were glued to grooved board and sanded using progressively fine grit until annual growth rings were visible (Stokes and Smiley 1996). In most cases, cross-sections were sanded without being glued. Annual rings were counted manually (e.g., Velmex®) or using a semi-automated program (e.g., WinDENDRO®). When the pith was missed from the sample the missing section was estimated using WinDENDRO® or approximated based on the size of the missing section.

5.2.4 DATA ANALYSIS

To understand how regional climate influences treeline dynamics, climate data were compiled from the closest long-term station to each site (Table A.2). The longest shared climate record for analyses was from 1960 to the year that samples were taken at each site, with the exception of the Yukon sites (Printer's Pass and Dempster), which had a shorter record. Growing degree-days (GDD) were calculated using a 5°C base temperature and were inferred from monthly mean temperatures. The GDD represents the biologically active period for most subarctic vegetation. Summer temperature (June, July and August), winter temperature (December, January and February) and GDD data were compiled for comparison with: (1) *seedlings* – mean values from the 10-year period before sampling and comparison of these values to the mean values from the previous 10-year period; (2) *saplings* – mean values from the period of 1986 to the year of sampling and comparison of these values to the mean values from the period of 1960-1985; and (3) *adult trees* – mean values and annual rates of change from 1960 to the year of sampling. Annual rates of change were based on slopes from linear regressions of mean summer and winter temperatures over the entire period (1960 to year of sampling).

Growth form

Height and DBH relationships were used to compare adult tree growth form between the forest and transition zones. Diameter data were not recorded at the Alaska sites and only basal diameter were recorded at the Nunavik site. Before including Nunavik diameter data, the DBH and basal diameter relationship was determined for the same species, larch [*Larix laricina* (Du Roi) K. Koch], from the Mealy Mountains site using a linear regression. This model was then used to convert basal diameter data to DBH values (Figs. A.1, A.2). For the Nunavik site, only trees <8 m in height were measured. For each region and species, linear regressions were fit to height and to DBH data. To examine the effect of climate on growth form, the slope estimates for each regression model were ordered by mean GDD. To compare the overall patterns between forest and transition zones, a *t*-test was performed on the fitted values from a generalized linear model for all regions and species combined, to determine if the slopes were significantly different from each other and hence if these height and DBH relationships were different between forest and transition zones.

Density: seedlings and saplings

Seedling densities were compiled for forest and transition zones, and compared to changes in GDD. Seedlings were also examined between forest and transition zones with the effect of stand density removed, as follows. The number of seedlings per adult tree was calculated by dividing seedling densities by the adult tree densities, at the per hectare scale. Due to low levels of seedling detectability and quick decomposition following seedling mortality, especially for first year seedlings that are within the surrounding mosses and lichens, the seedling densities reported are likely an underestimate of actual values.

Sapling densities were analyzed by looking at differences in the number of saplings per adult tree between forest and transition zones. As with seedlings, the ratio of saplings to adult trees was used to remove the effect of stand density on sapling number so that sapling number could be used as a measure of change in regeneration patterns and not just an indirect measure of stand density (i.e., sites with more adult trees are likely to have more saplings). For seedlings and saplings, higher densities in transition zones compared to forest zones are interpreted as responding or advancing treelines.

Age structure: saplings and adult trees

To compare age structure of saplings in the forest and transition zones, 5-year age class frequency distributions were used to reduce error associated with age determination while retaining resolution needed to examine patterns of recruitment. Median age values of saplings in the forest and transition zones were compared using a non-parametric Mann-Whitney test (M-W test). Sites were then categorized as either advancing or not, depending on the presence of significantly ($\alpha=0.05$) younger individuals in transition zones relative to the forest.

Adult tree age structure data included all living trees that were greater than 2 m in height. Age structures were compiled by species using 10-year age class frequency distributions to reduce error associated with age determination (Danby and Hik 2007, Caccianiga and Compostella 2012). Differences in age class frequency distributions used for saplings and adult trees was based on the assumption that saplings are generally younger and therefore less error is associated in age determination. For each site, age structures were compared between paired forest and transition zones using three statistics (Danby and Hik 2007): (1) age class distributions were compared using non-parametric Kolmogorov-Smirnov test (K-S test); (2) median age of individuals were compared using a non-parametric Mann-Whitney test (M-W test); and (3) establishment date was inferred using the five oldest individuals and compared using the M-W test. *A posteriori* comparison of establishment age in transition zones by treeline form was visualized using box and whisker plots. Transition zones that had younger median ages or were established after the forest zones were interpreted as advancing treelines.

What explains the variability in treeline response?

To predict treeline advance considering all life history stages separately and combined, a binary response variable was interpreted from seedling, sapling or adult tree data. Using all life history stages separately and combined allows for multi-scale determination of treeline advance, identifying the important climatic and ecological factors driving these patterns at different stages.

Modeling treeline variability

Binary response variables for seedlings, saplings and adult trees were fitted using Generalized Linear Mixed Models (GLMM) with a logit link function, which allow for consideration of the random effects of region and tree identity at each treeline. In all cases, tests were one-tailed since we were interested in advancing treelines. Continuous explanatory variables related to climate were: distance to ocean (km), latitude (decimal degree), elevation (m a.s.l.), mean summer and winter temperatures and GDD values, and for adult trees, annual rates of increase for summer and winter temperature and GDD values and treeline aspect (warm, cold or intermediate; c.f., Harsch et al. 2009). Related to ecological processes, the explanatory variables were: treeline type (latitudinal or altitudinal), tree form (abrupt, diffuse or persistent), dominant reproductive strategy (sexual or asexual), magnitude of natural disturbance (low, medium, high) and site soil moisture (dry, mesic, wet). For each response variable, explanatory variables were modeled separately to assess the strength of each variable on influencing treeline response and were then entered into the model based on their overall strength and removed using a backward selection approach. To assess model performance, we report the Concordance Index (C), which considers all possible pairs formed by taking one observation from each group and using the fitted model, classifies each pair (Chatterjee and Hadi 2006). The C-values range from 0.5 (model performs no better than guessing) to 1.0 (model is perfect at predicting). For significant variables in these models, we present odds ratios (with 95% confidence intervals), which are a measure of the effect size in GLMM. The odds ratio is the odds of the outcome in one group compared to the odds of it occurring in another group. When the ratio is near 1, the outcome is equally likely in each group. When the ratio approaches 0, the outcome is more likely in the first group and when the ratio becomes larger than 1, the outcome is more likely in the second group. All statistical analyses were performed in R (v. 2.14; R Development Core Team 2006).

5.3 Results

For climate data used in seedling analyses, 7/10 sites showed increases in mean summer temperature and GDD, with decreases observed at sites in Inuvik, Churchill and NW Russia (Fig. A.3). Winter mean temperature values for seedlings was highly variable, ranging from -3.6°C for the Alaska sites and -26.1°C at the Dempster site (Table A.2). For climate data used in sapling analyses, differences in mean summer temperature and GDD showed all sites experiencing increases with the highest values documented for sites in western Canada (Churchill, Dempster, Printer's Pass) and sites in the Mealy Mountains and Kola showing the least amount of increase (Fig. A.4). Winter mean temperature values for saplings ranged from -3.4°C in Alaska to -26.9°C at the Dempster site (Table A.2). For climate data used in adult tree analyses, mean summer temperatures and GDD were highest in Alaska (15.4°C/969.4 GDD) and Mealy Mountains (13.8°C/813.0 GDD) and the greatest annual rates of increase seen in Dempster (0.04°C/4.0 GDD) and Nunavik (0.01°C /3.9 GDD)(Figs. A.5, A.6; Table A.2). Sites in Alaska and Printer's Pass experienced the greatest annual rate of winter warming with mean temperatures at 0.22°C and 0.12°C, respectively (Fig. A.7; Table A.2). For adult trees, mean winter temperatures ranged from -6.9°C at the Alaska sites to -27.8°C at the Dempster site (Table A.2).

Growth form

Overall, height and DBH relationships were significant in the forest (Fig. 5.2; Adj. R^2=0.450, p<0.001) and transition zones (Fig. 5.2; Adj. R^2=0.385, p<0.001) with slopes of regression lines differing between the two zones (*t*-test: t_{1952}=14.8, *P*<0.001). Adult trees in the forest showed characteristics of true arborescent form (i.e., taller and thinner), whereas more variability in tree form was seen in transition zones (Fig. 5.2). No significant patterns were detected based on regression line slopes ordered by mean GDD from 1960 and 2010 between forest (F_8=0.0001, P=0.997) and transition zones (F_8=0.27, P=0.616; Fig. A.8), suggesting that climate alone, as expressed through mean GDD, which represents the biologically active period for trees, cannot alone explain variation in growth form relationships.

Density: seedlings and saplings

The number of seedlings per hectare was highly variable among regions and across zones, with no seedlings detected, and no apparent relationship between seedling density and recent climate warming within sites at Printer's Pass, Dempster, Inuvik and NW Russia (Fig. 5.3). For those sites where seedlings were found, there were generally more seedlings per adult tree in transition zones (n=7) compared to the forest zones (n=3). The greatest differences were seen in larch (*L. laricina*) in Churchill where two sites (RID and ROK) reported over 200 seedlings per adult tree in transition zones compared to 0 and 73 in the forest zones, respectively (Table 5.2A; Fig. 5.4). Odds ratios from GLMM indicated that diffuse treelines were far more likely to show a positive response by seedlings with the odds decreasing at more northerly latitudes (Table 5.3A). Regional and genera effects were not significant.

Twenty of 24 sites had more saplings per adult tree in transition zones than the forest zones, with values ranging from 1204.11 sapling per adult tree for black spruce in the Mealy Mountains to 0.04 saplings per adult tree for Siberian spruce in NW Russia while the opposite pattern was seen for the remaining four sites, with more saplings per adult tree in the forest zones with values ranging from 49.17 for larch in Churchill to 0.16 for white spruce in Alaska (Table 5.2B; Fig. 5.5). Lower latitude sites were more likely to have increased saplings per adult tree in transition zones, and though not significant, in treelines that reproduced predominantly by layering (Table 5.3B). Regional and genera effects were not significant.

Age structure: saplings and adult trees

The median age of saplings was significantly different between zones in 10/20 sites with 6 sites having older saplings in transition zones and 4 sites having older saplings in the forest zones (Table 5.2C; Fig. 5.6). Treeline response based on sapling age was not well explained by the climatic or ecological factors included in the models.

For all regions, adult trees were significantly younger in transition zones compared to forest zones (t-test: t_{3110}=24.4, P<0.001) with the three oldest trees located in the forest zones: (1) 503-year old white spruce in Monahan, Alaska; (2) 450-year old Siberian spruce in Rogovaya II, NW Russia; and (3) 430-year old white spruce in Churchill. Approximately 1/3 of the sites each had the younger median-tree age in transition zones, the forest zones, or showing no significant difference (Table 5.2D). Treeline response based on age of adult trees was not well-explained by the climatic or ecological factors, though latitudinal treelines seemed more likely to show an advancing treeline than altitudinal treelines.

Within 14/25 sites, establishment dates for adult trees suggested that transition zones established more recently than forest zones, 2/25 sites showed more recent establishment of forest zones, and there was no significant difference between forest and transition zones at 9/25 sites (Table 5.2E). Persistent treeline sites are older (median age=160 years) than diffuse-treeline sites (median age=110 years), suggesting that persistent treelines established before diffuse treelines (Fig. 5.7).

What explains the variability in treeline response?

Combining all life history stages, 20 of the 25 treelines studied showed evidence of change, with either a response (infilling with more seedlings or saplings in transition zones compared to the forest zones), or advance (adult trees being younger or more recently established in transition zones compared to the forest zones). In comparison, only 12 of 25 treelines showed evidence of a response or advance if only adult trees were considered. Combining all life history stages, diffuse treelines were more likely to respond positively and the odds of responding positively decreased when treelines were further from the ocean. Regional and genera effects were not significant.

5.4 Discussion

Ecological factors, not direct climate parameters, better explain variability in treeline response, and at identifying *which* and *how* treelines are changing. By looking at growth forms and different life history stages, we were able to identify the factors important in influencing treeline change and equally noteworthy, which factors were not important. Although we did not find evidence that treelines were directly influenced by seasonal or annual temperatures, we recognize that the positive response in seedlings, saplings and adult trees is in large part due to the direct and indirect effects recent climate warming has on ecological processes.

Growth form

Growth form of adult trees varied between forest and transition zones, with shorter and thicker diameter trees characteristic of transition sites, a result we expected given that treelines were classified as diffuse or persistent with no sites being classified as abrupt. We also observed greater variability in growth form in transition zones than in forest zones. We documented a general pattern of warmer sites, indicated by more GDD, having fewer stunted adult trees, though sites in Norway and Printer's Pass deviated from this pattern due to more prostrate growth forms.

If adult trees are responding to climate warming by increased height and radial growth, changes to the height and DBH relationship may not be sensitive enough to detect these changes, especially for old trees (>100 years) given the relatively small contributions that increased radial growth would have on the trees' overall diameter. More likely, this shift in growth form would be seen best in subsequent generations of trees if indeed the warming conditions manifest in higher growth rates. Others, however, have documented shifts in growth form by comparing the ages of single to multi-stemmed trees at treeline (Devi et al. 2008), but not as a function of height and DBH relationships. Further complicating growth-form relationships is the decoupling of temperature and radial growth patterns reported from treelines in Alaska (Wilmking et al. 2004) and across a moisture gradient in Northeastern Canada (Trindade et al. 2011), which would further detract from shifts in height and DBH relationships.

Climatic factors, such as wind and snow depth, could be driving the variability in growth form (Pereg and Payette 1998), as increases in tree height that result from recent warming may not be sufficient to exceed dieback due to winter abrasion, though few dead trees in the transition suggest that this is not the case. Another factor to consider is that many treelines reproducing predominantly by layering typically had more prostrate growth forms in transition zones (solid symbols; Fig. 5.2). This suggests that some of the variability seen in transition zones may be driven by different reproductive strategies. Climatic and ecological conditions in transition zones may prevent individuals from reproducing sexually, thus they predominately reproduce by layering, if possible. Overall, growth forms were only partially explained by climate, perhaps due to the magnitude of change required to shift growth forms, compounded by the growing evidence of decoupling temperature and growth relationships. Site-specific growing conditions and ecological plasticity of species may be key in understanding potential shifts in growth form (Aitken et al. 2008).

Density: seedlings and saplings

Seedling densities were highly variable across regions with less than half of the sites having no seedlings in the forest or transition zones. Substrate quality may constrain seedling establishment at treeline (Wheeler et al. 2011, Brown and Johnstone 2012), depending on the species-specific requirements. The absence of seedlings at these sites may also be partially explained by seedlings being difficult to differentiate from surrounding vegetation; but, even if values were underreported, the relative patterns would remain the same. Also, based on the notion that adult tree density decreases across treeline, we were surprised to see that for absolute seedling densities or the number of seedlings per adult tree, many of the treelines had more seedlings in transition zones compared to the forest zones. While we hypothesized that this positive seedling response would be seen more often in sites that were experiencing greater rates of summer or winter warming, we found no such evidence. Instead, we found that diffuse treelines were more likely to show a positive response than persistent treelines, which supports the findings of Harsch and Bader (2011). Persistent treelines may have established when the site conditions were more suitable for seedling recruitment. In comparison, diffuse treelines generally established more recently, and could be more in equilibrium with current climate and therefore are more likely to have higher seedling densities (Fig. 5.7).

Treelines with positively responding seedling densities were more likely to occur in lower latitude sites. If seed viability is limited across treeline (Sirois 2000), more southern sites would be able to reach GDD requirements more readily than northern treelines, thus, producing more seedlings. Factors influencing the life trajectory from seed to seedling could be crucial for understanding observed mismatch among sites that show high levels of seed production but limited recruitment, perhaps due to a combination of insufficient GDD to fill seeds and high levels of pre- and post-dispersal seed predation (Wheeler et al. 2011, Jameson

2012). However, GDD were not identified as an important factor in predicting seedling response. Without any direct influence of recent climate parameters on seedling densities and without specific data on seed viability, ecological factors such as seedbed availability and seedling mortality should be explored to better explain the observed patterns.

We found a positive treeline response of increased regeneration in transition zones, indicated by the occurrences of more saplings per tree in transition zones than forest zones and higher sapling densities more likely in sites at lower latitudes. Though not statistically significant, sites that were reproducing predominantly by layering were more likely to have a greater number of saplings in transition zones. Because none of the climate parameters were useful in predicting higher sapling densities in transition zones, the observed pattern may be explained by a light release that results from decreased canopy closure in diffuse and persistent treelines. This ecological explanation could stimulate infilling of saplings via seed as suggested by the increases in seedling density, or as our other findings suggest, sites with higher sapling density treelines could be partially explained by the higher prevalence of layering.

Age structure: saplings and adult trees

Unlike densities, age structure of saplings had fewer positively responding treelines, and we were unable to predict sites with younger saplings in transition zones using the climatic and ecological factors. Discrepancies in response for density and age of saplings (i.e., more, but generally older saplings in transition zones), suggest that layering, especially in transition zones, may be underestimated and perhaps plays a significant role in driving regeneration dynamics (Rossi et al. 2009). As a result, individuals originating from layering are likely underestimated since they can be many decades old when the layer is initiated, a type of 'sit and wait' strategy. Recent climate warming may allow adult trees to produce more biomass, which could result in increased layering. However, vegetative reproduction alone is not sufficient for landscape-scale forest expansion into tundra ecosystems. Thus, increased sapling density is not necessarily indicative of anything more than local stand infilling. In contrast, warmer temperature, if accompanied by soil moisture deficit, could have the opposite effect on sapling density by removing cool and damp conditions most conducive to layering (Greene et al. 2007). With life history stages determined by height and not age, we have found that differences in growth form patterns between the forest and transition zones result in a bias towards older trees being classified as saplings in transition zones.

Age structure of adult trees, based on differences in median age and date of establishment, were not well predicted by climatic and ecological factors. Establishment within zones was more sensitive as an indicator for advancing treelines than using median age, though it is likely that they are actually representing treeline advance at different temporal scales. Because the oldest trees in each zone were used to estimate when each zone was established, the treeline advance that is actually being reported occurred centuries ago as many of the sites had trees over 300 years of age. Other metrics of age structure, such as median age, offer insight into more current patterns of advance since this metric considers more recently established trees. Because trees are long-lived, and once established can have very low mortality rates, age structure may not capture recent changes in treeline dynamics and is best paired with other life history stages that may be more sensitive to recent change.

What explains the variability in treeline response?

Considering all life history stages together, we found that diffuse treelines closer to oceans were the most likely to show a positive response. Treelines that had predominant layering had better odds of responding positively, though not significantly so. Whether life history stages were examined independently or together, direct measures of regional climate and changes in climate did not influence whether treelines responded positively. The strongest climatic factor influencing treeline response was how far treelines were from the ocean. Oceanic climates are typically more temperate with lower chances of summer moisture deficits, reducing the likelihood of drought stress for tree species.

Ecological factors associated with treeline form, and the propensity for layering, were associated with positively responding treelines. Treeline form is indirectly influenced by climate but species ecology also plays a large role in defining tolerance limits, optimal growth conditions and form plasticity; all of which will contribute to an individual's persistence and response potential.

Examining life history stages separately and combined, we were able to rule out the direct climatic influences for each stage rather than diluting a potentially significant result. We also expected that the scale of response would be related to the extent of change to temperature and GDD, especially for seedlings, but this was not the case. Instead our results show that different life history stages are more influenced by ecological and biogeographical factors. Finally, with no regional or genera effects detected in any of the models, we are confident that our findings are representative of circumpolar treeline dynamics. While we acknowledge that, at broad spatial scales, treeline position may be controlled by temperature, we show that ecological factors are significant in understanding treeline dynamics. We expect that continued climate warming will become significant for treeline migration but until this threshold is passed, our results show ecological considerations drive treeline patterns.

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Table 5.1 Regional treeline characteristics for paired forest zones (F) and transition zones (T). Missing values represent sites where basal area was not calculated.

Region	Site	Treeline Type	Treeline Form	Treeline Elevation (m a.s.l.)	Individuals Sampled (n)		Plot Size (m²)		Density (trees/ha)		Basal Area (m²/ha)	
					F	T	F	T	F	T	F	T
Alaska^+	12 Mile	Altitudinal	Diffuse	945	131	87	4200	9000	312.0	87.0	0.74	0.01
	Eagle	Altitudinal	Diffuse	945	274	15	2000	2000	1370.0	75.0	0.52	0.04
	Usibelli	Altitudinal	Diffuse	760	65	5	1200	1200	3108.0	2633.0	N/A	N/A
Printer's Pass#*	North	Altitudinal	Diffuse	700	48	93	PCQ	PCQ	576.7	218.8	80.40	20.14
	South	Altitudinal	Diffuse	700	43	90	PCQ	PCQ	600.7	176.4	84.60	35.18
Dempster#*		Latitudinal	Persistent	550	288	93	PCQ	PCQ	745.9	207.2	2.80	0.28
Inuvik^*		Latitudinal	Persistent	20	54	88	625	11250	864.0	127.5	3.28	0.66
Churchill^+	BLK	Latitudinal	Diffuse	38	64	47	300	345	2133.3	1362.3	13.63	2.84
	RID	Latitudinal	Diffuse	22	66	51	699	204	944.2	2500.0	5.59	5.52
	ROK	Latitudinal	Diffuse	16	50	56	750	1200	666.7	466.7	23.21	0.29
Nunavik^*		Altitudinal	Diffuse	60	212	190	3200	25600	662.5	74.2	3.79	0.11
Mealy Mts.^*		Altitudinal	Persistent	550	250	122	1000	4600	2500.0	256.2	23.81	1.84
Norway^+		Altitudinal	Diffuse	450	179	80	7500	42500	224.0	18.4	4.42	0.21
Kola^+		Altitudinal	Diffuse	390	50	271	N/A	30000	N/A	83.7	N/A	0.03
NW Russia^+	Khoseda	Latitudinal	Diffuse	127	24	47	225	450	1066.7	1044.4	20.48	8.27
	Rogovaya I	Latitudinal	Diffuse	75	35	11	225	225	1555.6	488.9	17.11	N/A
	Rogovaya II	Latitudinal	Diffuse	73	39	20	225	225	1733.3	888.9	67.75	N/A
	Seida	Latitudinal	Diffuse	85	10	12	225	225	444.4	533.3	N/A	N/A

#density calculated from point-centered quarter (PCQ) plots
^density calculated from fixed area plots
*basal area calculated using basal diameter measurements
+basal area calculated using DBH measurements

Table 5.2 Comparison between forest zones (F) and transition zones (T) for: (A) change in seedling (height<0.15 m) density (T-F); (B) change in sapling (height between 0.15 and 1.99 m) density (T-F); (C) median age of saplings (5-year age class frequency distributions; M-W test); (D) median age of adult trees (height>2.0 m; 10-year age class frequency distributions; M-W test); and (E) adult tree establishment date (M-W test). Species codes are PIMA=black spruce (*P. mariana*), PIGL=white spruce (*P. glauca*), PISY=Scots pine (*P. sylvestris*), LALA=larch (*L. laricina*), ABBA=balsam fir (*A.* balsamea) and PIOB=Siberian spruce (*P. obovata*).

Region	**Site**	**Species**	**A) Δ Seedling Density (stems/ha)**	**B) Δ Sapling Density (stems/ha)**	**C) Sapling Median Age**	**D) Tree Median Age**	**E) Tree Establishment**
Alaska	12 Mile	PIGL	0	0.33	***P*=0.01**^{T}	*P*=0.44^{F}	***P*=0.04**^{F}
	Eagle	PIGL	0	0.26	***P*=0.021**^{T}	*N/A*	*P*=0.46^{F}^
	Usibelli	PIGL	1	-0.16	***P*<0.01**^{F}	*N/A*	***P*=0.01**^{F}
Printer's Pass	North	PIGL	0	8.71	*P*=0.21^{T}	*P*=0.34^{FT}	*P*=0.13^{T}
	South	PIGL	0	5.78	*P*=0.78^{T}	*P*=0.78^{FT}	*P*=0.11^{F}
Dempster		PIMA	0	-0.32	*N/A*	***P*=0.01**^{T}	***P*=0.01**^{T}
Inuvik		PIGL	0	0.16	*P*=0.84^{F}	***P*<0.01**^{T}	***P*=0.01**^{T}
Churchill	BLK	LALA	6	1.38	***P*<0.01**^{T}	*P*=0.21^{T}	*P*=0.40^{T}
	BLK	PIGL	19	15.45	*P*=43^{F}	*N/A*	*N/A*
	BLK	PIMA	38	-4.77	***P*=0.02**^{T}	***P*<0.01**^{T}	*P*=0.14^{T}
	RID	PIGL	172	0.15	*P*=0.24^{F}	***P*<0.01**^{F}	***P*=0.01**^{F}
	RID	LALA	5	-49.17	*P*=0.75^{T}	*N/A*	*N/A*
	ROK	PIGL	-1	12.79	***P*=0.01**^{F}	***P*<0.01**^{F}	***P*=0.01**^{F}
	ROK	LALA	222	1.38	*N/A*	*N/A*	*N/A*
Nunavik		LALA	0	0.42	***P*=0.03**^{F}	*P*=0.34^{FT}	***P*=0.03**^{F}
Mealy Mts.		ABBA	-31	5.99	***P*<0.01**^{T}	***P*=0.05**^{T}	*P*=0.13^{T}
		LALA	-6	*N/A*	N/A	***P*<0.01**^{T}	*P*=0.15^{T}
		PIGL	0	95.15	*N/A*	*P*=0.14^{T}	***P*=0.06**^{F}
		PIMA	11	1204.11	*P*=0.37^{F}	*P*=0.17^{T}	***P*=0.01**^{F}
Norway		PISY	0	0.40	***P*<0.01**^{F}	*P*=0.92^{FT}	***P*=0.01**^{F}
Kola		PISY	N/A	0.89	***P*<0.01**^{T}	***P*=0.01**^{F}	*P*=0.25^{F}
Russia	Khoseda	PIOB	0	0.04	*P*=0.46^{T}	*P*=0.15^{F}	*P*=0.31^{F}
	Rogovaya I	PIOB	0	0.31	*P*=0.44^{T}	***P*=0.05**^{*F}	***P*=0.01**^{F}
	Rogovaya II	PIOB	0	0.56	*P*=0.43^{F}	*P*=0.15^{F}	***P*=0.01**^{F}
	Seida	PIOB	0	0.68	*N/A*	*N/A*	***P*=0.01**^{F}

^includes trees of all age classes including saplings, **bolded** values are at least moderately significant (p<0.10)

$^{\text{F or T}}$ Specifies zone has older median age or established first

Table 5.3 Influence of climate and ecological variables using Generalized Linear Mixed Models (GLMM) with a logit link function on treeline, A) seedling response, B) sapling response and C) for all life history stages combined. There were no regional or species effects detected

	Odds ratio [95% CI]	**df**	**Wald Z**	***P***	***C***
A) Seedling response (density)				**0.02**	**0.89**
Treeline form	88.73 [1.00, 7870.00]	2	-2.31	0.02	
Latitude	0.63 [0.40, 1.00]	2	-2.26	0.02	
B) Sapling response (density)				**0.06**	**0.89**
Latitude	0.58 [0.33,0.99]	2	-1.85	0.06	
Non-significant variables					
Sexual or asexual		2	-1.29	0.19	
C) Treeline response (combined)				**0.08**	**0.90**
Treeline form	60.46 [0.99, 3672.85]	3	2.17	0.03	
Distance from ocean	0.99 [0.98,1.00]	3	-1.90	0.06	
Non-significant variables					
Sexual or asexual		3	-1.42	0.15	

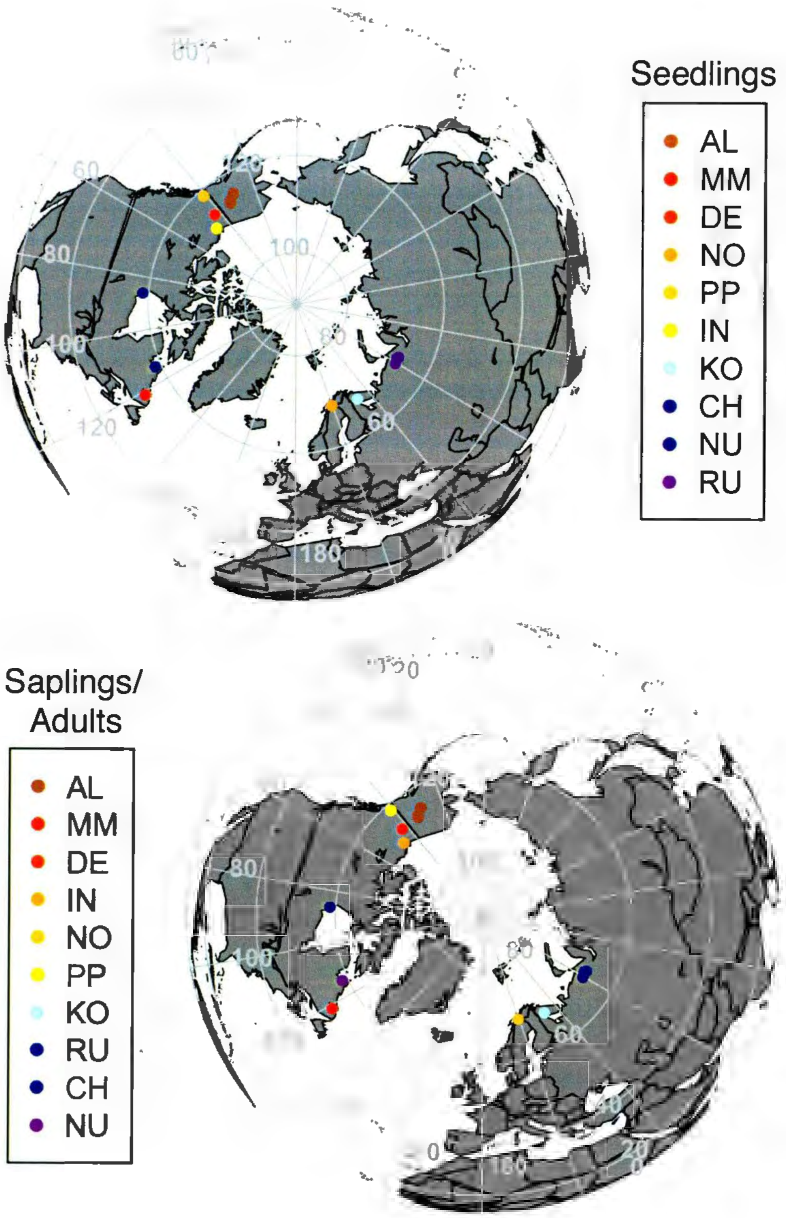
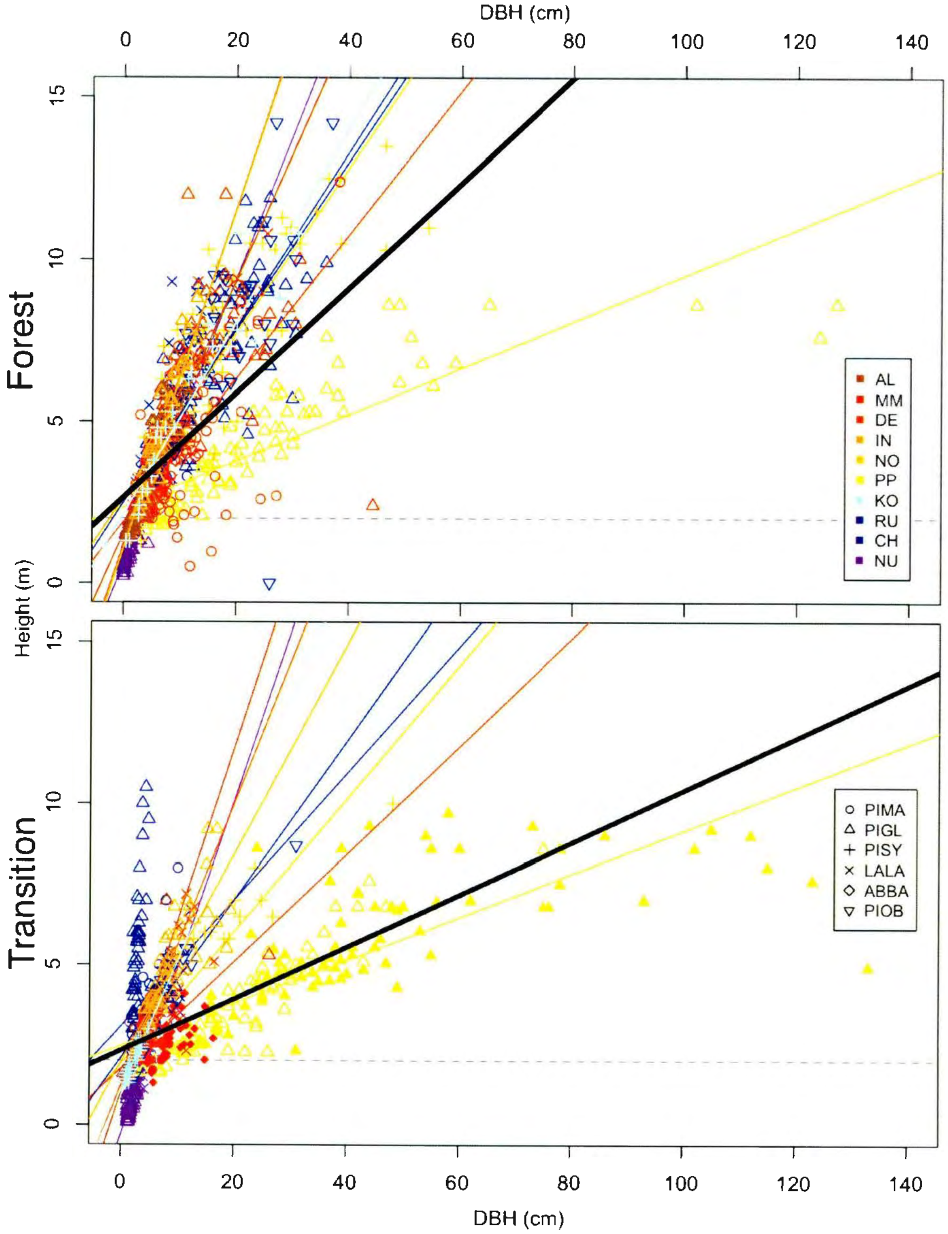


Fig. 5.1 Circumpolar map showing 10 regions with colour ordered by changes in growing degree-days (1990-2010 compared to 1960-1989) with warmer colours representing larger increases and cooler colours representing smaller increases (see Fig. 5.2 for values). Site codes are: AL=Alaska, PP=Printer's Pass, DE=Dempster, IN=Inuvik, CH=Churchill, NU=Nunavik, MM=Mealy Mountains, NO=Norway, KO=Kola, RU=NW Russia.



DBH (cm)
0
20
40
60
80
100
120
140
Forest
Transition
Height (m)
0
5
10
15
AL
MM
DE
IN
NO
PP
KO
RU
CH
NU
PIMA
PIGL
PISY
LALA
ABBA
PIOB

Fig. 5.2 Adult tree height by diameter relationships separated by forest (upper) and transition (lower). Sites ordered by mean GDD from 1960 to year of sampling. Grey dashed line represents sampling cut-off for adult trees (2 m). The black line for each zone represents the linear regression for all regions combined that are significant for the forest zone (F=1141, df=1283, $p<0.001$, Adjusted R^2=0.470), for the transition zone (F=616, df=939, $p<0.001$, Adjusted R^2=0.395) and were significantly different from each other (t-test: t_{1952}=14.8, $P<0.001$). In order of greatest to least rate of change for GDD, the site codes are: DE=Dempster, PP=Printer's Pass, NU=Nunavik, CH=Churchill, MM=Mealy Mountains, NO=Norway, IN=Inuvik, AL=Alaska, RU=NW Russia and KO=Kola. Species codes are PIMA=black spruce (*P. mariana*), PIGL=white spruce (*P. glauca*), PISY=Scots pine (*P. sylvestris*), LALA=larch (*L. laricina*), ABBA=balsam fir (*A.* balsamea) and PIOB=Siberian spruce (*P. obovata*). Filled in symbols represent those zones where asexual reproduction (i.e., layering) was the predominant form reproduction.

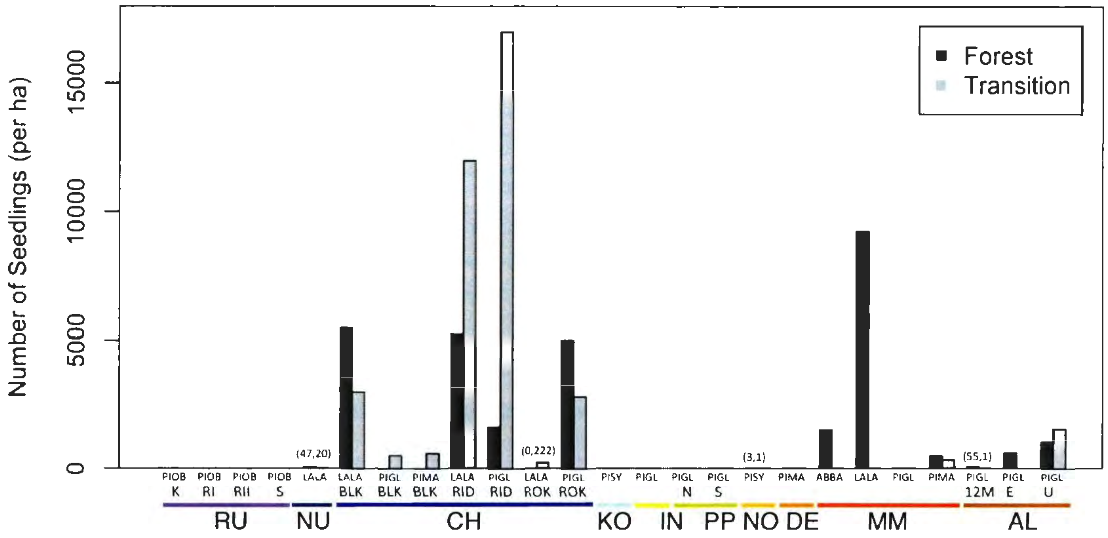


Fig. 5.3 Seedling densities per hectare in forest and transition zones ordered from left to right by extent of change in GDD from the 10 years prior to seedling counts to the previous 10 years (e.g., 1997 to 2007 – 1987 to 1996). In order of least to greatest change in GDD (see Seedlings legend in Fig. 5.1), the sites codes are: IN=Inuvik, RU=NW Russia, CH=Churchill, DE=Dempster, PP=Printer's Pass, KO=Kola, NU=Nunavik, NO=Norway, AL=Alaska, MM=Mealy Mountains. Species codes are PIMA=black spruce (*P. mariana*), PIGL=white spruce (*P. glauca*), PISY=Scots pine (*P. sylvestris*), LALA=larch (*L. laricina*), ABBA=balsam fir (*A. balsamea*) and PIOB=Siberian spruce (*P. obovata*). When needed to differentiate, abbreviated site codes are included from Russia (K=Khoseda, RI=Rogovaya I, RII=Rogovaya II), Churchill (BLK, RID, ROK) and Alaska (12M=12 Mile, E=Eagle, U=Usibelli).

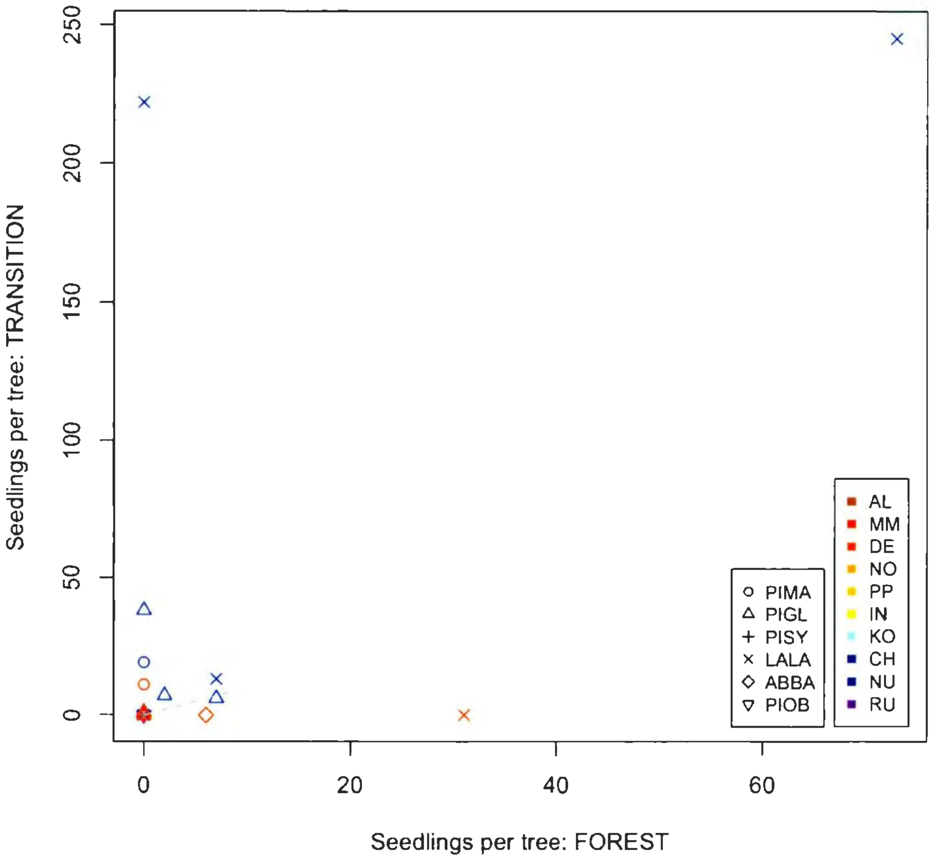
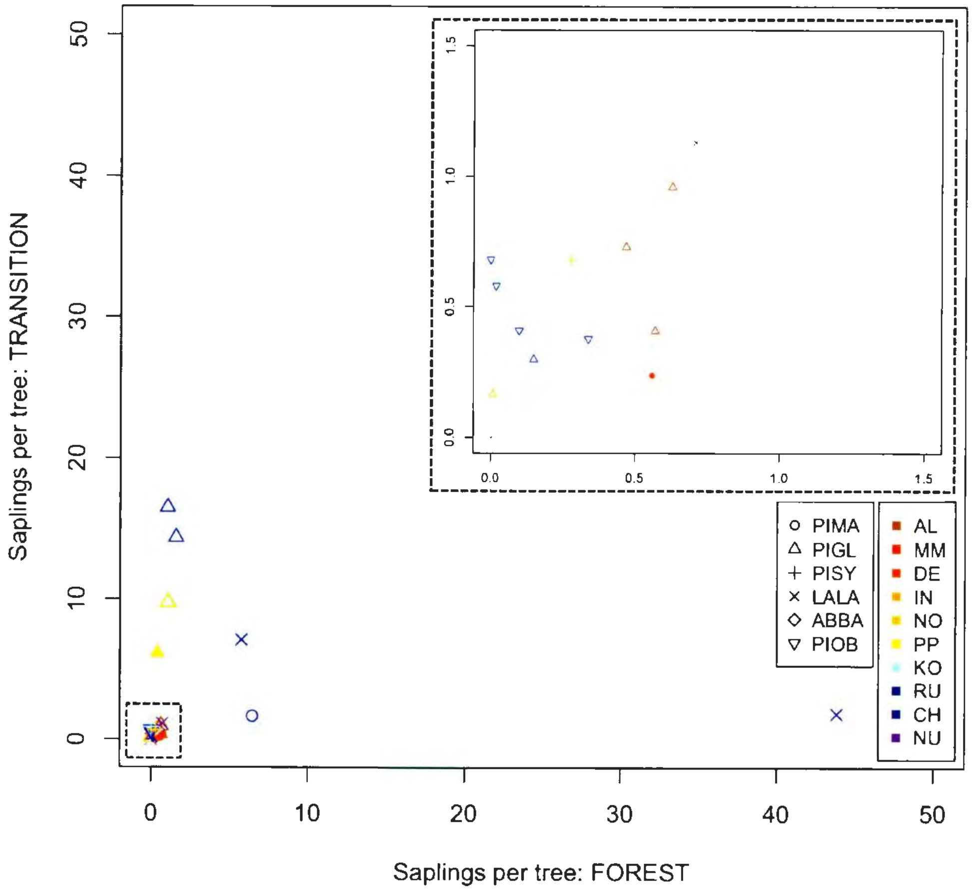


Fig. 5.4 Comparison of seedlings per adult tree between the forest and transition zones across all regions. Grey dashed line has a slope of 1. All symbols above the grey dashed line represent sites that have greater seedling densities in transition compared to forest zones, suggesting higher reproductive potential. Site codes are: AL=Alaska, PP=Printer's Pass, DE=Dempster, IN=Inuvik, CH=Churchill, NU=Nunavik, MM=Mealy Mountains, NO=Norway, KO=Kola, RU=NW Russia. Species codes are PIMA=black spruce (*P. mariana*), PIGL=white spruce (*P. glauca*), PISY=Scots pine (*P. sylvestris*), LALA=larch (*L. laricina*), ABBA=balsam fir (*A.* balsamea) and PIOB=Siberian spruce (*P. obovata*).



Saplings per tree: TRANSITION
Saplings per tree: FOREST
0
10
20
30
40
50
0.0
0.5
1.0
1.5
○ PIMA
△ PIGL
+ PISY
× LALA
◇ ABBA
▽ PIOB
■ AL
■ MM
■ DE
■ IN
■ NO
■ PP
■ KO
■ RU
■ CH
■ NU

Fig. 5.5 Comparison of saplings per adult tree between the forest and transition zones across all regions. Outliers were removed from visualizations (MM_{PIGL}: *F*=0, *T*=96.1, MM_{PIMA}: *F*=4.5, *T*=1208.9). Grey dashed line has a slope of 1. All symbols above the grey dashed line represent sites that have greater sapling densities in transition compared to forest zones, suggesting higher reproductive potential. Site warming index of growing degrees days (see Fig. 5.2) is ordered by extent of warming. Site codes are: AL=Alaska, PP=Printer's Pass, DE=Dempster, IN=Inuvik, CH=Churchill, NU=Nunavik, MM=Mealy Mountains, NO=Norway, KO=Kola, RU=NW Russia. Species codes are PIMA=black spruce (*P. mariana*), PIGL=white spruce (*P. glauca*), PISY=Scots pine (*P. sylvestris*), LALA=larch (*L. laricina*), ABBA=balsam fir (*A.* balsamea) and PIOB=Siberian spruce (*P. obovata*). Filled in symbols represent those zones where asexual reproduction (i.e., layering) was the predominant form reproduction.

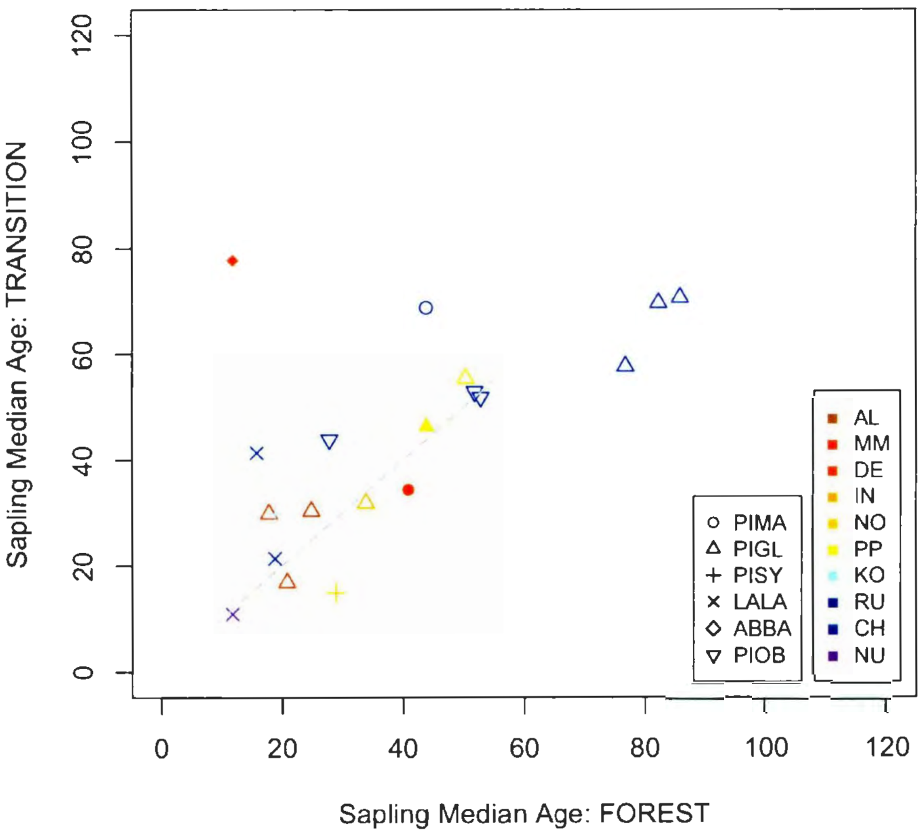


Fig. 5.6 Comparison of median age for all saplings (0.15-1.99 m) in the forest and transition zones across all regions. Grey dashed line has a slope of 1. All symbols above the grey dashed line represent sites that have greater median sapling age in transition compared to forest zones. Site warming index of growing degrees days (see Fig. 5.2) is ordered by extent of warming. Site codes are: AL=Alaska, PP=Printer's Pass, DE=Dempster, IN=Inuvik, CH=Churchill, NU=Nunavik, MM=Mealy Mountains, NO=Norway, KO=Kola, RU=NW Russia. Species codes are PIMA=black spruce (*P. mariana*), PIGL=white spruce (*P. glauca*), PISY=Scots pine (*P. sylvestris*), LALA=larch (*L. laricina*), ABBA=balsam fir (*A.* balsamea) and PIOB=Siberian spruce (*P. obovata*). Filled in symbols represent those zones where asexual reproduction (i.e., layering) was the predominant form reproduction.

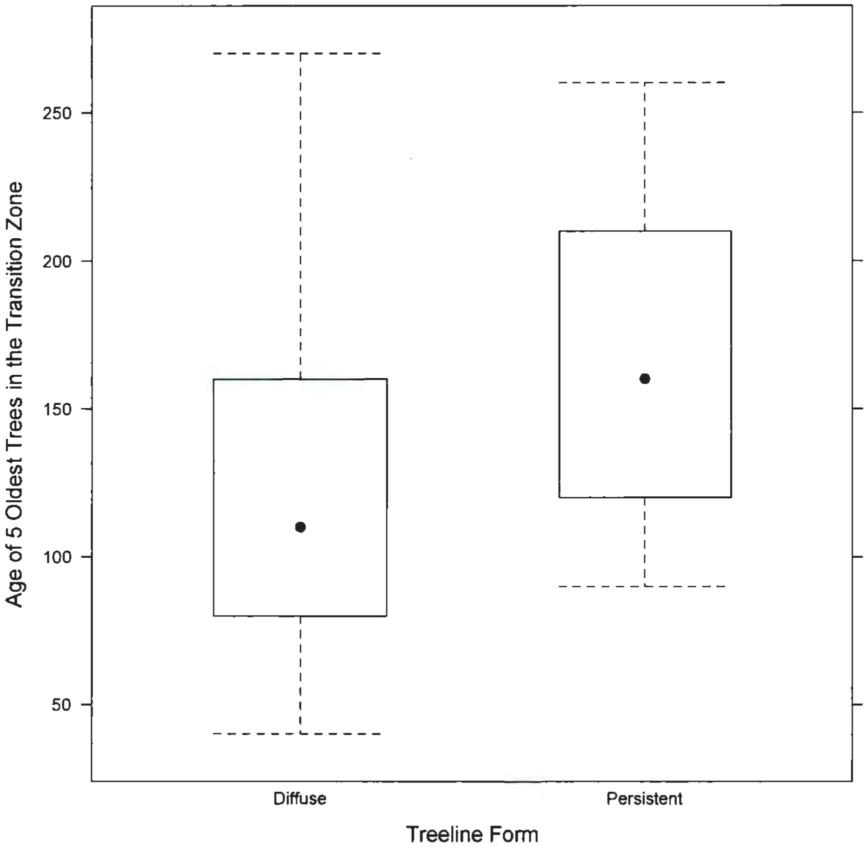


Fig. 5.7 Comparison of transition zone establishment dates between diffuse and persistent treelines based on 10-year age class frequency distributions of the 5 oldest trees per site. Solid circles correspond to median values with the box representing the 1st and 3rd quartile.

Chapter 6: Teaching and learning about climate change with Innu Environmental Guardians

Abstract

Impacts related to climate change are commonly reported in northern Canada. Labrador Innu have a multi-millennial history in this area, putting them in a good position to document and interpret these changes. Western Science monitoring initiatives are commonplace throughout northern areas and offer one approach for answering questions related to ecosystem change. Since 2001, the Innu Environmental Guardians Training Program has offered modules covering topics including fisheries, caribou, archaeology, and most recently on climate change and forest ecosystems. This paper provides an approach for detecting changes to the boreal forests of Labrador using empirical monitoring protocols that were determined in consultation with Labrador Innu and university-trained scientists, which ultimately led to the establishment of Innu Permanent Sample Plots (IPSP). In our experience facilitating these modules, much has been learned regarding the importance of culturally appropriate place and module content. Challenges encountered throughout the modules, including sustaining attendance, dealing with remote locations and attention to accuracy and precision, are explored. In our experience, the establishment of long-term monitoring plots with continued Innu

involvement will go far in bettering our understanding of how the boreal forests of Labrador are responding to climate change.

6.1 Introduction

In northern Canada, impacts related to climate change are being observed in most aspects of the natural environment (IPCC 2007). Both empirical studies and local knowledge are showing shifts in patterns that have persisted through recent memory. From berry productivity to sea ice coverage, there is a growing body of knowledge showing that the climate of the arctic and subarctic is changing (ACIA 2005). In Labrador, there has been an increase in summer surface air temperatures by 1.0°C to 1.5°C in the past decade (2000-2010), compared to the previous 30-year period (1970-2000) (Bell et al. 2008, Environment Canada 2011). This recent warming has important implications for the resources and people of Labrador.

It is recognized that forest ecosystems in the boreal region are particularly vulnerable to climate change, with major shifts expected within a century as global temperatures rise (Fischlin et al. 2007). For central Labrador, climate scenarios for the 2050s show winter temperatures warmer by 3 to 4°C and spring, summer and fall by 2 to 3°C, with precipitation increasing by 10 to 20%, relative to late 20th century climate baseline averages (Lemmen et al. 2008). With these changes one can expect more fall and winter rainfall events, later freeze-up and earlier break-up of water bodies, an earlier peak in spring runoff, but reduced summer streamflow due to increased evaporation and transpiration. Wildfire frequency and area burned can be expected to increase as well (Flannigan et al. 2005). The effects of such changes on forest ecosystems will include changes in phenology (Körner and Basler 2010) and potentially higher productivity, offset by effects of increased insect herbivory and disease (Fischlin et al. 2007).

In Labrador, trees are being supported across ecoregions ranging from high boreal forest to high subarctic tundra (Meades 1989). As a result of this variability, the forests play a diverse role in providing habitat, shelter and sustenance for the animals and people of Labrador. As climate warms, shifts in the number of growing degree-days, seasonal temperature extremes and length of growing seasons are all contributing to trees having the potential to establish and persist beyond their historic range limits. Some species can track suitable climate poleward (e.g. Malcolm et al. 2002, Thomas 2010), but in many other cases the responses are more subtle. Shifts in species growth rates (Trant et al. 2011) and productivity (Lévesque et al. 2012) are some of the early responses being documented for Labrador. For Labrador Innu, and many other northern peoples, the concern with climate change is focused primarily on the quality, quantity and access to renewable resources (Bell et al. 2008).

Innu occupation of Labrador extends at least 6000 years across much of inland and coastal regions (Tuck 1975, Loring 1992). Throughout this multi-millennial history, ecological processes and seasonality have become incorporated into Innu culture. Innu synchronicity with migratory resources allows for changes to be detected in the abundance and timing of these resources. However, changes like shifts in vegetation community composition, tree growth and soil/air temperature can be more difficult to detect due to the vastness of the Labrador landscape but these base components of the ecosystem will play a fundamental role in how the rest of the ecosystem will respond.

In terms of resources, Labrador Innu depend on many species of animals and plants throughout the year. For animals, the migratory woodland caribou (George River Herd) have long played a dominant role in the seasonal movement patterns and diet of Labrador Innu. Climate variability and change play a central causal role in the numbers and distribution of caribou in Labrador. Caribou are particularly vulnerable to changes in winter precipitation patterns as they affect forage availability (Couturier and Brunelle 1990, Jacobs et al. 1996, Jeffery 2008). In terms of plants, berry picking is an important cultural activity with berries representing a significant component of peoples diet (Armitage 2011). While warmer temperatures can result in increased plant growth (e.g., Kelly and Goulden 2008, McMahon et al. 2010), other factors such as increased variability in temperature extremes and summer moisture deficits may play a significant role in decreasing fruit set (Bokhorst et al. 2008) and net primary productivity (Zhao and Running 2010). Detection of ecosystem change requires extensive knowledge and landscape-specific experience (Lauer and Aswani 2010). When the objective is to detect long-term changes, one Western Science approach, henceforth referred to as 'Science', is to use monitoring programs to address specific questions and concerns. Science places value and importance on research questions and outcomes despite being perceived by many (including Science practitioners) as being objective. While often thought of as a method for uncovering universal truths, what the scientific method offers is a possible explanation for observed phenomena. When Science is perceived as being universal, it has the potential to displace or discredit other knowledge systems (Snively and Corsiglia 2001). Science is perhaps better seen as one approach that enables the answering of questions but still incorporates subjectivity when identifying what questions to ask. From a Science perspective, Indigenous Knowledge can direct these questions and identify important components to focus on when assessing the extent of ecosystem change. This is not to say that Indigenous Knowledge is incorporated into Science but rather that there would be communication between these different but complementary knowledge systems (Huntington 2000, Aikenhead 2001).

The purpose of this paper is to provide an overview of the climate change modules and a discussion focusing on the successes and shortcomings of these modules. This paper will begin with an overview of the Innu Environmental Guardians Program, which provides the framework for climate change monitoring initiatives followed by an examination of monitoring ecosystem change across the Labrador landscape. The successes and challenges of this monitoring initiative will be presented followed by possibilities for moving forward with future work.

6.2 Innu Environmental Guardian Training Program

The Innu Guardian Program began in 1992 in partnership with the Innu Nation and the Department of Fisheries and Oceans. In 1997, the Gorsebrook Research Institute at Saint Mary's University (GRI/SMU) in Halifax became involved when the federal environment department, Environment Canada, began collaborating with the Innu Nation (First Nation) of Labrador and social scientists from the GRI/SMU. The initial goal was to create a comprehensive baseline of ecological data of the Labrador landscape from both Innu Knowledge and Science perspectives, acknowledging the difficultly in establishing baselines in ever-changing environments. To provide an initial focal point for research, consultations were held with members of the Innu community to identify an aspect of the landscape that was deemed culturally significant and distinct. The landscape feature the Innu chose was *ashkui,* areas of open water in the river and lake ice where Innu camped every spring for subsistence and cultural livelihood activities, giving rise to what was referred to as the *Ashkui Project*. Funding for this research was primarily through the Environment Canada's Northern Ecosystems Initiative and Environment Canada, Atlantic Region (Sable et al. 2007).

In 2001, the Innu Nation Environment Office requested the GRI/SMU assist in developing culturally relevant educational programs to assist and strengthen the Innu Environmental Guardians, henceforth referred to as 'Guardians', in monitoring and sustainably developing their ancestral lands, Nitassinan. This would be the beginning of a series of modules referred to as the Innu Environmental Guardian

Program and henceforth as the 'Guardians Program', over the next ten years and involved up to fourteen Innu Environmental Guardians at various times. These modules included topics such as Understanding Ecosystems, Migratory Bird Management, Ethnographic Mapping, Caribou Management, Archaeology, Geology, Statistics, and, for the last three years, a series of modules concerning climate change. In 2006, The GRI/SMU through the Office of Aboriginal and Northern Research received two Social Science and Humanities Research Council (SSHRC) grants—the Aboriginal Program Research Grant and the Northern Development Research Grant—to continue the Guardian program and support ongoing research. Another grant from the Environment Canada's Northern Ecosystems Initiative (NEI) specifically focused on developing indicators for Climate Change from an Innu perspective. In 2008, the Office of Aboriginal and Northern Research was successful in obtaining further funding through the International Polar Year's Educational Outreach Program Grant in partnership with the Innu Nation, the Smithsonian Institution's Arctic Studies Centre, University of Alaska, and the University of the Arctic.

Most important to the modules was the incorporation of the following seven key ethical guidelines and pedagogical components in the delivery of the Guardians Program: First, the program is Innu driven, which means the Guardians decide the priorities, and learning is geared toward the preservation of their own land use and cultural practices. This knowledge is then used as the basis of decision-making processes in any development project; Second, learning and course content are related to on-going projects such as the forestry co-management agreement with the provincial government; Third, courses are offered in 1-2 week modules and delivered within the Innu communities (generally Sheshatshiu) or at field sites relevant to current projects affecting Nitassinan; Fourth, *tshishennuat* (Elders) are involved as advisors of Innu Environmental Knowledge to foster a dialogue and holistic learning from both an Innu and Western Scientific perspective; Fifth, programs are bi-lingual (Innu Aimun and English) when *tshishennuat* are present, with the Guardians acting as translators.; Sixth, modules are scheduled around "real" life situations, e.g., seasonal work, family obligations, and time at camps in the country; Seventh, training crosses disciplines so that the Guardians gain experience in all aspects of environmental monitoring, e.g., Fishery Guardians attend Caribou Management modules, and Forestry Guardians attend Fishery related modules (Sable et al. 2007). Beginning in 2007 to 2010, five modules examining climate change and boreal ecosystems were run in and around the Innu community of Sheshatshiu and the traditional caribou hunting area of Kamestastin (Figs. 6.1, 6.2; Table 6.1). While each of the modules focused on a different component of climate and boreal ecosystems, they were all structured around incorporating ecosystem components that the Guardians identified as being important.

6.3 Approach to Monitoring

The primary objective of the climate change and boreal ecosystem modules was to create an ecosystem approach to monitoring that was regionally specific and

Innu appropriate. It was important to incorporate all components of the ecosystems (i.e. the soil, the plants, the animals and the climate) and input from the Guardians and Elders, in order to tell the story of climate change in the Labrador boreal forest in a holistic way. In consultation with the Guardians, Innu Nation forestry staff and a review of the current provincial forestry guidelines and monitoring techniques used in other northern landscapes, a monitoring protocol for the climate change modules was created. On recommendation by one of the Guardians, David Hart, the monitoring sites would be referred to as Innu Permanent Sample Plots (IPSPs; Fig. 6.3). In doing so, the Innu were taking ownership of the plot as part of their ancestral land, as well as the process for monitoring it. Different modules would focus on different components of climate change and boreal ecosystems that would ultimately be integrated into the IPSPs. The overall intention with this approach is that there would be a legacy left behind of ecologically robust measurements that could one day be used to address questions relevant to the Guardians and other Labrador Innu.

The interplay between Innu Knowledge and Science is not intended to rank one knowledge system as being more important or relevant than the other. The monitoring approach draws on Science for methodology and epistemology but is directed and contextualized by Innu Knowledge and Guardian participation. Given that the effects of climate change manifest at multiple scales (e.g., from changes in berry size to the expansion of forests into the tundra), it is important for monitoring initiatives to focus on a similar wide-range, or scale, of ecosystems processes and components. In the following section, monitoring approaches for climate and forest components will be introduced and justifications will be made for the methodology used in our monitoring initiative. The climate and forest components will be addressed separately in order to explore the importance of each component and the required methodologies for detecting change. This separation is only for the purpose of clarity and in no way meant to detract from the interrelatedness of climate and forest processes.

6.3.1 CLIMATE

Permanent climate stations in the region provide baseline observational data and analyses that can be referred to when discussing long-term trends and variability in seasonal climate (e.g. Vincent et al. 2002). These may be supplemented at the community level by maintaining a narrative of seasonal and annual weather events based on observations and informal reports by members of the community. A limited suite of climate variables are monitored at the level of the IPSP. These include temperature and snow cover (duration and late-winter depth); two variables that best reflect local variation in bioclimatic conditions. It is generally not practical to maintain instruments for recording air temperature at the IPSP sites. However, as tree growth has been found to be tied to a critical soil temperature threshold in the root zone above approximately 3°C (Sveinbjornsson 1992, Körner and Paulsen 2004), it is possible to deploy miniature temperature loggers in the root zone (10 cm depth) at several points within the site. The sensors are deployed and retrieved annually. Set to sample on a 3-hourly interval, the records can be used to estimate the beginning and end dates of snow cover from changes in the amplitude of the temperature signal. Snow conditions at the IPSPs are sampled in late winter, using a central pit to measure depth, relative hardness, density, and presence of ice layers, with additional depth sampling using probes along 10 m transects outward from the pit. Site visits also provide opportunities for observations related to phenology, wildlife behavior and effects of weather-related effects such as blow-downs.

6.3.2 FORESTS

A multitude of approaches exist for monitoring long-term change in forest ecosystems. While many include establishing labour-intensive plot boundaries (e.g. see Dallmeir 1992, for descriptions of SIMAB plots), others only require one stake in the center of the plot (e.g. see Moroni and Harris 2010, for description of Temporary Sample Plots). From this center stake, it is possible to monitor a variety of forest attributes (e.g. forest density, age structure, species composition, wildlife trees). With specific objectives of incorporating climate change monitoring into this framework, an emphasis is placed on detecting changes to forest processes. An example of this would be changes to the frequency or abundance of forest pests, like insect herbivores, which may be more prevalent in a warming climate (e.g. Dale et al. 2001). Another monitoring component are plant communities that may be more sensitive to a changing climate and exhibit a faster response time compared to slower growing tree species. Monitoring shifts in plant communities can be accomplished by comparing relative abundance, changes to plant indicator species and documenting changes to exotic and uncommon species.

6.4 Innu Permanent Sample Plots

A total of four IPSPs were established throughout the climate change modules with the intention being that additional IPSPs would be established by Guardians in other parts of Labrador, as they saw fit. Three of these are located off the Trans Labrador Highway (53°07' N, 60°29' W; Fig. 6.1A) and the fourth is located at Kamestastin, which is a traditional hunting area for Mushuau Innu at Mistastin Lake (55°52' N, 63°26' W; Fig. 6.1B). The location of the IPSPs was selected based on their close proximity to Guardian activity to make it convenient to revisit the plots. The IPSP at Kamestastin is remote but this is a traditional caribou hunting site that is visited multiple times a year by some of the Guardians and numerous other Innu. At each location, the IPSP was established in what the Guardians decided upon as being representative of forests in that area. Another important criterion when selecting the location of the IPSPs was that they be in areas that are culturally and ecological significant to Labrador Innu, as determined by the Guardians. For example, the approach to selecting an appropriate site in Kamestastin involved meeting every morning in a communal cabin to decide where the Guardians wanted to go – taking into account the weather, group size, available time and other planned activities. The Guardians decided the specific location of the IPSP after spending time walking around different forests, having discussions about the significance of each area and how representative it was of forests in that region. The location of the IPSP is important for a few reasons. First, valuable information about climate change will be amassed at these locations. Second, these plots offer the possibility of long-term protection to areas where the surrounding landscape may be threatened by commercial forestry (e.g., near Sheshatshiu). While this consideration is less relevant for remote locations, emphasizing the idea of permanence while selecting sites may influence the ultimate placement of the IPSP. Third, these plots are supportive of ongoing monitoring mandates of the Innu Nation Environment Office especially in light of Innu moving towards self-governance.

The initial round of data collected from the IPSPs is summarized in Table 6.2. Due to the inherent differences in forest types represented by the four IPSPs, it was expected that there would be a lot of variability between sites. The reason the Innu were interested in establishing long-term monitoring plots was to understand how their forest ecosystems are changing, so the value of these data lie in comparing changes through time and not between forests. Because we expected different forest types to show a differential response to climate change, the high level of inter-site variability can be interpreted as indicating that the selected IPSPs are capturing the natural variability present across the Labrador landscape. One of the most striking differences between the IPSPs is the amount of forest regeneration – both in sapling and seedling abundance. Differences in site-specific moisture levels, species composition, nutrient availability and stand ages are possible factors that could be driving the observed differences in regeneration rates. Moisture levels and nutrient availability are often cited as variables that are vulnerable to climate change (Aitken et al. 2008, Finzi et al. 2011) and should therefore be given appropriate attention when these sites are resampled.

6.5 Lessons Learned

Education is a dynamic process that is in a continual state of critique and self-improvement. These climate change modules reflect this iterative approach to education in which the facilitators and the Guardians are continually learning from the module content and from each other. The following two sections will examine those approaches and content inclusions that were considered to be successful, followed by those that presented challenges which in some cases were overcome, and in other cases abandoned. The perspectives being offered are those of the module facilitators (university-trained natural and social scientists) and therefore do not reflect those of the administrators (host university) or the Guardians.

6.5.1 SUCCESSES

Throughout the three-year process, the climate change modules had many successes. Geographic *place* was an important consideration when planning these modules. Place is more than location: it includes interesting human and non-human interactions (Oakes 1997, Acevedo et al. 2008). With Indigenous Knowledge being not only content but also process, it is important that the place and the learning space reflect this (Simpson 2002). Simpson (2002) reinforces this point by stating that since Indigenous Knowledge comes from the land, Elders and other knowledge holders are more comfortable teaching and learning while on the land rather than in a classroom. To accomplish this, we gave priority to field-based over classroom-based activities, whenever possible. In our experience, it was easier to generate excitement and discussion with the Guardians about forest ecosystems when we were in the forest - closer to the origin of Innu Knowledge of forests. For the 2008 module, an Innu canvas tent was set-up near the locations of IPSP 1-3, about 30 minutes from Sheshatshiu. This space served as our classroom and communal space throughout the module. The advantages of this approach were many. First, an indoor space that was available to us was at an office where many of the Guardians from Sheshatshiu work. There, it was difficult to maintain focus on the modules when the Guardians were inundated with disruptions related to daily work life. *In situ* learning, especially when the Innu tent was set-up, is less formal than classroom scenarios allowing for more hands-on rather than theoretical discussions. The tent, as a warm shelter with food and tea available, served as a familiar and comfortable space for discussions. Lastly, maintaining attendance is a challenge for most educators and while unfavorable weather in field-based modules deterred some individuals, the majority of the Guardians put in long days in the field.

Innu-specific content was a key component to the climate change modules. Not surprisingly, when the impacts associated with climate change were appropriately contextualized, the information and application was more interesting to the Guardians. One way of ensuring that modules had an Innu focus was to have a loosely structured agenda in which daily activities can be responsive to the Guardians' interest. This free flowing approach is more engaging than following a rigid syllabus, as even a question can alter the direction of the day. In our experience, the lack of predictable punctuality and sustained attendance makes it unrealistic to have a firm agenda with exact timelines. This lack of structure also contributes to an informal atmosphere that encourages knowledge sharing and a freer exchange of information.

While Science is often thought of as being time sensitive, objective and able to provide definitive answers, what Science really provides are tentative explanations that change when better explanations become available. The informal nature of the modules provides a forum to discuss the importance and function of ecosystem components from both Science and the Guardians' perspective. This exchange benefits both perspectives by exploring complementary or alternative approaches to knowledge acquisition. In our experience, the Guardians were critical for determining the importance of ecosystem components while Science provided an option for acquiring knowledge when the Guardians' knowledge was incomplete. For example, Guardians do not have explicit knowledge of tree growth rates in the remote areas of Labrador but by using dendrochronology, the study of tree rings, a complete growth record for any individual tree can be obtained while the Guardians' knowledge of Innu land-use patterns that predates the individual tree in question helps to contextualize the Science.

Guardians that were involved in all of the climate change modules were often looked to by other Guardians to explain concepts developed in previous modules. The excellent attendance record and engagement of certain Guardians are considered to be an overall success of the project. In the most recent climate change module in Kamestastin, an Innu youth film group was simultaneously being trained in interviewing, filming, and editing techniques. Throughout this module, the youth were interviewing the Guardians on various scientific techniques and skills acquired through the climate change modules. These interviews were then edited into short videos that were integrated into an interactive website (www.kamestastin.com).

6.5.2 CHALLENGES

Attendance by the Guardians throughout the climate change modules was a constant challenge. This was especially an issue when the modules were based nearer to Sheshatshiu, where there was no sharp boundary between work and personal life. While accommodating and being understanding of the importance of unexpected personal situations is a tenet of the Guardians Program, it remains a major challenge from the perspective of the module facilitators. We do not have detailed knowledge of what factors facilitated or restricted participation, but we did find that holding the modules in remote areas improved Guardian attendance and allowed for more in-depth discussions of module topics.

The majority of the climate change modules were based near Sheshatshiu rather than Natuashish because it was more convenient for the majority of the

Guardians and also provided good indoor facilities, when needed. As a result of this, there was less involvement with the community of Natuashish and fewer IPSPs were established in that area. Some remotes sites of importance to the Innu could not be considered because of logistical costs and potential conflicts with other commitments that the Guardians may have had. With the climate change modules focusing on detecting change across Nitassinan, greater spatial coverage would have increased the diversity of landscapes captured in the IPSPs and would also have provided insight into potential differences in local and regional climate change impacts.

Lastly, difficulties arose in the emphasis that Science, specifically ecology and climatology, places on numerical accuracy and precision in field measurements and analysis. The hypothesis testing Science approach depends on the use of statistics to answer specific research questions. This attention to accuracy and precision is an integral component of Science training and in our experience requires more exposure than the climate change modules provided. Perhaps one of the major challenges in complementing Innu Knowledge with Science is that without statistics and reliable field measurements, the emerging story that Science can tell may not be fully understood.

6.6 Discussing 'Climate Change'

Supporting materials prepared for the modules made reference to the usual authorities on climate changes and its impacts, namely the Intergovernmental Panel on Climate Change (IPCC 2007) and the Arctic Climate Impacts Assessment (ACIA 2005). Given the setting, it seemed appropriate to briefly discuss changes in the landscape since the end of the last major regional glaciations (e.g., Lamb 1985); however, the focus was primarily on recent climate trends and variations from the mid-20th century, which is the period of instrumental record for meteorological stations in the region, and within the life experience of the more senior Guardians and Innu Elders. It became clear from the progress of discussions that, while most grasped the concept of climate change, it was short-term, even interannual *variability* that was of greater interest. Thus, an exceptionally warm winter and spring, such as occurred in 2009-10, was noteworthy for a variety of indicators, such as late freeze-up, early break-up and difficult winter travel conditions for lack of firm snow and ice, and unusually large numbers of overwintering birds and the early return of migrants. Better than any graphs or charts, it was the examination of the tree-rings, as noted, that best conveyed the concept of variability on decadal and longer time scales. Any discussion of future climate, assuming anthropogenic warming, was in terms of the likelihood of more or worse episodes of a kind they have experienced.

The distinction between adaptation to variations in climate as opposed to adaptation to some significantly different climatic regime is an important one in climate change adaptation studies (ACIA 2005), since boreal and arctic subsistence cultures have generally been found to acquire resilience under a varying and even changing climate, at least up to a point (Ford et al. 2010, Kofinas et al. 2010).

However, in the context of monitoring for biophysical changes in a boreal forest environment, such distinctions remained academic.

6.7 Moving Forward

Like many regions of the subarctic, the forests of Labrador are currently experiencing significant climate change, though the specifics for how they will respond are relatively unknown. Increased fire frequency and abundance of forest insects like eastern hemlock looper (Soja et al. 2007) figure largely into the overall vulnerability of the forests. We also expect that exotic plant and animal species which could previously not tolerate the harsh climate of Labrador will be able to establish and persist (ACIA 2005). Documenting and understanding these changes require detailed baseline information, such as that which is has been captured by the IPSPs.

Throughout the time that the climate change modules have been running, monitoring plots, which will be important for documenting change, have been established. In order to answer questions about how this ecosystem is responding to climate change, the IPSPs need to be resampled at regular intervals. The frequency of site revisits depends on the resources and schedules of the Guardians but we suggest returning to the IPSPs annually to document qualitative change and at five-year intervals for detailed quantitative surveys.

6.8 References

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Table 6.1 Specific information on climate change modules

Module Name	Focus	Year	Instructors	Participants	Location
Climate Change	Overview	2007	Jacobs	7	Sheshatshiu/Kamestastin
Climate Change and Boreal Ecosystems I	Innu permanent sampling plot, dendrochronology, local climate	2008	Jacobs/Trant	10	Sheshatshiu
Climate Change and Boreal Ecosystems II	Winter climate and ecology	2009	Jacobs/LeBlanc	7	Sheshatshiu
Seasonal Transitions	Phenology, berries, and repeat sampling	2009	Trant	5	Sheshatshiu
Climate Change and Boreal Ecosystems III	Innu permanent sampling plots, paleoenvironments, local climate	2010	Jacobs/Trant	2	Kamestastin

Table 6.2 Descriptive statistics for forest structure, vegetation, soil and climate data from the Innu Permanent Sample Plots (IPSP). IPSP-04 has only been partially set-up. Tree species are listed throughout the table are: ABBA (balsam fir; *Abies balsamea*), LALA (larch; *Larix laricina*), PIGL (white spruce; *Picea glauca*), PIMA (black spruce; *Picea mariana*), BEPA (white birch; *Betula papyrifera*). All numbers in parenthesis correspond to abundance values. Climate data are based on miniature temperature loggers placed a 10 cm depth in October 2008 and retrieved in June 2009. Snow surveys were carried out at site IPSP-4 on March 18, 2009. LHF = Litter – Humus – Fermentation.

	IPSP-1	IPSP-2	IPSP-3	IPSP-4
FORESTS				
Species present	PIMA, LALA, PIGL, PIGL	ABBA, PIMA, PIGL, BEPA	ABBA, PIMA	PIGL
Minimum Age (years)	107	220	225	
Trees (stems/ha)	23.5	12.0	14.5	8.5
Saplings (stems/ha)	31.9	4.0	11.9	
Seedlings (stems/ha)	15.7	816.4	392.5	
Height: 0-5 cm	bS(1)	bF(52)	bS(1), bF(24)	
5-15 cm		wS(1), bF(12)	bS(6), bF(7)	
15-30 cm	bS(3)	bS(12), bF(17)	bS(7), bF(6)	
30-200 cm	bS(10)	wS(1), bS(2), bF(26)	bS(4), bF(10)	
PLANTS				
Moss Cover (%)	79	73	72	
Most abundant species	*Kalmia angusifolia*	*Cornus canadensis*	*Cornus canadensis*	
Exotic species	Not present	Not present	Not present	
Rare species	Not present	Not present	Not present	
SOIL				
Thickness of LHF layer (cm)	8	10	8.5	2.2
Depth of A layer (cm)	12.5	>30	3.5	
Depth of B layer (cm)	>30	Not present	27.5	
Average thickness of organic layer (cm)	9.0	8.5	7.8	
CLIMATE (2008-09)				
Minimum soil temp (°C)	0	0		0
Snow-on date	21 Oct	3 Nov		16 Nov
Snow-off date	5 June	1 June		19 May
Late winter snow depth (cm)				143

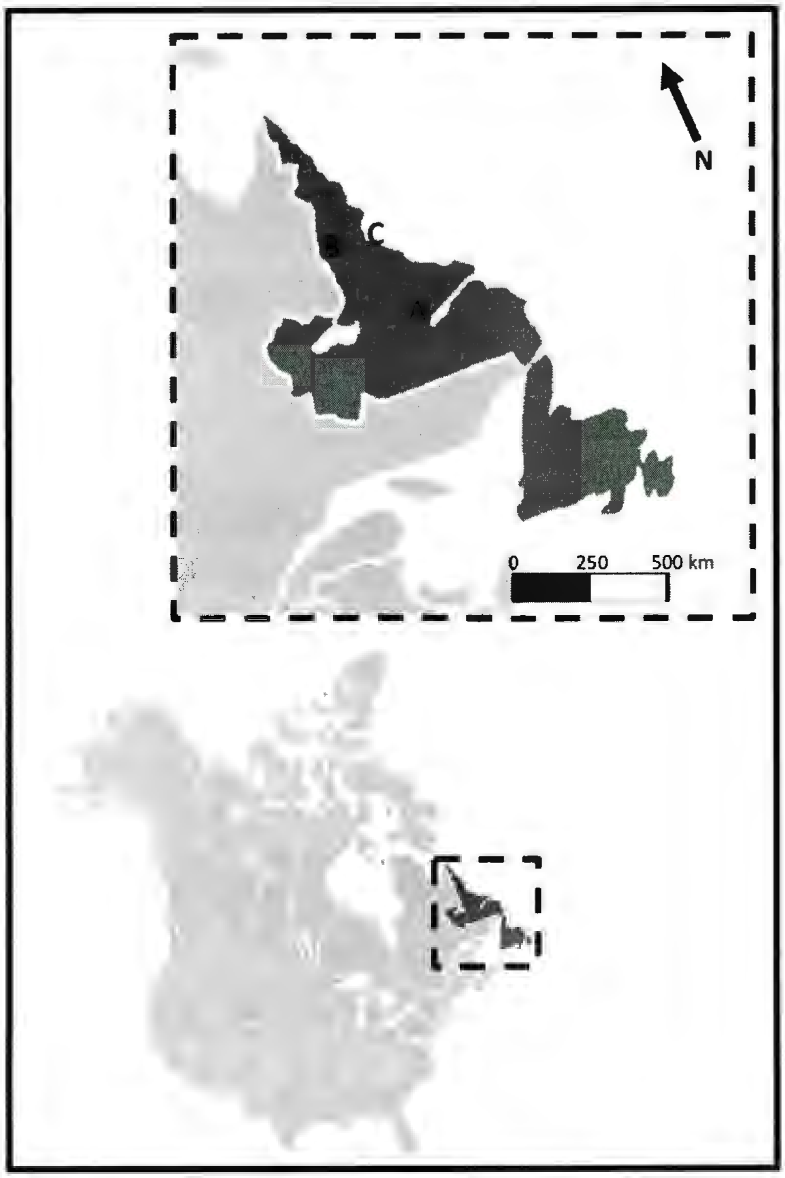


Fig. 6.1 Map showing locations of climate change modules outside of (A) Sheshatshiu, (B) Kamestastin and (C) Natuashish in Newfoundland and Labrador, Canada.

Fig. 6.2 Photographs from climate change modules from A) 2007: John Jacobs, Innu Youth Film Group, unidentified participant, Anthony Jenkinson and Hank Rich, B) 2008: Paul Pone and Sebastian Piwas, C) 2009: Hank Rich and D) 2010: Sebastian Piwas, Hank Rich and Innu Youth Film Group.

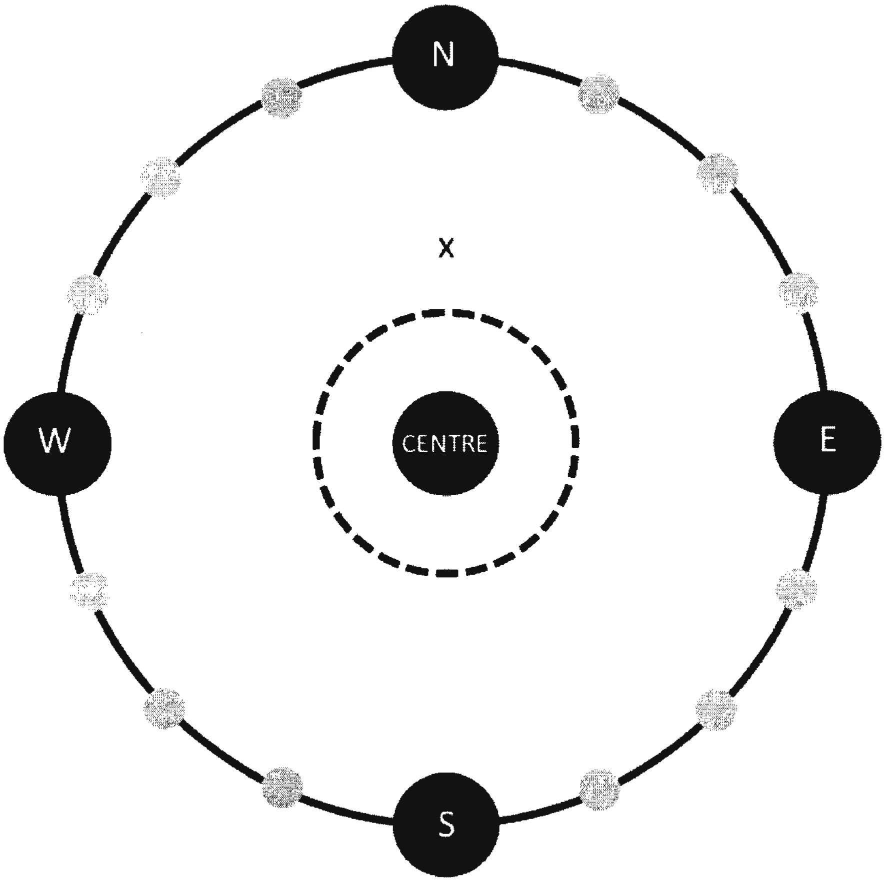


Fig. 6.3 Innu Permanent Sample Plot (IPSP) with plot sampling location for forest structure (open black circle: radius=11.28 m, n=1), vegetation (filled black circles: radius=1 m, n=5), forest regeneration (dashed circle: radius=4 m, n=1), soil (grey circles: n=12) with soil temperature logger 5 m north of the plot center (denoted by 'x').

Chapter 7: Summary and conclusions

Climate change continues to be manifested in warmer drier summers, warmer winters, higher variability and extreme weather events. What is also changing is our need to understand how ecosystems are responding to climate change, both from ecological and human land-use perspectives.

Using a multispecies approach, in Chapter 2, we reconstructed treeline dynamics in central Labrador over the past few centuries with climate relationships for the past century. Using linear regressions of height and diameter data, shifts in tree growth form were seen across treeline with individuals having shorter with thicker trunks, with the exception of larch (*Larix laricina*) that had the highest similarity in growth forms across the altitudinal gradient. Patterns of regeneration across treeline favoured larch for seedlings, while sapling density and age increased across treeline but diagnostic data suggested that the majority of saplings originated from vegetative reproduction. Based on tree age structure, there was limited evidence that treeline was advancing in the Mealy Mountains of Labrador. In this chapter, we also determined that black spruce (*Picea mariana*) and white spruce (*Picea glauca*) established at treeline prior to larch and balsam fir (*Abies balsamea*). Since the establishment of treeline, larch and balsam fir have had higher rates of infilling and lower mortality. Moving across treeline, we demonstrated that recruitment and climate correlations become increasingly variable with black spruce showing recruitment patterns that were most positively correlated to summer temperature. We expect a dramatic shift in treeline composition with larch and black spruce being the first to benefit from warming temperatures.

In a short discussion on the value of old trees at treeline, Chapter 3 discussed how persistent growth forms are well-positioned to capitalize on shifts in climate as it becomes more suitable. Using an example long-lived black spruce krummholz, a recent increase in radial growth suggests a response potential that may be explained by individuals having extensive below-ground biomass. Despite persisting on the landscape in an almost dormant state of minimal growth during inclement climate, these long-lived individuals may have profound implications for how treelines will respond to climate change.

In Chapter 4, we described the role of small-scale disturbance patterns at treeline in central Labrador using ecological data and insect outbreak reconstructions in four co-dominant tree species. By linking small-scale disturbance with tree mortality and regeneration patterns, we showed that despite occurring at a much smaller scale than most of the boreal forest, these disturbance patterns are significant for driving treeline dynamics. Our results also demonstrated in this chapter that small-scale disturbance, which leads to gap replacement dynamics, is an important process for regeneration as windthrow provide the suitable microsite conditions that seeds need to germinate and establish. We expected to see the frequency and magnitude of insect outbreaks decrease across treeline, as a result of the stress gradient, but based on the results of maximum herbivory, the magnitude of outbreaks is well-explained by stem density, as suggested by the Resource

Concentration Hypothesis (Root 1973). In this multispecies approach, larch and black spruce were identified as the species most affected by current disturbance patterns and also the species that showed the highest regeneration in forest gaps. With disturbance frequency and magnitude expected to increase with climate change, it is anticipated that higher levels of tree mortality and associated seedling regeneration, may facilitate the upward migration of larch and black spruce.

With the question arising from Chapter 2 of '*What do these regional patterns of treeline dynamics tell us about circumpolar treeline*?', Chapter 5 addressed this by synthesizing ecological and age structure data from 25 treelines across 10 regions. In this chapter, we showed that growth form across treeline could not be explained by the extent of warming at each site. This chapter showed that more southern treelines were useful predictors of seedling and sapling density and that persistent treelines were less likely to be associated with high seedling densities. Overall, our results demonstrated that positively responding treelines, those showing northward or upward movement, were best predicted by persistent treelines and nearness to the ocean. The ability of trees to reproduce vegetatively also increased the chances of treeline responding positively. In predicting which treeline would advance, an intriguing finding was that climate parameters (i.e., summer and winter temperature, growing degree-days) were not informative. The main message that emerged from Chapter 5 was that ecological factors are better predictors than the extent of warming at each site for understanding treeline patterns at broad spatial scales.

Returning to the idea that climate change will alter northern ecosystems and affect how people interact with their environment, Chapter 6 examined a series of climate change modules with Labrador Innu, that were implemented in efforts to understand changes to forest ecosystems. This chapter focused on integrating ecological methodologies and results from our treeline research with monitoring initiatives of the Innu Environmental Guardians. Field-based modules were successful in maintaining participant engagement, however, differentiating between short-term and long-term change presented difficulties for many of the Innu Guardians. Working with two complementary knowledge systems (i.e., western science and Indigenous knowledge), contextualized and validated the ecological questions presented throughout the other chapters. The interest shown by the Innu Guardians in treeline and vegetation change was primarily from a habitat perspective with concerns about the associated impacts to wildlife. Multidisciplinary approaches to understanding impacts associated with climate change were invaluable.

In conclusion, our research has addressed important questions pertaining to change across different spatial scales and by incorporating different knowledge systems. By better understanding how ecological factors interact with climate warming enables us to more accurately predict future change and move towards appropriate adaptation strategies. Landscape-level changes to the natural environment, as we expect with climate warming, cannot occur without substantial impacts on wildlife and other essential resources. Therefore, in a similar approach taken with our research, understanding these changes requires both ecological and human considerations.

7.1 References

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs **43**:95-124.

Appendix A

Table A.1 Comparison of study sites and methodologies

Region	Researchers	Period Sampled	Plot Type	Multiple Plots⁺
Alaska	Lloyd	1996-1998	Fixed area	No
Printer's Pass	Danby, Hik, Weir	2000	PCQ*	Yes
Dempster^	Brown, Johnstone	2007-2008	PCQ*	Yes
Inuvik^	Walker, Henry	2009	Fixed area	Yes
Churchill^	Mamet, Kershaw	2007-2008	Fixed area	No
Nunavik^	Dufour Tremblay, Boundreau	2010	Fixed area	No
Mealy Mountains^	Trant, Hermanutz	2007-2008	Fixed area	Yes
Norway^	Mathisen, Hofgaard	2007-2008	Fixed area	Yes
Kola^	Mathisen, Hofgaard	2007-2008	Fixed area	Yes
NW Russia	Wilmking	2007	Fixed area	No

^PPS Arctic funded initiative (for details see http://ppsarctic.nina.no/)

*PCQ = Point-centered quarters

⁺When multiple plots per zone were used, they were combined for comparison between sites

Table A.2 Region with closest climate station information. Fairbanks climate data were positioned in the middle of the Alaskan sites and therefore a specific direction was not available. Mean values and annual rates of increase for summer (June, July and August) temperature and growing degree-days (GDD) is based on the period of climate record available.

Region	**Climate Station**	**Distance and Direction from Site**	**Elevation (m.a.s.l.)**	**Tree: Mean Summer, Winter, GDD**	**Tree: Annual Increase Summer, Winter, GDD**	**Sapling: Mean Summer, Winter, GDD**	**Seedling: Mean Summer, Winter, GDD**
AL	Fairbanks, AL	~120	132.9	15.4, -6.9, 955.6	0.02, 0.22, 1.60	15.9, -3.4, 1005.3	16.1, -3.6, 1021.6
PP	Burwash Landing, YK	??	806.2	11.3, -20.0, 582.6	0.04, 0.12, 3.51	11.8, -18.4, 622.9	11.8, -19.5, 623.5
DE	Old Crow, YK	210 km NW	250.2	12.7, -27.8, 703.8	0.04, 0.11, 4.01	13.0, -26.9, 734.6	13.2, -26.1, 752.4
IN	Inuvik, NWT	10 km NW	67.7	12.0, -26.6, 649.3	0.02, 0.11, 1.67	12.4, -25.5, 682.0	11.6, -24.1, 608.8
CH	Churchill,	20 km NW	28.7	10.2, -24.6, 488.9	0.04, 0.05, 3.70	10.7, -24.1, 537.4	11.2, -23.0, 582.5
NU	Kuujjuaq, QC	533 km SE	39.3	9.9, -21.8, 453.6	0.10, 0.05, 3.91	10.3, -21.5, 495.6	11.0, -20.2, 551.8
MM	Goose Bay, NL	134 km SW	48.8	13.7, -15.3, 806.5	0.02, 0.03, 2.27	13.9, -15.6, 822.6	14.6, -14.2, 882.4
NO	Dividalen, NO	11 km SE	228	11.6, -8.1, 606.3	0.02, 0.03, 1.83	11.9, -7.6, 634.9	14.6, -7.8, 678.6
KO	Murmansk, RU	140 km N	81	11.1, -9.7, 561.0	0.01, 0.05, 0.78	11.2, -8.8, 575.2	11.6, -9.3, 608.7
RU	Khoseda-Khard, RU	138 km SW	114	10.5, -19.0, 514.7	0.02, -0.01, 1.50	10.9, -19.4, 547.4	10.5, -21.4, 503.7

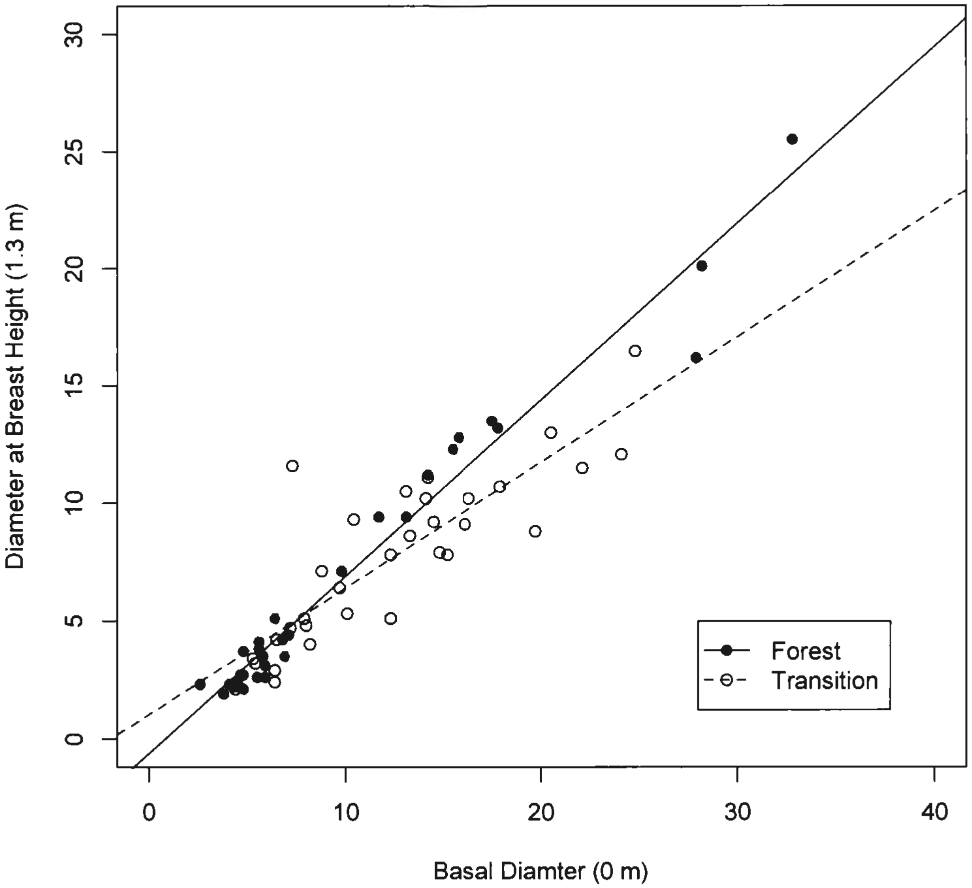


Fig. A.1 DBH and basal diameter relationship for larch (*L. laricina*) from the Mealy Mountains site for the forest zone (F_{28}=805.9, Adj. R^2=0.965, P<0.01) and the transition zone (F_{31}=85.0, Adj. R^2=0.724, P<0.001).

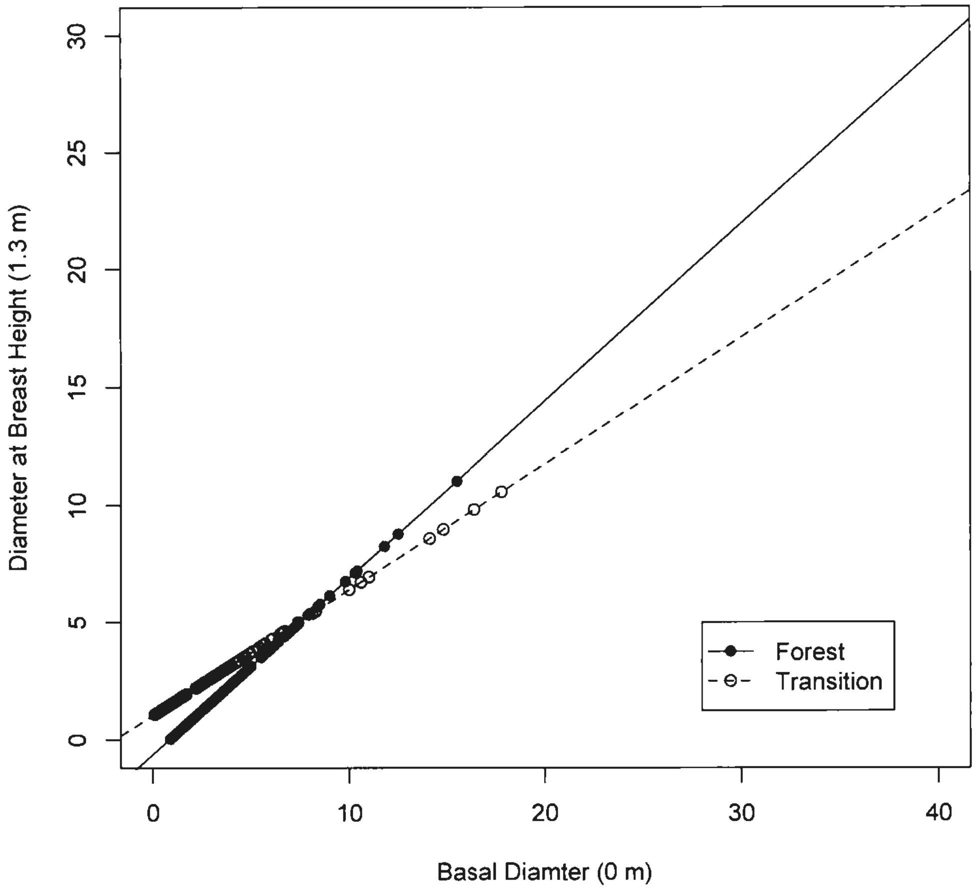


Fig. A.2 Modeled DBH from measured basal diameter for larch (*L. laricina*) from the Nunavik site using models from the Mealy Mountains forest (DBH=0.753*Basal-0.647) and transition sites (DBH=0.536*Basal+1.02).

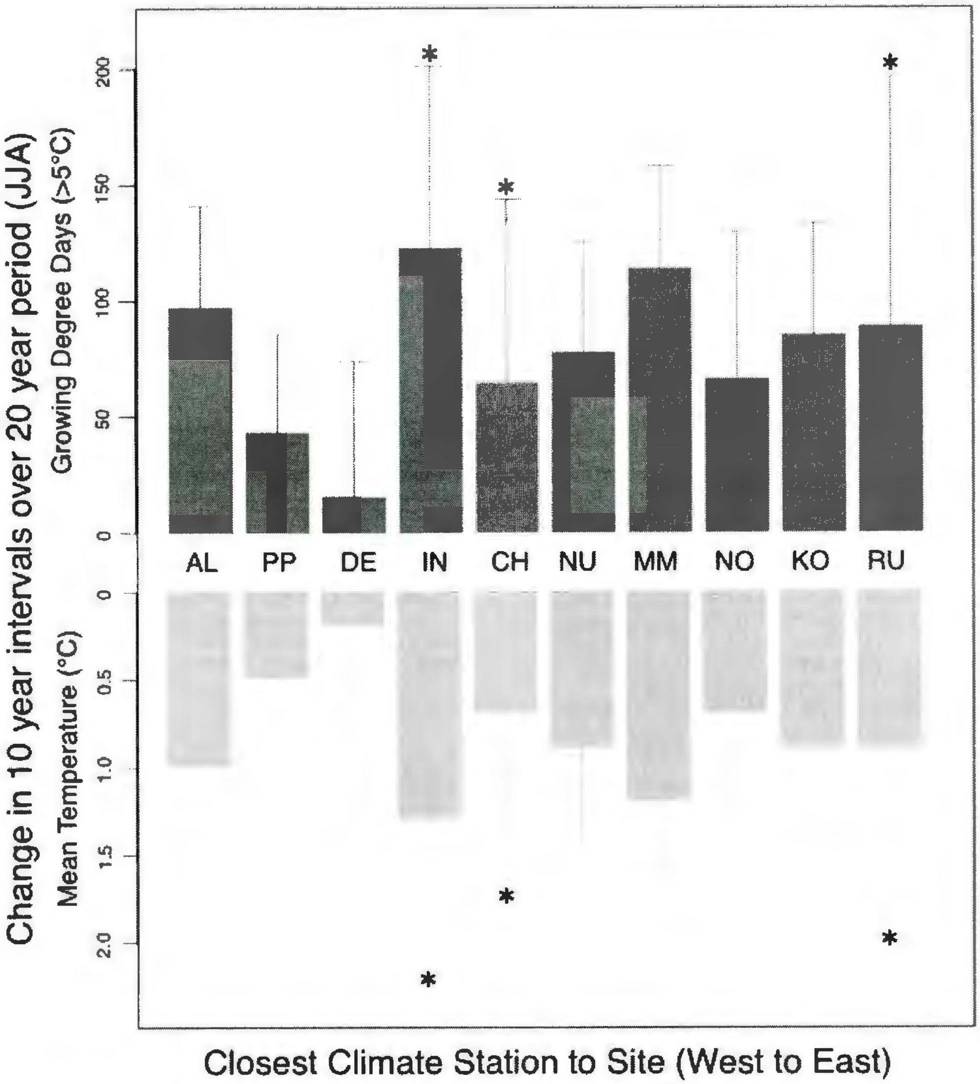


Fig. A.3 Seedling site warming index using growing degree-days (GDD; dark grey) and mean temperature (light grey) calculated from monthly climate data for differences between the 10 years prior to sampling and the previous 10 years for the months of June, July and August (Table A.1). Site codes are: AL=Alaska, PP=Printer's Pass, DE=Dempster, IN=Inuvik, CH=Churchill, NU=Nunavik, MM=Mealy Mountains, NO=Norway, KO=Kola, RU=NW Russia. Error bars show standard error.

*Indicate negative values

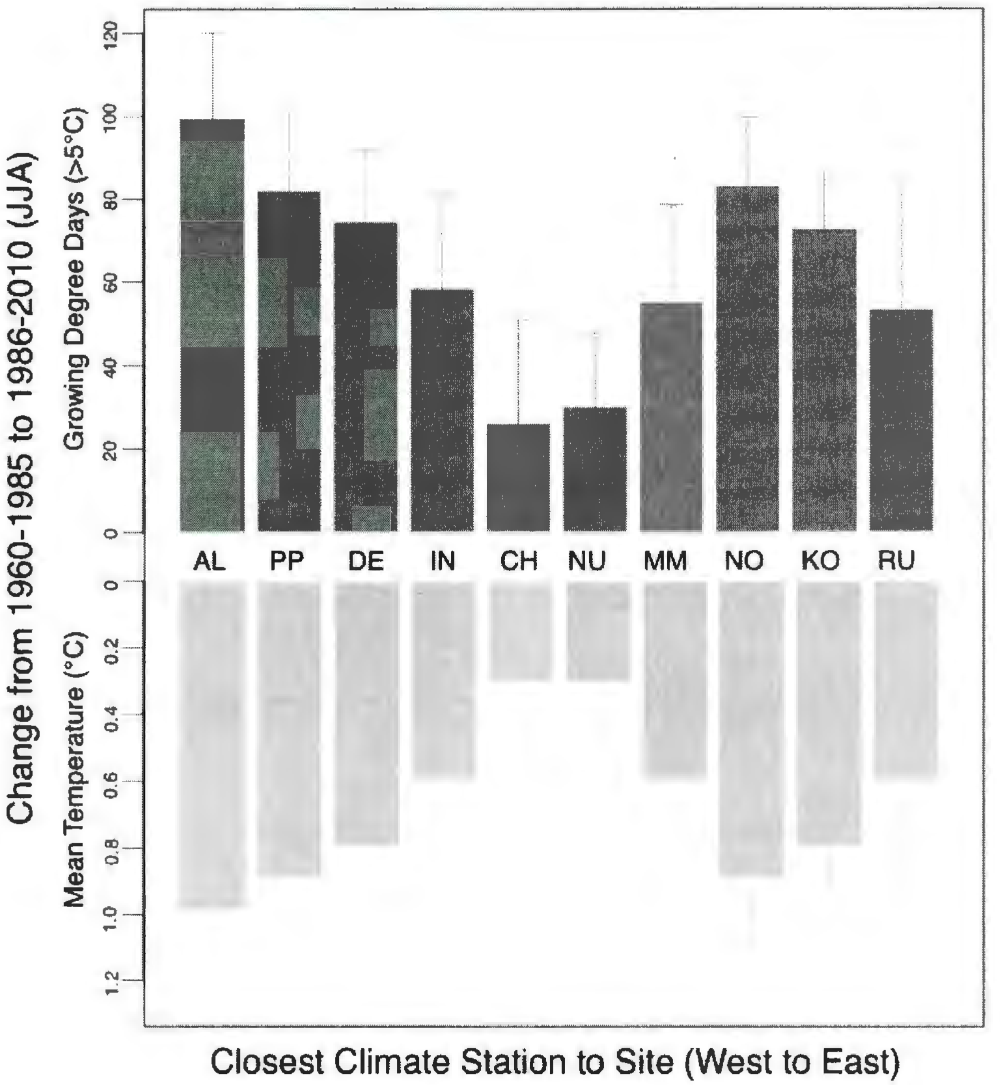
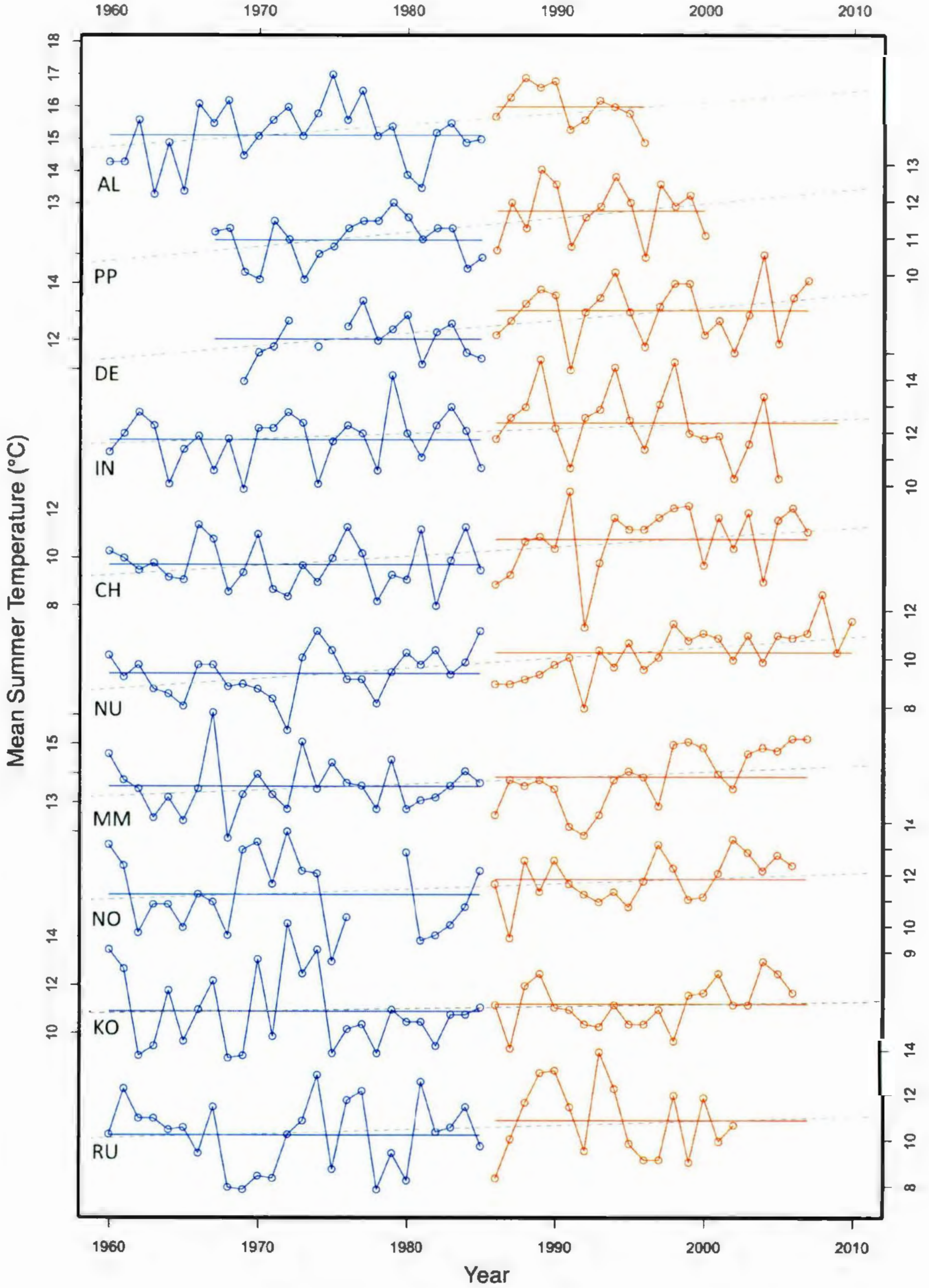


Fig. A.4 Sapling site warming index using growing degree-days (GDD; dark grey) and mean temperature (light grey) calculated from monthly climate data for differences between 1990-2010 and 1960-1989 for the months of June, July and August. Site codes are: AL=Alaska, PP=Printer's Pass, DE=Dempster, IN=Inuvik, CH=Churchill, NU=Nunavik, MM=Mealy Mountains, NO=Norway, KO=Kola, RU=NW Russia. Error bars show standard error.



1960
1970
1980
1990
2000
2010
AL
PP
DE
IN
CH
NU
MM
NO
KO
RU
Mean Summer Temperature (°C)
Year
18
17
16
15
14
13
14
12
12
10
8
15
13
14
12
10
13
12
11
10
14
12
10
12
10
8
14
12
10
9
14
12
10
8

Fig. A.5 Mean summer temperature (°C) for June, July and August from 1960 to year of sampling from closest climate station to each site. Using a piecewise regression, data are separated into pre-warming (1960-1985; blue) and post-warming periods (1986 to year of sampling; red) with grey dashed lines representing annual rate of increase in summer temperature (slope of regression for entire period). Site codes are: AL=Alaska, PP=Printer's Pass, DE=Dempster, IN=Inuvik, CH=Churchill, NU=Nunavik, MM=Mealy Mountains, NO=Norway, KO=Kola, RU=NW Russia. Broken lines correspond to missing data.

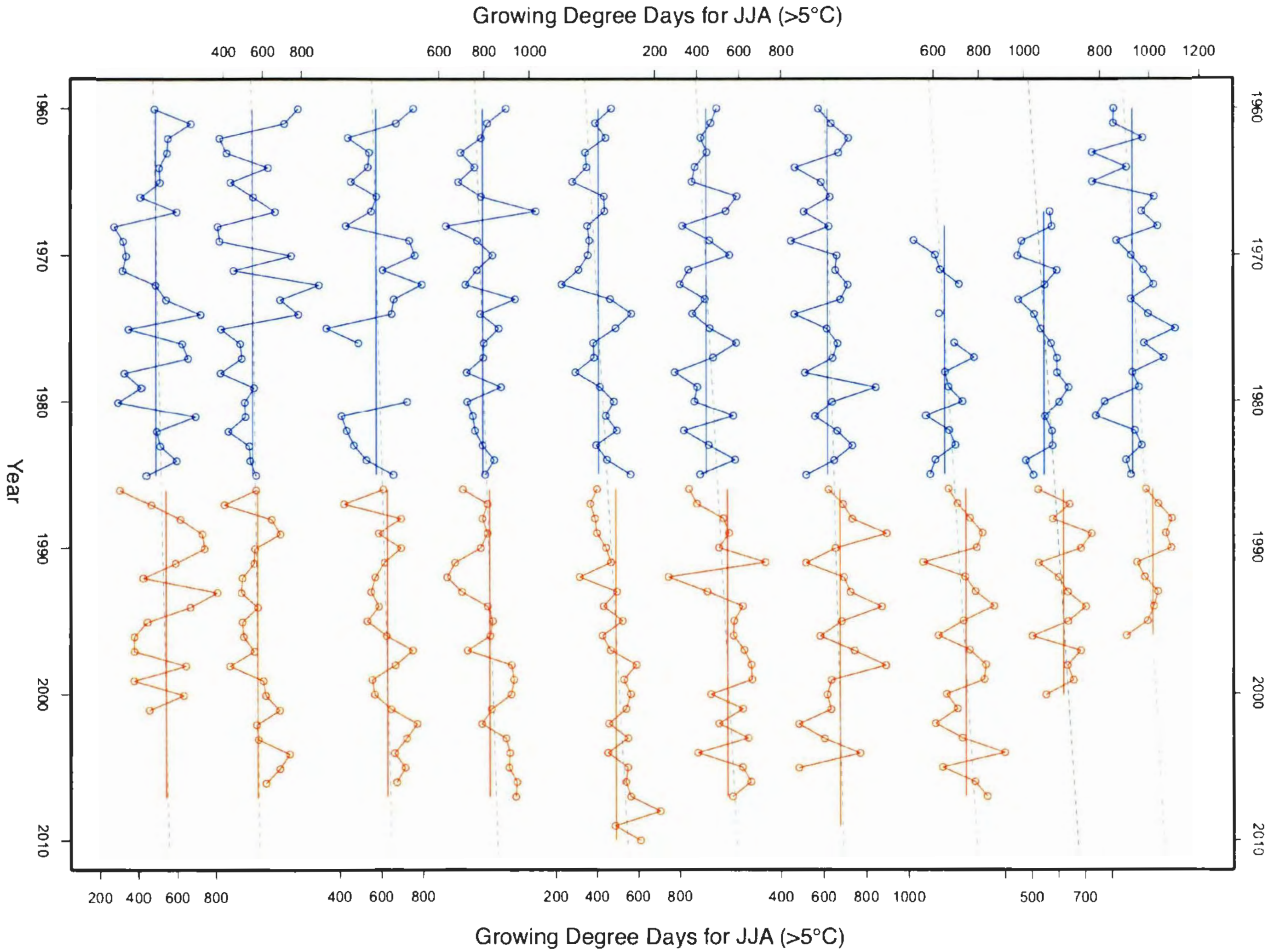

Growing Degree Days for JJA (>5°C)
400 600 800
600 800 1000
200 400 600 800
600 800 1000
800 1000 1200
Year
1960
1970
1980
1990
2000
2010
200 400 600 800
400 600 800
200 400 600 800
400 600 800 1000
500 700
Growing Degree Days for JJA (>5°C)

Fig. A.6 Growing degree-days (GDD; >5°C) for June, July and August from 1960 to year of sampling from closest climate station to each site. Using a piecewise regression, data are separated into pre-warming (1960-1985; blue) and post-warming periods (1986 to year of sampling; red) with grey dashed lines representing annual rate of increase in GDD (slope of regression for entire period). Site codes are: AL=Alaska, PP=Printer's Pass, DE=Dempster, IN=Inuvik, CH=Churchill, NU=Nunavik, MM=Mealy Mountains, NO=Norway, KO=Kola, RU=NW Russia. Broken lines correspond to missing data.

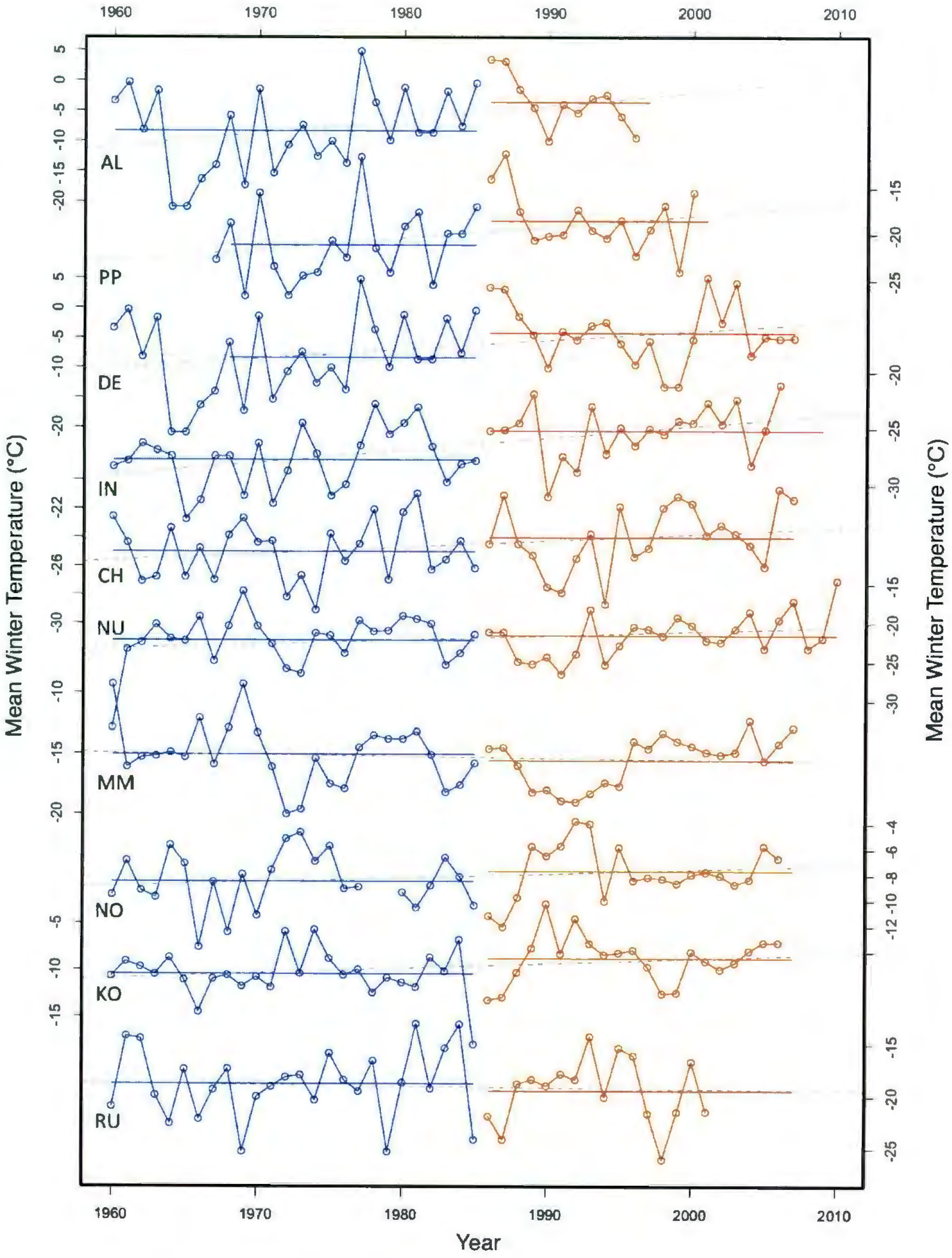

1960
1970
1980
1990
2000
2010
AL
PP
DE
IN
CH
NU
MM
NO
KO
RU
5
0
-5
-10
-15
-20
-22
-26
-30
Mean Winter Temperature (°C)
Year
-4
-6
-8
-10
-12
-25
Mean Winter Temperature (°C)

Fig. A.7 Mean winter temperature (°C) for December, January and February from 1960 to year of sampling from closest climate station to each. Using a piecewise regression, data are separated into pre-warming (1960-1985; blue) and post-warming periods (1986 to year of sampling 0; red) with grey dashed lines representing annual rate of increase in summer temperature (slope of regression for entire period). Site codes are: AL=Alaska, PP=Printer's Pass, DE=Dempster, IN=Inuvik, CH=Churchill, NU=Nunavik, MM=Mealy Mountains, NO=Norway, KO=Kola, RU=NW Russia. Broken lines correspond to missing data.

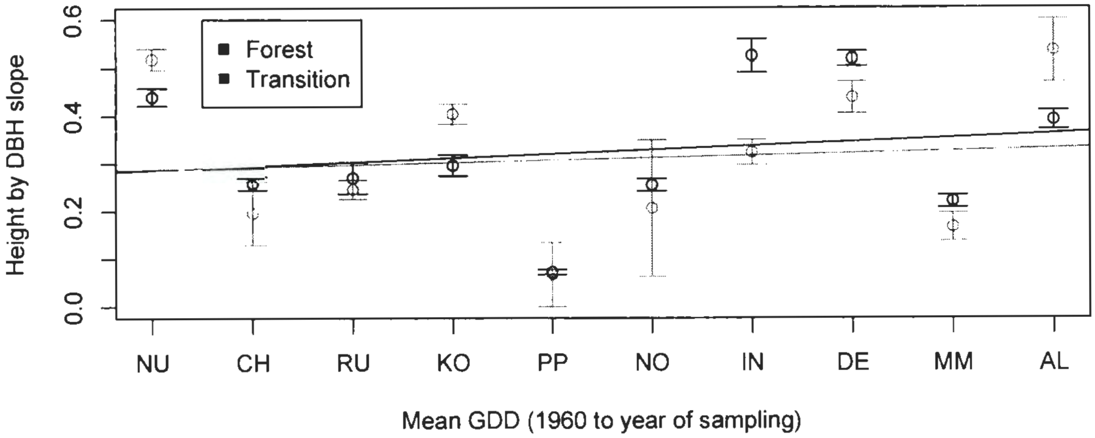


Fig. A.8 Comparison of slopes from height by diameter regressions for forest (solid line) and transition (dashed line) zones by site, ordered by sites decreasing mean GDD from 1960-2010. Site codes are: AL=Alaska, MM=Mealy Mountains, DE=Dempster, IN=Inuvik, NO=Norway, PP=Printer's Pass, KO=Kola, RU=NW Russia, CH=Churchill and NU=Nunavik.