SEEDLING ESTABLISHMENT AND CLIMATE CHANGE: THE POTENTIAL FOR FOREST DISPLACEMENT OF ALPINE TUNDRA (MEALY MOUNTAINS, LABRADOR, CANADA)

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by

© Anne Munier

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ABSTRACT

Loss of alpine habitat is of concern due to upslope migration of altitudinal tree-lines in response to climate change. The possibility of a rise in the tree-line of the Mealy Mountains of Labrador (Canada) was investigated by planting tree seeds and seedlings (*Picea mariana*, *Abies balsamea*, and *Betula papyrifera*) into experimental treatments along an elevational gradient in the tree-line ecotone. Treatments included passive warming with open top chambers; ground disturbance, and herbivore exclosures. Responses in seedling emergence, growth, damage sustained and mortality were monitored over one (*A. balsamea, B. papyrifera*) or two (*P. mariana*) growing seasons. Planted seedlings were able to establish and over-winter above present tree-line, but none were observed growing naturally. A lack of viable seeds may be limiting current tree-line migration, though seed viability improves with climate warming. While seedbed conditions and herbivory may eventually control the rate of seedling establishment, the results point to a strong possibility that tree-lines in the Mealy Mountains are capable of migrating upslope, with potentially significant changes or losses to the existing alpine habitat.

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LIST OF ABBREVIATIONS AND SYMBOLS

Open top chamber	OTC
Alpine tundra habitat	AT
Tree island habitat	TI
Open canopy forest habitat	OC
Temperature-enhanced treatment	T
Disturbance treatment	D
Temperature*Disturbance treatment	TD
Herbivore*Disturbance treatment	HD
Control	C

INTRODUCTION AND OVERVIEW

A host of complex and interacting factors affects the position of altitudinal tree-lines, and climate is considered the most important (Halliday and Brown 1943, Black and Bliss 1980, Grace 1989, Körner and Paulsen 2004). Up-slope migration of altitudinal tree-lines has been positively correlated with temperature warming in many parts of the world over the Holocene epoch (Lloyd and Graumlich 1997, Kullman 2002, Pisaric et al. 2003). More recently, as global temperatures have increased 0.6 ± 0.2°C over the 20th century (IPCC 2001), tree-lines have increased in elevation in alpine regions such as the Canadian Rockies (Luckman and Kavanagh 2000), Scandinavia (Kullman 2002), the Ural Mountains of Russia (Moiseev and Shiyatou 2003), and Alaska (Lloyd and Fastie 2003).

Thermal control is evident at every stage of a tree's life. Viable seed production at high altitudes is often only successful during particularly warm summers, and empty or underdeveloped seeds at tree-line are common (Stevens and Fox 1991, Arsenault and Payette 1992, Sirois 2000). Germination of viable seeds is temperature limited (Hobbie and Chapin 1998, Wang and Lechowicz 1998). Once established, the photosynthetic rate of seedlings and trees is limited by cool temperatures, as is their ability to utilize carbohydrates produced from photosynthesis (Körner 1998, Grace et al. 2002, Smith et al. 2003). Soil temperature influences root growth and longevity by affecting root respiration (Körner 1999). Temperature also indirectly affects tree establishment by influencing litter breakdown and nutrient availability to the plants (Berg et al. 1993).

The importance of temperature to tree-line migration is thus well-established, but other physical and ecological factors, and the interactions between them, can moderate or obscure the effects of warming on tree germination and establishment. Availability of suitable substrate, or safe sites, into which seeds can germinate may be the most important factor affecting successful seedling establishment (Harper 1981), and those of boreal tree seedlings can be quite specific in their substrate requirements (Germino et al. 2002, Calogeropoulos et al. 2004). Soil moisture is also critical, and studies have found that an increase in temperature without sufficient moisture will have a negative effect on seedling establishment (Black and Bliss 1980, Cairns and Malanson 1998). Wind can limit tree-line migration by killing seedlings and saplings through desiccation and defoliation once trees grow beyond the cover of neighbouring vegetation (Griggs 1938, Hessl and Baker 1997, Körner and Paulsen 2004). Herbivores control tree-line advance in Spain (Castro et al. 1999) and in Fennoscandia (Oksanen et al. 1995). Less research has been done on the impacts of herbivory on North American altitudinal tree-lines, but herbivores have been shown to affect boreal tree seedling establishment in Newfoundland (Noel 2004) and in northern Quebec (Côté et al. 2003). The mechanisms controlling tree-line migration are thus difficult to extrapolate over space and time, necessitating geographically specific research efforts to understand the likelihood of, and the mechanisms behind, tree-line advance.

Global mean temperatures are projected to rise 1.4-5.8°C by the year 2100 (IPCC 2001). This has lead to an increased interest in the effects that warming will have on altitudinal tree-lines around the world. One particular concern is the threat of displacement of alpine habitat by advancing forests. Alpine regions contribute disproportionately to global biodiversity due to their geographic isolation (Gottfried et al. 2002), steep environmental gradients (Fagre and Peterson 2002) and strong microhabitat differentiation (Körner 1999). This gives rise to a high numbers of endemic species (Gottfried et al. 2002) and to a high conservation priority (Orme et al. 2005). Experimental warming on the Tibetan Plateau revealed a rapid and significant decline in species richness for this alpine system (Klein et al. 2004). Upward migration of alpine plants has been recorded in the European Alps (Pauli et al. 1996), while an upward shift in tree-line in the Ural Mountains has led to a decrease of 10-30% of grassland and alpine heath vegetation over the past 70 years (Moiseev and Shiyatou 2003). Increasing forest cover is predicted to reduce biodiversity and alpine fauna habitat because species dislocated from geographic limits such as mountain tops cannot readily migrate and may be fated with local extinction.

The Mealy Mountains is one region of Labrador of particular interest with respect to the potential influence of climate change on altitudinal tree-line migration. Here, the tree-line appears to be largely climate-controlled, as the topography is relatively smooth and gradual, human disturbance is negligible, and there is no grazing of livestock. The Mealy Mountains are the highest uplands in southern Labrador, and they include treeless barrens of the High Sub-Arctic Tundra eco-region (Meades 1991), which are characteristically found much further north in Labrador. The unique alpine system and its importance to regional biodiversity make the potential upward migration of tree-line with climate warming a concern. The use of the alpine systems by fauna at risk such as the wolverine (*Gulo gulo*) and woodland caribou (*Rangifer tarandus caribou*) (COSEWIC 2002) makes the question of habitat displacement relevant to both the ecological and cultural fabric of the region. As the area lies within the proposed Akamiuapishku / Mealy Mountains National Park (Parks Canada 2005) there is much interest in the ecological integrity of this region.

Study Area

The Mealy Mountains are located in south-central Labrador, directly south of Lake Melville (Fig1.1). Research was conducted in the tree-line ecotone of the north-central part of the Mealy Mountains (N 53° 36.64' W 58° 49.03'), in an eastward tending valley, just south of an unnamed 1057 m high mountain.

The open canopy forest (~ 500 m a.s.l.) is composed of black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* [Moench.] Voss), balsam fir (*Abies balsamea* [L.] Mill.), and larch (*Larix laricina* [Du Roi] K.). Trees in the region are upright and many produce cones; however, tree seedlings are rare and tree height is seldom greater than 10 m. The understory and forest gaps are dominated by dwarf birch (*Betula glandulosa* [Michx.]) and mountain alder (*Alnus crispa* [Du Roi] Spreng). Small mammals and lagomorphs, known to be seed and seedling predators (Harrington 1998), have been observed and trapped in this area, including heather vole (*Phenacomys intermedius* Merriam), meadow jumping mouse (*Zapus hudsonius* Zimmermann), northern bog lemming (*Synaptomys borealis* Richardson), red backed vole (*Clethrionomys gapperi* Vigors), and snowshoe hare (*Lepus americanus* Erxleben) (Lewis et al. in press).

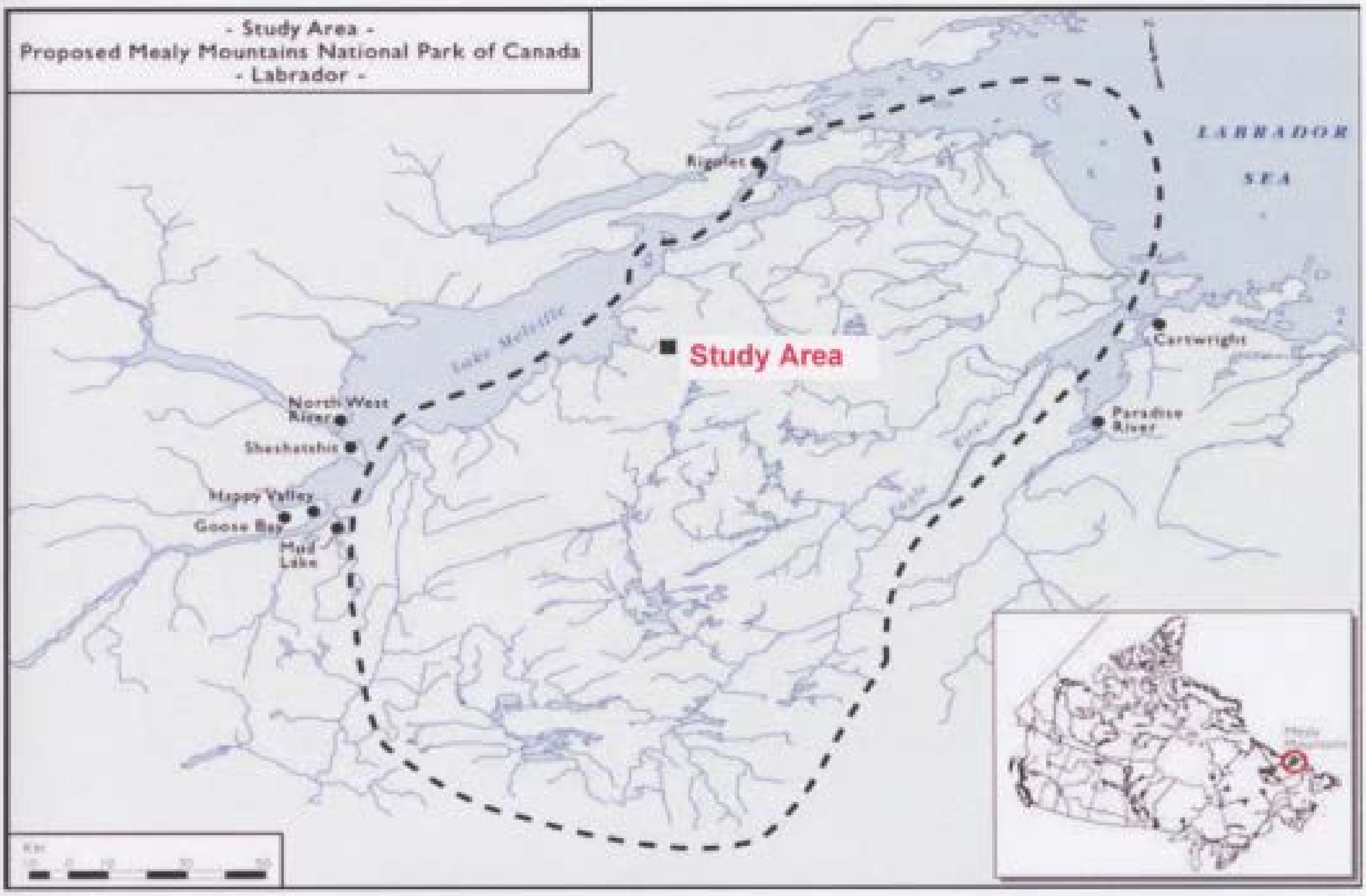

Fig. 1.1 Map of Mealy Mountains within Canada (inset), and of study area within the Mealy Mountains proposed National Park boundary (Parks Canada)

Trapping efforts over 2004 and 2005 yielded higher numbers of small mammals in the forest than further upslope, but numbers of trapped animals have been low (K. Lewis, unpublished data) compared to other northern areas (e.g. Institute for Environmental Monitoring and Research 2003, Klenner and Sullivan 2003).

Further upslope, at approximately 600 m a.s.l., isolated groups of trees, or 'tree islands', are surrounded by dwarf birch or by ericaceous vegetation. Commonly found beyond the limit of tree stands, these are either remnants of continuous forests from the past, or are outliers that have established in particularly favourable microhabitats (Körner 1999). Tree islands consist of either black or white spruce or balsam fir, and many are fertile, producing cones. They are potentially important sites for recruitment of tree seedlings beyond the forest limit, both as seed sources and as shelter from wind and climatic extremes (Germino et al. 2002, Holtmeier and Broll 2005). Krummholz patches are present along slope margins and exposed terrain beyond the limit of upright trees; few with cones. Dwarf birch meadows, tree islands and krummholz patches give way to alpine tundra vegetation at about 650 m a.s.l., where low-lying evergreen shrubs such as crowberry (*Empetrum nigrum* L.), partridgeberry (*Vaccinium vitis-idaea* L.), tundra bilberry (*Vaccinium uliginosum* L.), alpine bearberry *(Arctostaphylos alpina* L.), and Lapland diapensia (*Diapensia lapponica* L.) dominate. Lichens are common, mainly from the genera *Cladonia*, *Cladina*, and *Cetraria*. The rocky ground is disturbed through cryoturbation (successive frost heaving), with the resulting frost boils potentially important substrates for seedling recruitment (Sutton et al. 2006). Nomenclature for plant species follows Ryan (1978), and for animal species follows Banfield (1977).

Seeds and seedlings are obvious pre-requisites for the establishment of adult tree stands; as well, Cuevas (2000) noted that above the tree-line, seed viability and seedling emergence were the principle bottlenecks to tree establishment. Seedlings are particularly vulnerable to environmental stresses and climatic fluctuations, making them both the stage that tends to have the highest mortality, and the best indicator of climate change impact on forests (Shea and Grant 1985, Cuevas 2000, Germino et al. 2002).

It is with seeds and seedlings of black spruce, balsam fir, and paper birch (*Betula papyrifera* Marsh.) that the potential impacts of climate change on tree-line migration were investigated for this thesis. The objectives of this research were to better understand the potential for tree-line advance in the Mealy Mountains, and, if present, the means by which seedlings from local sources would be able to establish further upslope. All three species were planted into areas where near-soil temperature, ground disturbance, and herbivory were manipulated along an elevational gradient from open canopy forest through tree islands to alpine tundra habitat. Climate and climate change in south-central Labrador is examined in Section 2. This background provides context to the experimental temperature manipulations that were performed, which are examined in the same section. Seedling establishment among habitat gradients and experimental treatments is examined in Section 3. This study elucidates not only the likelihood but also the mechanisms behind a potential upslope migration of tree-line in the Mealy Mountains.

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CO-AUTHORSHIP STATEMENT

All manuscripts in this thesis were co-authored with Dr. Luise Hermanutz and Dr. John Jacobs. In all instances I was the principal contributor to project design and proposal, implementation of the field research component, analysis of the data and manuscript preparation.

2.0 CLIMATE AND TEMPERATURE MANIPULATION EXPERIMENTS IN THE MEALY MOUNTAINS STUDY AREA

2.1 Introduction

Climate is inextricably linked to tree-line position through the effects of temperature, moisture, wind, and extreme events on tree germination, growth, and reproductive capacity (Körner 1998, Alftine et al. 2003, Johnson et al. 2004). Climate monitoring has been ongoing in the alpine and tree-line regions of the Mealy Mountains study area since 2001; regionally, climate recording began in Cartwright in 1934, and in Goose Bay in 1941 (Keith 2001).

The climate of the Mealy Mountains is distinct from surrounding areas and is shaped by the cold Labrador Current to the east, the Lake Melville inland trough to the north, continental influences to the west, and variation in regional topography (Keith 2001). Summers are typically short and cool and winters long but relatively mild compared with the central Labrador Plateau to the west (Natural Resources Canada 1995). The study region is in discontinuous permafrost with the active layer extending into bedrock (Jacobs et al. 2005).

Seven decades of instrumental climate recording in central Labrador have not shown a significant long-term increase in air temperature (Jacobs et al. 2005). Recently, however, the region has begun to experience above-normal temperatures, mainly in the summer and fall. Annual temperatures in south-central Labrador have been at or above the 30-year (1951-1980) mean temperature for the past 10 years (Environment Canada 2005). The coming century is projected to see an increase in average annual surface temperature by 1-4°C for the region, as simulated by the Coupled Global Climate Model of the Canadian Centre for Climate Modeling and Analysis (Natural Resources Canada 2003). This same model projects an initial decrease in winter precipitation in the next five decades, followed by an increase of 0-20% of current precipitation patterns for the period 2080-2100.

In the summers of 2004 and 2005, tree-line tree seedlings were planted in experimental plots with the aim of improving our understanding of the potential for upslope tree-line migration in this region under a warming climate (see Section 3). Monitoring of air and soil temperatures was done at study plots along an elevational habitat gradient to measure microclimates near the planted seedlings.

To simulate climate warming, and to examine its effects on seedling establishment and survival, passive warming devices were established in all study plots along the same habitat gradient. These warming devices, or open-top-chambers (OTC), are common in experimental ecosystem warming studies (Hollister and Webber 2000). They are generally effective at warming air temperature, and less consistently, soil temperature, by amounts comparable to warming projected for the coming decades (Klein et al. 2005). There are several factors that influence the effectiveness of OTCs, including ground cover, humidity, solar radiation, wind, and season (Klein et al. 2005). These lead to a considerable amount of variation in temperature enhancement among different studies using OTCs, and over time within one OTC study (Marion et al. 1997).

This section summarizes the recent climate data that has been collected in the study area, and examines the effectiveness of the temperature manipulations performed. This provides a basis from which to investigate scenarios of future climate change and their effects on tree-line tree species in this area.

2.2 Methods

Climate Monitoring in study area

Climate monitoring in the Mealy Mountains study area began in the summer of 2001 with the installation of two automatic climate stations; one upper station in the alpine tundra at approximately 1000 m a.s.l., and another lower climate station in the open canopy forest, at approximately 570 m. a.s.l., and within 500 m. of the closest study plots. Air and soil temperature (at 1.4 m aboveground and 1 m underground respectively), solar flux, and air humidity are recorded hourly throughout the year, and bulk collection of precipitation is read annually (Jacobs et al. 2005).

Experimental temperature manipulations

Temperature manipulations were established to enable monitoring of planted tree seeds and seedlings under simulated warming conditions. Twelve study plots were established along an elevational gradient in the tree-line ecotone of the Mealy Mountains. Four plot replicates were set up in each of the open canopy forest (OC), tree island (TI), and alpine tundra (AT) habitats. OTCs were established in each study plot to provide passive warming (Plate 2.1). These were constructed with greenhouse plastic (6 mil) stapled to wooden stakes at a height of 0.7 m, with dimensions of 1.0 x 1.5 m. A gap of 3 cm was left between the bottom of the plastic and the ground surface to allow for normal water drainage, air movement, and travel by small animals. Chambers were uncovered to allow for normal precipitation. Controls were established at each plot so that the effects of the OTCs on seedling establishment could be compared to seedling establishment under natural conditions. OTCs were dismantled at the end of the field season in 2004 (Aug. 13) in anticipation of severe winter weather conditions, re-established in late June, 2005, and removed again Sept. 15-17, 2005.

Temperature monitoring at experimental study sites

A hand-held Traceable ® Hygrometer temperature sensor was used to measure air temperature inside the OTCs and in the controls. Temperatures were recorded at a height of 20 cm. above ground level, and were measured opportunistically at each plot throughout the 2004 and 2005 seasons during daylight hours. Four pairs of StowAway TidbiTs ® (Onset Corp.) were installed 5 cm below-ground in the centre of OTCs and controls, in two tree island plot

Plate 2.1 Study plot in open canopy forest with an open top chamber

replicates, one alpine tundra, and one open canopy forest plot replicate. A HOBO 4-channel outdoor / industrial data logger (Onset Corp.) was installed at each of the four 'corner plots', (i.e. those furthest east and west at the highest [AT] and lowest [OC] habitats). Each HOBO had temperature sensors measuring ambient air temperature at 1.4 m and soil temperature 5 cm below ground surface in OTCs and in controls. All of the sensors logged hourly temperature measurements. Laboratory calibration showed the maximum instrumental error of these sensors to be within $\pm$ 0.5°C.

Data Analysis

Information summarizing climate data collection in the study area and in study plots are presented to provide a climatological context. Differences in daytime air and soil temperature between OTCs and controls were both assessed first by 2-way ANOVA, General Linear Model, using SAS® version 9.1(SAS Institute Inc. 1996). Habitat and year were explanatory variables. Assumptions of normality and homoscedasticity were tested by plotting residual error values. Paired t-tests were then performed for air and soil temperatures between OTC and controls for each habitat gradient.

Differences in soil temperature between OTCs and controls were further investigated due to its diurnal cycle. A 2-way ANOVA tested the effects of hour of day (over the 24-hour period) and of habitat on temperature differences between OTCs and controls. The daily cumulative soil heat gain/loss in OTCs was then assessed for each habitat, by calculating the difference in degree*hours (Σ {Temperature difference * time interval}). The change in temperature over the time period of the study was not of interest, and no time series was performed.

2.3 Results

Climate monitoring in study area

The average summer temperatures (June through September) from 2001-2004 were 10.5°C and 7.3°C, and average growing degree days (> 5°C) were 621 and 372, at the lower and upper climate stations respectively (Jacobs et al. 2005). Average monthly temperatures ranged from approximately -21°C to

+14°C over the past 5 years (Fig. 2.1), with cooler winters and summers recorded at the upper station compared to the lower station. The last three years of records show an increase in mean monthly temperature in the spring. The particularly warm May of 2005 corresponds to observations that year of the snow pack melting earlier compared to the previous four summers, and thus extending the growing season considerably. The bulk precipitation gauge results suggest that the highlands in the study region receive annual precipitation of 2000 to 3000 mm (Jacobs et al. 2005).

Temperature monitoring at experimental study sites

Air temperatures were higher by approximately 1°C in the OC compared to the AT habitat, and were higher by approximately 0.5°C in 2005 compared to 2004 (Table 2.1).

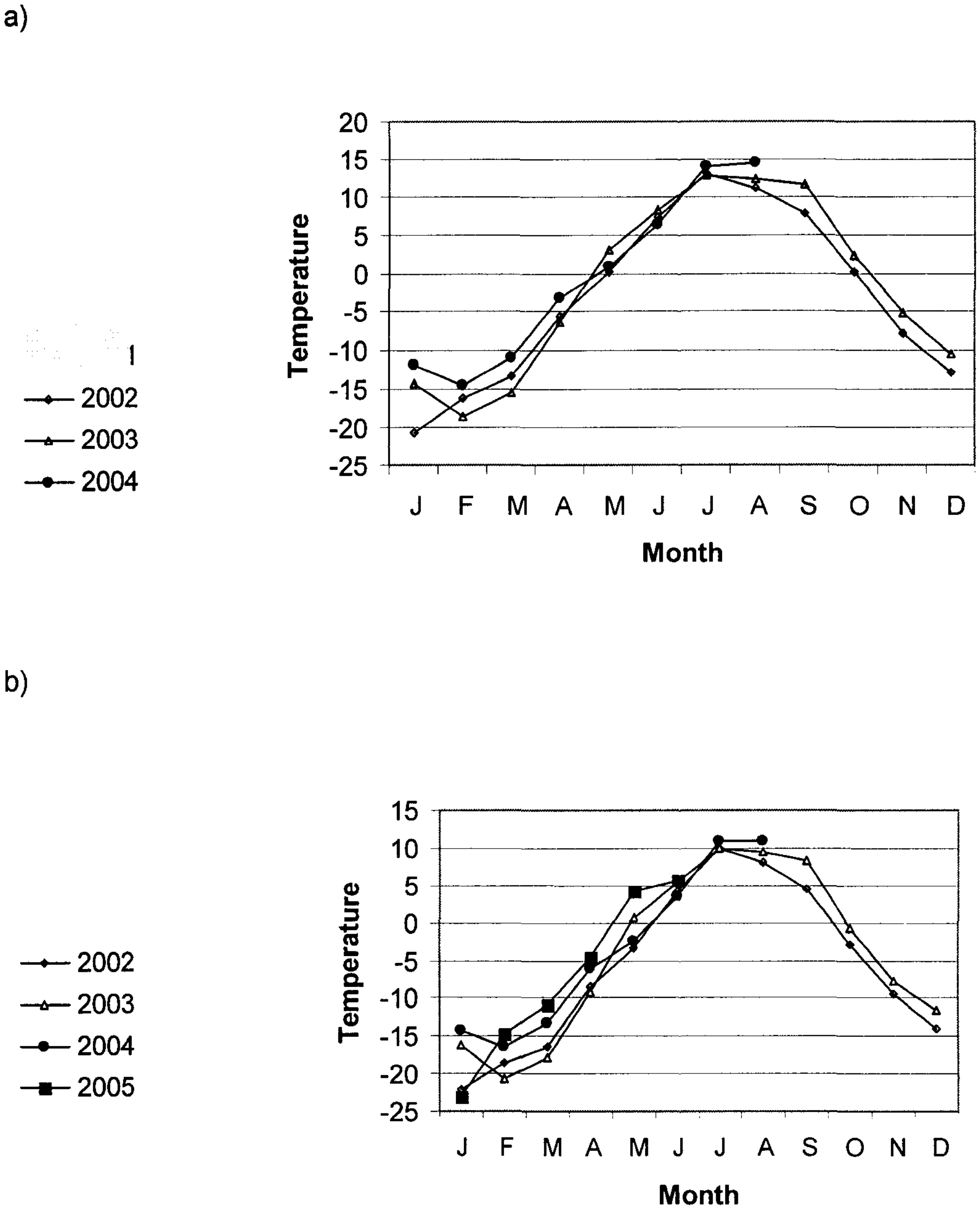

Fig. 2.1 Average monthly temperatures (^{0}C) at the lower (a) and upper (b) climate stations, January 2002 to August 2004 (for lower station) and to June 2005 (for upper station). Animal damage abbreviated the temperature records for the lower climate station.

Table 2.1 Average daily air and soil temperatures (°C) as measured by HOBO sensors in two alpine tundra and two open canopy forest study plots, July-August 2004 and 2005. Values are mean (SE)

	Habitat	2004	2005
Air temperature	AT	12.3 (0.15)	12.9 (0.53)
	OC	13.4 (0.26)	13.9 (0.66)
Soil temperature	AT	11.3 (0.22)	11.8 (0.34)
	OC	12.2 (0.24)	12.7 (0.30)

Effect of open-top-chambers:

Temperature

OTCs warmed air temperature by an average of 1.5°C compared to controls (Table 2.2). The temperature enhancement performed significantly differently among habitat gradients, with AT > T I > OC ($F_{2,9} = 12.81$, $p = 0.0023$), but not between years ($F_{2,3} = 0.10$, $p = 0.9014$). OTCs caused significant air temperature warming in each habitat.

OTCs caused a statistically significant soil warming in the alpine and tree island habitats during daylight hours (8:00 a.m. – 6:00 p.m.), though due to the margin of error of the temperature sensors, the temperature change in the alpine tundra is the only one that can be ascertained with confidence (Table 2.2). There was no significant difference in soil temperatures between OTCs and controls in the open canopy forest. The effects of habitat ($F_{2,5} = 1.91$, $p = 0.2421$) and year ($F_{1,5} = 1.03$, $p = 0.3558$) on soil warming were not statistically significant.

Table 2.2 Difference in air and soil temperatures (°C) between temperature-enhanced (**T**) and control (**C**) treatments at three habitat gradients. Values are mean temperature (SE) as recorded over daylight hours (8:00 am – 6:00 pm). Significant t-tests are indicated in bold.

	Air temperature			**Soil temperature**		
Habitat	**T-C**	**t**	***p***	**T-C**	**t**	***p***
AT	+ 2.2 (0.29)	7.66	**<0.0001**	+ 0.87 (0.18)	4.93	**0.0006**
TI	+ 1.3 (0.33)	3.96	**0.0003**	+ 0.39 (0.71)	3.02	**0.0128**
OC	+ 0.9 (0.24)	3.73	**0.0004**	- 0.17 (0.66)	-1.46	0.1742

OTCs had the general effect of raising soil temperatures during the day but rendering a slight cooling at night relative to the controls. There was a significant interaction between hour of day and habitat ($F_{2,64} = 6.81$, $p = 0.0021$), and this diurnal cycle was most apparent in the alpine tundra and tree island habitats (Fig. 2.2). There was a positive average 24-hourly cumulative heat gain in the OTCs compared to the controls in the alpine tundra habitat and tree islands, and in the open canopy forest there was a net loss of heat over the 24 hour period (Table 2.3).

Table 2.3 The cumulative heat gain/loss in soil temperature at 5 cm below ground surface in OTCs compared to controls, at three habitat gradients.

Habitat	**Cumulative heat change over 24 hours (°C*hr)**
Alpine Tundra	5.76
Tree Island	7.98
Open Canopy Forest	-4.33

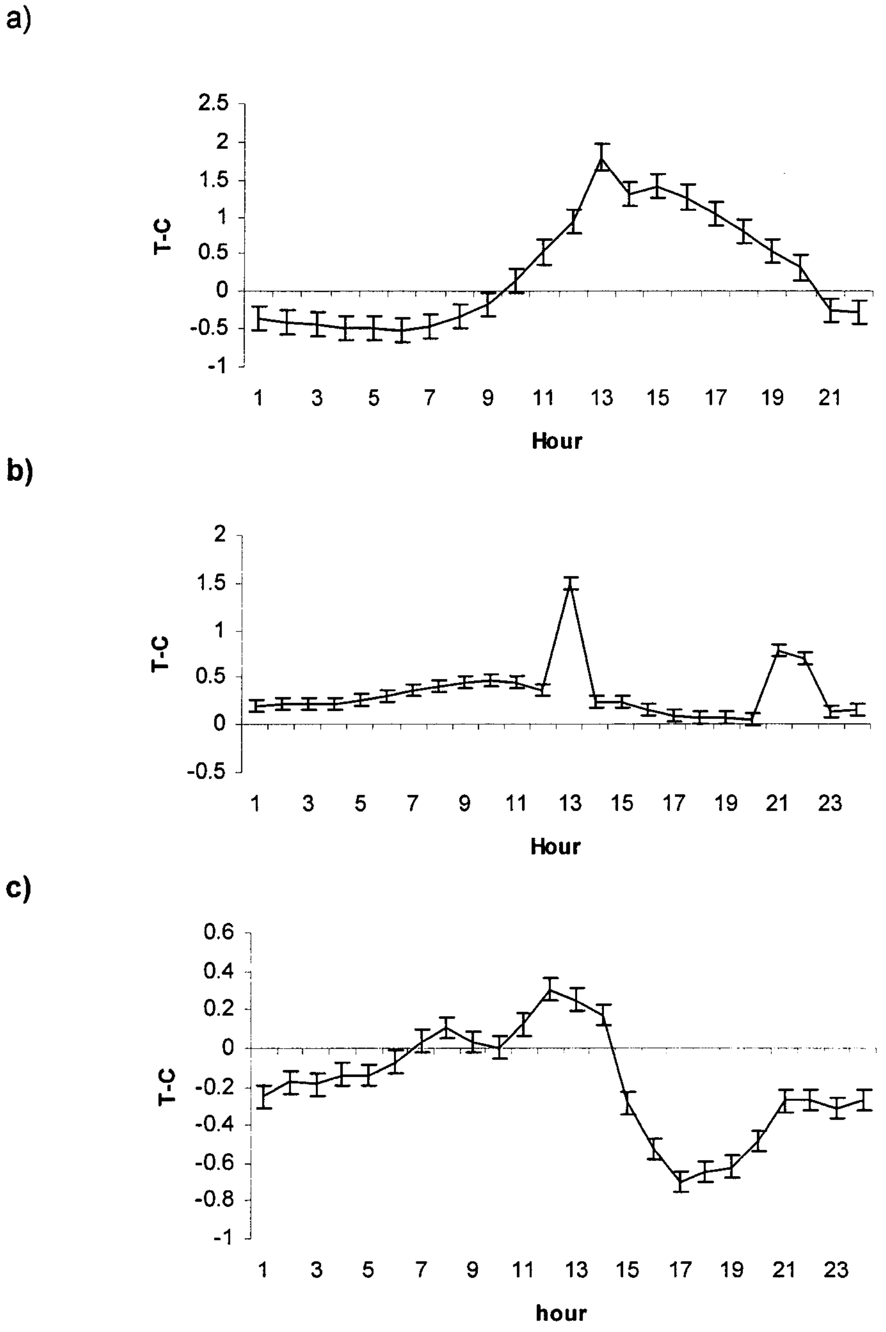

Fig. 2.2 Differences in soil temperature at depth of 5 cm between OTCs (T) and controls (C) in a) Alpine habitat, b) Tree Islands, c) Open Canopy Forest. Values are mean ±1 SE.

Discussion

While southern Labrador has not yet experienced significant climate warming, recent records point to a warming trend (Environment Canada 2005) that is projected to continue into the coming decades and centuries. The study of climate-vegetation dynamics in this region is very timely for forecasting landscape changes, particularly at geographical boundaries such as the tree-line ecotone. The plot-specific temperature monitoring cast light on the ambient and manipulated temperature regimes to which the tree seedlings were subjected over the course of the study.

The OTCs in our study increased air and soil temperature to a degree similar to that predicted for the region over the next 90 years (Natural Resources Canada, 2003). This compares to the 1.2 - 1.8°C near-surface air and soil temperature increase found in a meta-analysis of warming chambers used in the International Tundra Experiment (Arft et al. 1999). Temperature enhancement tended to increase with elevation, which could be due to wetter soils at lower elevations requiring more energy to warm, and their higher specific heat, than the drier alpine soils. The increased tree canopy at lower elevations sheltered the OTCs (and the growing seedlings) from the wind, which would also lessen the effect of chamber-warming compared to that in more exposed sites. As has been shown in other studies (Marion et al. 1997), the increased ground cover at lower elevation likely acts as insulation lessens heat conduction adding to the observed differences between habitats.

The diurnal cycle of excess heating during the daytime compared to nighttime was consistent with other studies using such passive warming devices, due to the correlation of solar radiation to temperature enhancement (Marion et al. 1997). We did not monitor nighttime air temperature, but nighttime soil temperature cooling was observed in the alpine tundra and the open canopy forest in this study. While not common, air and soil temperatures have shown such a response in other studies (Marion et al. 1997). Though OTCs were able to simulate daytime temperature increases similar to the level of climate warming projected over the next 100 years, the experimentally observed nighttime cooling is inconsistent with observations and predictions of current and future climate change. Rather, some climate models suggest a disproportionate increase in minimum (i.e. nighttime) temperatures compared to maximum (i.e. daytime) temperature for the future (Haines et al. 2000).

Climate change will have complex effects on the physical and ecological dynamics of a region that are beyond the scope of this study to investigate. Warming is expected to increase active layer depth, litter decomposition, nutrient mineralization and availability to plants, and hence plant species richness and composition (Arft et al. 2003). These outcomes are currently only predicted at a very general level, much less simulated. Nonetheless, the short-term ecological effects of OTC warming have been shown to be analogous to the ecological effects of natural climate warming when the two effects were compared in Alaska over seasons with significantly different temperatures (Hollister and Webber 2000). This adds confidence to the notion that OTCs are useful tools to monitor short- and medium-term changes in vegetation dynamics likely to occur with climate warming.

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3.0. WILL CLIMATE CHANGE LEAD TO FOREST DISPLACEMENT OF ALPINE TUNDRA HABITAT IN THE MEALY MOUNTAINS OF LABRADOR?

3.1 Introduction

Historical and current records show an unmistakable and well-documented picture of tree-lines that migrate in response to climate change (Rochefort et al. 1994, IPCC 2001, Kullman 2005). As global mean temperature has risen by 0.6°C over the last century (IPCC 2001) altitudinal tree-lines around the world have experienced increases in tree height (Lavoie and Payette 1994) and density (Lloyd and Fastie 2003), and upslope migration of seedlings and adult trees beyond present tree line (Hättenschweiler and Smith 1999, Luckman and Kavanagh 2000, Kullman 2002, Moiseev and Shiyatou 2003). Contemporary and future climate warming, projected to increase average global surface temperature by 1.4 - 5.8°C from 1990-2100, is expected to cause tree-lines to move up in altitude and latitude, often at the expense of alpine tundra habitat (IPCC 2001).

While the altitudinal tree-line has been described as "*perhaps the best known and most studied of all distributional boundaries of trees*" (Körner 1999) the large number of climatic, physical, and ecological factors that affect tree recruitment and tree-line position, and the regionally specific interactions among them, make it difficult to understand specific tree-line positions or to predict their future movements beyond a general level (Cairns and Malanson 1998, Malanson 2001, Holtmeier and Broll 2005). There is a strong correlation between tree-line position and temperature (Halliday and Brown 1943, Black and Bliss 1980, Grace 1989, Körner and Paulsen 2004); however, thermally controlled tree-lines do not always migrate in response to rising temperatures. The relative importance and interactions of climatic factors on tree-line position depend on the physical and ecological characteristics of the region. In the Canadian Rocky Mountains, for example, Luckman and Kavanaugh (2000) found that a 1.5°C temperature increase over the last century affected tree-line in some locations but not in others, and those that responded to the warming experienced a variety of responses.

Suitable ground substrate into which seeds can germinate is a basic necessity for tree establishment, and its availability is known to control tree-line advance in some areas (Cullen et al. 2001, Hättenschwiler and Körner 1995). The micro-site requirements of boreal tree seedlings can be quite specific (Germino et al. 2002), and generally the chances of seed germination success are improved with lower depths of litter or organic material (Greene et al. 1999). Herbivory is another potentially important factor affecting tree establishment, and vertebrate herbivores have been shown to control tree-line advance in Spain (Castro et al. 1999) and in Fennoscandia (Oksanen et al. 1995). The importance of these factors to tree-line advance is variable over space and time, and contributes to the difficulty of extrapolating trends in tree-line movement geographically.

This study examines the potential migration of the altitudinal tree-line in the Mealy Mountains. Seedling establishment of black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), and paper birch (*Betula papyrifera* Marsh.) was monitored along an elevational habitat gradient from open canopy forest to alpine tundra vegetation. Temperature, herbivory and ground disturbance were manipulated to investigate their effects on seedling establishment. Seedling emergence, height, damage sustained and mortality were recorded over the summers of 2004 and 2005. Through our experimental manipulations, we not only assessed the likelihood of tree-line migration (given availability of seed) under different environmental conditions, but also the factors responsible for seedling establishment at and beyond present forest limits in the Mealy Mountains.

3.2 Methods

Study area

Research was conducted in the north-central Mealy Mountains (N 53° 36.6' W 58° 49.0'), in an eastward tending valley, south of an unnamed 1057 m mountain. Study sites were established in the transition between open canopy forest and alpine tundra vegetation (approximately 550 m - 650 m a.s.l.), along a northeast facing slope.

Study Species

Not all of the tree species that occur in the study area were used as study species. These were chosen based on their frequency in the study area, and to represent a range of life history strategies.

Black spruce (bS) (*Picea mariana*)

Black spruce was the main experimental tree species used in this study, and was the most common tree species in the Mealy Mountains (Keith 2001), in

Labrador (Ryan 1978), and across boreal North America, where it commonly forms the tree-line (Viereck and Johnston 1990, Begin and Filion 1999). Black spruce seedlings have a particularly high tolerance to cold, wet, nutrient-poor conditions (Viereck and Johnston 1990), which, along with their phenotypic plasticity in the face of changing environmental conditions (Lavoie and Payette 1994), explains their predominance at the tree-line.

Balsam Fir (bF) (*Abies balsamea*)

Balsam fir is the next most common tree species in the Mealy Mountains (Keith 2001). Important differences between balsam fir and the other study species include its heavier seeds, which limits its dispersal ability. Seeds often fall directly into a forest patch, producing 'advance regeneration' (i.e. a slow-growing under-story layer), while the lighter spruce and birch seeds are long-distance dispersers (Safford et al. 1990, Gallipeau et al. 1997). Balsam fir is also tolerant to a wider range of seedbeds, is shade tolerant, and once germinated, can grow more quickly than can the other species (Anderson and Winterton 1999).

Paper Birch (pB) (*Betula papyrifera*)

Paper birch is an early successional species in the Mealy Mountains (Keith 2001), as it is elsewhere in the boreal forest, due to its low tolerance to shade, and relatively short life span (Safford et al. 1990). Although it was not observed directly in the study area, paper birch occurs sporadically in nearby forested areas (personal observation), and makes up continuous forest cover on steep slopes elsewhere in the Mealy Mountains (Keith 2001). Its very light, winged seeds allow for long-distance dispersal, making it a potentially important species to migrate into alpine areas (Safford et al. 1990). Deciduous species such as birch are often preferred over conifers by vertebrate browsers (Viera 2003), which can modify the species composition of expanding forests.

Based on the life history strategies of the different study species, it is predicted that should tree-line advancement occur, the light, wind-dispersed birch and black spruce seeds would be the first to establish beyond the tree-line. Birch seeds would likely be the first species to establish, with the more shade-tolerant, slower growing black spruce establishing more gradually. Balsam fir seeds are predicted to take longer to migrate, but could establish more successfully due to their tolerance for a variety of seedbeds and their present success in the upper tree-line ecotone.

Experimental design

A total of 12 study plots were established along an elevational gradient (Fig. 3.1). Four plot replicates were positioned in each of the open canopy forest (**OC,** Plate 2.1): adjacent to a tree island (**TI**, Plate 3.1a); and beyond the tree limit in alpine tundra (**AT**, Plate 3.1b) vegetation.

Seeds and seedlings of black spruce, balsam fir, and paper birch were planted into a series of five manipulated areas within each study plot. The manipulations, or treatments, (i – v) listed below, were positioned randomly in each plot, at a minimum distance of 1 m from neighbouring treatments. Each treatment area was 1.0 x 1.5 m, with one half randomly allocated to be planted in 2004, and the other half in 2005.

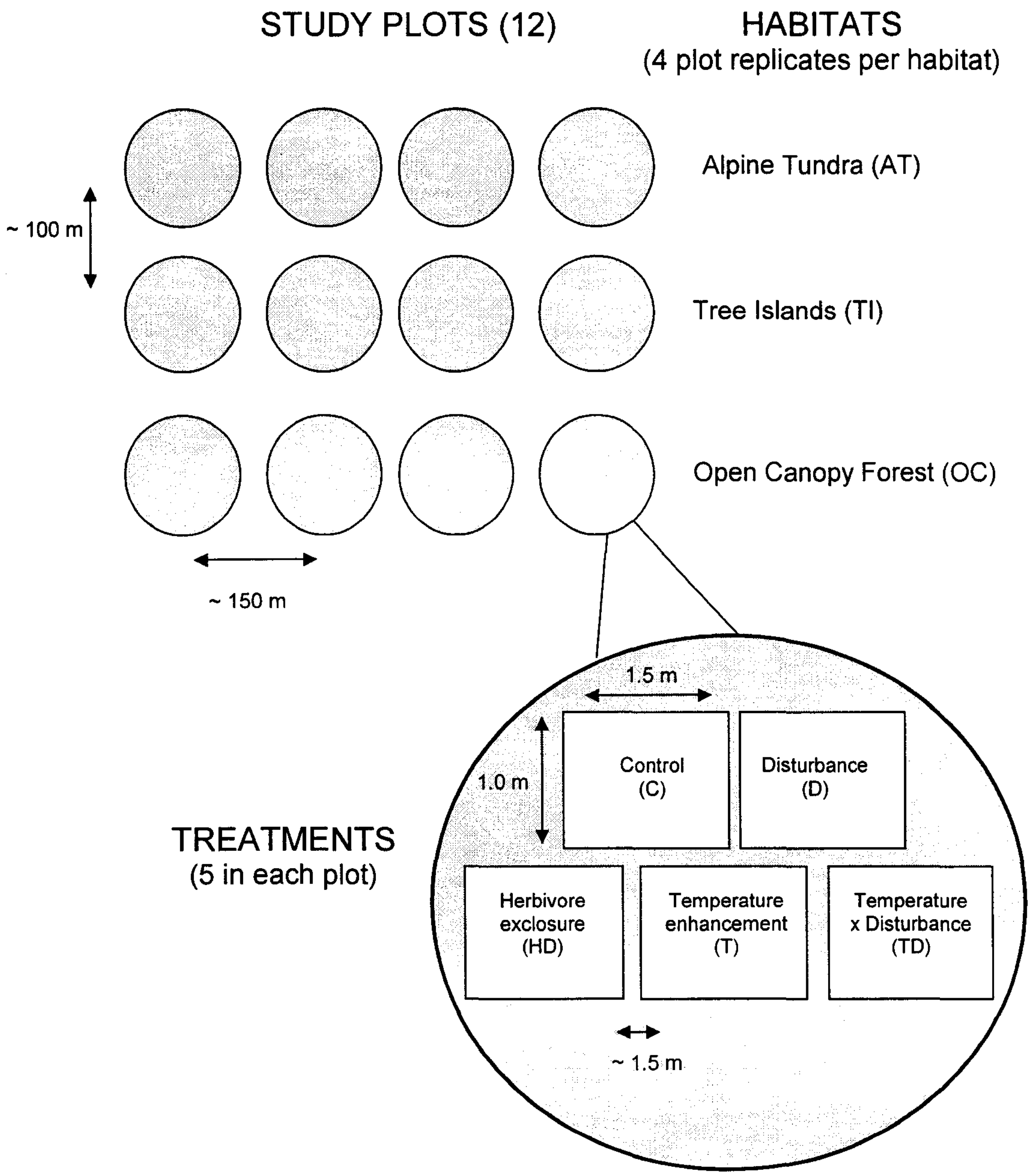


Fig. 3.1 Design of study plots over three habitats (AT, TI, OC) with five randomly assigned treatments (C, D, HD, T, TD) in each plot (not to scale).

a)

b)

Plate 3.1 Tree Island (a) and Alpine Tundra (b) habitat gradients used in study

i) Control (C): The control was used to monitor seedling establishment in a non-manipulated treatment. Direct comparisons could be made with the **T** treatment to determine the effects of temperature enhancement, because both treatments were on undisturbed ground.

ii) Disturbance (D): To simulate open seedbed conditions, ground cover was manually removed to expose mineral soil prior to sowing seeds. This treatment was also used as a control for Temperature x Disturbance (**TD**) and Herbivory x Disturbance (**HD**) treatments (Plate 3.2a).

iii) Herbivore exclosure x Disturbance (HD): To study the effect of seed and seedling predation by vertebrate herbivores, exclosures were erected using hardware cloth with mesh size of 12 x 13 mm (Plate 3.5b). Exclosures were covered at a height of 20 cm to exclude birds or jumping mammals. Hardware cloth was dug into the ground (10 – 20 cm, depending on the depth to rocks) to prevent entry by burrowing mammals. Disturbances were created in these treatments in order to provide a suitable seedbed for potential germinants. Cages remained in place over the winter.

iv) Temperature enhancement (T): Open-top-chambers (OTC) were formed to provide passive warming (OTC, Plate 2.1). Greenhouse plastic (6 mil) was stapled to wooden stakes at a height of 0.7 m. A gap of 3 cm was left between the bottom of the plastic and the ground surface to allow for normal water drainage, air movement, and travel by small animals. Chambers were uncovered so that precipitation was consistent with neighbouring treatments. OTCs were dismantled at the end of the field season in 2004 (Aug. 13) in anticipation of severe winter weather conditions, re-established in late June 2005, and removed again Sept. 15-17, 2005.

v) Temperature enhancement x Disturbance (TD): Treatments ii and iv were combined by creating soil disturbances within the OTCs to monitor seedling success under warmer temperature conditions where appropriate seedbed was made available.

a)

b)

Plate 3.2 Disturbance (a) and Herbivore x Disturbance (b) treatments into which seedlings were planted

Planting and monitoring of seeds and seedlings

In 2004, 32 black spruce seeds were sown, by being pressed into the ground, into each treatment in all study plots and marked with toothpicks. Seeds were unable to be sown in the ***HD*** treatment at one plot in each habitat gradient due insufficient exclosure material, so the total number of seeds planted was 1824. Half (16) of the seeds were sown on July 11, and the other 16 seeds were sown on July 29, to test the effect of growing season length on over-winter survival. All seeds were soaked in water for 16 hours prior to sowing. In addition to sowing seeds, seedlings of black spruce were germinated in peat pellets on-site, under more protected conditions, and 6-8 were planted into each of the treatments. The pre-germinated seedlings were planted provisionally so that should the sown seeds not develop, seedling development and survival could be still be monitored.

Surviving seedlings of those planted in 2004 were surveyed during June 25-27, 2005, and these seedlings continued to be monitored until September. On June 29, 2005, 16 seeds each of *P. mariana*, *A. balsamea*, and *B. papyrifera* were sown next to colour-coded toothpicks into all treatments, for a total of 2880 seeds. Again, all seeds had soaked in water for 16 hours and were sown by being pressed lightly into the ground. Paper birch and balsam fir were added in 2005 based on new observations in 2004 of paper birch in the region and of an unexpectedly high number of fir trees in the study area. To avoid over-exploitation of seeds found in trees in study area, all seeds planted were obtained from the Provincial Tree Nursery, Wooddale Newfoundland (Dept. of Natural Resources, Government of NL). The source for black spruce seeds

Goose Bay, Labrador, and balsam fir and paper birch seeds originating from Bay d'Espoir, Newfoundland. Fourteen pre-germinated seedlings of black spruce were planted into three treatments at each plot (***C, T***, and ***HD***) on July 2, 2005. The seedlings were not planted into ***D*** and ***TD*** treatments to increase sample size in fewer treatments, and because the purpose of these manipulations was to test their influence on seedling emergence and not on their growth and survival. On July 9, 2005, 10 pre-germinated paper birch seedlings were planted into ***C***, ***T***, and ***HD*** treatments in each of the plot replicates in the alpine tundra habitat gradient. Due to lower than anticipated germination of birch seeds, the seedlings were confined to only one habitat gradient, to increase the sample size in each treatment replicate. The alpine habitat was chosen as the most interesting gradient in the context of seedling invasion into previously non-treed areas.

Treatments were monitored every 3-6 days throughout the growing seasons of both 2004 and 2005. The date of first observation of seedling emergence was recorded for sown seeds; seedling height, damage sustained, and mortality were recorded for germinated seeds and planted seedlings. Seedling height was measured using calipers (accuracy 0.03mm) at the beginning and end of each season. Damage values were categorical and based on visual, above-ground observation of leaf or stem damage and removal, where 0= no damage, 1= < 25% damage, 2 = 25-50% damage, 3 = 50-75% damage, 4 = > 75% damage, and 5 = dead. The last measurements of all seedlings were taken on August 10-11 in 2004, and on September 15-17 in 2005.

Data Analyses

All statistical analyses were performed on SAS® version 9.1 (SAS Institute Inc. 1996). Measures of seedling establishment (number of seedlings emerging, time to emergence, seedling growth, damage, and mortality) were analyzed separately for each species, and the fixed effects of experimental treatments and habitats were used as explanatory (independent) variables. Data from treatments were pooled across habitats due to a low sample size in many individual plots (Sokal & Rohlf 1995).

Where the response variable consisted of binary or proportional data (i.e., proportion of seedlings that emerged, sustained damage or died) the logistic regression, a special case of the Generalized Linear Model, was used. Logistic regression is an appropriate test for such data, given the model's assumption that residuals have a binomial (as opposed to normal) distribution (Agresti 1996). It also shows a greater utilization of data and is a more sensitive test compared with traditional ANOVA or loglinear tests (Lewis 2004).

The time (number of weeks) to emergence was analyzed as a Poisson distribution, log link (Littel 2002), with homogeneity tested using a residuals vs. fits plot. Due to under-dispersion of the variance, the deviance scale parameter was used (Littel 2002). Based on the results of this test, it was of interest to compare the proportion of seeds that emerged in temperature enhanced treatments in early 2005 to those emerging in late 2005. This analysis was performed using the logistic regression in the Generalized Linear Model.

Seedling height was analyzed using Analysis of Variance (ANOVA) in the General Linear Model, as this response was a regression variable.

The performance of seedlings developed from sown seeds and those planted into peat pellets did not differ significantly for the factors being investigated in this study, therefore data from the two types of seedlings were pooled.

Differences among treatments were examined with the use of linear contrasts. To test the effect of temperature enhancement, treatments **T** and **TD** were contrasted with **C** and **D**; the effect of herbivory was tested by contrasting **HD** with **D**, and when the effect of ground disturbance was of interest **D** was contrasted with **C**.

3.3 Results

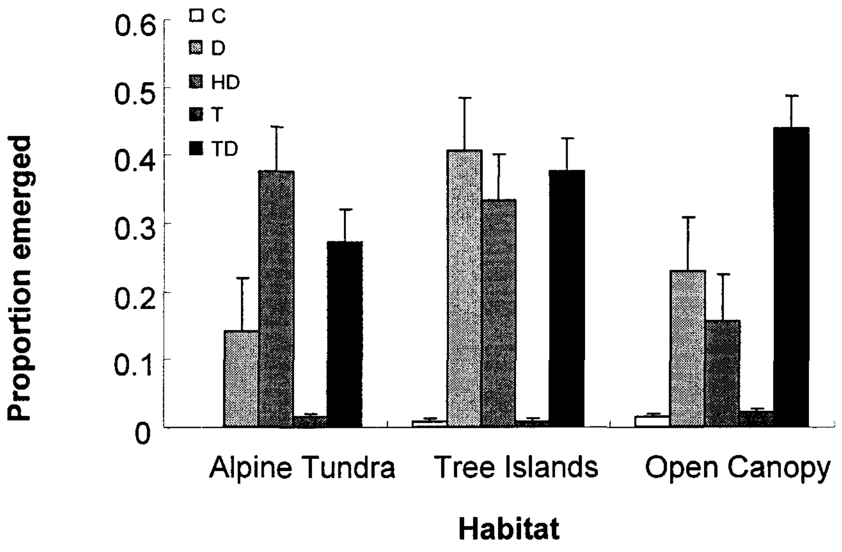
Due to low germination success and thus small sample size of balsam fir and paper birch, many of the analyses could not be performed for these species. Where data analysis was possible the results are included.

Seedling emergence among treatments and habitats

Black spruce

The overall proportion of black spruce seedlings emerging was 17.9 (± 6.9) % across habitats, treatments, and seasons. There was a significant interaction between treatment and habitat as factors affecting seedling emergence in both years (2004: $\chi^2 = 23.31$, d.f. = 8, $p = 0.0030$; 2005: $\chi^2 = 40.07$, d.f. = 8, $p < 0.0001$, Fig. 3.2). Both increasing temperature and excluding herbivores increased the proportion of black spruce seedlings emerging in 2004 and 2005

a)



b)

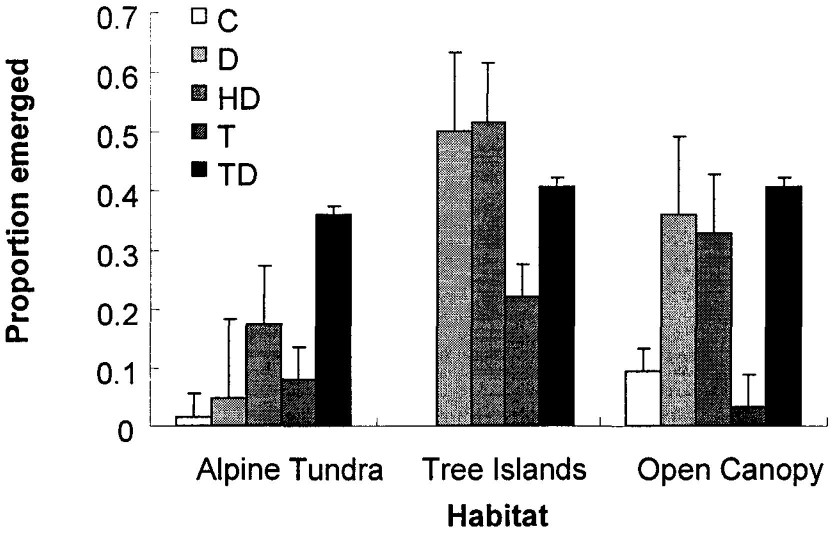


Fig. 3.2 Proportion of black spruce seedlings that emerged in each treatment and habitat in a) 2004 and b) 2005. Values are mean + 1 SE.

in the alpine tundra habitat (Table 3.1), while neither of these treatments affected emergence in the open canopy forest. Temperature enhancement increased seedling emergence in the tree islands in 2005, but not 2004.

Table 3.1 Differences in emergence of black spruce seedlings in disturbances (**D**), in temperature enhanced treatments (**T**), and in herbivore exclosures (**HD**) relative to controls in 2004 and 2005. Significant tests are indicated in bold.

Habitat	**Treatment**	**2004**			**2005**		
		d.f.	**X^2**	***P***	**d.f.**	**X^2**	***P***
AT	**D**	1	26.32	**<0.0001**	1	1.08	0.2990
	T	1	4.60	**0.0320**	1	14.37	**0.0002**
	HD	1	10.87	**0.0010**	1	5.42	**0.0199**
TI	**D**	1	76.50	**<0.0001**	1	55.23	**<0.0001**
	T	1	0.01	0.9277	1	13.09	**0.0003**
	HD	1	0.79	0.3733	1	0.03	0.8597
OC	**D**	1	28.59	**<0.0001**	1	36.96	**<0.0001**
	T	1	1.98	0.1590	1	3.07	0.0797
	HD	1	0.81	0.3695	1	0.14	0.7097

In both 2004 and 2005 the relative proportion of seedlings emerging per habitat decreased from TI > OC > AT. In 2004 these differences among habitats were not significant ($\chi^2 = 2.49$, d.f. = 2, $p = 0.2883$) but they were in 2005 ($\chi^2 = 34.81$, d.f. = 2, $p < 0.0001$).

Balsam fir

A total of 51 of the 960 (5.3%) balsam fir seedlings emerged in 2005 across treatments and habitats. There was no effect of temperature increase or herbivore exclusion on emergence. A significantly higher proportion of seedlings emerged in disturbed treatments (4.79%) compared with non-disturbed treatments (0.52%; $\chi^2 = 32.39$, d.f. = 1, $p < 0.0001$). Habitat did not significantly influence seedling emergence.

Seedling emergence over years and species

Time of planting

Over twice as many (black spruce) seedlings emerged of those planted early in 2004 (16.8%) compared to those planted later that season (8.6%). This difference was significant ($\chi^2 = 45.16$, d.f. = 1, $p < 0.0001$). Emergence of black spruce seedlings in 2005 (23.5%) was significantly higher than in 2004 (12.7%, $\chi^2 = 31.80$, d.f. = 1, $p < 0.0001$, Fig. 3.3).

Species comparisons

Overall seedling emergence in 2005 was 10.2%, with bS > bF > pB. The difference in emergence among species was significant ($\chi^2 = 281.42$, d.f. = 2, $p < 0.0001$), with black spruce producing over four times as many germinants (n = 226) as balsam fir (n = 51), which itself produced over three times as many germinants as paper birch (n = 15) for the same number of seeds sown.

Time to seedling emergence

The consistent date of planting and longer monitoring season in 2005 allowed us to examine the effect of temperature and habitat on time to seedling emergence.

Black spruce

There was a significant interaction between treatment and habitat on time to seedling emergence (number of weeks) ($\chi^2 = 19.73$, d.f. = 1, $p = 0.0062$). In all three habitats, temperature enhancement was accompanied by a longer time to emergence, though this effect was only significant in the tree islands (Table 3.2).

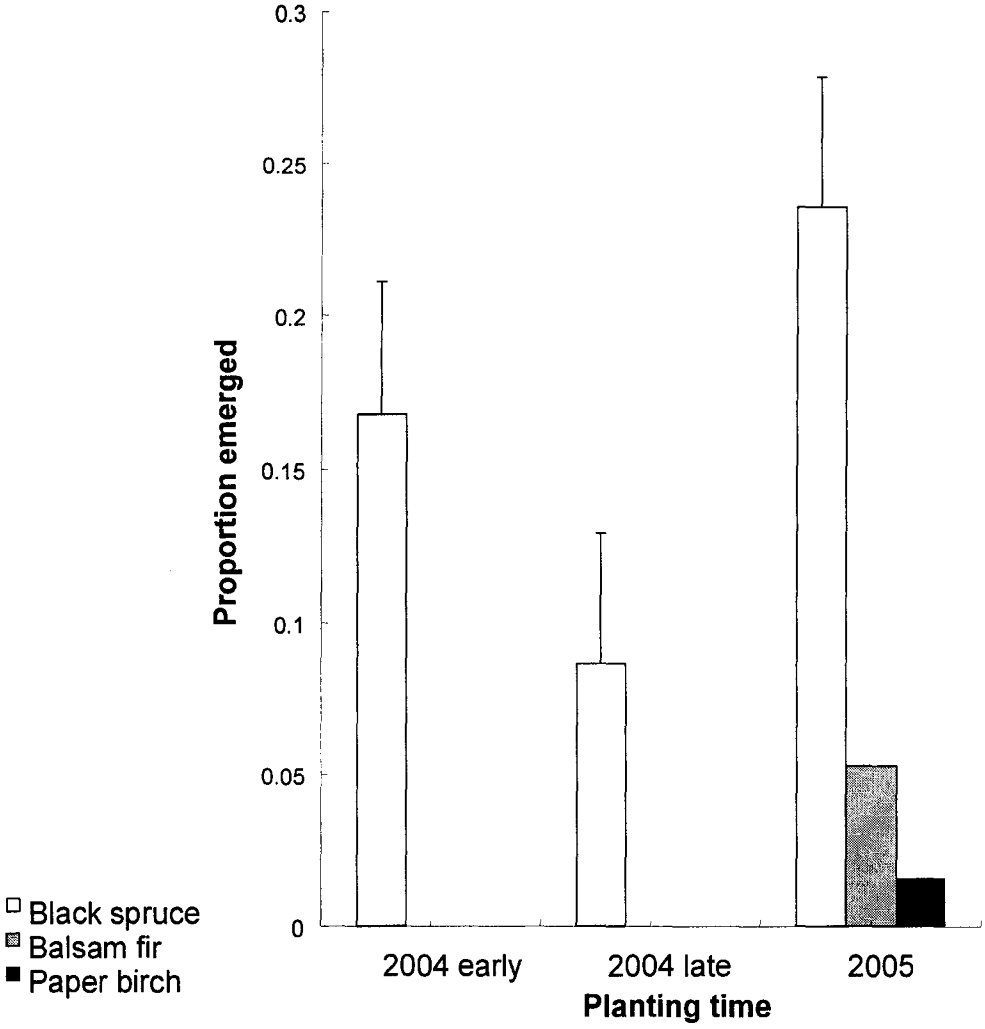


Fig. 3.3 Seedling emergence over two years, pooled over treatments; only bS was planted in both years, while all 3 species were planted in 2005. Values are proportion of planted seeds that emerged + 1 SE.

Table 3.2 The number of weeks taken for black spruce seeds to emerge in controls (**C,D**) compared to temperature enhanced treatments (**T,TD**). Values are means (SE)

Habitat	**Weeks to emerg.**		**d.f.**	**X^2**	***p***
	Control	**Temp.**			
AT	5.0 (0.71)	5.6 (0.28)	1	0.47	0.4910
TI	5.1 (0.25)	5.7 (0.23)	1	6.49	**0.0109**
OC	4.7 (0.19)	5.5 (0.30)	1	0.44	0.5095

A comparison was also made for the proportion of seedlings that emerged in temperature enhanced treatments earlier in the season (July 10-August 4, 2005) versus later in the season (August 5- September 17, 2005). The later, and cooler, part of the summer produced a significantly higher number of black spruce germinants in temperature enhanced treatments than did the earlier, warmer part of the summer ($\chi^2 = 13.05$, d.f. = 1, $p = 0.0003$). There was no significant effect of habitat on time to seedling emergence.

Balsam fir

Treatment did not significantly affect the time taken for balsam fir seedlings to emerge. There was a significant decrease in time taken for seedling emergence in the alpine tundra habitat (mean time = 4.7 weeks) compared to the open canopy forest and tree islands (mean time for both = 5.3 weeks) ($\chi^2 = 6.76$, d.f. = 1, $p = 0.04937$).

Comparison of species

Balsam fir seedlings took significantly longer to emerge (average = 6.0 weeks) than black spruce (average = 5.4 weeks) or paper birch (average = 4.8 weeks)

($\chi^2 = 4.80$, d.f. = 1, $p = 0.0285$). The latter two species did not differ significantly in time taken to emerge.

Seedling height

Black spruce

Treatments ($F_{4,15} = 9.52$, $p = 0.0039$) influence the height of black spruce seedlings grown over two summers. Increasing temperature caused a significant increase in height growth over two seasons for seedlings planted in 2004 ($F_{1,8} = 13.85$, $p = 0.0059$, Fig. 3.4), but not over one season for seedlings planted in either 2004 or 2005. Similarly, protection from herbivores caused a significant growth increase over two seasons for seedlings planted in 2004 ($F_{1,8} = 31.57$, $p = 0.0005$) but there was no significant effect of herbivory on seedling height over one season in either year. Over two growing seasons the effect of habitat gradient on black spruce growth was significant ($F_{2,14} = 45.38$, $p < 0.0001$), with seedlings growing taller as elevation decreased (OC > TI > AT).

Paper birch

Paper birch seedlings were all planted in the alpine tundra habitat. Those seedlings planted into temperature-enhanced treatments (average height = 5.87 mm) tended to grow taller than those in the control (average height = 4.71 mm) although this difference was not significant ($F_{1,60,} = 2.39$, $p = 0.1271$).

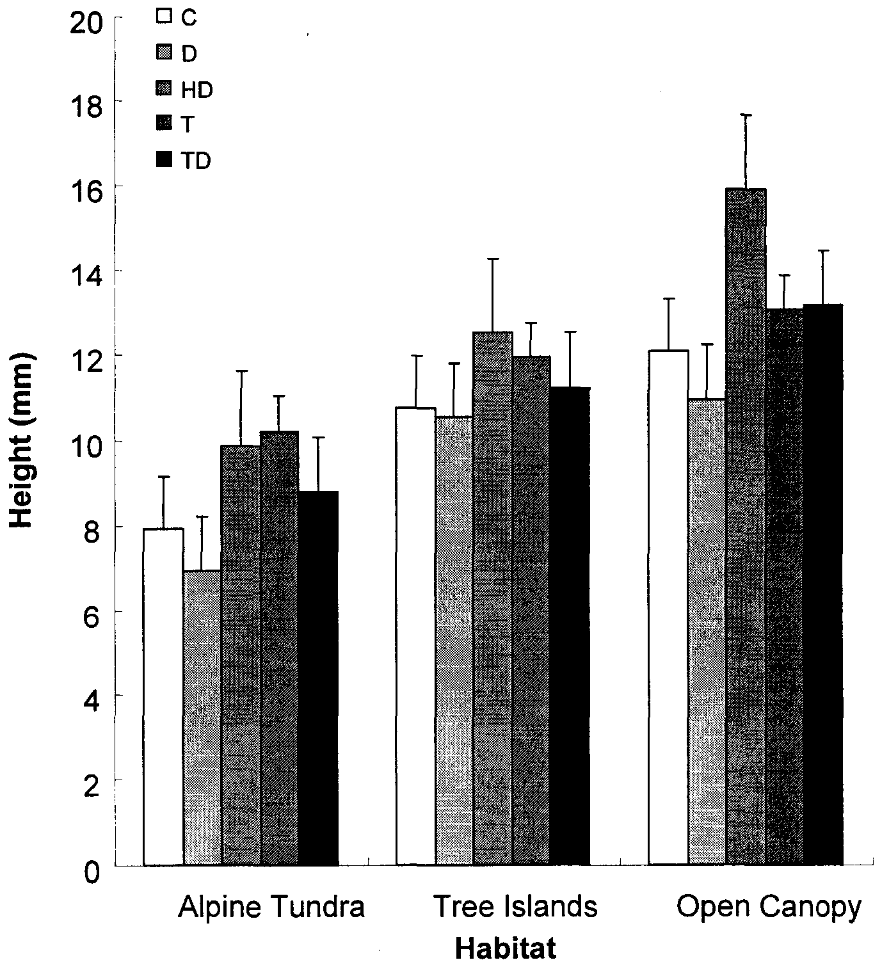


Fig. 3.4 Height (mm) of black spruce seedlings planted in 2004 as measured at last survey in 2005, across treatments and habitats. Values are mean ± 1 SE.

Damage sustained by seedlings

Black spruce

Approximately 17% of surviving black spruce seedlings that were planted in 2004 had sustained damage by the end of 2005. This included missing or broken leaves, presumably due to animal herbivory or trampling. Damaged seedlings were more frequently found in disturbed treatments than in herbivore exclosures ($\chi^2 = 42.93$, d.f. = 1, $p < 0.0001$, Fig. 3.5). Very few (~2%) surviving black spruce seedlings planted in 2005 sustained any damage. Damaged seedlings were again more frequently found in disturbed treatments than in herbivore exclosures, but the difference was not significant.

Second-year seedlings were more often damaged in the tree islands and alpine tundra habitats than they were in the open canopy forest ($\chi^2 = 5.68$, d.f. = 1, $p = 0.0172$). Damaged seedlings among those planted in 2005 were more frequently found in the open canopy forest than at higher elevation gradients, but these differences were not significant.

Most of the damaged seedlings had minimal damage values of '1' out of a possible range of 1-5 (5 = dead), and there was no significant effect of treatment or habitat on the severity of damage suffered by seedlings.

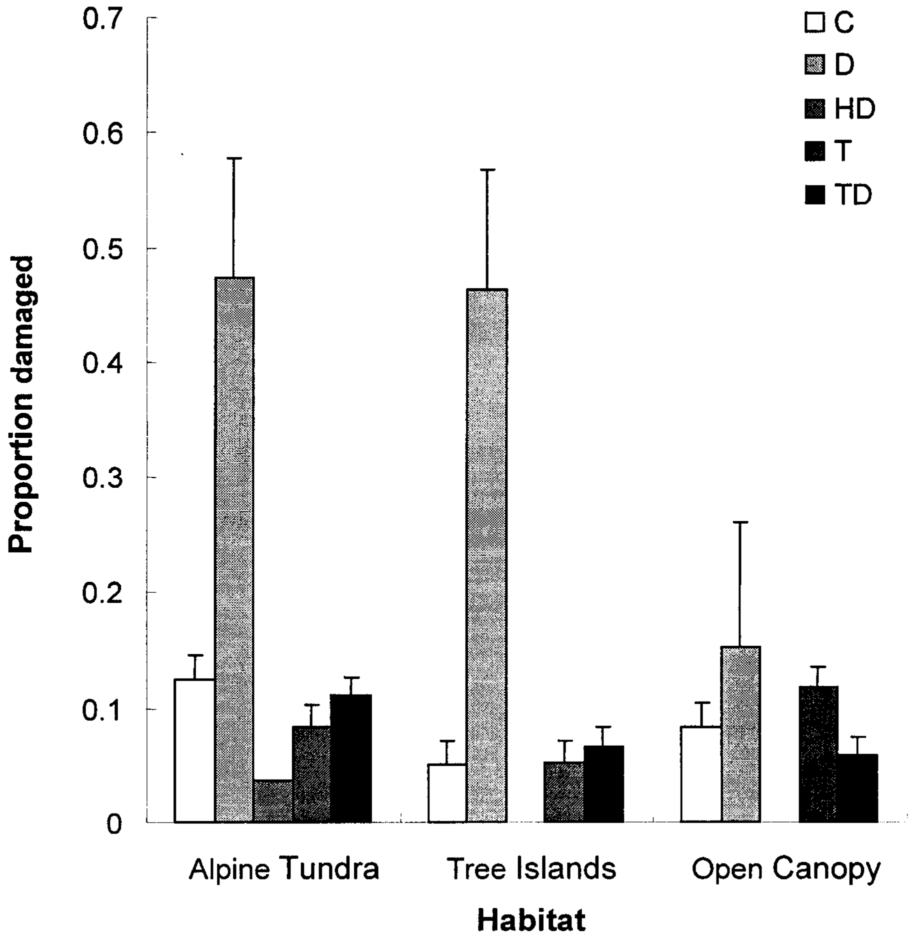


Fig. 3.5 Damage sustained by black spruce seedlings planted in 2004 by the last survey of 2005 across treatments and habitats. Values are proportion of seedlings damaged ± 1 SE.

Seedling mortality

Of the 566 black spruce seedlings planted in 2004, 186 died by September 2005 (32.86% mortality). Causes of mortality were not always evident but included predation, herbivory stress, and, in the AT habitat, stress from low temperature / soil moisture.

Black spruce

Seedlings planted in 2004 suffered significantly less mortality inside herbivore exclosures than in controls, as recorded in the last survey, 2005 ($\chi^2 = 4.27$, d.f. = 1, $p = 0.0388$, Fig. 3.6). Mortality was significantly lower in tree islands than in the open canopy forest and alpine tundra habitats ($\chi^2 = 19.54$, d.f. = 1, $p < 0.0001$). Seedlings planted in 2005 suffered little mortality and were not significantly affected by treatment or habitat.

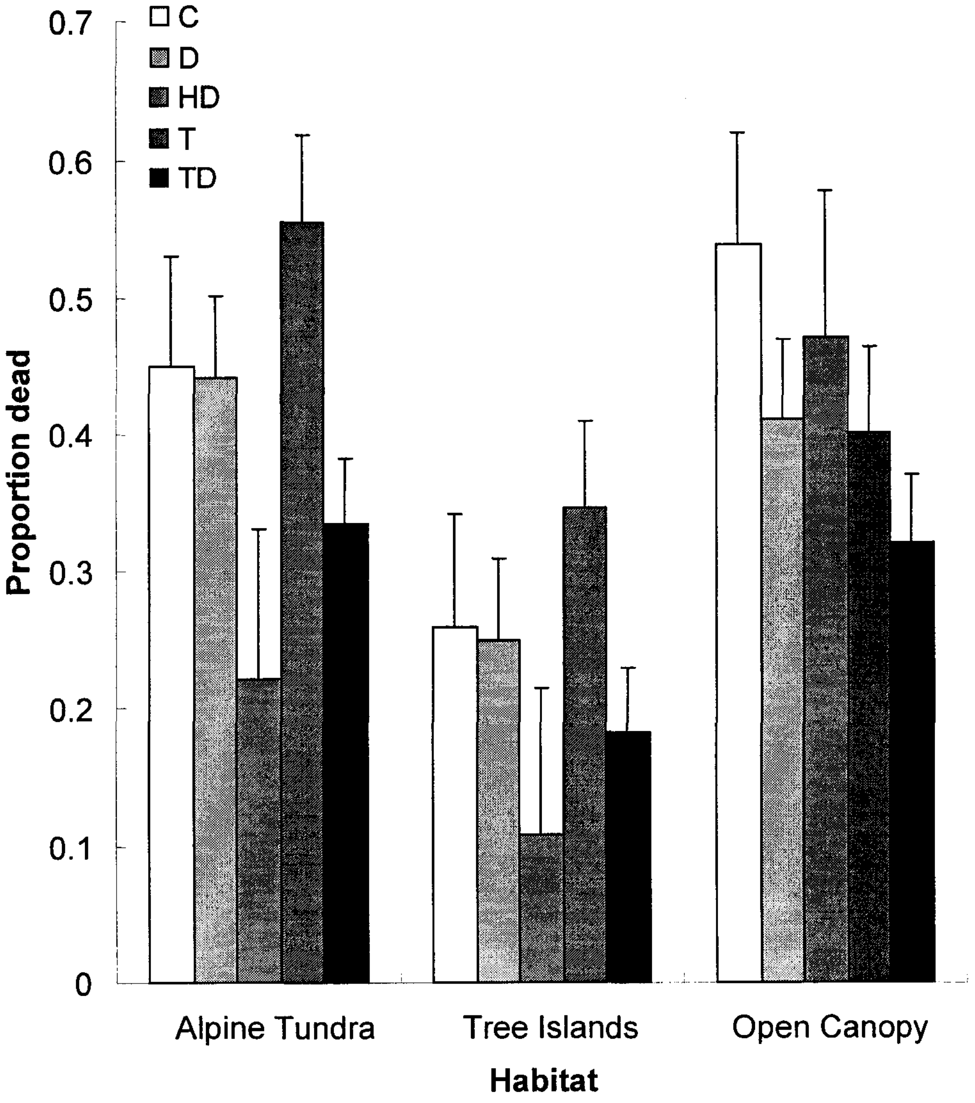


Fig. 3.6 Proportion of black spruce seedlings planted in 2004 that died by the last survey of 2005 across treatments and habitats. Values are mean ± 1 SE.

3.4 Discussion

This study has shown that black spruce seeds can germinate and seedlings can establish and over-winter in all habitats examined in the Mealy Mountains tree-line region. Temperature enhancement increased the probability of black spruce seedling emergence and seedling height growth, indicating that future warming could expand the distribution of this species beyond the present tree-line. Herbivore exclusion decreased seed predation and reduced damage and mortality in established seedlings, indicating that herbivores could be a constraint on future tree-line migration. Mineral substrates appear to represent optimal safe sites for all tree species, as seedling emergence in undisturbed seedbeds did occur, but rarely relative to when organic ground cover was disturbed. Black spruce was able to germinate much more readily than either balsam fir or paper birch, suggesting that this species will be at the “front line” of tree line expansion.

Due to genetic differentiation, local seeds may be more tolerant to regional environmental conditions than were the study seeds used in these experiments, which originated at lower elevation and latitudes. These results could therefore be conservative.

Seedling emergence success

Temperature enhancement increased black spruce seedling emergence in the alpine tundra habitat in both years, consistent with other studies (e.g. Hobbie and

Chapin 1998). The effect of temperature enhancement on tree establishment has been shown to increase as tree-lines are approached and environments become more stressful (Press et al. 1998; Hobbie et al. 1999). In the Mealy Mountains the larger response in the alpine habitat also reflects the higher degree of warming in OTCs at higher elevations. As OTCs did not affect soil temperature in the forest plots, little effect on seedling emergence would be expected from an increase in air temperature alone.

Herbivore exclusion increased black spruce seedling emergence, suggesting that local small mammals or other herbivores are seed predators. This result contradicts the suggestion by Keith (2001) that black spruce seeds are unpalatable to herbivores in the region; but is consistent with studies in Quebec that show a significant effect of small mammal predation on black spruce seeds (Côté et al. 2003). Small mammals were most frequently observed and trapped in the open canopy forest (Lewis et al. in press), where it might be expected that herbivore exclusion would significantly increase seed survival and thus germination by protecting seeds from predation, however no such effect was observed. The alpine tundra habitat, despite indications that it supported the fewest vertebrate herbivores (Lewis et al. in press), showed the strongest effect of herbivore exclusion in both years, perhaps due to a relative scarcity of food making the seeds more attractive to predators.

The tendency in boreal systems is for seedling establishment to decrease as the depth of the organic layer increases (Greene et al. 1999). A lack of natural disturbances into which seedlings can establish has influenced regeneration of trees at and beyond tree-line (Cullen et al. 2001, Grabher 2003, Pham et al. 2004), at times restricting forest expansion (Hättenschwiler and Körner 1995). This study also confirmed that seedling emergence was influenced by the availability of appropriate safe sites, and all species established more frequently in disturbed ground. The strength of the substrate effect was unexpectedly large for balsam fir seeds, which is the most likely species to germinate on vegetated soil, due to larger endosperm reserves and a faster growing taproot, allowing them to establish on litter (Anderson and Winterton 1999). The study area contained considerable areas of natural disturbance, including stabilized areas of frost activity and patches disturbed by animal activity, such as bear digging and rodent tunneling (personal observation). The availability of seedbed is thus likely only a modest restriction to tree-line migration. Some sown seeds of balsam fir and black spruce were able to develop in undisturbed seedbeds, such as mosses of the genera *Sphagnum* and *Dicranum*. Similar to other studies (Zhong and van der Kamp 1999), this observation suggests that ground disturbance, while considerably enhancing seedling establishment, is not a pre-requisite for seedling emergence.

The habitat gradient affected seedling emergence as expected, but in unanticipated ways. In natural systems seedlings are more common at lower, wooded elevations than in higher alpine elevations (Germino and Smith 1999). In this study emergence was greatest in tree islands, perhaps due to poor drainage of water that was observed infrequently in the forest habitat, which may have drowned some of the forest seeds or dislodged them from the ground. Germination was likely restricted at higher elevations by lower temperatures.

Time to seedling emergence

Seedling emergence was higher when seeds were sown in early July rather than late-July, which is consistent with many other studies (e.g. Wang and Lechowicz 1998, Seiwa 2000). Despite the abbreviated growing season for the seeds sown in late July, the proportion of the resulting germinants that survived to the end of 2005 was similar to the proportion of surviving seedlings of those planted earlier. This pattern suggests that in the study region, growing season length limits seedling emergence more than it limits seedling survival.

A decrease in temperature has been shown to retard germination in black spruce seeds (Wang and Lechowicz 1998), and it was thus expected that increasing temperature would decrease the time taken for seedlings to emerge. In fact, the opposite was found, with seeds taking longer to emerge in temperature-enhanced treatments. It appears that the OTCs were effective at enhancing seedling emergence only below a certain temperature threshold. When the temperature was relatively warm, as in July 2005, the enhancement of temperatures by 1.5°C in the OTCs may not have conferred any meaningful advantage to the germination process. However, as the weather cooled in August and September, seedling emergence became greater in temperature enhanced treatments than in controls. Black and Bliss (1980) suggested that below 11-14°C black spruce germination is limited, which is consistent with the above results. In July 2005, when then mean temperature was just above 14°C, OTC's did not appear to significantly enhance black spruce emergence, while in August and the first half of September, when mean temperature was just below 10°C, OTCs did significantly enhance seedling emergence. This surge of emergence in **T** and **TD** later in the season correspondingly lengthened the average time taken for seedlings to emerge in these treatments, but not in the **C** and **D** treatments.

The time to seedling emergence for balsam fir in the alpine tundra habitat was less than it was in the lower-elevation plots. Seeds were able to germinate longer into the season in the milder, lower-elevation sites, but were curtailed in the alpine tundra sites once the weather had cooled in late summer. There were no significant differences among habitats in the time to seedling emergence for black spruce or for paper birch. Differences in time to emergence among the species were consistent with other studies (Anderson and Winterton 1999), with the small-seeded spruce and birch emerging on average more quickly than the large-seeded fir. It is more critical for seedlings with smaller endosperm reserves to establish earlier in the season when moisture levels are higher and when they will have time to grow and successfully over-winter (Wright 1968).

Seedling growth

Seedling growth has been positively correlated with survival for some tree seedlings (Orlander and Karlsson 2000, Seiwa 2000). Seedling height can therefore be an indicator of tree establishment success. Consistent with other researchers (Brand 1991, Hobbie and Chapin 1998), we found that temperature enhancement increased black spruce seedling height growth in all habitats over two field seasons. A height increase relative to controls due to temperature enhancement over one season was not observed in this study, though the height difference of paper birch seedlings in and out of OTCs may warrant further investigation, given the relatively small sample size of birch seedlings. An increase in growth in this species due to temperature enhancement would perhaps be more likely than in the spruce or fir, reflecting the greater growth potential of paper birch (Vasiliauskas and Chen 2002).

Herbivore exclusion increased the growth of seedlings, likely due to the seedlings' ability to grow without being clipped or disturbed by animals. This effect was particularly marked in the open canopy forest, which contained the highest numbers of small mammals (Lewis 2005, unpublished data). The increase in black spruce seedling height as elevation decreased was expected, as temperature and canopy protection for seedlings are greater in the forest.

Seedling damage and mortality

Herbivores in the Mealy Mountains tree-line region appear to increase damage and mortality sustained by tree seedlings. Most injuries involved the breaking off or damaging of needles and leaves, thus limiting the seedling's ability to obtain resources through photosynthesis, and compromising its survival. Though few, there were damaged seedlings present inside exclosures. The HD treatment was capable of excluding vertebrate herbivores but not invertebrates such as slugs, ants and other arthropods, all known to be in the study area (McDonald 2005, unpublished data) and known to predate boreal tree seeds and seedlings (Côté et al. 2005). The effect that these animals have on seedling establishment would be of interest. Pathogens, intense precipitation and wind are other possible sources of damage. Some evidence of climatically induced damage to seedlings was observed, but no diseased seedlings were apparent.

These results are consistent with other studies suggesting that herbivores have a significant influence not only on forest tree succession (Côté et al. 2003, Noel 2004), but also on tree-lines (Cairns and Moen 2004). While not surprising, the significance of seedling predators in this study is noteworthy due to the low levels of small mammal populations in the study area in 2004 and 2005 (Lewis, unpublished data). Several of the small mammals observed in the area are known to predate seeds and seedlings (Harrington 1998), including *Phenacomys intermedius* Merriam (heather vole), *Zapus hudsonius* Zimmermann (meadow jumping mouse), *Synaptomys borealis* Richardson (northern bog lemming), *Clethrionomys gapperi* Vigors (red backed vole), and *Lepus americanus* Erxleben (snowshoe hare) (Lewis et al. in press). Abundant signs of past small mammal activity were observed in the area, such as shrub debarking, tunneling, and scat piles, suggesting that populations were previously larger and that the small mammals were at a low point in their cycle during the study period. Thus far insufficient regional data have been collected on small mammals to understand their local population dynamics and variation in their effect on seeds and seedlings.

The habitat in which seedlings were most often damaged was not consistent between first- and second-season seedlings, nor did it correspond to the habitat where seedlings most frequently died. There are different stressors affecting seedlings at different habitat levels: first year seedlings were damaged most often in the open canopy forest, where vertebrate herbivores were found most often and thus had more opportunity to damage them. Second year seedlings were more damaged at higher elevations, perhaps due to the accumulation of climatically-induced (i.e. wind) damage. Mortality in second-season seedlings was apparently due to a combination of both stressors, with the open canopy forest and alpine tundra habitats containing the highest proportions of dead seedlings.

Comparison of species

The emergence of black spruce was greater than the other two species, as reported in other studies (Hobbie and Chapin 1998, Anderson and Winterton 1999). Seedling growth and survival are often higher for fir than for spruce, however (Griggs 1938, Gallipeau et al. 1997, Feller 1998), so longer monitoring of balsam fir would be useful to determine the importance of this species to tree-line migration. While higher germination does not lead us to conclude that black spruce will dominate future tree migrations, its abundance in the study area, its affinity for cooler, nutrient poor substrates, and its successful establishment over two seasons in this study suggests that it would be a likely species to expand forest range. Paper birch had very few germinants, and, based on results over one season in this study, would not be a strong component of an expanding forest in this region.

Implications

Even seedlings that were planted without the benefit of OTCs or exclosures in this study successfully established in all habitats. We are compelled to ask why there was no evidence of natural seedling establishment in tree islands and upslope. Seedlings often develop beyond tree-lines only to be constrained by wind or herbivores (Körner and Paulsen 2004), but there was no evidence of stunted or dead seedlings in this area. One possibility for the inconsistency is that the high temperatures experienced in the study area in recent years has made seedling establishment feasible only recently, and that we are now in a time lag between the development of favourable conditions for seedling migration and their actual establishment. It is also possible that the rodent populations were at a low point in this study, allowing the establishment of seedlings that will later be predated.

Seed viability is an important factor influencing tree-line movement that may also be contributing to the current lack of apparent forest extension. Though there are many cone bearing trees in the study area, preliminary results indicate that seed viability of all species near the upper tree limit is low, due in large part to unfilled and incompletely developed seeds (Munier and Hermanutz, unpublished data). This is consistent with other studies showing high numbers of non-viable seeds at and near the tree-line (Stevens and Fox 1991, Arsenault and Payette 1992). This phenomenon is considered one of the principle bottlenecks to seedling establishment above the tree-line (Cuevas 2000, Sirois 2000). As boreal tree seed viability increases with temperature (Kullman 1996, Sirois 2000), this factor would likely become less limiting as the climate warms.

The process of tree-line migration can happen in different ways, including infilling of areas with low tree density; tree establishment radiating out from tree islands; and direct elevational expansion of trees. In the Mealy Mountains, it is likely that should the forest expand upslope, the process will be facilitated by the presence of tree islands, as these provide shelter from extreme climatic conditions, and many are already producing cones. This cone production suggests that trees would be able to respond readily to a sustained temperature increase by producing seeds that develop to maturity (Sirois 2000). Tree-line monitoring in Alaska and elsewhere have shown significant increases in shrub density as the climate warms (Sturm et al. 2001, Wharen et al. 2005). The more plastic growth response of deciduous shrubs compared to evergreen trees make them likely to respond more quickly to climate change (Chapin et al. 1995), and it is probable that in the Mealy Mountains, the locally common dwarf birch will migrate in response to warming before any of the tree species.

As is the case in many other alpine regions of the world, there is reason to believe that climate warming will promote upslope tree-line migration with the potential displacement of alpine habitat in the Mealy Mountains in coming decades. Abiotic and ecological factors will modulate the shape of the future tree-line, but two seasons of monitoring suggest that they will not stop its migration.

While most of the stages of seedling establishment can occur at and above the tree-line already, many of these processes, including seed development, seed germination, and seedling growth, will be enhanced by warmer temperatures. Even with relatively moderate climate warming, changes in the future tree-line and alpine habitat of the Mealy Mountains are likely, and should be considered when planning for conservation, recreation, and resource use in the region.

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4.0 THESIS SUMMARY AND CONCLUSION

Loss of alpine habitat is of concern due to upslope migration of altitudinal tree-lines in response to climate change. Thermal control of tree-line, however, is mediated by local physical and ecological factors, making trends in tree-line migration difficult to extrapolate geographically.

Little research into the ecological effects of climate change has been done in Labrador. The Mealy Mountains is a region of particular interest with respect to the possibility of tree-line migration. They are the highest uplands of southern Labrador and contain alpine tundra that is regionally unique and contributes significantly to biodiversity and wildlife habitat. Forest displacement of this alpine system is therefore a concern for the ecological integrity of the region, for regional biodiversity, and for the fate of alpine-affinity fauna and flora that use the habitat. This study investigated the potential impacts of climate warming on the altitudinal tree-line of the Mealy Mountains.

Monitoring of seedling establishment was conducted along a habitat gradient in the tree-line ecotone of the Mealy Mountains over two summers. Temperature, herbivory, and ground disturbance were manipulated to examine the effect of these treatments, and of habitat, on seedling emergence and survival.

The climate of the study area was examined in Section 2, to provide a context for any potential climate change. The effectiveness of open top chambers used to simulate temperature warming in the seedling experiments was also investigated.

While no significant long-term warming has yet occurred in southern Labrador, temperatures in this region have been showing an apparent warming trend in recent years. Climate models project increases in annual temperature of between 1-4°C over the next 100 years for this region.

Open top chambers used in the experiment create a daytime air temperature increase of approximately 1.5°C, which approximates the degree of warming projected for summer air temperatures in this region for the year 2100. Soil temperature showed an increase in diurnal range of heating within the OTCs, and tended to warm the soil during the day and cool it slightly below normal temperatures overnight. The effectiveness of the warming devices was greater in the alpine tundra and tree island habitats than in the open canopy forest, and the differences in results obtained from warming experiments on seedling establishment among the different habitats appear to reflect this difference.

Section 3 examined the responses of tree seedlings to environmental manipulations in study plots along a habitat gradient. Seedlings were monitored in temperature-enhanced, ground-disturbed, and herbivore-excluded treatments in each of the plots. Seedling emergence, time to emergence, growth, damage sustained, and mortality were recorded.

Temperature enhancement increased black spruce seedling emergence, and growth of black spruce and of paper birch seedlings. Herbivore exclusion decreased seed predation, increased height, and decreased seedling damage and mortality in black spruce seedlings. Disturbed ground substrate significantly enhanced seedling emergence in all species. Black spruce establishment far exceeded that of balsam fir or paper birch.

Despite successful establishment and over-wintering of seedlings over the course of this study, even when planted into controls, no seedlings were observed growing naturally above the tree limit in the study area. This could be due to low seed viability of trees in the tree-line region, as indicated by preliminary studies. Seed viability is expected to improve as climate warms, suggesting that this may not remain a limiting factor to tree-line migration in the future.

Limitations to the research that could be conducted related mainly to the remoteness of the Mealy Mountains field camp. Access was by helicopter or float plane, which limited the amount of equipment (i.e. greenhouse and exclosure materials) that could be transported. To accommodate the travel and lodging logistics, plans had to be made with considerable advance notice, which could pose challenges to anticipate the ideal time to take advantage of the growing season given the current changes in temperature. As this treeline ecotone is at an ecological boundary and there are limited fertile trees, seeds used in the study were not from the immediate surroundings, though were sourced in the province.

There is scope for much research to follow up on the findings of this study. The principle activities that should be followed up on include continued monitoring of the experimental seedlings over time, giving particular attention to their ability to grow above the height of surrounding vegetation. Studies of seed viability of the main tree species found in the study area are essential to elucidate the probability of natural regeneration, and these should also be continued over time, to monitor their receptiveness to changes in ambient temperature. Surveys of natural seedling establishment, taking note of seedbed and other requirements for germination and survival, should also continue over time.

Results of this study suggest that the altitudinal tree-line in the Mealy Mountains is capable of migrating upslope. Seedling recruitment and growth are expected to be enhanced as temperature increases due to climate warming. Constraints to tree-line migration may include herbivores, which could lower germination, height, and survival of seedlings. The availability of appropriate seedbed into which tree seedlings can establish will also shape the future tree-line. Based on two seasons of monitoring however, neither of these potential constraints appears likely to restrict tree-line migration in the Mealy Mountains, but rather to modify its movement.