Treeline dynamics: Pattern and process at multiple spatial scales

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The primary hypothesis of treeline formation, low growing season temperature limitation of growth, predicts that treeline position will track climatic changes. These hypotheses were generated from broad treeline patterns, which may overlook critical local variability. To assess the hypothesis that all treelines are limited by low temperature and will respond in kind, treeline response over the last 100 years was evaluated at 166 treeline sites in a meta-analysis. Treeline advance was variable and not related to climate warming in the way expected. Treelines that experienced strong winter warming were more likely to have advanced and treelines with a diffuse form were more likely to have advanced than those with an abrupt, Krummholz or island form. Diffuse treelines may be more responsive to warming because they are more strongly growth limited, whereas other treeline forms may be subject to additional constraints. The results suggest that mechanisms other than growing season temperature, such as winter dieback and recruitment failure, may also determine treeline position and dynamics.

As treeline responses worldwide confirm a close link between form and dynamics, variability in treeline response may be explained by identifying the mechanisms controlling treeline form. The varying dominance of three mechanisms affecting tree performance - growth limitation, seedling mortality and dieback – modified by species traits, local climatic conditions, stressors and neighbour interactions is proposed to result in different treeline forms and the expected response of treelines to climatic change. The proposed mechanisms controlling treeline form and expected responses to climate warming were subsequently tested at the abrupt *Nothofagus* treeline in New Zealand.

The role of growth, mortality (across all size classes) and recruitment in controlling treeline dynamics were evaluated using long-term data collected along seven abrupt *Nothofagus* treeline transects in the South Island, New Zealand. Demographic parameters were modelled over two periods, 1991-2002 and 2002-2008 within a Bayesian framework. Stem number increased above treeline over the 15-year study duration but stem distribution above treeline did not change; 90% of all stems and of new recruits occurred within 10 m of the treeline edge. Modelled growth, mortality and recruitment rates varied by period, transect and stem size. Results do not provide clear evidence of treeline advance but do indicate that recruitment is ultimately limiting advance.

The causes of recruitment limitation were then tested through transplanted *Nothofagus solandri* var. *cliffortioides* and *Pinus contorta* seedlings along a 200 m vertical transect starting 50 m below treeline and with passive warming. Survival and growth of seedlings transplanted 150 m beyond the *Nothofagus* treeline did not decrease with distance from the treeline edge or improve with passive warming (repeated measures ANOVA, $p > 0.05$). Survival varied by species; *P. contorta* exhibited a greater overall probability of mortality than *N. solandri*. Relative growth rates did not significantly differ between species but pine exhibited a net increase in height whereas *N. solandri* exhibited a net decrease in height. At the seedling stage, low temperature is not limiting and *N. solandri* does not appear to be less well adapted to treeline conditions than northern hemisphere conifer species. The role of facilitation was subsequently tested by removing vegetation around *N. solandri* seedlings. Vegetation removal negatively affected N. *solandri* seedling survival. No effect of passive warming was observed. The results confirm that *N. solandri* can survive beyond their present limit but that growth and survival are limited to facilitative microsites. Treeline advance at the *Nothofagus* treeline in New Zealand is proposed to be limited by germination ability in dense vegetation and intolerance in the early life stages to sky exposure. Positive feedback, whereby established trees create ideal microsites for germination and seedling establishment, is proposed to be critical in determining recruitment patterns and the relative inertia to climatic change observed at the treeline.

The results overall indicate that, globally, treeline response to climate change will be highly variable and not necessarily directly related to climate warming. Treeline form is a good indicator of the mechanisms controlling treeline dynamics and the potential response by treeline to climatic change.

Keywords: abrupt, advance, climate change, demographic rates, diffuse, forest dynamics, global meta-analysis, interspecific interactions, Krummholz, mortality, *Nothofagus menziesii*, *Nothofagus solandri* var. *cliffortioides*, *Pinus contorta*, recruitment, survival, treeline

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Table of Contents

List of Tables

List of Figures

Chapter 1
Introduction

1.1 Treelines as indicators

Considerable variability exists in the direction and rate at which plants species' distributions are responding to climatic change (Kelly & Goulden 2008; le Roux & McGeoch 2008; Harsch *et al.* 2009). The causes of variability in response can have considerable effects on community composition, ecosystem functioning (Gomez-Aparicio & Canham 2008; Wookey *et al.* 2009) and species survival (Halloy & Mark 2003; Thomas *et al.* 2004; Brooker *et al.* 2007; Baez & Collins 2008). For example, whether the variability in response results in novel communities or transient dynamics will depend upon whether species differ in their sensitivity or ability to respond to climate change. Local extinctions may result when species are unable to shift to more favourable climatic conditions, either from adverse climatic conditions or encroachment of shifting species (Halloy & Mark 2003; Thomas *et al.* 2004; Brooker *et al.* 2007; Baez & Collins 2008). Unfortunately, the relative importance of species sensitivity and species ability to respond to climate change is poorly understood.

Developing plans to manage the effect of climatic changes requires understanding species sensitivity and ability to respond to climate change, which can vary between species or sites. This information, however, is not always known, especially at low elevations and latitudes where the degree or length of time since climate warming began has been insufficient to induce a response. For many species, it may also be difficult to identify the margins of the distribution. Further, few plant species exist in unmodified environments, so it is uncertain whether the plant species is responding to climatic or land-use changes. Finally, it is not always possible to identify plant species responses to climate warming if shifts in distribution began prior to when monitoring of the species began.

Treelines are considered to be early indicators of plant response to climate warming. Treelines occur at high elevations and latitudes, which are generally less heavily modified by human land-use than at lower elevation or latitude and where warming has been the longest in duration and most pronounced (Holtmeier 2009). Current and historical changes in treeline distribution are identifiable because treelines are conspicuous boundaries formed by long-lived species. The longevity of trees also means that they are less sensitive to interannual variability than short-lived plants and tree rings can be used to age trees and reconstruct past responses to climate change (Carrer & Urbinati 2004; Bekker 2005; Carrer *et al.* 2007). In this thesis, I use treelines to address some of the basic questions regarding plant species response to climate warming: 1) how universal is plant species response to climate warming; 2) how do plant traits affect ability to respond to climate warming; and 3) how do biotic interactions affect ability to respond to climate warming.

1.2 Treeline definition

A single conventional definition of the treeline does not exist. Definitions vary by the growth form (arborescent or shrub-like) and minimum height (not defined, 2 m, 3 m) designating the upper limits of the treeline. Defining the treeline by minimum height is subject to error as both taxon-specific traits and site-specific conditions can affect the maximum achievable height (Holtmeier & Broll 2005). Further, height is not always a good indicator of reproductive ability above treeline (reviewed in Holtmeier 2009). Still, it is beneficial to define a minimum height when evaluating changes in treeline position as established trees are less sensitive to short-term climatic fluctuations than seedlings and the presence of a recruitment band is not necessarily indicative of a shift in treeline position. The decision to include shrub-like growth forms (Krummholz) is also subjective as Krummholz are not arborescent and often do not produce seed. Krummholz, however, are formed by tree species and can shift back to an arborescent form, often before treeline advance occurs. Krummholz are, therefore, important indicators of limiting climatic conditions and potential ability of treelines to shift position in response to climatic change. In this thesis, I have chosen a relatively general definition of treeline in order to minimize inadvertent exclusion of treeline sites. The treeline refers to the transition zone between the upper boundary of the closed forest (forest limit) and the upper boundary of trees at least 2 m high (tree limit) or, if Krummholz are present, the upper boundary of Krummholz regardless of Krummholz height (species limit).

This thesis focuses on four primary treeline forms - diffuse, abrupt, Krummholz and island. The four forms are defined by both spatial structure and growth form. Diffuse and abrupt treeline exhibit arborescent growth forms, Krummholz are shrub-like and islands can be either arborescent or shrub-like. In terms of spatial pattern, diffuse refers to treelines that exhibit a gradual decline in tree density and height along the transition zone. Abrupt refers to treelines in which tree density does not change along the transition zone. In other words, the forest limit is also the tree limit. Island treelines are characterized by clumped patches above the forest limit and may be formed by shrub-like or arborescent growth forms. Changes in density at Krummholz treelines may be gradual or abrupt but these treelines always exhibit shrub-like growth forms.

Treeline form could also be classed within six categories based on spatial structure and growth form – diffuse arborescent, diffuse Krummholz, abrupt arborescent, abrupt Krummholz, island arborescent, and island Krummholz. The decision to include Krummholz as a separate form, rather than as a modifier of diffuse and abrupt forms, reflects my initial hypotheses, that separate processes control difference in spatial structure and differences in growth form. Once the mechanisms controlling structure and form are defined then they can be applied to intermediate forms. For example, abrupt Krummholz would reflect both the mechanisms causing abruptness and the mechanisms causing Krummholz.

The treeline form is unlikely to be stable. If form were determined by climatic conditions, then climatic change would result in a shift in treeline form. Treelines that do not fit into one of the four treeline form classes may represent a change in limiting climatic conditions. Shifts in treeline form may also be an early indicator of climatic change, especially if shifts in form occur before treeline advance initiates.

1.3 Causes of treeline formation

Treelines may result from several different factors, including climate, orographic and edaphic features, and anthropogenic causes (Holtmeier & Broll 2005). Although non-climatic factors do influence treeline position and form, treelines in which the primary limiting factors is not climate are unlikely to represent the true tree species limit and will provide little insight into the mechanisms controlling plant species response to climatic change. As this thesis is focused on understanding why some treelines are responding to climate change but not others, analyses and discussions are limited to those treelines in which climatic factors exert a greater effect on treeline pattern and dynamics than non-climate factors.

Climatic treelines occur where climatic conditions limit at least one process – growth, survival or recruitment (Table 1.1). Most of the proposed mechanisms describe regional or taxon-specific variability rather than global patterns (Tranquillini 1979; Grace & Norton 1990; Stevens & Fox 1991; Wardle 1993). Only one hypothesis was developed from quantitative data collected at treeline sites globally, the growth limitation hypothesis. This hypotheses proposes that treelines occur where growing season temperature is too low for carbon assimilation or accumulation to occur (Körner & Paulsen 2004; Körner & Hoch 2006). An alternative hypothesis, the facilitation hypothesis, was developed from observations globally but lacks the extensive empirical data used to develop the growth limitation hypothesis. The facilitation hypothesis proposes that treelines occur because recruitment is limited above treeline and the availability of suitable facilitative microsites is an important factor determining treeline position (Smith *et al.* 2003). The two hypotheses contrast in that the growth limitation hypotheses focuses on the limits of already established trees and the facilitation hypothesis focuses on the limitation of treeline expansion. The reproductive constraints hypothesis encompasses adult reproduction/germination and seedling growth and survival. Although the factors controlling seed production and seedling growth likely differ, these two processes are frequently grouped into a single hypothesis, the reproductive constraints hypothesis (e.g. Körner 1998; Smith et al. 2003; Sveinbjörnsson *et al.* 2002).

Hypothesis	Factors	Proponents
Frost-related stress	Frost and frost drought damage tissues and impair growth and survival	(Tranquillini 1979)
Mechanical disturbance	Partial or whole tree damage from wind abrasion, ice, snow loading and herbivory	(Grace & Norton 1990)
Reproductive constraints	Seed germination, seedling growth and survival	(Wilmking & Juday 2005)
Annual carbon balance	Photosynthetic carbon gain is insufficient to support maintenance and minimum growth of trees	(James *et al.* 1994)
Growth limitation	Low temperatures limit carbon assimilation greater than photosynthetic carbon accumulation	(Körner & Hoch 2006)
Facilitation	Amelioration of stressors through plant-plant and plant-abiotic object interactions	(Smith *et al.* 2003)

Table 1.1: The six primary hypothesized causes of treeline formation with associated factors and proponents.

Throughout this thesis, facilitation refers to plant-plant and plant-abiotic object interactions that result in a net benefit for the plant of interest and no net cost for the other plant. Whether interactions are facilitative or not is temporally and spatially variable, depending upon several factors, including climate stress and life stage. For example, microsite conditions facilitating seedling survival may not be suitable for germination. In this thesis, evaluation of plant-plant interactions is limited to seedlings.

1.4 Treeline pattern and scale

Treelines are not uniform in form or structure. When viewed globally, the treeline elevation is closely linked with latitude (Ward 2001; Gellhorn 2002). Within a mountain range, the treeline is subject to variation in position based on aspect and topography (Camarero *et al.*

2000; Danby & Hik 2007a). Finally, within a site, the treeline can vary considerably and it is often hard to identify where the actual treeline is (Wardle *et al.* 2006).

The mechanisms controlling treeline pattern will also vary at different spatial scales. Global patterns are most likely influenced by temperature which declines predictably with elevation and distance from the equator (Körner 2007), whereas regional patterns are influenced by regional climatic conditions and variables related to aspect such as growing season length and snow duration (Camarero & Gutierrez 2002; Danby & Hik 2007b). Local patterns are influenced by fine topographic and climate variation (Holtmeier & Broll 2005).

Although general patterns in treeline position and dynamics are more readily observed at a coarse global scale, the mechanisms controlling treeline formation and position ultimately act upon individual trees, necessitating that controlling mechanisms be observed at a fine spatial scale. Observing patterns only at a fine spatial scale will ultimately result in understanding local variability and will likely miss the critical variables controlling global patterns. In this thesis, I assess treeline pattern and process from global, regional, and fine spatial scales using observations and experiments at one scale to inform experiments or support hypotheses at another scale.

1.5 The New Zealand treeline

The New Zealand treeline is principally composed of southern beeches (genus *Nothofagus*). *Nothofagus menziesii* (silver beech) is common on the western sides of the South and the North Islands, and *Nothofagus solandri* var. *cliffortioides* (mountain beech) on the eastern and inland parts of the South Island. In certain areas, including a section on the west side of the South Island and Steward Island, *Nothofagus* is absent and the treeline is composed of podocarps and mixed hardwoods (Figure 1.1). The form of these two treelines differs markedly. The *Nothofagus* treeline is abrupt whereas the podocarp-hardwood treeline is diffuse. The elevation of both treeline types across both islands follows an altitudinal gradient. Treeline elevation is greatest on the North Island, reaching an elevation of 1500 m at 38 °S and decreasing to 900 m at 42 °S (Wardle 2008). In assessing changes in treeline position at the *Nothofagus* treeline in New Zealand, I use the conventional definition of treeline advance; an upward shift in trees (stems ≥ 2 m high). The use of height to define changes in treeline position is not indicative of reproductive ability as stem height can be significantly affected by growing conditions such as local soil properties, neighbouring vegetation and climate (Wardle 1984) but is used to ensure that changes in treeline positions represent true shifts, not transient dynamics. Growth rate is also variable by growing conditions, a seedling may be 40 cm high after two years when grown at a nursery but only 15 cm high beneath the forest canopy (Wardle 1984). I therefore classify stems according to diameter throughout this thesis with seedlings referring to stems ≤ 1 cm diameter and saplings referring to stems between 1 and 4 cm diameter.

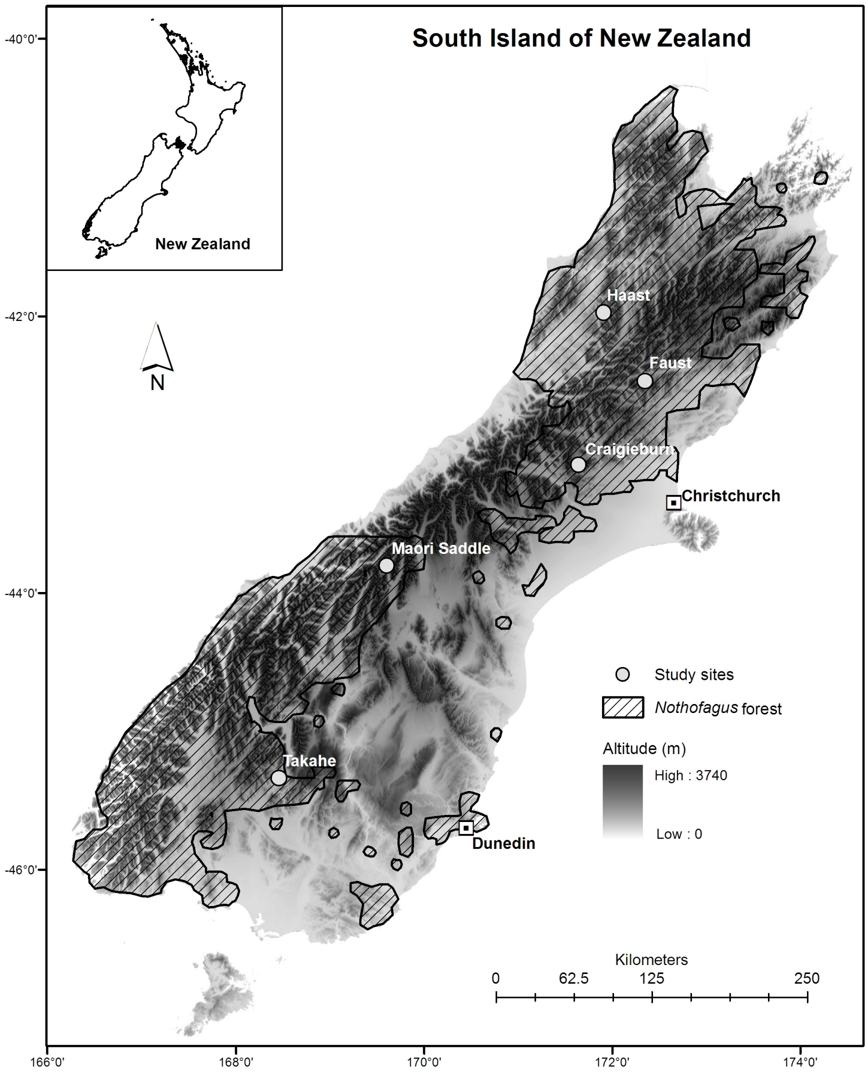

Figure 1.1: Distribution of the *Nothofagus* forest across the South Island, New Zealand.

Here, I focus on the *Nothofagus* treeline because it contrasts more strongly with the majority of treelines around the world which are diffuse in form and are evergreen conifers (Richardson & Friedland 2009). The *Nothofagus* treeline in New Zealand is similar in structure to other *Nothofagus* treelines in South America. Both are abrupt in form and exhibit minimal recruitment beyond the treeline edge but differ in that *Nothofagus pumilio* in South America is deciduous and *Nothofagus* species forming treeline in New Zealand are evergreen (Cuevas 2000). The differences in physiognomy and form between the New Zealand *Nothofagus* treeline and the majority of treelines globally indicate that there may not be a single mechanism controlling treeline formation and position globally.

1.6 Thesis objectives

The main research question in this thesis is: *How does pattern indicate processes and dynamics at treeline?* To answer this main question, the following questions were addressed:

A. Can treeline form be used to indicate treeline response to climate warming?
B. What mechanisms control the major differences in treeline form?
C. Are these mechanisms reflected in treeline pattern and dynamics?
D. Do site- or taxon-specific factors limit the treeline position below the life form limit?
E. How do biotic interactions affect growth and survival beyond the treeline?

I have approached these questions by first exploring global patterns in treeline dynamics (A) and form (B), then evaluating the hypotheses put forward in (B) against long-term observations of treeline patterns and dynamics across seven *Nothofagus* treeline transects in New Zealand (C). The expected causes of the patterns observed across New Zealand (C) as outlined in (A, B) are then tested at a single site (D, E).

I have taken the approach that treelines in equilibrium with climatic conditions are ultimately limited by low growing season temperature and should respond to climate warming. This corresponds with long standing observations of the global relationship between treeline position and temperature (Daubenmire 1954; Körner 1999; Gellhorn 2002; Körner & Paulsen 2004). I then ask the question, why are some treelines not responding to climate warming and/or not occurring at their thermal limit? By taking this approach, I am able to focus my research objectives on the mechanisms that differentiate between expected patterns based on global descriptions and observed patterns.

1.7 Outline of thesis

In Chapters 2 and 3, I evaluate pattern and dynamics globally. In Chapter 2, I quantitatively synthesize the published treeline literature on treeline dynamics. I use a meta-analytical approach to evaluate the relationship between treeline response to climate warming and several variables that could explain response including methodology, site-specific factors and treeline specific factors. In Chapter 3, I synthesize the published literature on treeline formation and propose a new framework for understanding the causes of different treeline forms and responses to climate warming. This framework uses treeline form as an indicator of the mechanisms controlling treeline position and response to climate warming.

In Chapter 4, treeline pattern and processes are evaluated at a landscape scale. Here, I use demographic data from the past 15 years to model growth, mortality and recruitment at seven transects across the South Island of New Zealand.

In Chapters 5 and 6, I test the hypotheses set out in Chapter 3 at an abrupt treeline site in New Zealand. At this site, I am testing fine scale processes proposed to result in abrupt transitions. In particular, Chapter 5 examines whether site-specific climatic conditions or taxon-specific intolerances limit the treeline position below the potential thermal limit. Chapter 6 examines the role of facilitation and competition under current and warmer temperatures in seedling survival above treeline.

Finally, in Chapter 7, the results from all the previous chapters are synthesized, some general conclusions are drawn and directions for future research are suggested.

Chapter 2 was published in Ecology Letters in 2009 (12: 1040-1049) and is co-authored with Drs. Richard Duncan, Phil Hulme and Matt McGlone. Chapter 3 has been submitted to Global Ecology and Biogeography and, at the time of submission of this thesis, was still in review. The manuscript is co-authored with Dr. Maaike Bader. Chapter 4 has been significantly modified from the original version in preparation for publishing. The revised draft is co-authored with Drs. Richard Duncan, Phil Hulme, Peter Wardle and Janet Wilmshurst. Chapters 5 and 6 have not been submitted for publication yet.

Chapter 2

Are treelines advancing? A meta-analysis of treeline response to climate warming

2.1 Abstract

Treelines are temperature sensitive transition zones that are expected to respond to climate warming by advancing beyond their current position. Response to climate warming over the last century, however, has been mixed, with some treelines showing evidence of recruitment at higher altitudes and/or latitudes (advance) whereas others reveal no marked change in the upper limit of tree establishment. To explore this variation, I analyzed a global dataset of 166 sites for which treeline dynamics had been recorded since 1900 AD. Advance was recorded at 52% of sites with only 1% reporting treeline recession. Treelines that experienced strong winter warming were more likely to have advanced, and treelines with a diffuse form were more likely to have advanced than those with an abrupt, Krummholz or island form. Diffuse treelines may be more responsive to warming because they are more strongly growth limited, whereas other treeline forms may be subject to additional constraints.

2.2 Introduction

Average temperatures have risen globally over the past century, with the most pronounced and rapid changes at high altitudes and latitudes (IPCC 2007). Within these zones, treeline position is widely thought to be temperature sensitive and potentially responsive to climate warming (Kupfer & Cairns 1996; Holtmeier & Broll 2005). For this reason, the dynamics of the upper alpine or arctic tree limit have been studied around the globe with the aim of detecting change, understanding responses to temperature variation, and evaluating the threat to alpine and arctic biota in response to treeline movement in high altitude and latitude communities (Foley *et al.* 1994; Holtmeier & Broll 2007).

Temperature is widely considered to be the primary control on treeline formation and maintenance (Mikola 1962; Körner 2007). Supporting evidence includes global relationships between treeline position and temperature isotherms (Grace 1977; Körner & Paulsen 2004), fluctuations in treeline position in accordance with past temperature changes (Grace 1989; Foley *et al.* 1994; Lloyd & Graumlich 1997), and recent recruitment beyond historical treeline limits consistent with observed rates of recent warming (Suarez *et al.* 1999; Gamache & Payette 2005; Truong *et al.* 2006; Shiyatov *et al.* 2007). In particular, the prevailing view is that high altitude and latitude treelines are controlled by summer temperature (Holtmeier & Broll 2007; Gehrig-Fasel *et al.* 2008; MacDonald *et al.* 2008), with treeline position over much of the globe coinciding with a mean growing season temperature of 5-6 °C (Körner & Paulsen 2004). This implies that treelines should be particularly responsive to changes in summer temperature, although other studies suggest that the effects of winter temperature on survival may also play a role (Kullman 2007; Rickebusch *et al.* 2007).

Although treelines are considered thermally limited and average temperatures have increased globally over the last century, treeline advance is not a worldwide phenomenon (Holtmeier & Broll 2007). This disjunction between rising average temperatures and expected treeline response could be due to spatially non-uniform patterns of temperature change. There can be marked variation in the degree to which local sites or regions have warmed or even cooled on average over the last century (Lindkvist & Lindqvist 1997; Körner 2007), along with differences in the extent to which sites have experienced summer or winter warming (Armbruster *et al.* 2007). Variation in treeline response may reflect this local spatial variability in average and seasonal temperature changes, rather than mean global trends.

In addition, temperature may not be the dominant factor controlling treeline position at some sites. This is because the direct influence of temperature may be masked by interactions with other factors such as precipitation (Daniels & Veblen 2003; Wang *et al.* 2006) cold-induced photoinhibition (Danby & Hik 2007a), disturbance (Lescop-Sinclair & Payette 1995; Cullen *et al.* 2001b) or plant-plant interactions (Germino *et al.* 2002; Bekker 2005). Furthermore, tree responses may be asynchronous with the rate of warming, either lagging behind or occurring only after a threshold level of warming has occurred (Rupp *et al.* 2001).

The considerable variability in topography and local climates associated with treelines worldwide, and their differing taxonomic composition, undoubtedly complicates the picture and limits the conclusions that can be drawn from single studies. On the other hand, global overviews that ignore local differences may overemphasise coarse-scale drivers such as temperature (e.g. Körner & Paulsen 2004). To avoid the limitations of both these approaches, I compiled a global dataset of individual treeline studies in relation to local and regional environmental variables with the aim of comparing changes in treeline position over the last century.

Here, I determine the global extent to which treelines have advanced, specifically testing the hypothesis that the probability of treeline advance since 1900 AD is linked to the degree of local temperature warming, and explore the possibility that factors other than temperature may influence treeline response to climate warming.

2.3 Materials and Methods

2.3.1 Database

Treeline studies published prior to June 2008 were identified using journal search tools (Web of Science, BIOSIS, JSTOR, Proquest Dissertations and Theses search), internet web searches, and by direct communication with the authors of studies. To reduce error associated with publication bias, whereby reports of treeline advance were expected to be published more often than reports of no advance, I used a general search criterion to identify studies that may not have set out to document treeline changes, but where appropriate methods to detect changes were used.

Treelines are conventionally defined as the transition zone from the closed forest to the upper alpine or arctic limit in which upright trees reach either two or three metres in height, but may also be defined by the presence of Krummholz trees. As the definition of a treeline varies considerably among studies, I included only those studies in which the authors explicitly stated that the study area included the upper tree (at least 2 m in height) or Krummholz limit. Studies in which the uppermost tree height was greater than 3 m were included only if it was noted that no other trees or Krummholz existed beyond the treeline. Treelines were classed as having advanced or not since 1900 AD according to explicit statements in each study regarding the nature of treeline movement. Treeline advance was not limited to changes in trees 2 m or more in height but included seedlings and saplings. In comparing those studies in which the authors classed treelines as having advanced, versus those that had not, treeline advance was reported if there was evidence of recruitment since 1900 AD at least 10 m beyond the historic position of alpine treelines, and at least 80 m beyond the historic position of arctic treelines. Where authors reported the size of trees used to infer advance (159 of 166 studies), 53% reported new recruits >2 m tall (i.e., a clear shift in treeline position) while the remainder of studies inferred advance from recent recruitment of trees that had not yet reached 2 m in height. Although some studies reported advance prior to 1900 AD, my analyses were limited to responses observed after this date. Changes in density below current treeline, or a change in growth form from Krummholz to upright, were not classed as evidence of treeline advance. Studies were omitted where no data on recruitment beyond the current upper tree limit or Krummholz belt were reported. Treelines reported as receding (2/166) were included but classed as not advancing. Data quality limited the response to a binary variable "advance or not" since quantitative estimates of the rate of change were not reported consistently.

I examined 243 treeline studies, for which treeline advance or not since 1900 AD could be classified for 103. These 103 studies reported responses from 166 treeline sites (36 studies included data from multiple sites), comprising 126 alpine and 40 arctic treelines from around the world, but with most sites in North America or Europe (Fig. 2.1). Of the 36 studies reporting data from multiple sites, 25 reported the same response at all sites examined. The studies had used three general approaches to assess treeline response: long-term monitoring of permanent plots (43 sites), remote sensing, mostly aerial photographs (27 sites), and treeline/stand history reconstruction using growth rings to age trees and date establishment (96 sites).

To determine whether treeline advance was related to recent temperature changes, I used a dataset of global historical land surface temperatures (GHCN; Peterson & Vose 1997) comprising monthly temperature data from about 7000 stations around the world. I removed duplicate station records and retained only stations with at least 50 years of complete monthly data since 1900 AD (2651 stations). For each of the 166 treeline sites, I identified the nearest climate station (using great circle distance) and downloaded the historical mean monthly temperature data for that station. I calculated mean annual temperature as the average of the mean monthly temperatures for each year. The annual rate of change in temperature over the duration of the study, defined by study start and end dates, was estimated as the slope of the least squares regression line for the relationship between mean annual temperature and year for the period ten years prior to the start of the study through to when the study finished. End date refers to the final year observations were made and start date refers to either the first year of observations (e.g. repeat photography, long-term monitoring) or the first year after 1900 AD in which trees were dated in stand history reconstructions. I included temperature data for ten years prior to the start of the study because treeline change may lag behind temperature change, and, at some sites, there was evidence of advance prior to the start of the study. When the study start date preceded 1900 AD (i.e., prior to the onset of recent human-induced warming), I calculated change in annual temperature from 1900 AD to when the study finished. I also calculated rate of temperature change for the summer months (June-August in the northern hemisphere and December-February in the southern hemisphere) and winter months (December-February in the northern hemisphere and June-August in the southern hemisphere).

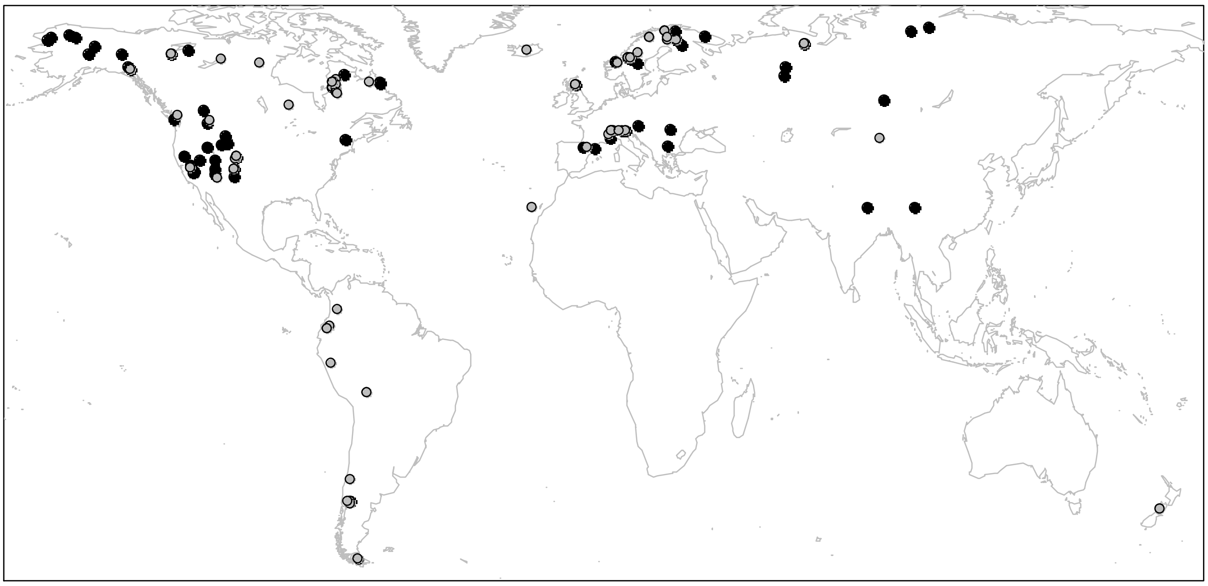

Figure 2.1: The location of the 166 treeline sites across the globe analyzed in this study grouped according to whether they are advancing (black circles) or not advancing (grey circles).

For each site, I collated additional explanatory variables that are routinely reported as proxies for exposure to environmental stress (reviewed in Smith *et al.* 2003): treeline form, elevation, latitude, distance from the ocean, aspect and treeline type. I also included variables that could affect my ability to detect a response: study duration, study start date, study scale, and disturbance (Table 2.1; Appendix A), along with the taxonomic family of the treeline species, because treeline position and potentially response have been identified as having a taxonomic component (Körner & Paulsen 2004).

Variable	Class	No. of sites	Range
Aspect	Warm	30	
	Cold	36	
	Neutral	67	
Distance from ocean		166	13.8 km – 2883 km (539 km)
Disturbance	None	110	
	Natural	16	
	Anthropogenic	33	
Elevation		155	4 masl – 4330 masl (1560 masl)
Family		166	
Form	Abrupt	10	
	Diffuse	82	
	Krummholz	69	
Latitude		166	-54.13° – 70.52° (51.44°)
Annual temperature change		166	-0.026° – 0.049 °C/y (0.006 °C/y)
Summer temperature change		166	-0.038° – 0.09 °C/y (0.011 °C/y)
Winter temperature change		166	-0.044° – 0.084 °C/y (-0.002 °C/y)
Study duration		166	1 – 108 years (63 years)
Study start date		166	1900-2006
Study scale	Coarse	27	
	Fine	139	
Treeline type	Alpine	126	
	Arctic	40	

Table 2.1: Definition and sample size of variables used in model formulation. The range (minimum - maximum) and mean (in parentheses) of continuous variables are shown.

Elevation, latitude, aspect and treeline type were obtained from information in the published studies. Aspect was classed as warm (south facing in the northern hemisphere and north facing in the southern hemisphere), cold (north facing in the northern hemisphere and south facing in the southern hemisphere) or neutral (east and west facing). Treeline type was classed as alpine or arctic. Distance to the ocean was calculated as the distance from the study site to the nearest coastline using ArcView 9.1 (ArcGIS Version 9.1).

Treeline form refers to the spatial structure of the treeline at the start of the study. I recognised three treeline forms: 1) diffuse- characterized by decreasing tree density with increasing altitude or latitude; 2) abrupt- a continuous canopy with no decline in density right up to treeline; 3) Krummholz- the treeline may be diffuse or abrupt but is characterised by severely stunted or deformed polycormic trees; and 4) island – the treeline may be formed by Krummholz or arborescent growth form but is characterized by clumped patches above the forest limit. Tree height often declines with altitude or latitude in both diffuse and abrupt treelines but was not considered indicative of these forms. When more than one treeline form was recorded at a study site, I used the form recorded at the uppermost alpine or arctic treeline limit. In the case where both Krummholz and upright trees occur at the upper limit, the treeline was classed as Krummholz. Treeline form was inferred primarily from written descriptions and, when necessary, photographs or direct communication with authors.

Evidence for disturbance at each site was classed as unknown (no information on disturbance recorded), none (an explicit statement that there was no evidence of disturbance at the site), natural (e.g. evidence of wind, natural fire, earthquake) or anthropogenic (e.g. evidence of agriculture, livestock grazing, fire suppression). I did not record data on the timing or intensity of disturbance because this was reported inconsistently. I used study methodology as a proxy for the effect of scale on my ability to detect treeline advance. In general, field based studies (long-term monitoring and stand history reconstructions) were at a finer scale and smaller spatial extent than those relying on remote sensing (repeat photography and satellite imagery) methods.

2.3.2 Analysis

I used logistic regression models to determine whether treeline advance or not was associated with the explanatory variables. I fitted these models in a Bayesian framework so that I could accommodate plant family as a random effect in the model, and to deal with missing values (Gelman & Hill 2007). The dataset had 56 missing values for explanatory variables: aspect (33), elevation (11), disturbance (7), and treeline form (5), mostly where information was not available from published sources. Rather than omitting sites with missing values, which is the conventional approach assuming missing values occur at random (Gelman & Hill 2007), I modelled missing values for continuous variables as if they were drawn at random from a normal distribution having mean and variance estimated from the data, and missing values for categorical variables as if they were drawn from a multinomial distribution with the probability for each category estimated from the data (Gelman & Hill 2007). This allowed us to include all of the relevant data in the model while incorporating the uncertainty associated with estimating those missing values.

Our response variable was whether treeline advance had occurred since 1900 AD or not. I modelled this as a Bernoulli process with a logit link function, including rate of temperature change (annual and seasonal), treeline form, distance from ocean (log transformed), elevation (log transformed), latitude, study duration, study start date, aspect, disturbance, study scale (field observation *vs.* remote sensing), and treeline type as explanatory variables. The continuous explanatory variables (rate of annual and seasonal temperature change, distance from ocean, elevation, study duration and latitude) were standardised by subtracting their mean and dividing by twice their standard deviation to assist with model convergence and to put the parameter estimates for both continuous and categorical variables on a comparable scale (Gelman & Hill 2007). Categorical variables (treeline form, aspect, disturbance, study scale and treeline type) were included by coding them as dummy variables and choosing one of the classes as a reference class with the coefficient set to zero. Plant family was included as a random effect, with the regression coefficients describing the effect of each family assumed to be drawn from a common normal distribution with a mean of zero and a standard deviation estimated from the data.

Data on rate of temperature change were taken from the GHCN climate station closest to each treeline site, but the site-station distances varied from <1 km to 626 km (median = 77 km). To assess the significance of this, I investigated how differences among GHCN stations in their rate of temperature change varied as a function of both distance apart and difference in elevation (Appendix B). Temperature trends differed among stations but there was no strong tendency for stations located further apart or those having a greater difference in elevation to differ systematically from stations located closer together or at similar elevation. Thus, while using temperature trends from climate stations located close to, but not at, treeline sites may introduce noise to the data, it should not generate any systematic bias.

I first included each explanatory variable alone in a logistic regression model to identify the variables with the greatest influence on treeline response. I then included in a multivariate model the subset of variables that tended to differ from zero in the logistic regression models, in order to assess their relationship with treeline advance having accounted for the effect of other variables. Plant family was also included as a random effect in the multivariate model to account for the possibility that species in the same plant family showed similar responses. Several studies included more than one site, which might result in correlated responses, but I did not include a study-level effect in the model because most studies (67 of 103) comprised only a single site. No variables included in the final model were collinear.

The model was fitted using OpenBugs called from the BRugs library (Thomas *et al.* 2006) in R v. 2.8 (R Development Core Team 2008). I used non-informative prior distributions to reflect a lack of prior information about the model parameters, specifying a normal prior with variance 1000 for regression coefficients and a uniform prior in the interval 0-10 for variance parameters. I ran three chains each with a burn-in of 5000 iterations, which was sufficient to ensure convergence as judged by inspection of the chain histories, and then sampled the posterior distributions from a further 10000 iterations of each chain. The importance of explanatory variables was assessed using 95% Bayesian credibility intervals on these posterior distributions. Further details of the development of the models and interpretation are provided in Appendix C.

2.4 Results

Mean annual temperature increased at 111 of the 166 sites at an average rate of 0.013 °C/year over the study duration, although the rate of temperature increase was less than 0.01 °C/year at over half of the sites experiencing warming (Fig. 2.2a). Summer warming occurred more often (117/166 or 71% of sites, mean rate = 0.0189 °C/year), than winter warming (77/166 or 46% of sites, mean rate = 0.0199 °C/year; Fig. 2.2).

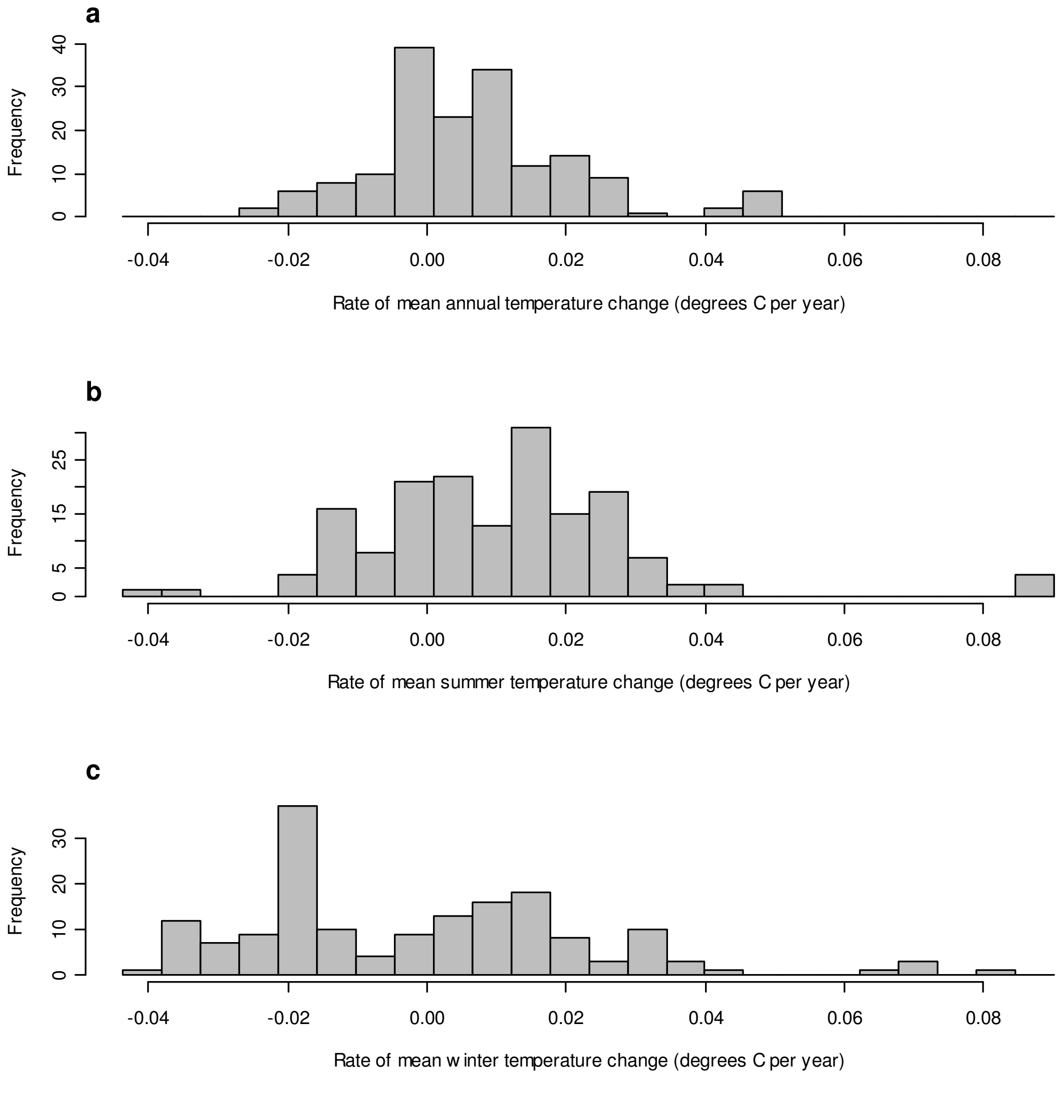

Figure 2.2: Histogram of the rate of annual (a), summer (b), and winter (c) temperature change (°C/year) for the 166 study sites for the period ten years prior to study start date to the study finish date.

Treelines had advanced since 1900 AD at 87 of 166 sites (52%). Of the sites that showed no advance, 77 had remained stable whereas two had receded, with the two sites where treelines had receded also showing evidence of disturbance. There was no clear association between probability of treeline advance and rate of mean annual or summer temperature increase. For example, of the 111 sites in which annual temperature had increased over the study duration, 63 (57%) had advanced, and of the 55 sites that had cooled, 24 (44%) had advanced. Indeed the 95% credible intervals for the parameter estimates describing the relationship between the probability of treeline advance and rate of annual and summer temperature change, when these were included alone in a model, overlapped zero (Fig. 2.3a). In contrast, treelines were more likely to advance at sites that had warmed during the winter months: the parameter estimate for the relationship between probability of treeline advance and rate of winter temperature change, when included alone, was positive and 95% credible intervals did not include zero (Fig. 2.3a). The positive relationship between winter temperature change and treeline advance may also relate to cooling, in which sites were less likely to advance if winter cooling occurred. Treelines were more likely to advance if winter temperatures warmed (43/77 sites) and were just as likely to advance if winter temperatures cooled (45/89 sites).

Disturbance, study duration, study start date, latitude, aspect, treeline type, and scale did not show strong relationships with probability of treeline advance when each variable was included alone in a logistic regression model (the 95% credibility intervals around the parameter estimates all overlapped zero; Table 2.1, Fig. 2.3a,b). In contrast, the parameter estimates for rate of winter temperature change, elevation, distance to ocean, and treeline form tended to differ from zero. I therefore fitted a multivariate model that included these four explanatory variables along with plant family as a random effect.

Having accounted for the effects of the other variables in the model, elevation and distance to ocean failed to show a clear relationship with probability of advance (Fig. 2.3c). Rate of winter temperature change was associated with probability of advance, with 95% credible intervals excluding zero: sites that had warmed more during the winter months were more likely to have advanced. The strongest relationship was with treeline form: diffuse treelines were more likely to have advanced than abrupt, Krummholz and island treelines (Fig. 2.3c). Of the 82 treeline sites classed as diffuse, 67 (80%) had advanced, whereas of the 79 sites classed as abrupt, Krummholz or island, only 17 (22%) had advanced (five sites were unclassified with regards to treeline form).

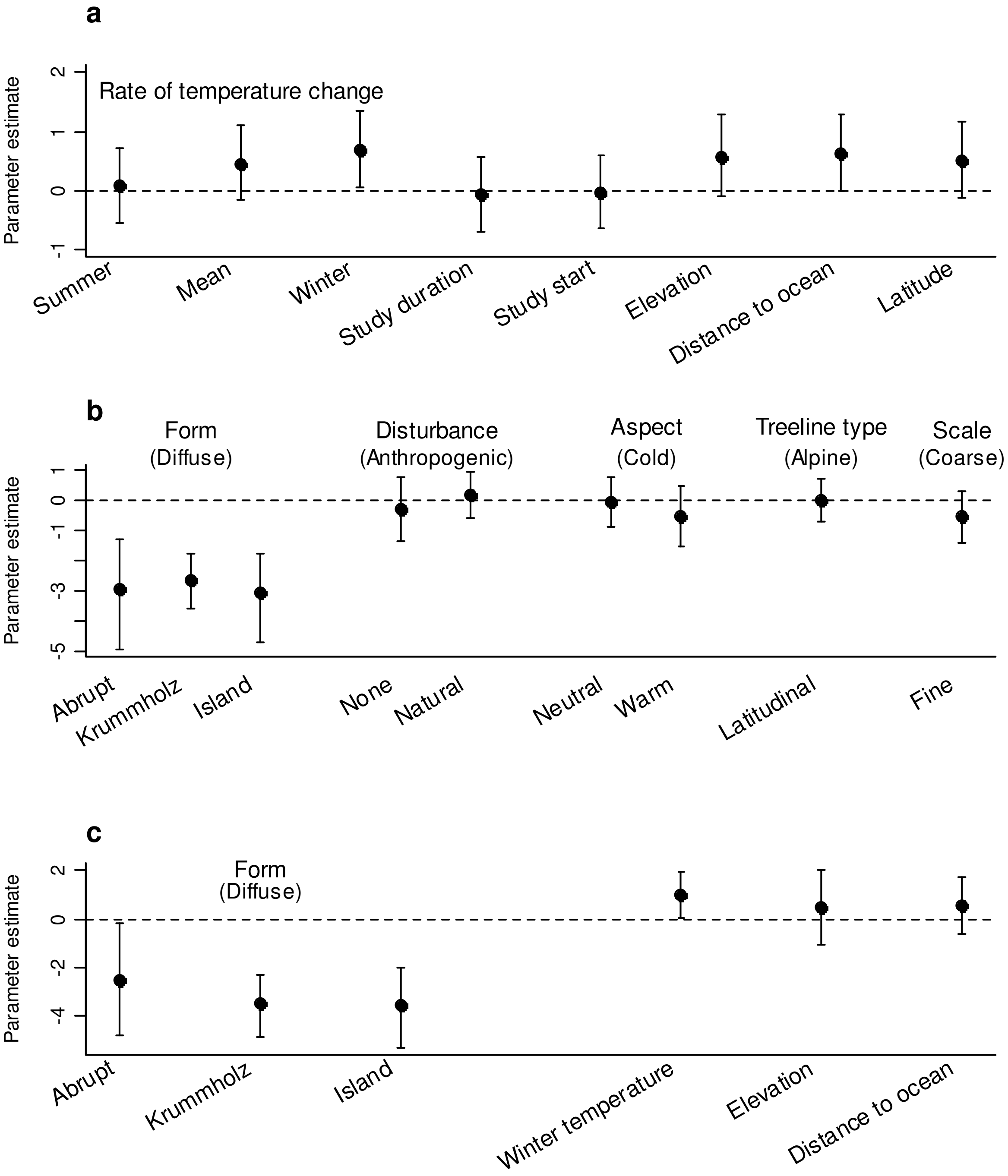

Figure 2.3: The mean and 95% credible intervals for the parameter estimates describing the effect of each explanatory variable on the probability of treeline advance when those variables are included alone in a logistic regression model (a, b) or together in a multivariate logistic regression model with plant family included as a random effect (c). The continuous variables (rate of temperature change, distance from ocean, elevation, study duration and latitude) were standardised by subtracting their mean and dividing by two times their standard deviation. The parameter estimates for the levels of the factor variables are with regard to a reference class (shown in parentheses), which is set to zero. Credible intervals crossing the zero line (dashed) are not significant.

There were no clear differences among plant families in their probability of advance having accounted for other variables in the model (Fig. 2.4). This may reflect the strong bias towards species in the Pinaceae and Betulaceae, which formed the treeline at 136 sites (82%). Species in other families occurred at few sites, limiting my ability to detect differences.

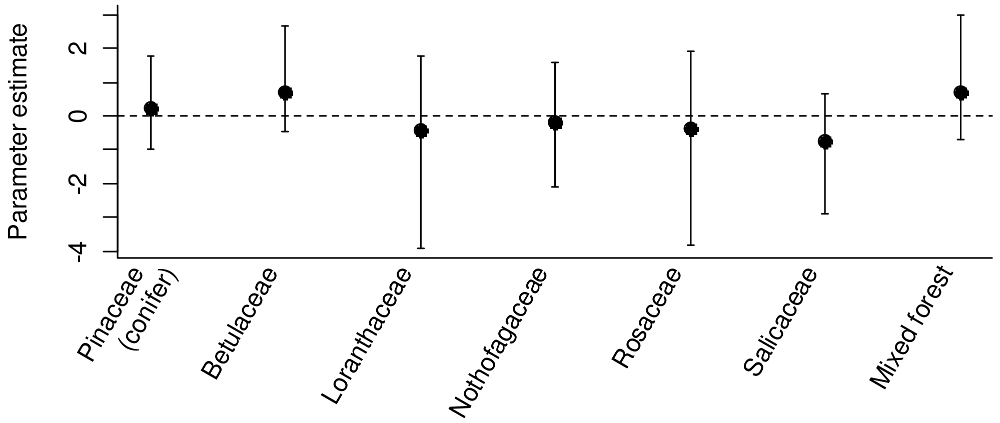

Figure 2.4: The mean and 95% credible intervals for the parameter estimates describing the effect of plant family on the probability of treeline advance. Conifer treelines comprise only the family Pinaceae, while all other families are angiosperms. Mixed forests are treeline sites composed of both gymnosperm and angiosperm families. Credible intervals crossing the zero line (dashed) are not significant.

Finally, to explore the relationship between temperature change and treeline form further, I modelled the relationship between rate of mean annual, summer and winter temperature change and probability of advance, separately for diffuse treelines and for abrupt, Krummholz and island treelines combined (Fig. 2.5). There is evidence that treelines with differing form have different temperature responses (Camarero 2000; Danby & Hik 2007b). Diffuse treelines were more likely to advance when warming occurred (mean annual, summer or winter), having the strongest association with mean annual and winter warming. In contrast, abrupt, Krummholz and island treelines were more likely to advance only with winter warming.

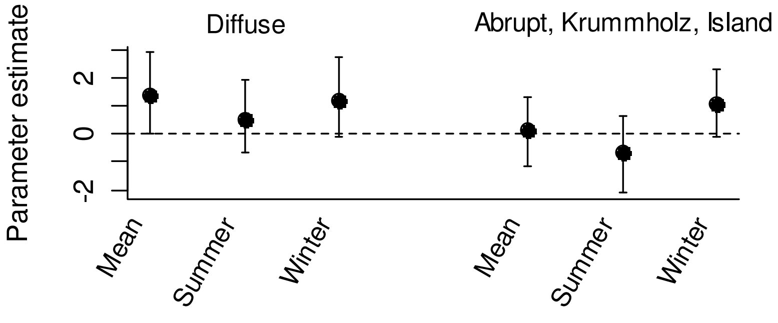

Figure 2.5: **The mean and 95% credible intervals for the parameter estimates describing the effect of rate of mean annual, summer and winter temperature change on probability of treeline advance, for diffuse and abrupt, Krummholz and island treelines separately. Credible intervals crossing the zero line (dashed) are not significant.**

2.5 Discussion

Our global analysis indicates that, regardless of form, location and degree of temperature change experienced over the last century, treeline positions have either advanced or remained stable. At only two sites were treelines recorded as receding and both of these sites showed evidence of disturbance. This is consistent with what might be expected if treelines were responding to increasing global temperature but were also constrained by other factors. In contrast, I would expect to observe no advance or random fluctuations around a zero trend line (approximately equal numbers of advances and retreats) in the absence of directional change. Unless receding treelines have been systematically under-reported, the net global outcome is that treelines are rising. Advance, however, was not universal.

Of the variables I considered, two were strongly associated with treeline response: treelines that experienced stronger winter warming were more likely to advance, and treelines with a diffuse form were more likely to advance than treelines with abrupt, Krummholz or island forms. At a global scale, treelines are considered to be constrained primarily by growing season temperature (Körner & Paulsen 2004). That treeline advance is more strongly associated with winter, rather than summer, warming is therefore surprising. The observed relationship with winter warming alone was apparent only for abrupt, Krummholz and island treelines; diffuse treelines appear to be responding to overall increases in temperature (Fig. 2.5). This variation in the response of treeline forms to seasonal and annual temperature change may result from different primary constraints on treeline position; diffuse treelines, in contrast to abrupt, Krummholz and island treelines, are more likely to form where climatic factors, particularly growing season temperature, primarily limit growth rather than survival (Camarero & Gutierrez 2002; Danby & Hik 2007a). Although there is a body of evidence suggesting that diffuse treelines are limited by growing season temperature (Ellenberg 1988; Wiegand *et al.* 2006), the presented results do not provide such evidence but do suggest that diffuse treelines are responding to overall warming, of which summer warming is a component (Fig. 2.5).

In contrast, abrupt, Krummholz or island treelines may be more strongly influenced by stress factors associated with winter conditions that lead to plant damage and limit survival. Krummholz form, in particular, is commonly attributed to damage associated with factors such as wind abrasion, snow and ice damage (Norton & Schöenberger 1984; Hadley & Smith 1986) which can be severe during late autumn, winter and early spring. Considering that recruitment by seed is infrequent during unfavourable periods (Laberge *et al.* 2001;

Caccianiga & Payette 2006) and that tall seedling growth is likely limited by the same factors that limit vertical growth in Krummholz (Smith *et al.* 2003), recruitment beyond the Krummholz belt is unlikely to occur unless conditions limiting vertical growth are lessened. Likewise, the step-like structure of abrupt treelines can arise because harsh winter conditions limit survival in open sites due to factors such as winter desiccation (Cairns 2001). These factors may be ameliorated by the presence of tall, closed canopy trees leading to an abrupt boundary at treeline. Such feedback effects in turn may constrain the response of these treelines to climate warming (Bader *et al.* 2007b). Hence, advance in Krummholz and abrupt treelines may occur only when winter warming is sufficient to ameliorate other constraints, or when temperature increases sufficiently to compensate for those constraints.

Although treelines with higher rates of winter warming were more likely to show advance, there was much variability around this relationship, with many sites classed as advancing even when mean winter temperature over the study duration had cooled. Several reasons are frequently proposed to explain why treelines fail to respond to temperature changes as expected. First, study methodology could have a pronounced effect on ability to detect change. The inclusion of remotely sensed (coarse-scale) methodologies may decrease my ability to detect a response because they may be less effective at detecting small shifts in altitude or latitude. However, there was no significant difference between coarse- and fine-scale studies in their ability to detect advance (Fig. 2.3b).

Second, ecological time lags (e.g. slow-growing species, rare seeding events) may delay recruitment. Treeline advance has been shown to lag behind climate warming at some sites, but typically by only a few decades (Lescop-Sinclair & Payette 1995; Kullman 2001; Lloyd *et al.* 2003). Most of the included studies began well after the onset of 20th century warming, or were of sufficient duration to exceed these lag periods. Disturbance legacies may further influence treeline position and its ability to respond to climate changes. Past disturbances can shape treeline structure and influence initial recruitment patterns but subsequent patterns of recruitment and spread may be more strongly controlled by climate (Holtmeier & Broll 2005; Bolli *et al.* 2007; Vittoz *et al.* 2008). Hence, rather than affecting the probability of recent advance, disturbance may influence when advance initiates and act as a potential lag source. I found no evidence in the data of different responses at sites that varied in known disturbance history, suggesting any long-lasting effects of disturbance cannot explain the patterns observed in this study.

Finally, interannual variation can have a significant effect on treeline advance. Recruitment and survival are both highly sensitive to short periods markedly cooler or warmer than the general temperature trend (Kitzberger *et al.* 2000; Gray *et al.* 2006). For example, recruitment observed at a site with a cooling trend may have occurred during a brief warm period, and recruitment at a site with a warming trend may have been hindered by a short cold period that killed new recruits. Until the general warming trend consistently exceeds interannual variability, treeline advance may depend upon the coincidence of favourable conditions over sufficient years to permit establishment, growth and survival (Szeicz & MacDonald 1995; Wang *et al.* 2006). This is less likely to be critical for diffuse treelines if summer growth limits treeline position, because growth gains in warmer summers are likely to be retained through cooler summers. In contrast, where treeline advance is limited by winter survival, a single cold year could destroy the gains made over several warmer winters.

In summary, approximately half the treeline sites examined globally have advanced since 1900 AD, with a link between probability of advance and the degree of local winter warming at those sites. These results are consistent with what I would expect if treelines were responding to increasing global temperatures but were also constrained by other factors. In particular, diffuse treelines are more likely to advance than abrupt, Krummholz or island treelines. I speculate that diffuse treelines may be strongly limited by growing season temperatures and hence particularly responsive to overall temperature increases. Abrupt, Krummholz and island treelines, in contrast, may be more strongly limited by winter temperatures in association with other constraints that act on tree survival, such as damage due to wind, snow or winter desiccation. Advance at these sites may require an increase in winter temperature sufficient to ameliorate the impact of these other constraints.

Chapter 3
Treeline form – a potential key to understanding treeline dynamics

3.1 Abstract

Treelines occur within a narrow range of mean growing season temperatures globally, suggesting that low temperature growth limitation determines treeline position. However, treelines also exhibit features that indicate that other mechanisms, such as biomass loss not resulting in mortality (dieback) and mortality, determine treeline position and dynamics. Debate regarding the mechanisms controlling treeline position and dynamics may be resolved by identifying the mechanisms controlling prominent treeline spatial patterns (or ‘form’) such as the spatial structure of the transition from closed forest to tree limit. Recent treeline studies worldwide have confirmed a close link between form and dynamics. In this review, I describe how varying dominance of three general ‘first-level’ mechanisms (tree performance: growth limitation, seedling mortality, and dieback) result in different treeline forms, what ‘second-level’ mechanisms (stresses: e.g. freezing damage, photoinhibition) may underlie these general mechanisms, and how they are modulated by neighbour interactions (‘third-level’ mechanisms). This hierarchy of mechanisms should facilitate discussions about treeline formation and dynamics. I distinguish four primary forms: diffuse, abrupt, Krummholz and island. Growth limitation is dominant only at the diffuse treeline, which is the form that has most frequently responded as expected to growing-season warming, whereas other forms are controlled by dieback and seedling mortality and are relatively unresponsive. Treeline form provides a means for explaining the current variability in treeline position and dynamics and for exploring the general mechanisms controlling treeline responses to climatic change. Form indicates the relative dependency of tree performance on various aspects of the external climate (especially summer warmth vs. winter stressors) and on internal feedbacks, thus allowing inferences on the type as well as strength of climate-change responses.

3.2 Introduction

Treelines worldwide exhibit striking similarities as well as differences in structure and position. Some researchers prefer to address the similarities (e.g. Körner, 1998, Paulsen & Körner, 2004) whereas others prefer to emphasize the differences (e.g. Butler *et al.*, 2009; Holtmeier, 2009). In the following review, I take an intermediate stand, recognising broad categories of treeline structures, based on spatial patterns, and discussing how each structure (or 'form') may be controlled by a few general processes and may exhibit its own typical response to climatic change.

The prevailing hypothesis regarding the cause of treeline formation is that growing season temperature limits tree growth (Körner & Paulsen 2004; Hoch & Körner 2009). This idea is based upon notable similarities in various temperature parameters at treelines worldwide, the most consistent being average growing season temperature, at least at northern hemisphere conifer treelines (Paulsen & Körner 2001). The importance of growing season temperature seems to be in contradiction to results from regional and global analyses, in which treeline advance was positively associated with winter warming and not significantly associated with summer warming (Kullman 2007; Rossler *et al.* 2008; Harsch *et al.* 2009). Also, negative effects of winter stress and damage on recruitment, tree survival and growth appear to contradict the dominance of summer growth control (Tranquillini 1979; Pereg & Payette 1998; Rickebusch *et al.* 2007). The seemingly inconsistent and even contradictory response of treelines to observed climate warming necessitates a deeper understanding of the mechanisms controlling treeline dynamics (Halloy & Mark 2003; Holtmeier & Broll 2007).

One reason why increased growing season temperature often does not lead to a treeline shift may be the disjunction between the mechanisms that control stable and dynamic treeline states. A stable treeline, one that is not clearly shifting in position, even if demographic rates are fluctuating, is primarily associated with mechanisms limiting mature tree performance, especially growth. Recruitment below the treeline is important for long-term stability but does not affect treeline position. In contrast, a dynamic treeline, by definition, is either advancing or receding and therefore exhibiting either recruitment with low mortality beyond the treeline (advance) or high mortality of established trees at and below the treeline and little or no recruitment (recession). Thus, the mechanisms and environmental conditions primarily associated with stable treelines (i.e. growth limitation in established trees, determined by low summer temperature) are reflected in the prevailing hypothesis on treeline formation but are not necessarily the same as those associated with dynamic treelines (i.e. establishment and mortality, determined by conditions, including but not exclusively, temperature, year-round;

Camarero *et al.* 2000; Daniels & Veblen 2004; Moen *et al.* 2008; Rickebusch *et al.* 2007). This disjunction between the conditions controlling treeline maintenance (stable treelines) and treeline advance (dynamic treelines) may explain why just over 50% of treelines around the world have recently advanced despite annual temperature warming occurring at nearly 70% of treeline sites (Harsch *et al.* 2009).

Spatial patterns at treeline ecotones, the transition zone from the forest line to the tree limit, can range from abrupt lines to diffuse zones and from straight transitions to complex patchworks. Such distinct spatial patterns are certain to differ in both their origin and their functioning (Levin 1992; Grimm *et al.* 1996). Patterns may be directly attributable to underlying topographical features (Butler *et al.* 2007), but, in many cases, these are emergent patterns on relatively homogenous slopes. The different origins of treeline spatial patterns, in particular abrupt vs. diffuse treelines, have been discussed, with varying conclusions, by e.g. Ellenberg 1966, Tranquillini 1979, and Holtmeier 2009. Here, I review how treeline spatial patterns, hereafter referred to as four treeline 'forms', may indicate the processes that control current treeline position and, importantly, how they link to the potential response to climatic changes (Armand 1992; Bader *et al.* 2008). The presence of a link between form and response is indicated by the fact that treeline response to climate change appears to differ between different treeline forms (Lloyd 2005; Harsch *et al.* 2009). I briefly discuss physiological mechanisms but these are reviewed elsewhere more comprehensively (Tranquillini 1979; Grace 1989; Wardle 1993; Körner 1998). I discuss how different mechanisms, at the levels of direct tree performance, causative stresses and modifying neighbour interactions, determine typical treeline forms and dynamics. I focus on the mechanisms controlling treeline advance since treelines are expected to advance rather than recede in response to climate warming. The global distribution of different treeline forms and the frequency of advance and of disturbance in these forms are assessed from an extended database modified from Harsch *et al.* (2009; Appendices D and E).

3.3 Linking form and dynamics: outline of the framework

Treelines are conventionally defined by a strong decline in tree height and density, with the critical values of these properties varying between authors (summarized in Holtmeier 2009). My definition of the treeline follows that in Holtmeier & Broll (2005): an ecotone, delimited at the upper end by the tree species limit, the uppermost elevation or latitude at which tree species occur as trees at least 2 m in height or Krummholz, and at the lower end by the forest line, the uppermost elevation or latitude at which there is a continuous forest canopy. The zone between these limits can vary greatly in width and character, thus comprising different 'forms'. I recognize four globally reoccurring primary forms (Fig. 3.1):

- Diffuse, characterized by a gradual decrease in single-stemmed tree height along the treeline ecotone. Tree density also tends to decrease along the treeline ecotone.
- Abrupt, characterized by a continuous forest > 2 m high directly bordering low alpine vegetation. Trees may be present above the continuous forest but their presence is infrequent.
- Island, characterized by clumped patches or linear strips ('fingers') of Krummholz or trees above the continuous forest limit.
- Krummholz, characterized by a band of severely stunted or deformed multi-stemmed trees above the continuous forest limit. Krummholz growth form can occur in clumped patches above the upright forest (class as island treeline) or as a dispersed or contiguous band above the upright forest (classed as 'Krummholz treeline'). The characteristics of Krummholz treelines also apply to Krummholz-island treelines, whereas other features of island treelines are more specific for this form only.

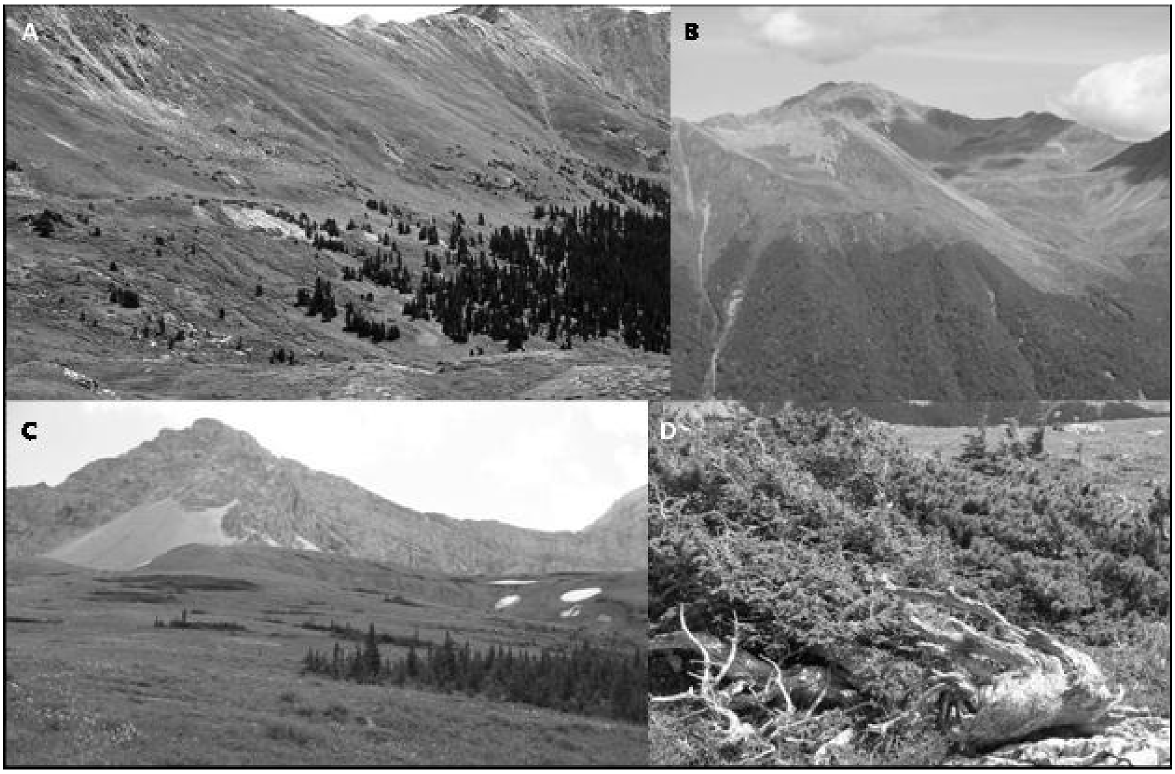

Figure 3.1: Examples of the four treeline forms: a) diffuse treeline Loveland Pass, CO, USA, photo F-.K. Holtmeier); b) abrupt *Nothofagus* treeline near Lewis Pass, New Zealand; c) Krummholz-island treeline on Lee ridge (Glacier NP) - islands are relatively few here, making this an ambiguous case between Krummholz or Krummholz-island, and mechanisms typical for both will play a role; d) Krummholz island close-up (prevailing wind direction is from right to left) with likely founder (established behind rock), now (partly) died off, and younger individuals established to the lee (*Abies lasiocarpa* and *Pinus albicaulis* Glacier NP, MT, USA).

Although classifying a continuum of forms into discrete classes based on several characteristics creates ambiguous cases, it is necessary and helpful to clarify general patterns. Treeline sites may be classed differently depending on the author's reference frame. For example, the sharp (abrupt) treeline described by Armand (1992) would be gradual (diffuse) according to Bader *et al.* (2007a), which is due to the very diffuse and abrupt treelines they were compared to, respectively. Still, once clearly defined, treeline forms are ideal indicators of the mechanisms controlling treeline formation and dynamics. They are readily recognized, easily distinguished, and have a wide geographic distribution (Fig. 3.2). The suitability of treeline form as an indicator of treeline dynamics is further suggested by the relationship between treeline response and form: nearly four out of five diffuse treelines identified by Harsch *et al.* (2009) had advanced in response to recent climate warming, whereas only one out of four abrupt, island or Krummholz treelines had advanced (Fig. 3.3).

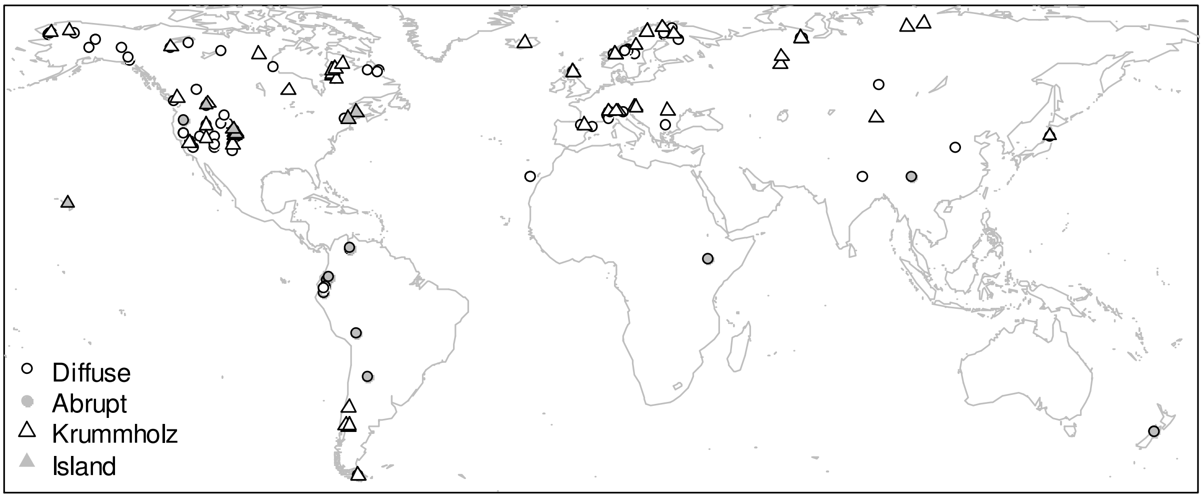

Figure 3.2: Location of 195 treeline sites analyzed in this study grouped according to whether they are diffuse (white circles), abrupt (grey circles), Krummholz (white triangles) or island (grey triangles) in form. For information on database, see Appendix D. For references, see Appendix E.

Several forms may occur simultaneously within one mountain range or even on a single mountain. Local differences in climate, aspect, substrate, land-use and other disturbances may account for such local differences (Lloyd 2005; Holtmeier 2009). As long as the tree limit is not controlled by topography (e.g. a vertical rock face delimiting the treeline), local variability in form should be indicative of controlling factors and potential local responses similar to larger scale patterns (e.g. nearly all New Zealand treelines being abrupt).

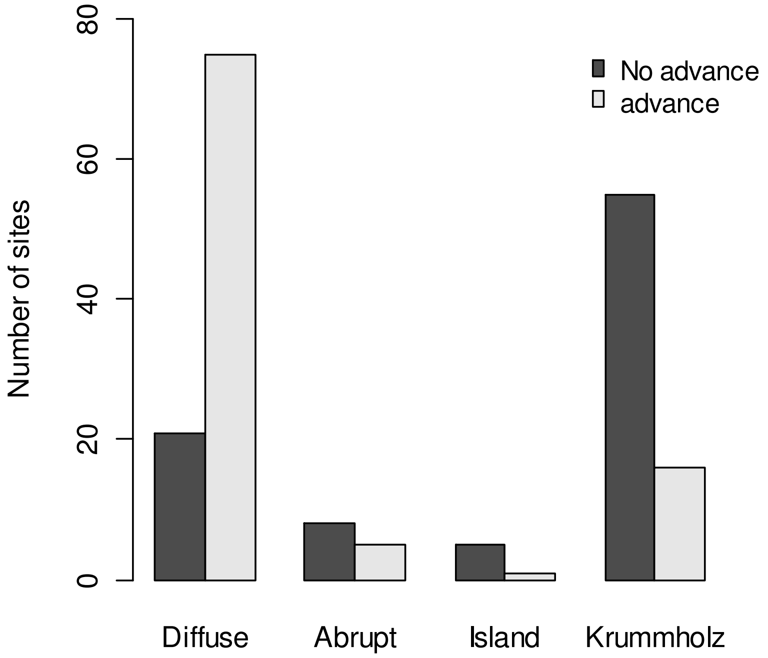

Figure 3.3: Frequency of diffuse, abrupt, island and Krummholz treelines observed to have advanced or not since 1900 AD. Modified from Harsch *et al.* (2009).

Treelines represent the distributional limit of tree species and reflect the local tree species tolerance to environmental stress, at least at those not limited by topography (Holtmeier & Broll 2007). Thus, treeline position is frequently described in terms of climatic stressors (Table 3.1). Accordingly, at environmentally stressful conditions (e.g. high elevations and latitudes), growth, recruitment and mortality are determined more by environmental stress than by competition or biotic interactions (e.g. browsing) (Menge & Sutherland 1987; Maestre *et al.* 2009). In the development of the proposed framework, I consider treelines to be at their climatic limit or upper end of the environmental stress-gradient and that climatic stress exerts a greater influence on treeline form and dynamics than competition or biotic interactions. How changes in the stressors will affect tree performance and observed treeline form and dynamics are briefly discussed throughout this chapter.

I postulate that treelines result from three major mechanisms controlling tree performance: growth limitation (ability to develop new biomass), dieback (biomass loss not causing mortality), and seedling mortality (Fig. 3.4). The relative dominance of these three general ‘first-level’ mechanisms determines both treeline form and dynamics (Fig. 3.5). These mechanisms are the result of various types of physiological stress or damage (second-level mechanisms). For example, growth can be impacted by an insufficient carbon balance or by direct low-temperature restrictions on tissue formation, seedling mortality can result from snow fungi, freezing damage, or summer drought and dieback can result from freezing damage, wind abrasion or snow breakage (Table 3.1, Fig. 3.4). The second-level mechanisms are further modified by neighbour interactions (third-level mechanisms) that modify microclimate and microsite conditions (e.g. soil) through e.g. a redistribution of wind (sheltering, wind funnelling) and snow, shading, or resource competition. Microsite conditions are also determined by macroclimatic and geographic conditions, which depend on site location (e.g. exposure, latitude, continentality). The effects of the second-level mechanisms on tree performance further depend on tree-species characteristics such as shade dependence, freezing tolerance and photosynthetic capacity (Fig. 3.4).

	Stress	**Stressor**
Growth limitation	Limited carbon assimilation/ impaired biosynthesis	Low growing season temperature Nutrient deficiency Short growing season
Dieback	Breakage	High snow load
	Freezing damage	Frost
	Winter desiccation	Sky exposure and frozen soil
	Photodamage	Excess radiation
	Mechanical damage	High wind
Seedling mortality	Snow fungi	High snow load
	Freezing damage	Frost
	Winter desiccation	Sky exposure and frozen soil
	Photodamage	Excess radiation
	Heat stress	
	Summer desiccation	Low precipitation and high temperature

Table 3.1: Each of the primary mechanisms controlling treeline form results from several types of stress which, in turn, result from several stressors (adverse microsite conditions).

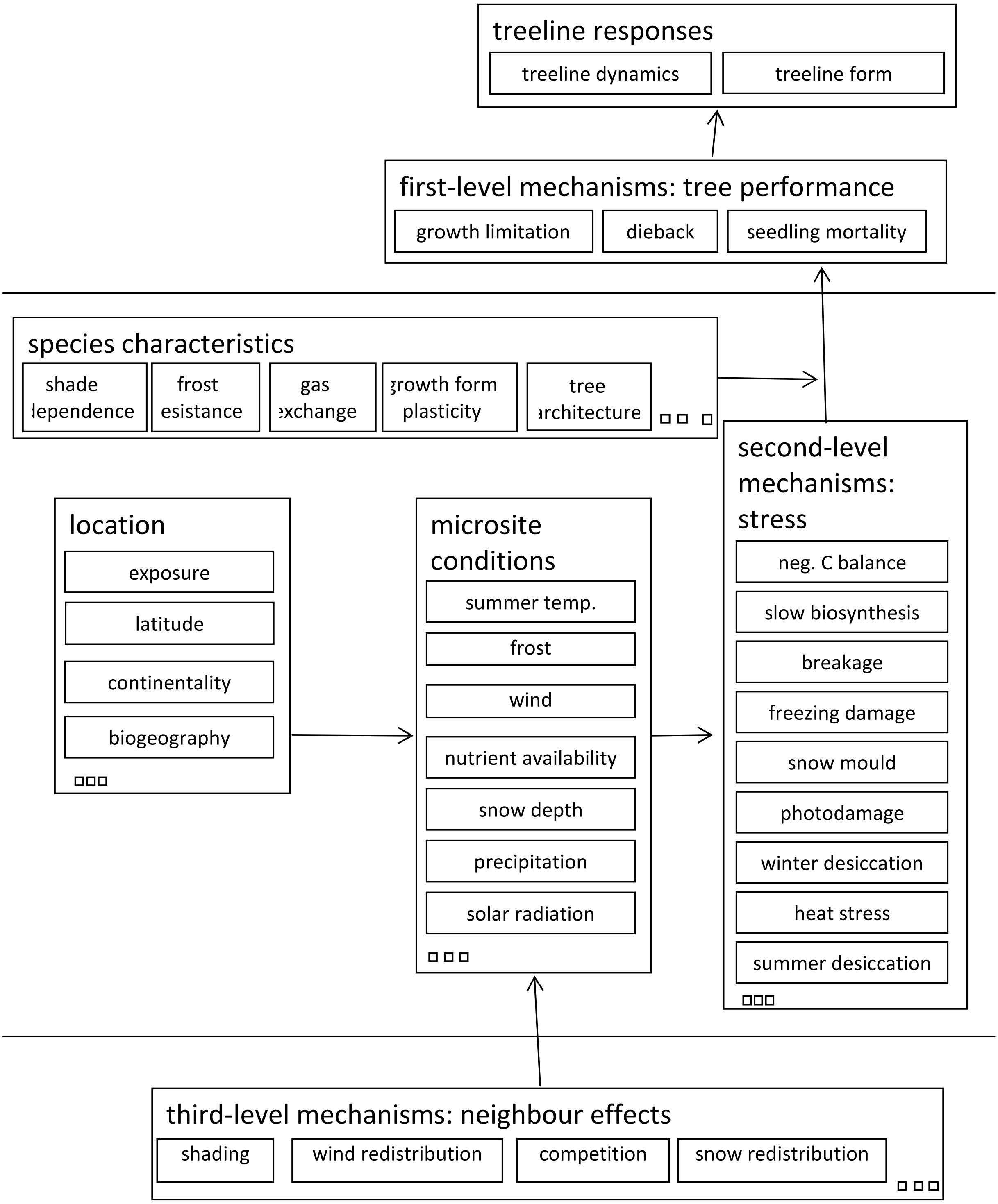

Figure 3.4: Outline of the framework, showing three orders of mechanisms controlling treeline form and dynamics and the factors and conditions that determine how these mechanisms operate. Small boxes indicate that the listing of mechanisms is not exhaustive.

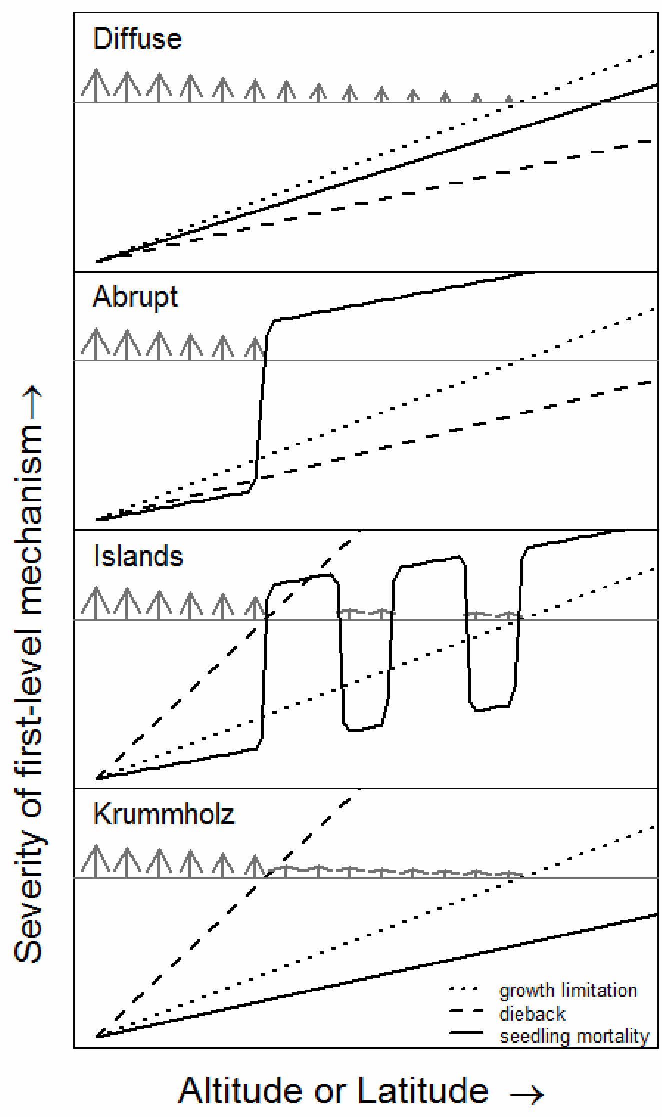

Figure 3.5: Conceptual diagram illustrating how treeline form can result from growth limitation (dotted black line), dieback (dashed black line) and seedling mortality (solid black line). The three primary mechanisms become inhibitory at a theoretical threshold level (horizontal grey line with trees). The sharp increases and decreases in seedling mortality in abrupt and island treelines are both the effect and a reinforcement of the treeline pattern itself (positive feedback).

Studies of survival have primarily focused on seedlings because treeline advance depends on the establishment of seedlings, which tend to have high mortality. Given that mortality in mature trees is very rare except after severe disturbance or prolonged periods of stress (Kullman 1997) and that treelines are expected to advance in response to recent climate warming, I focus on seedling mortality. Seed production, viability and germination are also not included as a separate performance mechanism but were considered a component of seedling establishment and survival, and, therefore, seedling mortality. Fecundity often declines with elevation (Allen & Platt 1990; Mencuccini *et al.* 1995; Jump & Woodward 2003) and does affect treeline dynamics. However, fecundity is initially limited by the same factors limiting growth (Johnsen *et al.* 2005; Richardson *et al.* 2005) and biomass retention (Lescop-Sinclair & Payette 1995; Caccianiga & Payette 2006). Monitoring fecundity, therefore, provides minimal gains to understanding treeline dynamics beyond what may be gained by studying growth limitation and dieback. Further, at treeline, recruitment is ultimately limited by germination or subsequent survival (Cuevas 2000, 2002).

How growth limitation, dieback and seedling mortality could interact to form diffuse, Krummholz and abrupt treelines has been demonstrated by Wiegand *et al*. (2006) in a simple model. The three different treeline forms resulted from differences in the relative importance of two gradients, as well as the level of facilitation from neighbouring trees. In this model, growth limitation and dieback were encompassed into a single gradient, growth-inhibition, and seedling mortality was encompassed within the general mortality gradient. A strong age-dependent mortality gradient combined with weak growth inhibition and strong facilitation resulted in an abrupt change in tree height and density. The explanation is that, once established, trees would grow to a relatively large size and only seedling establishment would be restricted at the unfavourable end of the mortality gradient. Diffuse treelines formed where the growth inhibition gradient increased as a function of distance beyond the forest line. Krummholz formed under strong ‘growth inhibition’ (in the present paper I consider this dieback rather than growth limitation as Krummholz are limited by biomass retention rather than biomass formation), with differences in density and patchiness (island formation) related to facilitation strength and the mortality gradient. This simple model produced treeline patterns similar to many of those observed in the Spanish Pyrenees (Wiegand *et al.* 2006), but underlying mechanisms leading to the required gradients were not explicitly tested but were included phenomenologically.

Land-use (anthropogenic disturbance) can strongly influence treeline form (Holtmeier 2009). Although I do not explicitly address land-use effects in this review, it is inevitable that some treelines have been shaped more by anthropogenic disturbances than by processes specific to the local tree species or climatic conditions. Here, land-use refers to repeated human modification (e.g. cattle grazing, controlled burns) whereas natural disturbance refers to both infrequent but intense events (e.g. earthquakes) and frequent but low intensity events (e.g. windfall). The first-level mechanisms would, in such treelines, be controlled by an additional set of second-level mechanisms, e.g. browsing, trampling or fire damage. In such cases, land-use is likely to mask treeline responses to climatic changes; continued land-use may impede recruitment above treeline whereas recolonization of alpine areas after cessation or deintensification of land-use could be misinterpreted as response to climatic changes

(Hofgaard 1997; Camarero & Gutierrez 2007; Gehrig-Fasel *et al.* 2007; Kullman 2007). The effect of natural disturbances tends to be more ephemeral and spatially patchy than land-use. Although land-use is more frequently associated with some forms than others (Fig. 3.6; χ^2 test, $p < 0.05$), all forms may be influenced by it and there appears to be no form that generally indicates land-use (human disturbance), natural disturbance (wind, fire) or absence of human or natural caused disturbance (Fig. 3.6) (Tranquillini 1979; Holtmeier 2009).

In the next section, I discuss each of the three first-level mechanisms and how they result from the various second- and third-level mechanisms. In the subsequent section, I will discuss how the four primary treeline forms arise because of interactions between the three first-level mechanisms and what bearing this brings with respect to expected responses of treelines to climate change.

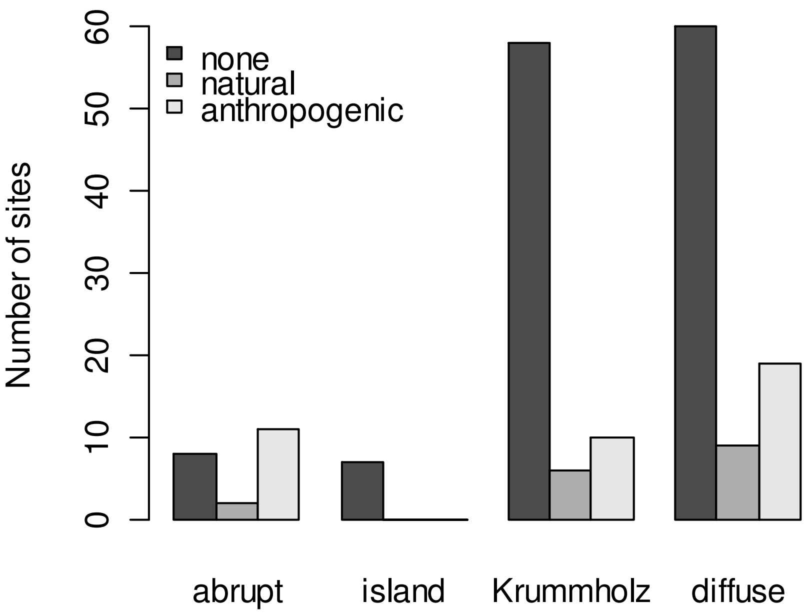

Figure 3.6: The percentage of abrupt, island, Krummholz and diffuse treeline sites that are undisturbed, disturbed by natural means and disturbed by anthropogenic land-use. For details on the database and references, see Appendices D and E.

3.3.1 Growth limitation

Restricted tree growth can be broken down into two mechanisms: limited biomass gain (i.e. growth limitation *sensu stricto*) and biomass loss (i.e. dieback, discussed below). Both are due to stress, i.e. sub-optimal conditions, but growth is limited by long-term mild stress (low growing season temperature, limited nutrient availability), whereas dieback is usually due to more severe stress caused by shorter-term stressors (wind, frost, snow load). Limited growth ultimately results in small but upright trees, whereas dieback ultimately results in small deformed trees or Krummholz. Differentiating between growth limitation and dieback is important not only because of their effect on tree form, but also because they are controlled by different climatic parameters, acting at different times of the day and year. Growth takes place during the growing season, per definition, and requires sufficient warmth, whereas dieback may also be suffered in the dormant season, i.e. winter, and is more sensitive to low temperature extremes and other climatic stressors such as frost and wind.

One of the consistent patterns among all alpine and arctic treelines is the gradual decline in tree height as the treeline is approached, which may start a few hundred meters below the actual treeline. Similarly, growth rates, usually measured via growth rings, also tend to decline with elevation (Li *et al.* 2003). There are two potential causes of decreased growth with proximity to the tree limit: limiting availability of essential nutrients (due to low uptake or supply), in particular carbon, or impaired tissue formation due to low temperature (Sveinbjörnsson 2000). Traditionally, the formation of treelines has been attributed to carbon shortage (source limitation), based on the argument that photosynthesis should be impaired at low temperatures and trees could thus no longer afford their carbon-intensive trunks (Wardle 1993). Measurements of gas-exchange and non-structural carbon compounds, however, have shown little indication of carbon limitation in treeline trees (Körner 1998; Piper *et al.* 2006).

Attention has therefore turned to low-temperature limitations to tissue formation i.e. carbon use or sink limitation (Körner 2008; Hoch & Körner 2009). Trees are more closely coupled to the atmosphere than low-growing plants and, therefore, experience less warming and lower average temperatures (Grace *et al.* 1989; Körner 1998); this difference does not apply for tree seedlings, especially those embedded in the low alpine vegetation, suggesting that other parameters determine performance at this life stage. Tissue formation, when not limited by carbon availability, is limited either directly by low-temperature limits to biosynthesis or indirectly by soil nutrient availability. Nutrient availability can be relatively low at treeline due to low microbial mineralization and nitrogen fixation rates at low temperature (Loomis *et al.* 2006). Increasing nutrient availability has been shown to alleviate low-soil-temperature-induced growth limitation in both arctic and alpine treelines (Wardle 1985b; Weih & Karlsson 1999) but may affect other first-level mechanisms very differently. For example, experimentally enriched alpine shrub communities were selectively killed by snow fungi (Körner 1999).

Although growth rates at treeline can be influenced by many factors, including moisture and nutrient availability (Gamache & Payette 2004; Kessler *et al.* 2007), growing season temperature appears to be the main driver for most alpine and arctic treelines. Treelines exhibit a high consistency in temperature parameters like warmest-month mean or days with air temperature means above 5 °C (parameters reviewed in Körner 1998). According to a recent survey, treelines occur within a narrow band of mean growing season temperature (between ca. 5 and 8 °C; Körner & Paulsen 2004), which is just above the minimum temperature required for tissue formation in plants (5 °C; Körner 2008). This coincidence may be due to a direct temperature limitation to growth at treeline, thus supporting the carbon sink limitation hypothesis, although the physiological mechanism of this mean-temperature effect is still unclear (Hoch & Körner 2009). Another temperature-related parameter often considered, growing season length, may also affect yearly growth and the balance between growth and tissue loss and thus all first-order mechanisms. However, as growing seasons at treeline vary from year-round at tropical alpine treelines to a few months at arctic treelines, this parameter cannot explain treeline positions worldwide.

Growth rates vary across a site according to small-scale environmental variation and neighbour interactions. For example, temperatures are lower on northern than southern aspects in the northern hemisphere (Treml & Banaš 2008) and mean and maximum temperatures under forest cover are consistently lower than above the treeline (Körner & Paulsen 2004; Bader *et al.* 2007a). Temperature also varies as a function of microtopography with critical impacts on nutrient supply, soil moisture, and vegetation (Holtmeier & Broll 2005). Neighbour interactions can either decrease or increase temperatures through shading and sheltering, respectively. Self-shading of the tree root zone decreases soil temperature and has been suggested as a mechanism limiting tree growth at treeline (Körner 1998). Conversely, shading may provide protection from soil heat-loss in winter and associated winter desiccation (Grace 1989). In any case, shade-induced low temperature does not appear to limit seedling establishment, probably because shelter from radiative stresses (photoinhibition, overheating, and increased drought risk) outweighs the disadvantages of cooler temperatures (Ball *et al.* 1991; Germino & Smith 1999; Smith *et al.* 2003).
Despite the strong evidence of growth limitation at treelines globally, there remains a considerable number of treelines that occur at higher mean temperatures (8-11 °C) than expected if only temperature were limiting growth, notably southern hemisphere, island (e.g. Hawaii), and tropical cloud forest treelines (Körner & Paulsen 2004; Bader *et al.* 2007a; Wardle 2008). Low temperature will still slow tree growth at these treelines but the higher

growing season temperatures may indicate that other parameters, possibly also related to temperature, ultimately limit tree growth at these treelines (Wilmking & Juday 2005). Alternatively, these treelines may be controlled primarily by tree (seedling) survival rather than growth, and hence not by growth temperatures but by other factors (Gieger & Leuschner 2004). Of course, this possibility is also open to treelines that do fall within the 'global' range of mean growing season temperatures.

3.3.2 Dieback

Whereas growth limitation affects tree size, it does not account for the strong deformations often observed in treeline trees, extreme cases fittingly called 'Krummholz' (bentwood in German). Deformations in trees at the treeline can be induced by dieback resulting from tissue loss or damage caused by a range of stressors, including wind, snow, frost, and excess radiation (Table 3.1). Dieback can occur year-round but is more often associated with winter wind and snow stress and with cold spells in late spring and early autumn (Grace 1977; Butler *et al.* 2009). Wind can provoke dieback directly through cooling and desiccation, but it is especially damaging in combination with blown dust- or ice-particles (dust-/ice blasting), which exposes leaves to winter desiccation. Wind can also affect damage levels indirectly by redistributing snow cover, exposing some stems and burying others under heavy snow loads. Exposed stems are vulnerable to windborne particle abrasion, temperature stress, and winter desiccation (Grace 1977; Cairns 2001) whereas stems burdened by heavy snow loads are vulnerable to physical damage through settling or creeping snow or infections by various species of snow fungi (Kullman 1997; Holtmeier 2009).

The severity of these stressors acting on treeline trees is modified by exposure and neighbour interactions (Pereg & Payette 1998; Cairns 2001; Smith *et al.* 2003). Exposure is determined by many factors such as treeline position within a mountain range, on a mountain (aspect, slope, and distance from ridgeline), distance from ocean, elevation, prevailing wind direction, and sky exposure (Pereg & Payette 1998; Cairns 2001; Alftine & Malanson 2004). At more exposed sites, trees often experience climatically severe conditions, including high winds and strong solar radiation (Butler *et al.* 2009). The negative effects of exposure are modulated by self-facilitation and neighbour interactions, e.g. through shelter from wind and reductions of incoming and outgoing radiation (Germino & Smith 1999; Wardle 2008). The latter can be due to a direct reduction in radiation and frost damage, or to a reduction of winter desiccation by limiting heat loss from the soil in winter (Grace 1989). Many of the processes causing partial dieback can, when sustained or excessive, also lead to mortality, especially in young recruits. The effects of mortality on treeline form, however, are very different from those of dieback and resulting tree deformations.

3.3.3 Seedling mortality

Mortality of established trees at treeline is a relatively rare event, except in the case of large-scale disturbances such as fire, insect outbreaks, avalanches, or sustained periods of unfavourable climatic conditions (Kullman 1997). In contrast, a single bad weather event during the growing season can be sufficient to kill seedlings (Wardle 1985b; Kullman 1986; Smith *et al.* 2003). Seedling mortality in summer can be caused by inadequate carbon gain, desiccation, overheating, photodamage or nightly frost damage, whereas in winter it can be caused by frost, winter desiccation or snow fungi (Table 3.1; Stevens & Fox 1991; Piper *et al.* 2006; Danby & Hik 2007a). Seedlings are over-proportionally affected by some of these stresses, due to their small root system (drought), low stature (lesser coupling to the atmosphere: overheating, night frosts) and low biomass (little water storage: summer or winter desiccation; and little carbohydrate storage for replacing lost tissue: photodamage, frost damage, snow fungi). As a result, tree seedlings at treeline often suffer mortality greater than 90% in their first year with lower subsequent rates (Noble & Alexander 1977; Cui & Smith 1991; Castro *et al.* 2004; Maher & Germino 2006). Although tree seedlings should not be inherently more sensitive to climatic conditions above treeline than seedlings from alpine species, in practice this does appear to be the case. A potential reason might be that constant genetic mixing between trees at different elevations limits potential evolutionary adaptation. In contrast, alpine species are excluded from lower altitudes by competition, so that selection pressure for surviving the alpine is likely to be high in the entire population. Seed production and dispersal are also prerequisites for successful recruitment. However, where seed availability has been explicitly studied it does not appear to ultimately limit tree establishment at treeline (Cuevas 2000, 2002).

Shelter from direct sky exposure is a critical facilitative neighbour interaction enhancing survival and controlling the distribution of new recruits (Wardle 1985a; Germino & Smith 1999). At lower elevations, competitive interactions tend to dominate and recruitment is negatively associated with proximity to neighbours (Olofsson 2004) whereas the pattern is reversed near the treeline (Eränen & Kozlov 2008). By creating its own benign microclimate, the treeline forest becomes relatively insensitive to climatic deterioration. Beyond the forest, however, the alpine zone experiences the harsh mountain climate in full and seedling mortality can represent a strong limitation to treeline advance (Tranquillini 1979).

3.4 Application of the framework to four treeline forms

Growth limitation, dieback and seedling mortality are evident at all treelines but vary in dominance. I here adopt the viewpoint that low-temperature-induced growth limitation is the most general phenomenon at all treelines worldwide and thus consider growth-limitation-only as a type of 'null-model' for treeline control, determining the 'potential' or 'climatic' treeline elevation or latitude (*sensu* Körner 1998). That is, in the absence of all other limiting factors, the treeline would, in many cases, occur beyond the current position (Holtmeier & Broll 2005). The observed treeline forms and positions are, thus, the result of interactions between growth limitation and additional causative stresses and disturbances that influence mortality (and thereby tree density) and dieback (and thereby growth form; Figs 3.4, 3.5). The importance of the different mechanisms depends both on local environmental conditions and on the tree species involved, and is modified by neighbour interactions. Changes in climatic conditions can shift the dominance of the mechanisms at a given treeline site and thus result in changes in treeline form (e.g. release from Krummholz; Holtmeier & Broll 2007, increased tree density in diffuse treelines; Camarero & Gutierrez, 2004; Lloyd, 2005), perhaps before resulting in altitudinal or latitudinal shifts. Changes in treeline form can therefore be considered an early indicator climatic change effects, especially at sites where low growing season temperature is not the only stressor or time lags are evident between the onset of climatic change and treeline advance (Camarero & Gutierrez 2004; Lloyd 2005).

3.4.1 Diffuse treelines

Diffuse forms can be found in both alpine and arctic treelines (Fig. 3.2) and, on a global scale, are the most frequently studied form (92 of 195 sites; App. F), although there are a few regions where research on diffuse treelines is under-reported (e.g. New Zealand, where treelines tend to be abrupt). In contrast to the relatively tall trees at abrupt treelines and the step-wise changes in height at Krummholz treelines, tree height and density at diffuse treelines tend to gradually decline with proximity to the tree limit (Figs. 3.1, 3.5).

I hypothesize that diffuse treelines are formed and maintained primarily by growth limitation with the primary stressor being low growing season temperature, which has been identified by Körner & Paulsen (2004) to be below 5 – 8 °C (Figs 3.4, 3.5). Growth limitation is suggested by the negative correlations between elevation and tree height and growth rate (Carrer & Urbinati 2004; Bunn *et al.* 2005), whereas its importance relative to other processes is suggested mostly by the absence of strong tree deformations (Krummholz) or a steep mortality gradient (treeline sharpening). Even if not dominant, seedling mortality and dieback can also be important at diffuse treelines and would contribute to the decline in tree density evident at most diffuse treelines (Fig. 3.5). This decline with proximity to the tree limit may also result from the diffuse nature of seed dispersal and the spatial heterogeneity in microclimatic conditions such as temperature, moisture and nutrients (Johnson & Miller 2006; Moen *et al.* 2008). However, if the relevant microsite conditions were improved by the trees themselves, distributions would become more clumped, as in abrupt and tree island treelines (see below). At diffuse treelines, in contrast, negative neighbour interactions are more likely to dominate. For example, treelines in dry areas tend to consist of widely spread trees (e.g. *Pinus hartwegii* on Pico de Orizaba, Mexico, or *Polylepis tarapacana* on Sajama volcano, Bolivia), which may be due to root competition. Similarly, light-demanding species (e.g. *Pinus* and *Larix* species) tend to form relatively open forests, due to competition for light (Holtmeier 2009).

If diffuse treelines are limited primarily by growth, this implies that diffuse treelines are more likely to be in equilibrium with growing season temperature than the other treeline forms and should exhibit greater sensitivity to changes in minimum growing season temperature. It is therefore expected that growing season warming should increase growth rates and seedling survival resulting in more rapid recruitment above the diffuse treeline. Indeed, diffuse treelines have exhibited an earlier, stronger response signal than the other treeline forms; over 80% of diffuse treelines are advancing compared with 22% of abrupt, Krummholz or island treelines (Fig. 3.3). At the 86 sites identified in Harsch *et al.* (2009) as having advanced, advance in diffuse treelines initiated, on average, 20 years earlier than in abrupt treelines, 40 years earlier than in island treelines and 10 years earlier than in Krummholz treelines. In addition, advance has been associated with mean annual warming, of which growing season is a component, only for diffuse treelines (Harsch *et al.* 2009).

3.4.2 Abrupt treelines

Abrupt treelines tend to occur at lower elevations than expected based on global patterns of growing season temperature at treeline (Körner & Paulsen 2004). For this reason, and because these sharp boundaries may be rather ‘unnatural-looking’ (Fig. 3.1b), many abrupt treelines are considered to be non-climatic treelines that have been suppressed by disturbances. However, disturbance is not the only cause of abruptness; many of the abrupt treelines in the database were undisturbed (Fig. 3.6). In addition, the lack of advance at abrupt treelines in the absence of reoccurring disturbance events (Didier 2001; Lepofsky *et al.* 2003) indicates that these treelines are not primarily maintained by disturbance and that recruitment is unlikely to occur unless the causative stressors are diminished (Daniels & Veblen 2004; Gieger & Leuschner 2004; Bader *et al.* 2008).

Abrupt treelines are not growth limited, as evidenced by their often tall tree height (> 2 m), high growth rates and high seed number and viability at the tree limit (Cuevas 2000; Danby & Hik 2007b; Wardle 2008). Even though seed numbers at treeline in New Zealand and Chile were high, recruitment remained low above the treeline (Cuevas 2000; Wardle 2008). Still, beyond the establishment stage, growth in such treelines can occur well beyond the established treeline. *Nothofagus solandri* var. *cliffortioides* seedlings transplanted under artificial shade showed positive growth rates up to 150 m beyond the New Zealand abrupt treeline (Wardle 1985b). Seedlings and branches outside of the shade boxes, however, died after the first autumn frosts, indicating the importance of damage and seedling survival at these treelines. At other abrupt treelines, permafrost and wind-snow interactions negatively impact seedling survival and growth (Danby & Hik 2007a). The superposition of seedling mortality on the growth limitation gradient probably explains the relatively low elevations of abrupt treelines (Gieger & Leuschner 2004).

The critical role of seedling mortality in controlling abrupt treeline formation is evident at two sites in which abrupt and diffuse treelines, closely located but on opposite aspects, were monitored. In both the Spanish Pyrenees (Camarero *et al.* 2000) and the Yukon in Canada (Danby & Hik 2007b), the primary difference between the abrupt and diffuse sites is the primary limiting factor - low temperature at the diffuse site and permafrost or wind at the abrupt sites. Seedling mortality was monitored in the Yukon and was higher at the abrupt treeline, resulting from greater photoinhibition and winter desiccation (Danby & Hik 2007a, b). Similar patterns undoubtedly exist at other regions globally but few have been documented (e.g. Moen *et al.* 2008; Elliot & Kipfmueller 2010).

In contrast to the dominance of conifers in the majority of treeline sites included in the presented database (different functional tree type distributions in diffuse (83.5% conifers), abrupt (52.8% conifers), island (100% conifers) and Krummholz (93.3% conifers) treelines, χ^2 test, $p<0.001$), half of the abrupt treelines were composed of broadleaved tree species (11/22), a large proportion of which were evergreen (9/11). The dominant species were various tropical treeline species and *Nothofagus* species in New Zealand and the southern Andes. This reflects the dominance of this treeline form in these regions and is likely to reflect a causal effect of tree type on treeline form. Evergreen broadleaved species may be particularly sensitive to winter frost and hence more dependent on shelter by neighbours (Woodward & Kelly 1997). Indeed, seedling preference at treeline for microsites with low sky exposure has been found for evergreen broadleaved *Eucalyptus pauciflora* (Ball *et al.* 1991) but not for deciduous *Betula litwinowii* (Hughes *et al.* 2009). Seedlings of evergreen broadleaved tropical cloud forest treeline species and *Nothofagus solandri* var. *cliffortioides*, all species forming abrupt treelines, likewise perform better under shade (Wardle 2008). Such preference was also observed for the evergreen needle-leaved *Abies lasiocarpa* and *Picea engelmannii*, which form island treelines (Germino & Smith 1999).

In stressful environments, such as above treeline, seedling establishment may be enhanced by positive plant-plant interactions (facilitation). Facilitation is evident at all treeline forms but abrupt treelines in contrast to diffuse treelines exhibit abrupt changes in mortality above the forest limit (Fig. 3.5). This situation arises when seedling establishment requires shelter from the harsh climatic conditions beyond the forest limit (Szeicz & MacDonald 1995; Malanson 1997; Batllori *et al.* 2009). Abrupt treelines are thus formed due to a dependence on facilitative neighbour interactions leading to a positive feedback switch, which limits the range of suitable plant-plant interactions (Armand 1992; Wilson & Agnew 1992). Such a switch is often mediated by the microclimate with trees providing protection from summer drought (Cuevas 2000), excess solar radiation (Ronco 1970), and winter desiccation (Danby & Hik 2007a). Alternatively, a switch can be mediated by soil conditions (e.g. mycorrhizae) and fire or other disturbances (Ball *et al.* 1991; Germino & Smith 1999; Bader *et al.* 2008). Several switches, mediated by different mechanisms, can also occur simultaneously. Positive feedback has been found to increase treeline abruptness in several models (Malanson 1997; Wiegand *et al.* 2006; Bader *et al.* 2008). In one of these models, positive feedback caused a more rapid response to environmental amelioration, which was due to non-equilibrium conditions before the amelioration (Malanson 2001). In another model, positive feedback slowed down the rate of advance in response to climatic warming, which was due to the neighbour-dependency of recruitment (Bader *et al.* 2008). Consistent with these latter model results, abrupt treelines have not been responding to recent climate warming (Harsch *et al.* 2009). Of the two abrupt sites classed in Harsch *et al.* (2009) as advancing, one was formerly disturbed by human land-use and one had warmed in both the winter and summer seasons.

3.4.3 Krummholz treelines

Krummholz does not meet the conventional definition of a tree because it rarely reaches the commonly applied 2 m height requirement. We, however, included Krummholz as a unique form because it is composed of tree species and can switch in growth form between Krummholz and upright trees (Lescop-Sinclair & Payette 1995; Hessl & Baker 1997; Smith *et al.* 2003). Krummholz can occur in patches (see below under island treelines) or as a continuous or diffuse belt above the closed forest. The conventional definition of a tree may mean that Krummholz treelines are underreported in the literature. Despite this limitation, Krummholz treelines have been recorded extensively (77/195 sites; Appendix E) in both alpine and arctic treelines globally (Fig. 3.2), usually in sites described as being wind exposed (Hadley & Smith 1986; Pereg & Payette 1998; Camarero *et al.* 2000).

Dieback is strongly evident at Krummholz treelines (Fig. 3.1c). In Glacier National Park, 9% of the Krummholz canopy was lost to winter desiccation during the 1998/99 winter (Cairns 2001). In addition, trees have been observed to respond positively to shelter; natural or experimental shelter from wind resulted in decreased winter desiccation and increased survival rates (Hadley & Smith 1986; Cairns 2001).

The Krummholz form is a response rather than an adaptation to stress, although the ability to form Krummholz can be adaptive at treeline. For example, Krummholz does not exhibit a growth advantage at low temperature (Pereg & Payette 1998; Cairns 2005), even though meristem temperatures can be higher under Krummholz mats than trees (Grace 1989). Krummholz is not primarily growth limited: vertical stem growth often occurs during summer months but new growth is lost by subsequent winter damage (Wardle 1968). Krummholz-like deformations are also common in other wind-exposed marginal habitats like coastal dunes (Barrick 2003), indicating an interaction between poor growth and physical damage. The common directional shape of Krummholz is due to increased dieback in shoots and leaves facing the prevailing winds (Hadley & Smith 1986).

Krummholz persist in exposed environments presumably because of reiterative layering and self-facilitation (Norton & Schöenberger 1984; Laberge *et al.* 2001). Seedling recruitment is less frequent because seedling mortality is generally high except within the facilitative shelter of Krummholz mats (Camarero *et al.* 2000; Resler & Stine 2009; but see Elliott & Kipfmueller 2010). Still, recruitment from seed does occur occasionally, as evidenced in mixed-species Krummholz (*Pinus albicaulis*, *Abies lasiocarpa* and *Picea engelmannii*) in the Rocky Mountains (Tomback & Resler 2007).

Advance has been less commonly observed in Krummholz than in diffuse treelines (Fig. 3.3). Still, increased growth (i.e. vertical stem development) and recruitment of seedlings have been noted at many Krummholz treelines and appear to be correlated with improved winter conditions (i.e. warmer temperatures, more snow) but not summer conditions (Lescop-Sinclair & Payette 1995; Harsch *et al.* 2009). Advance, in response to warmer growing season temperatures, is unlikely to occur at these treeline unless the climatic factors limiting stem and seedling survival are also ameliorated.

3.4.4 Island and finger treelines

Island and finger treelines (also ‘ribbon forest’) occur as patches of upright trees or Krummholz growing above a continuous forest line (Fig. 3.1d). Treelines with single, often relatively large, forest patches above the closed forest limit are not considered island treelines here because these patches are probably tied to favourable microsites (e.g. sheltered valley slopes) or caused by (anthropogenic) disturbance (Kessler 2002) and are not indicative of treeline-forming mechanisms in the sense presented here. Island treelines occur predominantly in North America (Fig. 3.2), with the best studied examples in Glacier National Park, Montana (Butler *et al.* 2009) and are either less common or underrepresented in the literature outside this region.

The direction, shape, and size of the islands are controlled by seedling mortality and dieback but may also be influenced by microtopography (Holtmeier & Broll 1992; Resler & Stine 2009). Growth in Krummholz islands is predominantly through layering, the direction of which is determined by dieback, which tends to occur at the windward side of the islands and, in the case of Krummholz islands, in shoots protruding through the snow (Bekker 2005). As a result, tree stature is lower and die-back greater on the windward side of tree islands (Fig. 3.1c) and tree height increases with distance from the exposed frontline (Cairns 2001). As a second result, islands can migrate in downwind direction and thus ‘walk’ across the tundra (Holtmeier & Broll 1992).

Islands generally start to form where small topographic features (e.g. treads and risers or rocks) modify conditions, improving survival in localized patches and subsequently by existing trees through positive feedback (Wilson & Agnew 1992; Alftine & Malanson 2004; Bekker 2005). The importance of positive feedback, often even inferred from the degree of clumping of plants, tends to increase with environmental severity (e.g. Bekker & Malanson, 2008; Elliot & Kipfmueller, 2010). For positive feedback to result in stable patches rather than a closed abrupt treeline, the local positive effect needs to be accompanied by a negative effect at some distance (a reaction switch *sensu* Wilson and Agnew 1992). This can be achieved at island treelines through the redirection of wind and snow (Alftine & Malanson 2004). Alternatively, a patchy treeline may represent a transient state, patches being outposts of an advancing treeline. This scenario appears more likely where patches consist of tall upright trees, indicating relatively mild conditions for growth and persistence. In such treelines, facilitation of seedling survival near islands may result in a slow infilling of the spaces between islands.

All reported undisturbed island treelines as well as most undisturbed Krummholz treelines are composed of needle-leaved trees, which may be due mainly to the geographical bias, because most of these treelines are reported from North America, where the grand majority of alpine treelines, of all forms, is composed of evergreen conifers. As argued for abrupt treelines, positive feedbacks will stabilise the island treeline, unless it represents a transient state. In the case of stable island treelines, directional growth does allow for slow migration of individual islands, but an advance of the ecotone as a whole will not occur without an improvement in the climatic conditions limiting survival (Bekker 2005).

3.5 Conclusions

The treeline is amongst the most readily recognized bioclimatic boundaries and, as such, has been suggested to be a critical indicator of responses to climate warming. Treelines, however, are not universally responding to warming through changes in treeline position (Harsch *et al.* 2009), suggesting that use of treelines as a bioindicator of warming responses will be ineffective if the variability in treeline-forming mechanisms is not taken into account. Treeline form provides a handle for explaining the variability in response and exploring the general mechanisms, at three explicit levels, controlling treeline response to climatic change. For example, diffuse treelines, controlled by growth limitation (level 1) due to low growing season temperatures (level 2), are advancing, whereas abrupt, island and Krummholz treelines, controlled by seedling mortality and dieback (level 1) due to a variety of mechanisms (level 2) and modified by positive neighbour interactions (level 3), are not (Fig. 4). Consistent with these expectations, abrupt, island and Krummholz treelines, which are not limited by growing season conditions, are not responding to summer warming, but some are responding to changes in the severity of winter conditions (Szeicz & MacDonald 1995; Hessl & Baker 1997; Vallée & Payette 2004; Caccianiga & Payette 2006).

Using treeline form to predict dynamics is complicated by non-linear responses to climate warming, principally due to third-level mechanisms (neighbour interactions), and interactions between temperature and other climatic factors. The current lack in response by abrupt and island treelines, where facilitation plays an important role, could change to a rapid one (catastrophic phase shift) once certain climatic thresholds are reached, e.g. a higher frequency of mild winters allowing enough tree establishment for commencing a positive feedback. Interactions between temperature and other climatic factors may lead to reduced tree growth, cessation of advance, or treeline recession under warming conditions (Lloyd & Fastie 2002, Daniels & Veblen 2004). In the light of this complexity, recognising and understanding four general treeline forms is clearly only a first step towards being able to predict specific treeline responses.

The use of treeline form to determine the mechanisms controlling local treeline formation and dynamics is further complicated by the absence of hypothesis testing globally. Growth limitation has been tested globally, resulting in the conclusion that limitations to carbon assimilation most likely limit growth (Hoch & Körner 2003; Sala & Hoch 2009). Carbon assimilation limitation has also been associated with low temperature (Körner 2008; Hoch & Körner 2009). In Chile, treeline formation was best explained in terms of carbon assimilation and seedling mortality (Piper *et al.* 2006). Support for the proposed mechanisms comes from localized experiments and observations. This, however, does not preclude the possibility that alternate mechanisms could result in the four treeline forms. Needed here are experiments specifically designed to test the proposed framework. For example, growth limitation could be assessed by monitoring growth of seedlings planted above the current treeline, dieback could be assessed by building shelters around individual stems, and seedling mortality could be assessed by sowing seed and planting seedlings in modified microsite conditions above treeline.

Detailed predictions of changes in treeline form or position require a greater understanding of species- and site-specific processes. Treeline form depends strongly on tree species characteristics. For example, Krummholz can only develop if the species exhibits growth form plasticity and abrupt treelines are most likely to develop in shade-tolerant species. However, the available information, especially regarding species' tolerances to stressors such as drought, frost and solar radiation, may not always be applicable to the treeline situation or to the seedling stage. Knowledge of seedling tolerance is critical as advance is a function of recruitment and seedlings tend to be less tolerant to stress than mature trees due to their small root systems, lower stature and lower biomass. Needed here are basic data on species tolerances at treeline, preferably for all critical life stages, including germinants and seedlings.

Site conditions may differ strongly at different treelines even within mountain ranges, but data on environmental parameters acting at this scale (e.g. wind, radiation, precipitation) are not readily available globally and can therefore not be analyzed at this scale. Needed here are super-regional, if not global, datasets, most likely derived from remote sensing, linking treeline form and position to environmental parameters at multiple scales (Walsh *et al.* 2009). On a still finer scale, microsite conditions are critical in determining seedling distribution and survival and hence treeline form and advance. Although the effects of microtopography (e.g. rocks, turf-banked terraces) have been addressed for certain northern-temperate treeline types

(Butler *et al.* 2009; Holtmeier 2009), the dependence of treeline dynamics on such features, combined with vegetation-based microsite modifications, still needs to be evaluated for most situations. The multi-factorial nature of the problem at this scale precludes global generalisations of results, but addressing the problem in its full complexity may be prerequisite for accurate local, as well as regional, predictions of future treeline dynamics.

In short, there are numerous limitations to our understanding of plant species response to climate warming but treelines provide an exciting example of how observed pattern (form) can indicate controlling mechanisms and response to climatic change. Spatial and temporal patterns thereby reflect in the same treelines, diffuse forms reacting most directly and gradually, and abrupt treelines and tree islands exhibiting complex behaviours, including strong time lags and potential rapid shifts.

Chapter 4

Observed shifts at the southern New Zealand *Nothofagus* treeline using growth, recruitment and mortality rates measured over 15 years

4.1 Abstract

Treelines, limited by low temperature, are expected to shift to higher elevation or latitude in response to climate warming. Despite considerable warming, not all treelines globally are shifting. In this study, I evaluated changes in growth, mortality and recruitment at five *Nothofagus* treeline regions in southern New Zealand. All *Nothofagus* stems at or above treeline along transects in these regions were mapped and measured (basal area) three times (in 1991, 2002 and 2007), allowing for estimation of growth, recruitment and mortality rates over 15 years. Stem number increased above treeline over the 15-year study duration but stem distribution above treeline did not change; 90% of all stems and of new recruits occurred within 10 m of the treeline edge. Modelled growth and mortality decreased with increasing stems size and did not vary significantly over the study duration. Recruitment increased over the study duration (1991-2002, 2002-2008) and tended to occur closer to the treeline edge than further away. No climatic variables considered (mean annual, minimum annual and mean winter temperature, annual precipitation and potential solar radiation) were significant in explaining variability in demographic rates between transects or periods. The results do not provide clear evidence that the New Zealand *Nothofagus* forest has begun expanding above the current treeline edge but do indicate that recruitment is ultimately limiting advance.

4.2 Introduction

The position of the treeline is expected to shift upward in response to climate warming. This expectation is based upon the well-established relationship between treeline position and temperature globally (Daubenmire 1954; Tranquillini 1979; Körner 1998; Jobbagy & Jackson 2000; Körner & Paulsen 2004). Consistent with expectations of a thermal limit of treeline position, shifts in treeline position have been observed globally since the early 1900's (Suarez *et al.* 1999; Shiyatov 2003). Some treelines are shifting in concert with the rate of climate warming (Butler & DeChano 2001; Kullman 2002; Camarero & Gutierrez 2004; Shiyatov *et al.* 2007) whereas others are not shifting (Harsch *et al.* 2009).

Understanding why some treelines are shifting upward in response to climate warming and others are not is of considerable importance in terms of predicting the effects of shifting plant species' distributions in response to climate change. Stable treelines, those not shifting upward in response to climate warming, are generally considered to occur because of insufficient warming, disturbance or because the treeline is not in equilibrium with climatic conditions (Körner & Paulsen 2004). However, the influence of taxon-specific tolerances and traits related to seedling establishment and survival (Bader *et al.* 2008), seed production (Cuevas 2000) and dispersal ability (Malanson 1997) are increasingly being recognized as asserting a strong effect on the ability of tree distributions to shift in response to climatic change. Mortality is also recognized as potentially influencing treeline position but has more often been recognized as causing the treeline to recede rather than inhibiting treeline expansion (Kullman 2007).

Recruitment limitation of treeline advance has been demonstrated in both empirical (Batllori *et al.* 2009; Green 2009) and simulation (Malanson 1997; Dullinger *et al.* 2004; Bader *et al.* 2008) studies. Despite the increasing recognition of the role that recruitment exerts on the rate and timing of treeline response to climate warming (Smith *et al.* 2003; Smith *et al.* 2009, Malanson & Cairns 1997), few studies have assessed if recruitment is ultimately limiting treeline advance and if recruitment limitation will decrease with climate warming (Hobbie & Chapin 1998; MacDonald *et al.* 1998; Cullen *et al.* 2001b). If recruitment were limiting treeline position and ability to respond to climate warming, then shifts in treeline position in concert with climate warming would not be expected.

A strong link between treeline structure and treeline response to climate warming has been identified, in which treelines with an abrupt transition between the continuous canopy and the alpine zone are less likely to shift upward in response to climate warming than treelines with a gradual or diffuse transition (Harsch *et al.* 2009). Treeline structure has also been identified to be a function of growth and mortality rates (Wiegand *et al.* 2006), so analysis of growth, recruitment and mortality trends over time at abrupt treelines may provide insight as to why some treelines are not expanding. For example, although the dominant treeline species in New Zealand, *Nothofagus* spp., similar to many other treeline species around the world, has experienced considerable warming over the last century (0.9 °C; Mullan *et al.* 2008), a clear change in treeline position is not evident (Wardle & Coleman 1992; Cullen *et al.* 2001b). Growth limitation is evident in the decline in growth with increasing altitude (Wardle 1985b) but annual growth rates of *Nothofagus menziesii* have not responded to warming in the last half of the 20th century (Cullen *et al.* 2001a) as expected if temperature were limiting. Recruitment has been extensive above treeline across 17 sites in the South Island, New Zealand but only within the first 7-10 m (Wardle & Coleman 1992) and stand-history reconstructions suggest that the recruitment is transient and unlikely to result in a new treeline (Cullen *et al.* 2001b).

In this study, I build upon the work established by Wardle and Coleman (1992) by monitoring growth, mortality and recruitment over 15 years above treeline in five regions spanning the South Island, New Zealand. I determine if the treeline is shifting upward by evaluating changes in recruitment and mortality rates along with recruitment distance and the number of stems reaching tree height (2 m high) over the study duration. Here, I assess whether the treeline has begun shifting upward and explore the possibility that stable or slowly advancing treelines are limited more by recruitment or mortality than growth.

4.2.1 *Nothofagus* treelines in New Zealand

New Zealand *Nothofagus* treelines are remarkably abrupt in form; the upper edge of the continuous canopy occurs at the upper edge of the tree limit. Two species of *Nothofagus* commonly form the treeline in New Zealand: *Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole, which is dominant in the eastern areas, and *Nothofagus menziesii* (Hook. f.) Oerst, which is dominant in the western mountains (Wardle 2008). *Nothofagus* treelines are floristically simple and characterised by a very abrupt transition between the forest limit and the alpine zone (Wardle 2008). Tree height decreases from a maximum of 20 – 25 m at low elevations to 3 – 5 m at treeline although much shorter or taller stems can be observed on exposed or sheltered slopes respectively (Norton & Schöenberger 1984). Trees tend to be single-stemmed but multi-stemmed trees are common at treeline. Krummholz are not present at the treeline. Regeneration is primarily achieved through seed production although lateral branching may also be important at treeline (Schönberger 1984). Seed production is variable in quantity and frequency and is synchronized between *Nothofagus* species across their geographic ranges (Schauber *et al.* 2002). Small to moderate mast years occur, on average, at 3-5 year intervals and large mast years at 6 – 11 year intervals (Wardle 1984). In the last 30 years, seed production has increased in response to recent climate warming, mostly resulting from increased frequency of moderate mast years (Fig. 4.1; Richardson *et al.* 2005). Seed are small (5 – 8 mm long), contain minimal reserves and establish readily in disturbed soils but not in thick litter or vegetation (Wardle 1984; Wardle 1985b). Dispersal is unspecialised and generally poor (within 20 – 30 m) although much further seed dispersal distances are possible (Wardle 1984). Mortality is greatest in the first growing season following seedling establishment and results primarily from seedling intolerance to water stress although browsing and absence of ectomycorrhizal fungal associations can also negatively affect survival rates (Wardle 1984; Ledgard & Davis 2004). Mortality declines rapidly after the first year (Wardle 1984). *Nothofagus* stems have been observed primarily within 10 m of the treeline edge (Wardle & Coleman 1992) but can, when planted in heavily shaded microsites, survive 150 m above the current treeline edge (Wardle 2008). Shade and shelter are important to decrease the rate of water loss (Wardle 1984) but may also be important in reducing frost damage (Wardle 1985b).

Broad treeline patterns in New Zealand are consistent with expectations if temperature were limiting. First, growth rates of both species declines with increasing elevation (Wardle 1984). Second, consistent with global patterns, the treeline elevation across New Zealand tends to decrease with latitude. Treeline sites decrease from 1400 m at 38° latitude to 900 m at 46° latitude near the coast, with inland sites reaching 200-300 m higher in elevation (Wardle 2008). Finally, seed production and viability decreases with elevation and is positively related to temperature (Allen & Platt 1990; Richardson *et al.* 2005). There are also indications that temperature is not limiting at the treeline. First, growth and recruitment have not responded to climate warming that occurred between 1950 and 2000 (Cullen *et al.* 2001a; Cullen *et al.* 2001b). Second, the treeline occurs at a higher mean growing season temperature than expected based on global relationships between treeline position and mean growing season temperature (Körner & Paulsen 2004).

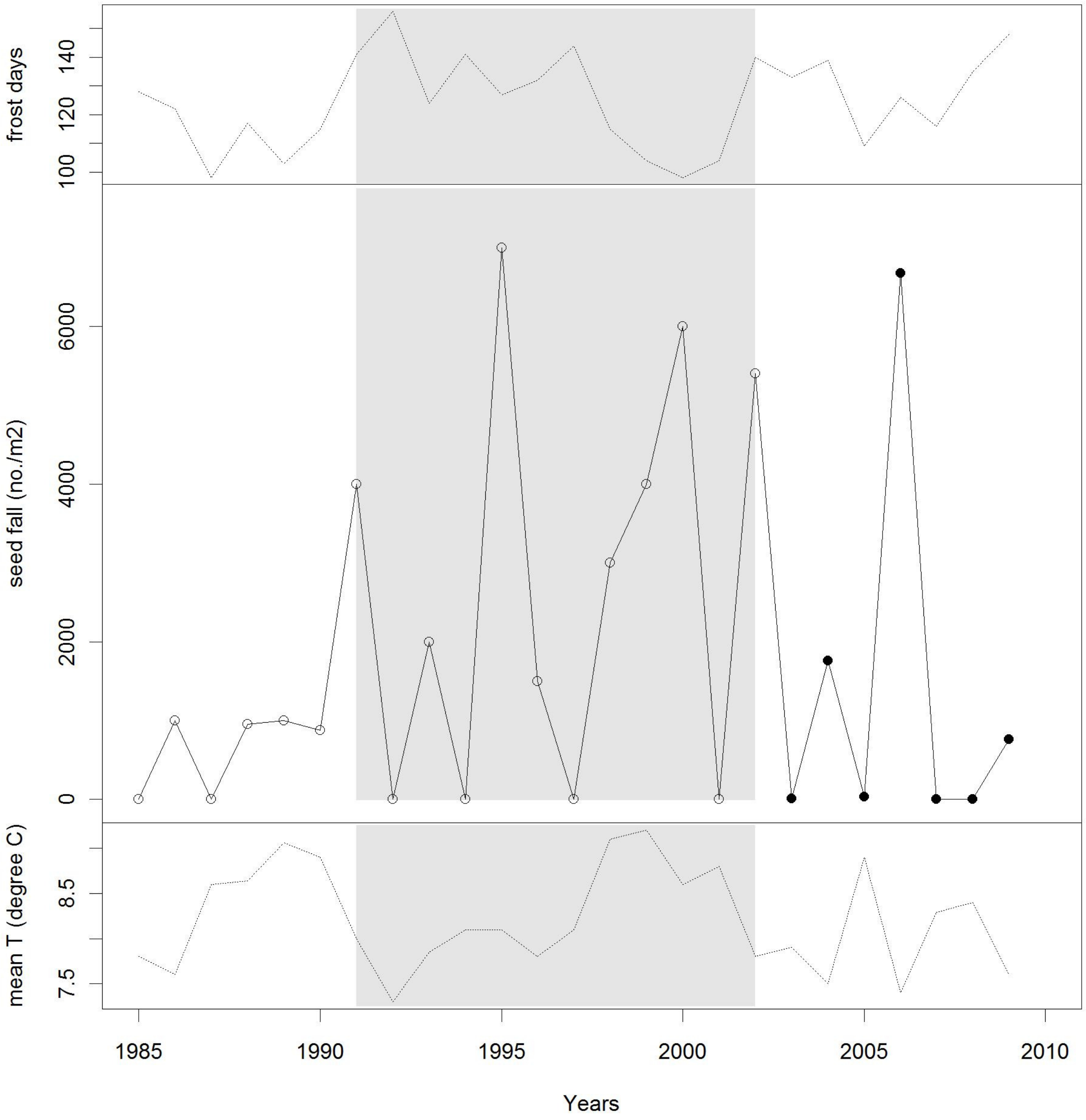

Figure 4.1: Frost days (top panel), seed fall per m^2 (middle panel) and mean annual temperature (bottom panel). Climate data was downloaded for the Craigieburn climate station located at 940 masl (NIWA 2009). Seed fall data for 1985-2002 was adapted from Richardson *et al.* (2005) and for 2002-2009 from unpublished data collected by the Department of Conservation. Seed fall traps were located at 1340 masl in Craigieburn Forest Park (open circles) and at 700 m at Nelson Lakes National Park (filled circles).

4.2.2 Site descriptions

The climate of the South Island is oceanic with moisture laden winds blowing predominantly from the west to southwest (Salinger 1988). A steep west- to east-coast precipitation gradient is generated by a prominent mountain range, the Main Divide, which runs from the southwest to the northeast of the island. Temperature tends to be warmer on the east coast than the west and inland during the summer. The pattern is reversed in the winter (Salinger 1988). Frosts are present throughout most of the year (Salinger 1988).

Seven treeline transects were established on mid- or upper-mountain slopes of five mountain ranges in the South Island, New Zealand, three on the western side of the Main Divide and two on the eastern side by Peter Wardle between 1991 and 1993 (Table 4.1, Fig. 4.2). These transects were chosen by P. Wardle to be representative of the region in which they are located. Treelines at each transect reach the maximum altitudes characteristic of each region and are apparently undisturbed by fire in the last 50 years. Fire is likely to have occurred at Maori Saddle at the end of the 19th century. All transects have different climates, topography and composition of alpine vegetation above the treeline (Table 4.2, Appendix F). Vegetation varies from complex shrub-grass-bare soil mosaics (Faust) to dense tussock grasslands (Maori Saddle, Haast East, Takahe West).

Within each region, a single transect was established, except the most northern (Haast) and southern (Takahe Valley) regions, where transects were set up with both western and eastern aspects. This was necessary to obtain sufficient transect length within the region. Each transects is dominated by either *Nothofagus solandri* var. *cliffortioides* or *Nothofagus menziesii*, and sometimes by a mixture of the two (Table 4.1). The transects exhibit minimal disturbance and are situated, as far as possible, on relatively uniform slopes.

Transect	Latitude	Longitude	Elevation (masl)	Transect Length (m)	Aspect	Species	PSR (MJ cm^{-2} y^{-1})
Haast East	-42.318	172.088	1220	93	ne	M, S	0.84
Haast West	-42.311	172.087	1240	193	w	M, S	0.64
Faust	-42.505	172.409	1328	549	w-sw	M	0.70
Craigieburn	-43.111	171.713	1350	347	se-ssw	M	0.55
Maori Saddle	-43.821	169.281	1082	277	nw-sw	S	0.75
Takahe East	-45.283	167.670	1100	86	ne	M	0.77
Takahe West	-45.287	167.668	1106	164	ssw	M	0.49

Table 4.1: The latitude, longitude, elevation, transect length, aspect, species composition and potential solar radiation (PSR) at each transect. Species codes: *N. solandri* (M), *N. menziesii* (S).

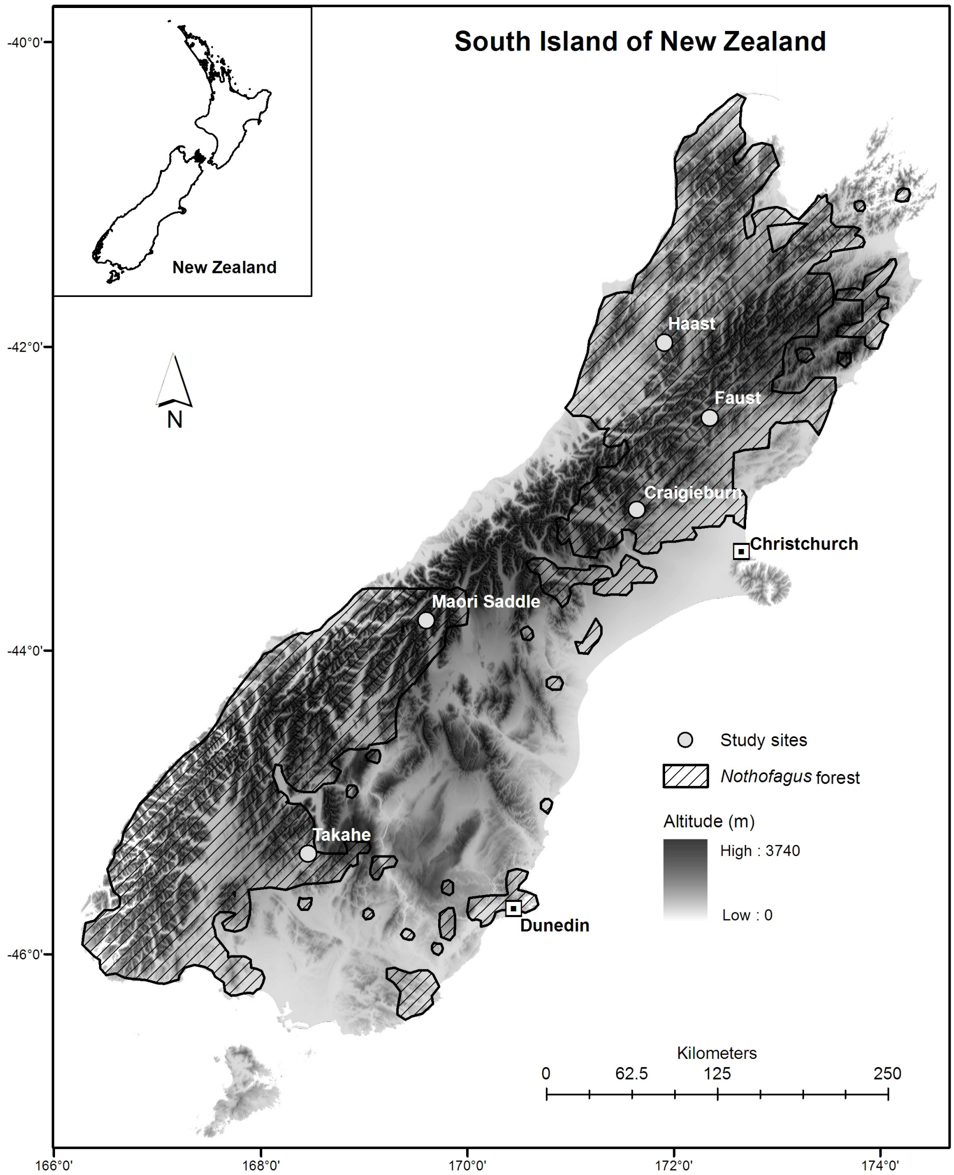

Figure 4.2: The location of treeline regions within the South Island, New Zealand.

4.3 Methods

4.3.1 Data collection

A single transect running along the treeline edge was established at three sites. The topography was such that two transects were established at two sites (Haast and Takahe Valley), one on the eastern and one on the western aspect. Transects were established in the austral summer between November 1990 and December 1991, except Takahe Valley which was established in March 1993. Transects were set up to sample a length of continuous treeline with the length of transects dictated by topography; treeline edge is often broken by features such as gullies or rock outcrops. Each transect was between 86 m and 549 m long

(Table 4.1) and divided into 20-50 m long sections, with each section permanently marked using metal posts. Transects were surveyed when they were first established and then re-measured in the austral summers of 2002/03 and 2007/08. Transects were censused by Peter Wardle in 1991 and 2002 and by Melanie Harsch in 2007.

		Mean T (°C)		Winter T (°C)		Minimum T (°C)		Total annual precipitation (mm)	
Transect	Period	Mean	Slope	Mean	Slope	Mean	Slope	Mean	Slope
Haast East	1991-2002	4.92	0.063	-0.274	-0.111	-12.27	0.270	1825.9	24.107
	2002-2008	4.67		-0.462		-13.38		1794.7	
Haast West	1991-2002	4.79		-0.287		-12.40		1825.9	
	2002-2008	4.53		-0.30		-12.51		1794.7	
Faust	1991-2002	5.14	0.066	-0.274	0.053	-11.00	0.128	1956.1	-24.502
	2002-2008	5.27		0.175		-12.26		2137.9	
Craigieburn	1991-2002	5.67	0.007	1.18	-0.019	-10.27	0.077	1448.9	45.795
	2002-2008	5.51		0.857		-10.49		1866.8	
Maori Saddle	1991-2002	4.29	0.176	0.10	0.151	-8.14	0.013	4433.0	-43.140
	2002-2008	4.80		1.05		-8.97		4016.9	
Takahe East	1991-2002	5.40	0.047	-1.90	-0.005	-7.31	-0.027	6679.5	-30.317
	2002-2008	5.36		-2.07		-7.11		6375.7	
Takahe West	1991-2002	5.36		-1.90		-7.35		6679.5	
	2002-2008	5.45		-2.07		-7.15		6375.7	

Table 4.2: Mean annual (mean T), mean annual winter (June, July, August), and minimum annual temperature (all in °C) and total annual precipitation (mm) averaged for the specified time period. All mean climate values are averaged annual records collected between 1991 and 2001 or 2002 and 2008. Climate data are obtained from the nearest climate station to each transect. The effect of the difference in elevation between treeline transects and climate station on temperature is corrected for by assuming a lapse rate of 0.66 °C/100 m elevation (Norton 1985). The slope refers to the slope of the least squares regression line for the relationship between the climate variable and year (1991-2008) and was calculated for each site (Haast, Faust, Craigieburn, Maori Saddle, Takahe).

In each census year (labelled 1991, 2002, 2007, although Takahe Valley was initially measured in 1993), a base tape was laid out between the metal poles and used to map the position of the outermost edge of the forest canopy at the treeline, with treeline defined as the continuous canopy ≥2 m high (Figure 4.3). The canopy edge was mapped as *x*, *y* coordinates with *x* being the distance along the base tape from the start of the transect, and *y* being the distance from the base tape to the outermost edge of the canopy. Measurements of the treeline edge were taken at intervals of 2 – 12 m along the base tape, with the frequency of measurement determined by the irregularity of the treeline edge. Discrete clumps of trees ≥2 m high above the continuous canopy were not considered part of the treeline edge. In the first census year, 33 points were taken at Haast East, 54 at Haast West, 117 at Faust, 129 at Craigieburn, 85 at Maori Saddle, 74 at Takahe East and 143 at Takahe West. In the second and third census years 33 canopy points were taken at Haast East, 66 points at Haast West, 153 at Faust, 142 at Craigieburn, 91 at Maori Saddle, 78 at Takahe East, and 151 at Takahe West.

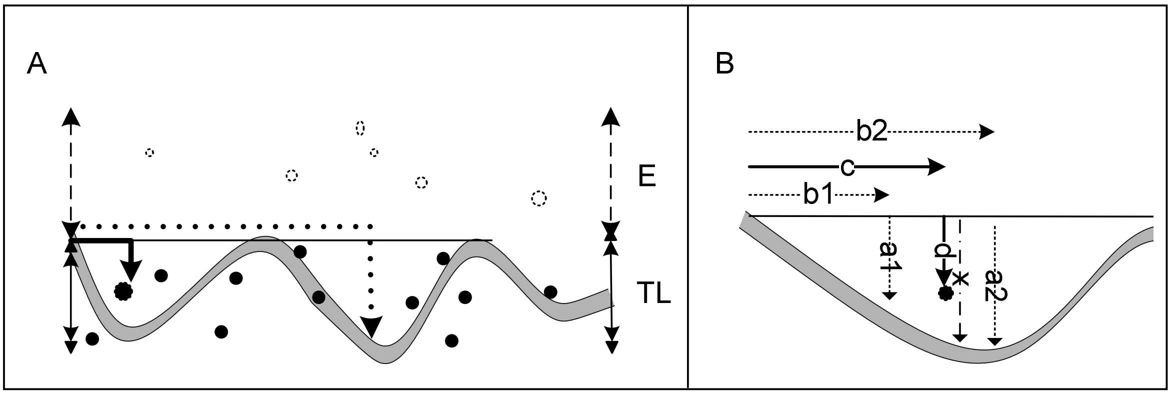

Figure 4.3: Conceptual diagram of the layout of the transects and two primary processes by which treelines may advance (A) and how stem distance from treeline edge was estimated (B). The thick grey line represents the current treeline. Recruitment occurs within an expanding canopy (TL) (filled circles) or beyond the canopy (E) (open circles). Treelines were monitored along a permanent transect (thin black line). All stems were recorded along and from the transect (thick black arrow) and the canopy position was measured at subsequent years at the same location along the transect (dotted arrow). Stems distance from treeline is estimated as the difference in the measured distance from the transect line to the stem (d) and the estimated distance from the transect line to the treeline edge (x).

The position of all *Nothofagus* stems ≥0.05 m tall that occurred above the treeline edge were mapped as *x*, *y* coordinates with *x* being the distance along the base tape from the start of the transect, and *y* being the distance from the base tape to the base of the stem measured at right angles to the base tape. At the second census (2002), stems were relocated using these *x* and *y* coordinates but, to help with subsequent relocation, all stems 0.05 – 0.5 m tall were then marked with individual tree tags attached with wire around the base of the stem. The species of each stem was recorded and its height measured from the ground to the apex using a tape measure for all mapped stems 0.05 - 3 m in height. Height of stems taller than 3 m was estimated. Diameter was measured at the base of the stem with callipers for stems with a diameter less than 10 cm and with a diameter tape for larger trees. For stems with more than one basal stem, the largest stem was measured and the number of stems recorded.

The distance of each stem from the treeline edge was calculated by determining the position of the treeline canopy edge as a straight line between the two canopy measurement points either side of the stem, and then calculating the perpendicular distance from that edge to the stem.

$$X = (((a2 - a1)/(b2 - b1)) * (c - b1)) + a1) \qquad \text{(eqn 4.1)}$$

Where c (position along base tape to be estimated) is between b1 and b2 (consecutive points along the base tape from which canopy distance was measured), which correspond to successive distances to the canopy from the base tape (a1 and a2; Fig. 4.3b). The estimated distance of the stem (Y) is then calculated by subtracting the distance of the stem from the base tape (d) from the estimated distance of the base tape from the canopy (X) at the same point along the base tape (Fig. 4.3b):

$$Y = X - d \qquad \text{(eqn 4.2)}$$

The estimated distances from the treeline edge are based on the assumption that the canopy forms a straight line between measurement points. This assumption may be violated if canopy-distance interpolations underestimate the distance to the treeline edge or, especially at greater distances, the distance between seedlings and the base tape were not taken at right angles. This error was minimized by comparing recorded distances of the same stems to the base tape between years. This ensured that methods were consistent between years and that any differences in distance from the treeline edge following the first year are due to changes in canopy position rather than measurement error. I used the treeline edge calculated from canopy measurements at the first census (1991) to identify stems found above treeline.

To detect changes in recruitment, growth, and survival with distance from treeline between census years (1991-2002, 2002-2008), the stem distances from the canopy are all estimated from the 1991 canopy positions. The changes in treeline demographics and dynamics were evaluated for the time period between census years (1991-2002, 2002-2008). Distance in the following sections refers to the estimated distance beyond treeline edge.

Changes in canopy position were evaluated from canopy distance measurements made at the same point along the transect line in consecutive measurement years (Fig. 4.3a). Positive changes in distance indicate canopy extension and negative changes indicate canopy recession. Changes in canopy position were evaluated during the first period (1991-2002) from 635 points and in the second period (2002-2008) from 714 points. The rate of canopy extension was then calculated for all transect as the difference in distance at the beginning of the period from the end of the period, divided by the length (in years) of the period.

4.3.2 Climate data

Climate data were downloaded directly from the NIWA National Climate Database for the closest climate station to each site in which temperature was recorded between 1991 and 2008 (Table 4.3). Annual climate data (mean temperature, absolute maximum and minimum temperature, and total precipitation) were averaged for the two periods (1991-2002, 2002-2008). The effect of difference in elevation between climate station and treeline site on temperature measurements was corrected for by assuming a temperature lapse rate of 0.66 °C per 100 m change in elevation (Norton 1985). Potential solar radiation, the maximum energy received on the earth's surface assuming no atmosphere to reduce its intensity, was included as an index of evaporative demand, soil moisture content and exposure of vegetation to photosynthetically active and ultra-violet wavelengths (Bennie *et al.* 2008). The annual potential solar radiation (MJ $cm^{-2}y^{-1}$) was calculated for each sector along the transect as a function of latitude, aspect and slope relative to a flat surface at the equator (latitude, aspect, slope = 0) and takes into account the hourly position of the sun for each day of the year (Galicia *et al.* 1999; Allen *et al.* 2006).

Site	Climate Station	Elevation (masl)	Distance (km)
Haast	Reefton Ews	421	28
Faust	Boyle River Lodge	600	2.8
Craigieburn	Broken River Skifield	914	4.6
Maori Saddle	Lake Moeraki Ews	9	11.4
Takahe Valley	Te Anau Downs	22	17

Table 4.3: The elevation (masl) of the nearest climate station to each site and the Euclidean distance between sites and climate stations.

4.3.3 Analysis

The direction of canopy position change was evaluated for each transect in each period using paired t-tests. I then evaluated whether the mean rate of canopy change varied between transects in both periods using one way analysis of variance (ANOVA). Changes in treeline position occur when recruits above the treeline reach tree height (2 m). How distance from treeline and tree size affect the rate of tree growth was assessed by separately regressing tree size (height or diameter) against growth for stems at the treeline edge, within 5 m of the treeline edge, within 10 m of the treeline edge and more than 10 m from the treeline edge. Changes in treeline position also depend on survival and recruitment rates at or above treeline edge. Although it is possible to use statistical models to determine the effects of stem, site and climate specific factors on treeline position, I chose to analyse the demographic processes (growth, mortality and recruitment) separately since the processes may respond differently to changes in climate between the periods, to transect-related factors and to distance from the treeline.

To identify if demographic processes can be generalized across all South Island *Nothofagus* treelines or if processes were site-specific, I calculated the rate of growth, survival, mortality (1- survival) and recruitment for each transect in each period. The calculations were conducted in R v 2.10 (R Development Core Team 2008) using equations 4.3, 4.5, 4.7, and 4.8 as detailed below. Mean relative growth rates for each transect in each period were subsequently analyzed with ANOVA followed by TukeyHSD (Honest Significant Difference) post hoc comparisons to examine differences between transects.

All subsequent models were built in a Bayesian framework in order to accommodate unequal census period lengths and the hierarchical structure of the data (trees were sampled within sectors within transects). Although it is well recognized that demographic patterns at treeline can vary over short spatial scales (Holtmeier 2009), such as between sectors, I chose not to explicitly evaluate the causes of variation between sectors because I was more interested in the general trends of the region, in which case transect is more indicative. I did, however, include sector as a random effect in all models to account for the largely unexplained variability that exists between sectors.

I was interested in rates of stem growth, mortality and recruitment, and whether these rates would lead to an increase in stems above the current treeline, and hence a potential upward shift in treeline position at the five study sites. To determine this, I estimated these rates from the individual stem data, constructing models to account for factors likely to influence growth, recruitment and mortality. Specifically, I modelled differences among transects, species, census periods (1991-2002 and 2002-2008) and included stem basal area, distance from treeline edge, potential solar radiation and climate as covariates. The annual climate (mean, minimum, winter temperature, precipitation) was included to evaluate if climate explains variability between periods. Climate was included in this model as the annual rate of change (e.g. warming, cooling), over the study duration and was estimated as the slope of the least squares regression line for the relationship between the climate variable and year (1991-2008). Only stems above the treeline edge were included in model development. I first included each explanatory variable alone to identify the variables with the greatest influence on growth, survival and recruitment. I then included in a multivariate model the subset of variables that tended to differ from zero in the univariate models, in order to assess their relationship with growth, survival and recruitment having accounted for the effect of other variables.

4.3.3.1 Growth

Growth was measured in terms of basal area increment, a more accurate measure of tree growth (i.e. biomass accumulation) than height or diameter increment. For each stem that was alive throughout each census period (1991-2002 and 2002-2008), I calculated relative annual basal area increment (g) as the difference in basal area ($BA = \left(\left(\frac{diameter}{2}\right)^2 pi\right)$) at the ground at the beginning and end of the period divided by the basal area at the beginning of the period, divided by the length of the period (t, in years).

$$g = \left(\left(BA_2 - BA_1\right)/ BA\right)/ t \qquad \text{(eqn 4.3)}$$

The relative growth rate follows a Gaussian probability distribution with mean $\hat{g}$ and standard deviation σ. Growth was modelled as a linear equation with an overall intercept, an individual random effect to take into account that multiple observations of growth on the same stem are not independent, and a sector random effect. I included explanatory variables measured for stems (BA, distance from treeline, species), sectors (potential solar radiation) and transects (interaction between transect and period, climate).

The stem and sector random effects were included by coding each stem and each sector across all transects with unique values so that each stem, with its own unique code, was defined as occurring within one of 58 unique sectors. I included the interaction between periods and transect because I was interested in identifying if changes in demographic processes between periods at *Nothofagus* treelines were generalizable across the South Island, New Zealand, or were site-dependent.

4.3.3.2 Mortality

For each stem alive at the start of a census period, I know whether it was alive or dead at the end of that period, coding stems that were alive as 1 and stems that were dead as 0. I modelled these data as if they represented draws from a Bernoulli distribution in which the outcome, *S* (whether a tree was alive or dead), after *t* years was related to the annual probability of mortality, *m*, during that period:

$$S \sim Bernoulli\left((1-m)^t\right) \qquad \text{(eqn 4.4)}$$

The annual probability of mortality was then related to explanatory variables using a logit link function to constrain the probabilities to between 0 and 1. I modelled mortality in relation to the same explanatory variables as described in the growth model. Basal area was included as an index of size to test for the effects of age on survival.

4.3.3.3 Recruitment

For each stem alive at the end of each census period, I know whether it was alive at the start of the period or whether it was newly recruited during that period, coding stems alive at the start 0 and new recruits 1. I modelled these data as if they represented draws from a Bernoulli distribution in which the outcome, R (whether a stem had recruited or not), after t years was related to the annual probability of recruitment, r, during that period:

$$R \sim Bernoulli\left(1-(1-\hat{r})^t\right) \qquad \text{(eqn 4.5)}$$

The annual probability of recruitment is then modelled in relation to explanatory variables as defined for the survival model except that the covariate tree height was not included in the model formulation.

To determine if the treeline population is increasing in density or if recruitment above treeline represents a constant turnover, I compared recruitment and mortality (1 – survival) rates. For this analysis, recruitment and survival rates were not modelled but were calculated directly from the data using a modified version of equation 4.5 to calculate annual mortality:

$$M = (1-\hat{S})^t \qquad \text{(eqn 4.6)}$$

and equation 4.7 to calculate annual recruitment.

4.3.3.4 Model specification

Models were built in a Bayesian framework and were fit using Markov chain Monte Carlo (MCMC) methods using OpenBugs (Thomas *et al.* 2006) called from the BRugs library in R v. 2.10 (R Development Core Team 2008).

The height and potential solar radiation continuous variables were standardized by subtracting their mean and dividing by twice their standard deviations to assist in model convergence and to put the parameter estimates of both continuous and predictor variables in the same numerical range (Gelman & Hill 2007). Distance was standardized by dividing the values by twice the standard deviation, putting the variable in a similar range as other variables while retaining the original structure of the distance variable, in which 0 is set at the treeline edge rather than the mean of the distribution. Categorical variables (species, transect, period) were included by coding them as dummy variables and then setting one category as a reference class (*N. solandri*, Craigieburn, 1991-2002) with the coefficient set to zero (Gelman & Hill 2007). The interaction between transect and period was included by setting the coefficient for the period 1991-2002 to 0 so that changes in growth, recruitment and survival within a transect are relative to 1991-2002 rates.

Low temperature limitation of growth is a hypothesized cause of treeline formation (Körner 1998). Low temperature influences treeline elevation by limiting growth and survival and should be evident as a decline in height or diameter with increasing elevation. An interaction between distance and height or diameter was included in the initial model formulation of the growth and survival models but was retained in the final model only if the interaction was significant. No other interactions were assessed. The regression coefficients describing the effect of each category of the random effects (sector, stem ID) were assumed to be drawn from a common normal distribution with a mean of zero and a standard deviation estimated from the data (Gelman & Hill 2007).

Non-informative prior distributions were assigned to all parameters to reflect lack of prior information and to allow the data to drive parameter estimation. The fixed effect parameters (height, distance) were assigned normal prior distributions with mean 0 and variance 1000. Variance parameters were assigned uniform distributions in the interval 0-10. The variance term for the random effect terms were given broad uniform priors on the standard deviation (Gelman & Hill 2007).

Performing three MCMC (Markov chain Monte Carlo) runs with a burn-in phase of 100 000 iterations was identified as suitable for all models through visual examination of the chain traces. I continued each MCMC run for a further 100 000 iterations and used the last 50 000 iterations of all three runs (i.e. a sample of 150 000 in total) to obtain posterior distributions for each parameter, from which I derived mean values and 95% credible intervals.

4.4 Results

4.4.1 Treeline canopy

On average, the treeline canopy extended at all transects in both periods (Fig. 4.4). The canopy extended at 489 points, retracted at 116 points and did not change at 30 points during the 1991-2002 period. The canopy extended at 604 points, retracted at 61 points and did not change at 49 points during the 2002-2008 period. The canopy extended at a greater rate in the first period (0.135 m/yr) than the second period (0.083 m/yr; Paired t-test, $t = 2.627$, $df = 634$, $p < 0.05$). The average rate of extension differed significantly between transects in the first period (ANOVA, $F = 9.42$, $p < 0.05$) but not the second period (ANOVA, $F = 1.66$, $p > 0.05$; Fig. 4.4).

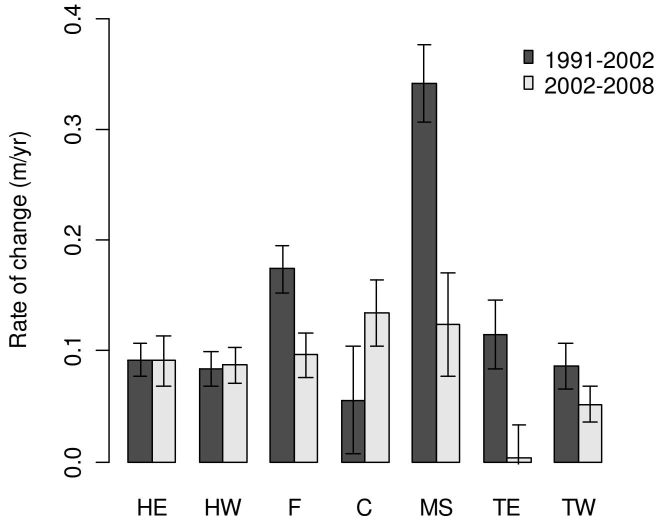

Figure 4.4: Average rate of canopy extension (m/yr) and standard errors during the 1991-2002 (dark grey) and 2002-2008 (light grey) periods in each transect. Rate of canopy change is based on 635 canopy points in the first period and 714 points in the second period. Transect codes: Haast East (HE), Haast West (HW), Faust (F), Craigieburn (C), Maori Saddle (MS), Takahe East (TE), Takahe West (TW).

4.4.2 Growth

Across all transects, growth did not significantly differ between periods or with potential solar radiation and species (Fig. 4.5). Growth tended to be lower for larger stems than smaller stems. No climate variables were significant in explaining variability in growth (Table 4.4). In both periods, growth varied minimally between transects (Fig. 4.5b).

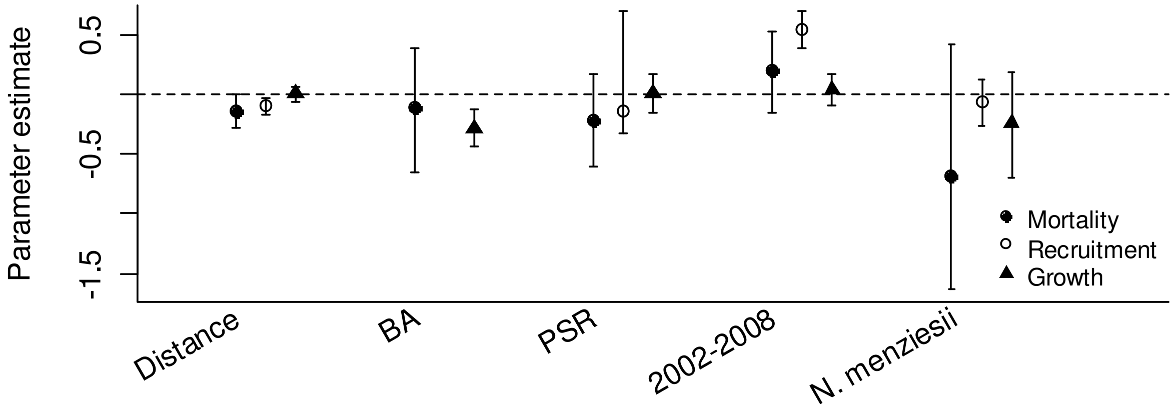

Figure 4.5: The mean and 95% credible intervals for the parameter estimates describing the effect of explanatory variables on growth (triangle), mortality (filled circles), and recruitment (open circles). Random effects for the growth models are not shown. Rates in period 2002-2008 are relative to period 1991-2002. *N. menziesii* is shown relative to *N. solandri*. Credible intervals crossing the zero line (dashed) are not significant. Details of standardisation for distance and potential solar radiation (PSR) are detailed in text.

		Growth	Survival	Recruitment
Mean annual Temperature(°C)	mean	0.025	-0.098	0.262
	CI	-0.21 – 0.22	-1.01 – 0.74	-0.48 – 3.17
Mean winter Temperature (°C)	mean	-0.027	-0.474	-0.009
	CI	-0.20 – 0.09	-1.79 – 0.92	-2.94 – 1.04
Minimum annual Temperature (°C)	mean	-0.011	-0.350	0.139
	CI	-0.40 – 0.09	-1.11 – 1.64	-1.54 – 0.62
Precipitation (mm)	mean	-0.286	0.377	-0.612
	CI	-0.59 – 0.02	-2.24 – 1.57	-2.05 – 0.16

Table 4.4: Posterior means and credible intervals (CI) of parameters describing the effect of mean annual, minimum annual and mean winter temperature, and precipitation on growth, survival and recruitment over the entire study period in the univariate models. Credible intervals that do not overlap zero are considered to be significant.

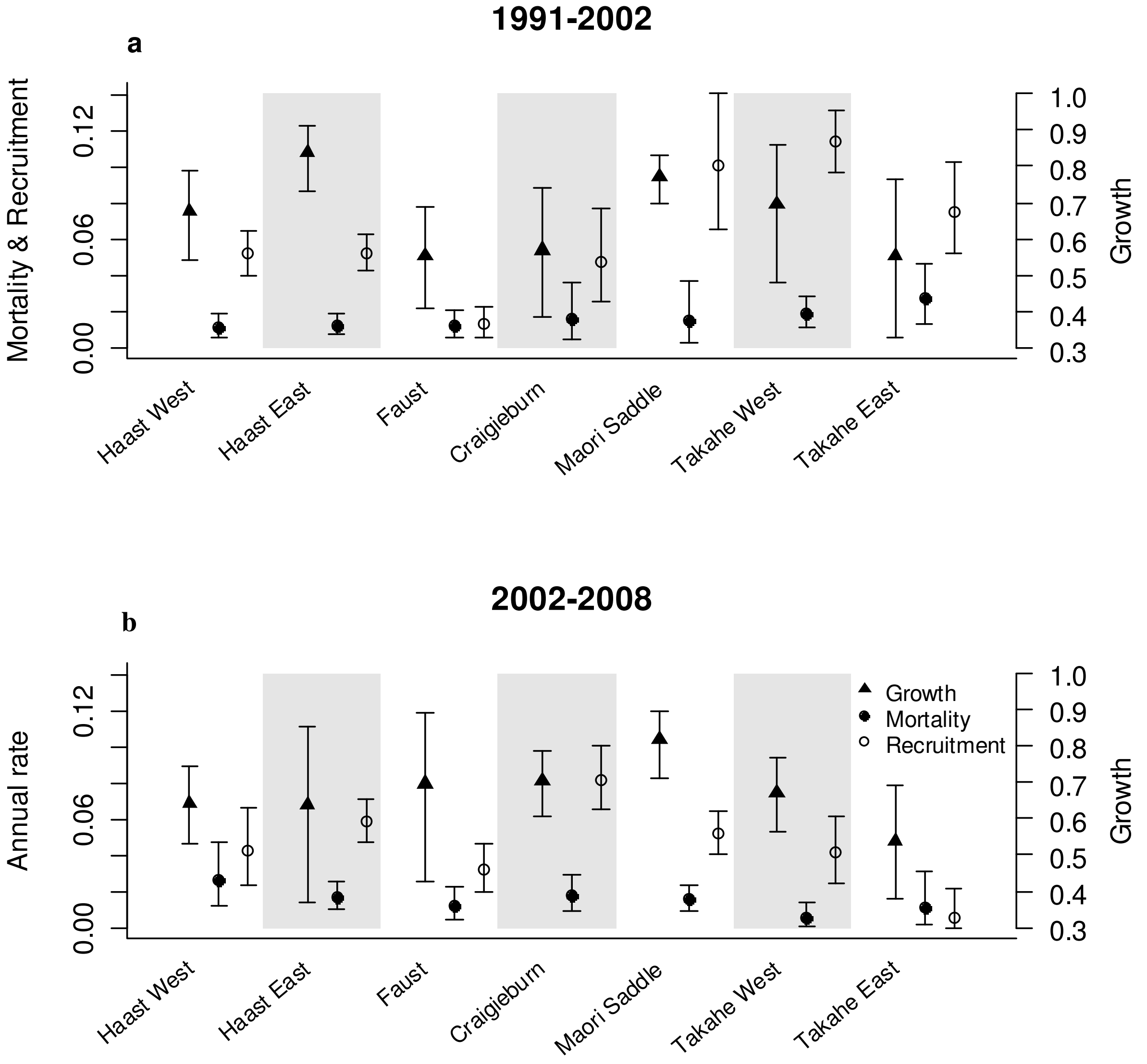

Figure 4.6: Modelled annual growth (triangles), mortality (filled circles) and recruitment rates (open circles) with 95% credible intervals at each transect in 1991-2002 (a) and 2002-2008 (b). Credible intervals that do not overlap are considered to be significantly different.

4.4.3 Mortality and recruitment rates

Across all transects and periods, mortality did not significantly differ between species or with basal area and potential solar radiation (Fig 4.5). The only variable that was significant in explaining variability in mortality was distance, in which mortality tended to decrease with further distance (Fig. 4.5). No climate variables were significant in explaining variability in mortality or recruitment in the univariate models (Table 4.4). Between transects there was little variability in mortality rates. Mortality tended to be greatest at Takahe Valley East during the first period and Haast West during the second period but this was not significant (Fig. 4.6).

Recruitment was evident at all transects in both periods (Fig. 4.7) but varied considerably between transects. In the first period, recruitment was significantly lower in Faust from all other transects and, in the second period, significantly lower in Takahe East from all other transects except Faust (Fig. 4.6). Recruitment tended to be greatest, although not significantly, at Maori Saddle, Takahe West and Takahe East in the first period and at Craigieburn in the second period (Fig. 4.6). Across all transects, recruitment was less likely to occur at further distances from the treeline edge and increased in the second period relative to the first (Fig. 4.5). Potential solar radiation and species were not significant in explaining variability (Fig. 4.5).

Recruitment was insufficient to replace mortality at most transects both above and below the treeline in the first period (Fig. 4.7a,b). During this period, recruitment was greater than mortality only below treeline at Haast East and Maori Saddle, the two transects in which no mortality was observed. In the second period, recruitment was greater than mortality at most transects both above and below treeline (Fig. 4.7c,d). Only at Haast East, Maori Saddle and Takahe West above treeline and Craigieburn and Maori Saddle below treeline, was recruitment not sufficient to replace mortality. Overall, mortality tended to be greater above treeline than below treeline, although the pattern was reversed at Craigieburn in both periods and in Takahe East and West in the second period. Recruitment tended to be greater below treeline than above in the first period (all transect except Haast West and Maori Saddle) and above treeline than below in the second period (all transects except Haast East, Maori Saddle and Takahe West).

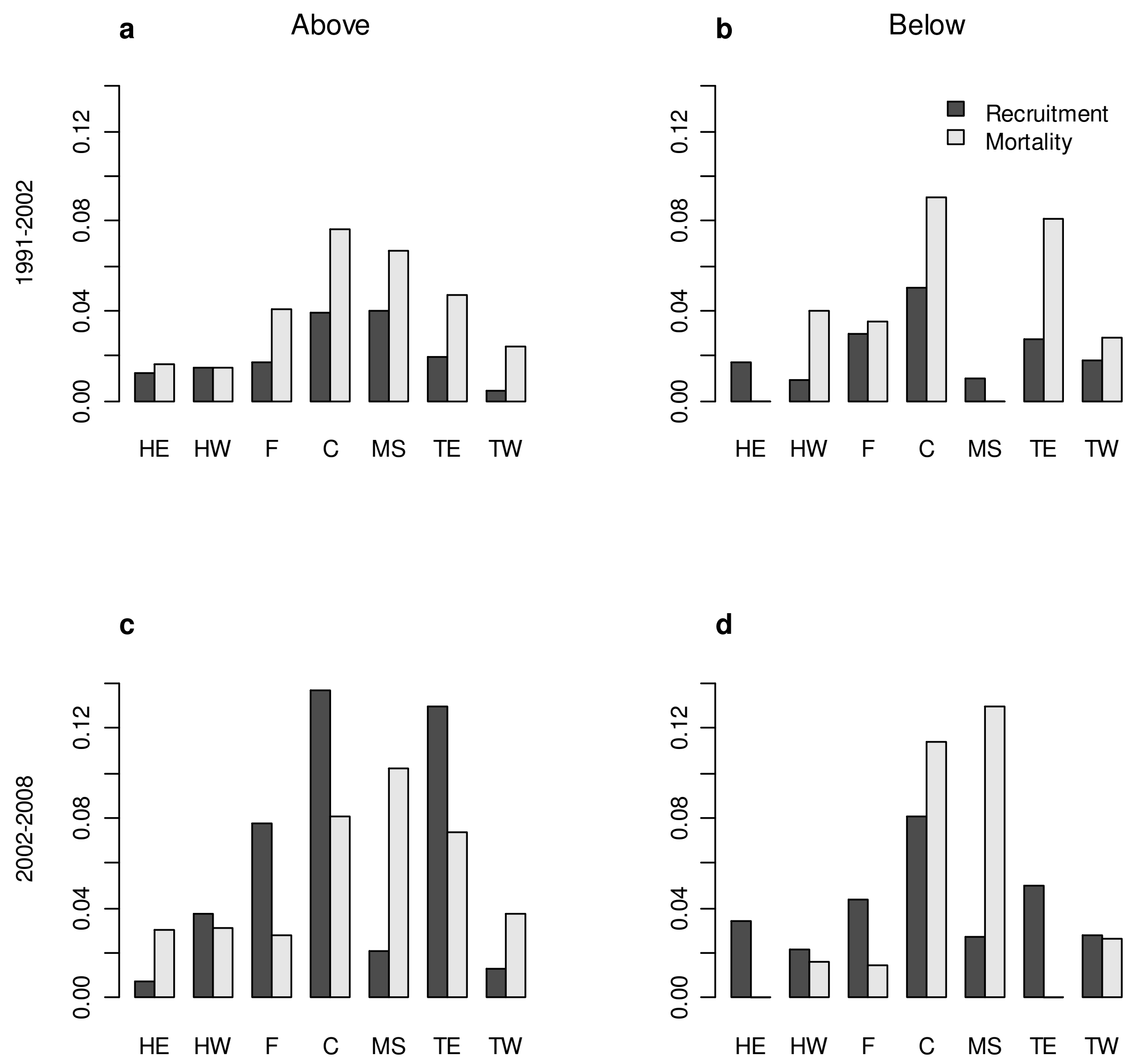

Figure 4.7: Calculated recruitment (dark grey) and mortality (light grey) rates of seedlings and saplings (diameter ≤ 4 cm) for each transect for the 1991-2002 period (a, b) and 2002-2008 period (c, d), above (a, c) and below (b, d) treeline. Transect codes as in Figure 4.4. Rates are calculated directly from the data using equations 4.6 and 4.7.

The total number of stems found above the treeline increased over the study duration from 587 stems in 1991 to 1117 stems in 2007. Over the same period, the number of stems ≥2 m tall also increased (148 stems in 1991, 243 stems in 2007) but at a slower rate than the rate of increase for all stems (1.6, 1.9 fold increase respectively; Fig. 4.8a). The majority (90%) of stems at each census were found within 10 m of the treeline edge, with no individuals found beyond 30 m (Fig. 4.8b). The median distance of all stems above treeline was less than 4 m across all census years and shifted closer to the treeline by 0.53 m over the study duration, from 3.58 m in 1991 to 3.06 m in 2007 (Fig. 4.8b).

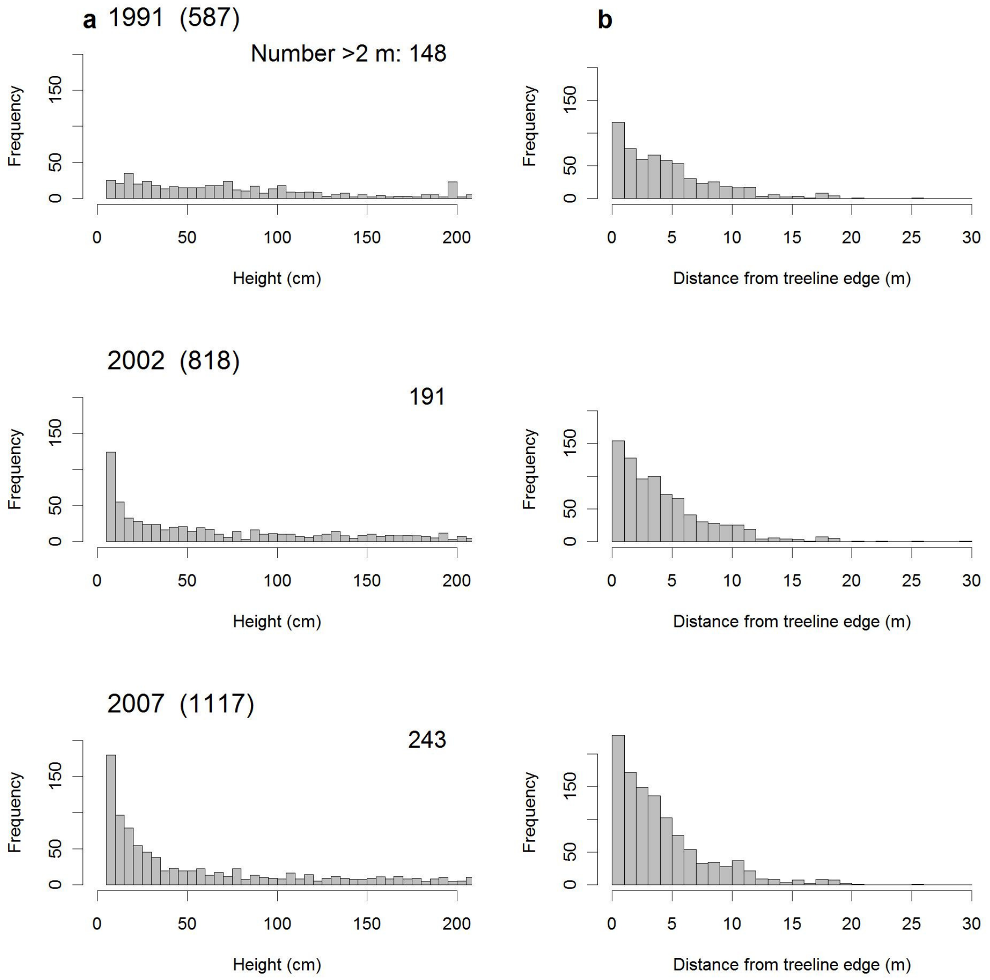

Figure 4.8: The frequency of stems observed across all transects in each height class along with the total number of stems observed (in brackets) and the total number of stems greater than 2 m (a) and the frequency of stems observed across all transects in 1 m distance classes in each census year (b). Dashed lines represent the median distance beyond the treeline edge in which all stems occurred.

4.5 Discussion

4.5.1 *Nothofagus* population dynamics

The analysis of treeline demographics indicates that a change in the New Zealand *Nothofagus* treeline position may occur, given sufficient time. Even under the short time-frame in which the treeline was monitored over (15 years), observable changes in stem number were evident above treeline. The observed changes, however, do not provide clear evidence that the forest is expanding. Although stem number increased above treeline, the majority of recruitment occurred within 10 m of the treeline edge and the distribution of the majority of stems did not shift upward (Fig. 4.8). In addition, mortality was size-dependent and tended to be greater near the treeline edge, which may limit establishment of a new treeline.

How rapidly any changes in treeline position occur at will depend upon both local and macro environmental conditions. For example, recruitment and mortality for stems with a diameter ≤ 4 cm varied considerably between transects and periods (Fig. 4.7). Climatic variables considered (annual mean, annual minimum and mean winter temperature, annual precipitation) were not directly related to recruitment, growth or mortality and are insufficient to explain variability in demographic rates between transects or periods (Table 4.4). It is possible that mortality and recruitment were influenced by climate variables but other variables such as distance from treeline, soil nutrient properties and mycorrhizae exert a stronger influence than annual climatic trends. If temperature were the primary factor limiting growth, then a positive response to warming over the past 15 years (Table 4.5) or even century (Cullen *et al.* 2001b) should have been evident and growth would be inversely related to distance from the treeline edge (Fig. 4.5). Of course, climatic conditions vary annually and intermittent monitoring may not fully represent the relationship between climatic conditions and growth, recruitment and mortality between census years.

As mortality rates did not change over the study duration, lower seedling mortality is unlikely to explain changes in recruitment rates over the study duration. Instead, the increase in recruitment most likely resulted from increased seed production. Seed production has increased in the last 30 years of the 20th century, primarily resulting from more frequent moderate mast years following climate warming (Fig. 4.1; Richardson *et al.* 2005). The frequency of mast years, however, is not a good indicator of recruitment rates for this study; recruitment was lower in the first period than the second, despite greater frequency of moderate mast events in the first period. Recruitment rates may have been influenced by the timing of mast years relative to census years, especially if masting events occurred a year prior to a census year. As mortality is greatest in the first year following germination and decreases thereafter (Wardle 1984), recruitment rates for periods ending just after a mast year (second period) may be artificially high relative to the first period in which more time had elapsed between mast and census years (Fig. 4.1).

Recruitment may also be limited by seed dispersal and germination. Seed dispersal limitation has been demonstrated in model simulations to limit advance rates (Malanson & Cairns 1997; Dullinger *et al.* 2004) but has rarely been observed as the primary limiting factor in the field (Green 2009) because other factors, such as seedling emergence and seedling survival, limit advance rates more than dispersal ability (Cuevas 2000; Holtmeier 2009). Dispersal may slow the rate of advance at the New Zealand *Nothofagus* treeline but given that presence of stems above treeline and occurrence of seedlings 30 m above treeline (Fig. 4.8), dispersal is not likely limiting recruitment. Germination studies are lacking above the *Nothofagus* treeline, but, given that the number of stems increased by 20-50% in both periods at all transects except Maori Saddle and Takahe East (Fig. 4.8) and that *N. solandri* seed can germinate 150 m beyond treeline in specific microsite conditions (Wardle 1985b), germination is unlikely to be the primary factor limiting recruitment unless the availability of suitable microsites is limited. Microsite availability may explain, in part, the limitations to recruitment as the three transects with the lowest recruitment rates also tended to be dominated by tussocks with less bare soil above treeline (Appendix F). Biotic interactions, especially mycorrhizae availability, may have influenced advance rates but cannot explain the differences in recruitment rates observed between periods. Disturbance is also unlikely to be limiting treeline advance; none of the treeline transects monitored are currently being used for human means. Even if historical land-use occurred, rapid treeline expansion should be evident following cessation of land-use (Motta & Nola 2001; Shiyatov *et al.* 2007), unless some factor not related to disturbance inhibits recruitment, in which case treeline expansion would not be expected regardless of historical disturbance (Cierjacks *et al.* 2008; Green 2009).

Finally, recruitment may be limited by differential tolerances to microsite conditions at different life history stages. For example, germination is maximized under low light conditions (e.g. under the canopy) but growth is maximized under high light conditions (e.g. open canopy; Wardle 1984). This may be why recruitment at the *Nothofagus* treeline edge has been positively associated with disturbance rather than changes in temperature (Cullen *et al.* 2001b). How important gap openings are above treeline are less clear. Wardle (1985b) planted *N. solandri* seedlings up to 150 m above treeline under varying degrees of artificial shade within Craigieburn Forest Park. Survival, as expected, was maximized under low light conditions but seedlings never developed into trees, even after 35 years. The seedlings grew beyond the confines of the shelter (35 cm high) but growth was subsequently lost in the dormant period. Further evaluation of the importance of light exposure on growth above treeline is necessary.

Historically, the frequency of fires in New Zealand has been insufficient for New Zealand species to evolve fire resistance or tolerance to fires. The arrival and subsequent use of fires by Maori from Polynesia circa 1300 A.D. and Europeans in the 1800's wrought significant effects on the distribution of *Nothofagus* forests (McGlone & Moar 1998; Wardle 2001). Given the slow rate of recovery by *Nothofagus* species, areas burnt 200 years ago have, most likely, not fully recovered. The limitations to recolonization by *Nothofagus* species following fire in New Zealand is likely to be similar to the factors limiting treeline advance, such as poor ability to germinate in vegetated microsites (Wardle 2001).

4.6 Conclusions

Nothofagus treelines in New Zealand are unique globally. They are extremely abrupt and occur below the expected elevational limit based on global patterns of mean growing season temperature at treeline. Even when compared against *Nothofagus* treelines in South America, which can form Krummholz above the upright tree limit, the treelines in New Zealand are low. The low treeline position and, consequently, low recruitment above treeline, has been suggested to result because the *Nothofagus* species forming treeline in New Zealand, similar to broadleaved evergreen species worldwide, are less cold-tolerant than deciduous and needle-leaved species (including *Nothofagus* species in South America).

In the northern hemisphere, treelines formed by winter cold limited species is associated with localized absence of conifers, such as *Quercus semecarpifolia* in the Himalayas (Ohsawa 1990). In New Zealand, the absence of species more tolerant of winter cold than *N. solandri* and *N. menziesii* is associated with isolation and insufficient time for adaptation to cold conditions. Insufficient time (2 million years) has passed in which climatic conditions have been sufficient to support evolution of hardier trees (Gage 1980). In contrast, conditions have been suitable for evolution in the Andes, where the local *Nothofagus* species is deciduous, for the past 4.6 million years (Mercer & Sutter 1982; Thomson 2002). Currently, few parts of New Zealand experience winter temperatures associated, globally, with deciduous broadleaved species (McGlone *et al.* 2004).

Despite the difference in cold tolerance and treeline elevation, broadleaved evergreen *Nothofagus* species in New Zealand and broadleaved deciduous *Nothofagus* species in South America are both relatively stable and treeline advance is limited by seedling emergence and survival (Cuevas 2000). Further, when planted at high elevation conditions in New Zealand, coniferous treeline forming species from the northern hemisphere do not always perform as well as expected based on cold tolerance alone (Wardle 1985b). Winter cold tolerance alone cannot explain the relative inertia of the New Zealand *Nothofagus* treeline. The answer may lie in Holocene dynamics. *Nothofagus* did not form the upper forest limits until the second half of the Holocene, probably because there was little difference between summer and winter temperatures and frequent growing season frosts in the first half of the Holocene (McGlone 1996). Similarly, *Nothofagus* treelines in New Guinea, which are below the expected elevation based on global temperature patterns, are negatively affected by frosts (Brown & Powell 1974).

In summary, the abrupt *Nothofagus* treeline results primarily from limits to recruitment. Greater recruitment rates in the second period relative to the first resulted in both increased observed and projected number of stems above treeline. The lack of clear evidence of treeline advance, however, indicates that the abrupt treeline is not limited directly by low temperature. Observed and experimental manipulation of seedling establishment at abrupt treelines globally suggests that seedling survival and growth are maximized in microsites with strong shade, such as experienced under trees. I postulate that the stable nature of the New Zealand *Nothofagus* treeline probably results from recruitment limitation, of which germination and seedling survival are components.

Chapter 5
Are treelines limited below the potential thermal limit by site-specific climatic conditions or taxon-specific intolerance?

5.1 Abstract

The upper altitudinal or latitudinal limit of the treeline is hypothesized to be determined, globally, by tolerance of tree species to low growing season temperature. However, some local species distributions do not reach the treeline elevation based on low temperature, either because taxon-specific tolerances or site-specific climatic conditions limit their distribution. Whether treeline elevation is limited by site- or taxon-specific limitation has implications for general applicability of using climate along to predict changes in species distribution. I evaluated site-specific and taxon-specific limitation by planting two treeline-forming species with contrasting life-history traits: an evergreen angiosperm (*Nothofagus solandri* var. *cliffortioides*) and an evergreen conifer (*Pinus contorta*) along elevation transects from 50 below to 150 m above the low New Zealand treeline in natural and experimentally warmed microsites. Growth and mortality did not negatively respond to cooler temperatures (distance from treeline) or positively respond to warming (passive warming). Mortality contrasted between species and seasons. Overall, *P. contorta* mortality was greater than *N. solandri* mortality. *N. solandri* seedlings were more likely to survive through the growing season and *P. contorta* seedling survival did not significantly differ between seasons. Results indicate that climatic conditions, such as early season frosts, limit native and introduced treeline forming species to similar elevations when but taxon-specific tolerances limit the native species ability to grow to tree height and ultimately limit treeline position.

5.2 Introduction

The upper altitudinal or latitudinal limit of the treeline is determined by tolerance of tree species to unfavourable abiotic conditions. Most research, to date, has focused on the effects of one abiotic factor, low growing season temperature (Cabrera 1996; Körner 1998; Körner & Paulsen 2004; Bansal & Germino 2008). All other abiotic factors are considered to not act globally or exert less of an influence than low growing season temperature and, therefore, to be negligible (Körner 1998, 2007). Variation in taxon-specific tolerances to abiotic stress has also largely been overlooked, despite the considerable phylogentic differences between treelines globally. In addition, treelines not clearly limited by low growing season temperature, have been dismissed as being non-true treelines, formed in the absence of tree species better-adapted to high elevation conditions (Körner & Paulsen 2004).

Treelines, however, may be determined as much by winter conditions as by growing season conditions (Jobbagy & Jackson 2000; Danby & Hik 2007a; Harsch *et al.* 2009). The local tree species forming treeline represents tree life form (evergreen needle-leaved, deciduous broadleaf) adaptations to winter conditions and a physiological limit across all tree species to low growing season temperatures (Jobbagy & Jackson 2000). Based on a global analysis of treeline position, the tree life form at treeline is determined by winter conditions and the elevation is determined by growing season temperature (Jobbagy & Jackson 2000). There are, however, treelines that occur at growing season temperatures greater than expected if low temperature were limiting, principally those in the southern hemisphere, tropics and on islands (Körner & Paulsen 2004).

There is good reason to expect that southern hemisphere treeline forming species are less well adapted to high elevation conditions than northern hemisphere treeline forming species. Treeline forming species in the southern hemisphere have been isolated from northern hemisphere treeline forming species since Pangaea broke up 200 million years ago (Francis 1991; Manos 1997). In the case of New Zealand treeline forming species, insufficient time has elapsed in which mountains were high enough with temperatures cold enough for evolution of hardier species (Gage 1980). Evergreen broadleaved species, the tree life form for which New Zealand treeline species fall within, are the least hardy life form to cold winter temperatures (Jobbagy & Jackson 2000).

Alternatively, local treeline forming species may fall below the expected elevations based on growing season temperature because site-specific climatic factors limit distributions below limits imposed by broad-scale environmental gradients. For example, low soil temperature is limiting treeline position on a north-facing aspect in the Yukon, as expected by global treeline-temperature patterns. In contrast, the treeline position on a south-facing aspect is limited below the thermal limit by cold-induced photoinhibition and winter desiccation (Danby & Hik 2007b). The treeline sites were composed of the same species, the only difference between sites was the local climatic conditions.

The occurrence of taxon-specific limitation has, thus far, been assessed through identification of climatic stressors limiting the distribution of local treeline forming species (e.g. Bader *et al.* 2007b, Ball *et al.* 1991, Danby & Hik 2007b) but whether stressors relate to taxon-specific limitations or local climatic conditions has rarely been assessed (e.g. Odum 1979, Wardle 1985b, Instituto Forestral 1986). A trial was established in 1968 in which three northern hemisphere evergreen needle-leaved tree species and two evergreen broad-leaved species were planted along with the native evergreen broadleaved species, *Nothofagus solandri* var. *cliffortioides*, above the native *Nothofagus* treeline in New Zealand (Wardle 1985b). Only one species, *Pinus contorta*, was able to grow beyond the confines of shelter at higher elevations than planted *N. solandri* seedlings, indicating that local climatic conditions exert, in part, strong influences on treeline position and that life form alone was not a good predictor of potential species distribution. The experiment, however, did not assess if growing season temperature, the primary broad-scale environmental gradient limiting treeline position globally, is limiting the local treeline position, or how winter conditions affect survival. The modified microsite conditions, continuous and consistent degree of shade surrounding seedlings and no neighbouring vegetation, are infrequent above treeline. Microsite conditions above treeline are heterogeneous, so taxon-specific tolerance to competition for resources and tolerance to light exposure may be critical for survival.

Here, I evaluate if low treeline position is a feature of the local treeline forming species (taxon-specific) or whether low treelines are a general feature of site conditions in New Zealand (site-specific). I compare growth and survival of the evergreen broadleaved species, *N. solandri*, and the evergreen needle-leaved species, *P. contorta*, in natural and experimentally warmed microsites above treeline. Disturbance at the site is infrequent and insufficient to impede recruitment above the treeline. If site-specific conditions limit treeline position then both species would be expected to perform poorly above treeline in natural microsites and either not respond or respond negatively to experimental warming. This is because conditions other than temperature are expected to limit treeline position below the potential life form limit. If taxon-specific tolerance limits treeline position below the expected tree life form limit, then differences in response to temperature, seasonal conditions and light exposure should be evident between species. Conifers occur at lower mean coldest month temperatures than broadleaves (Jobbagy & Jackson 2000). Taxon-specific limitation of the *Nothofagus* treeline, therefore, should be evident as lower tolerance of the *Nothofagus* species to dormant period conditions than in the growing season. I expect vegetated microsites to enhance *N. solandri* survival, by providing shelter, and negatively affect *P. contorta* survival. Although taxon-specific limitation can occur at any life history stage, I focus on seedling survival because the seedling stage is a principle limiting stage; seedlings are less sensitive to desiccation and more likely to exhibit temperature limitation than new germinants, plants in the first year following germination (Wardle 1984). The research is conducted at a relatively undisturbed New Zealand treeline that is below the potential thermal induced tree life form limit (Körner & Paulsen 2004). Although the climate is mild, conditions at treeline may be unfavourable because of early and late season frosts and spatially and temporally variable snow cover.

5.3 Methods

5.3.1 Field site

The studied treeline is located on a steep, highly eroded east-facing slope in the Craigieburn Range, South Island, New Zealand (43°10´S, 171°71´E). The site is characterized by hot, dry summers and mild winter conditions. Precipitation is relatively evenlu distribution throughout the year, with 40% occurring as snow. Frosts occur regularly throughout most of the year. Although the site is protected from the prevailing westerly winds, strong winds are common, especially during spring. The forest is composed of a single tree species, *Nothofagus solandri* var. *cliffortioides*, which extends up to treeline at 1320 masl. Tree height at low altitudes ranges between 12 - 15 m but rarely exceeds 3 m at the treeline (Wardle 1984). Vegetation above the treeline is dominated by tussock, *Chionochloa pallens*, and two low-statured evergreen shrubs, *Dracophyllum uniflorum* and *Podocarpus nivalis.*

The field site is located adjacent to a larger long-term treeline monitoring program that covers most of the South Island, New Zealand (Chapter 4). Although Craigieburn is the warmest and driest of the long-term monitoring sites (Table 4.2), it is representative of *Nothofagus* treelines in the South Island, New Zealand in that treeline position in Craigieburn has remained stable despite considerable warming (0.9 °C) over the past century (Mullan *et al.* 2008). The site was also chosen because several introduced pine species have been planted on a nearby slope (Ledgard & Baker 1988). Pines were planted in 1964 at 1320 masl and have been spreading to higher elevations (Ledgard & Baker 1988).

5.3.2 Species

The dominant native tree species within the Craigieburn range is *N. solandri*, an evergreen angiosperm found primarily at dry high elevation sites. The species is moderately hardy to low summer and winter temperatures (Wardle & Coleman 1976). Seeds are small with limited resource reserves, which may explain, in part, the poor germination ability in dense aboveground vegetation. Seedling establishment is maximized under moderate shade (65%) and growth beyond the seedling stage is maximized under full light (Wardle 1974, 1984).

Pinus contorta was chosen to contrast *N. solandri* because it is an evergreen conifer that occurs across a wide elevation band, including at high elevations throughout its native range, the western region of North America. In addition, in a high elevation experiment at Craigieburn, *P. contorta* exhibited greater survival and growth at high elevations than the seven other trialed treeline forming species (Wardle 1985b, c). Of the species introduced into New Zealand, *P. contorta* is the most tolerant of high elevation conditions in New Zealand (Wardle 1985b) and, therefore, the best species to contrast with *N. solandri* survival and growth to identify if taxon-specific tolerances limit *N. solandri* treeline position.

P. contorta was introduced into New Zealand circa 1880 and widely planted as a commercial forestry species. It has subsequently spread into natural grasslands and is perceived as a major threat to alpine tussock ecosystems (Swaffield & Hughey 2001). The species occurs extensively throughout the Craigieburn Range both as planted trees and natural regenerating trees (wilding pines) but it has not yet colonised the field site. *P. contorta* is shade intolerant (Pfister & Daubenmire 1975), very hardy to cold winter temperatures (Sakai & Larcher 1987), moderately hardy to cold summer temperatures (Nilsson 2001), and regenerates best under full sunlight (Despain 2001). Both *N. solandri* and *P. contorta* are susceptible to wind and snowpack damage on exposed sites and will form stunted multi-stemmed trees (Norton and Schoenberger 1984, Ledgard and Baker 1988b).

5.3.3 Field observations

N. solandri seedlings in transects 1, 2, and 4 were initially sourced from a nursery. Subsequent replacement of dead seedlings and establishment of transect 3, which occurred three months after the other three transects were established, were sourced from seedlings below the treeline. The source of seedlings was changed because canopy sourced seedlings contained less resource reserves and therefore should exhibit less inertia to stress than nursery obtained seedlings. This was ideal under the short timeframe of the study (3 years). Seedlings obtained from the nursery and below treeline exhibited similar diameter (≤ 1 cm) but, on average, 33 cm differences in height, reflecting differences in growing conditions. Nursery obtained seedlings were let to harden for a month at the nursery (200 masl) before planting. Although nursery seedlings were not inoculated with mycorrhizae, mycorrhizae may have been present at the time of planting. Canopy sourced seedlings were not checked for mycorrhizal colonization. *P. contorta* seedlings were sourced from naturally seeded seedlings at 1300 masl on an east facing slope 1.5 km from the field site. Care was taken to ensure that all naturally sourced seedlings were of similar height within species.

Four transects extending from 50 m below the treeline to 150 m beyond the treeline were established on an east-facing aspect between November 2007 and April 2008. *N. solandri* seedlings were planted in November 2007 and *P. contorta* seedlings were transplanted in April 2008. Along all four transects, a single *N. solandri* seedling was planted directly into the microsite next to the transect line at 10 m intervals. To reduce transplanting stress, as much of the seedling rootmat and surrounding soil as possible was retained during transplanting. Along transects 1 and 2, an additional seedling was placed at ten metre intervals from 5 - 45 m above treeline. Along transect 3; a *P. contorta* seedling was planted in the closest microsite similar to the *N. solandri* microsite. Along transect 4, an additional *N. solandri* seedling and two *P. contorta* seedlings were planted in as similar as possible microsites to the *N. solandri* seedling (Fig. 5.1). In total, 25 *N. solandri* seedlings were planted along the first two transects, 20 along the third transect and 35 along the fourth. *P. contorta* seedlings were only planted above the treeline because of permit regulations, 15 in transect 3 and 30 in transect 4. Microsites were classed by whether the object neighbouring the transplanted seedling was vegetated (*C. pallens, P. nivalis, D. uniflorum*) or not (soil bank, rock). All seedlings in transect 4 were planted into vegetated microsites. The height of the neighbouring microsite object (vegetation, bank, rock) was measured along with the location of the neighbouring object (vegetation, bank, rock) relative to the seedling (above, below, left right). Seedling height and diameter at the base were recorded at the time of transplanting and again, along with whether or not the seedling survived, at the beginning of each interval (November, April) through March 2010. In this study, growing season comprises the four months December through March and dormant period the eight months April through November. Seedling height was measured with a metre-ruler to the nearest 1 mm and diameter was measured with callipers to the nearest 0.1 mm. Dead seedlings for both species were replaced in April 2008 and November 2008 with locally sourced seedlings.

The effect of transplanting was assessed with a reciprocal transplanting experiment at 910 masl. The degree of canopy cover at the reciprocal transplanting experimental site was similar to the degree of canopy cover evident above treeline; open cover by disconnected individual trees. In November 2007, at the time that the experiment was installed, ten naturally seeded *N. solandri* seedlings were removed and then replanted in the same location. Survival was subsequently monitored at the same period that vertical transects were monitored.

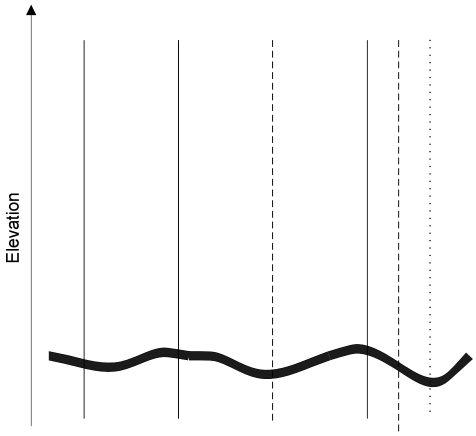

Figure 5.1: Layout of experimental design. The thick line represents the treeline edge with the are below the line being within the forest canopy. Thin solid lines represent *N. solandri* seedlings, dashed lines represent *P. contorta* seedlings and dotted lines represent the OTC treatment.

Temperature around a single *N. solandri* and *P. contorta* seedling at each 10 m interval along transect 4 was passively warmed using open top chambers (OTC) from January 2008 through October 2009 (Fig. 5.1). The second *N. solandri* and *P. contorta* seedlings at every 10 m interval served as the control. OTC were constructed from 2 mm thick acrylic sheeting. Several design elements were trialled in the field, including a hexagon, square, and triangle. The triangle was most effective in withstanding damage from wind, snow and keas. Each side of the OTC was shaped as trapezoid with a length of 0.5 m at the bottom edge and 0.33 m at the top edge and height of 0.5 m. At each 10 m interval along transect 4, one *N. solandri* and one *P. contorta* seedling were placed in the centre of the OTC (OTC treatment) and one beach and one *P. contorta* seedling were placed within a metre from the OTC (control treatment). The open top design allowed precipitation to reach seedlings but chamber walls may have decreased exposure to wind and lowered the risk of photodamage because of condensation on the plastic.

Temperature differences between unwarmed and warmed treatments (control, OTC) and along the elevation gradient were assessed by simultaneously measuring soil temperature 10 cm below the soil surface inside and outside the OTC using iButton® Thermochron® temperature loggers (Dallas Semiconductor Corporation, Dallas, TX, USA) in all paired replicates from December 2008 through March 2009. Dataloggers were placed adjacent to the seedlings. The effectiveness of OTC in warming microclimates was assessed with a repeated measures analysis of variance (ANOVA) with treatment (OTC, control) and distance above treeline as the fixed effects and an index of microsite position (1 through 15) as the repeated measure. This test allowed us to assess the interaction between treatment and distance from treeline on temperature while taking into account that treatments were paired. Analysis was conducted in R v. 2.10 (R Development Core Team 2008). An additional datalogger was placed 10 cm belowground under a tree at the canopy edge to evaluate if the *Nothofagus* treeline is below the estimated global temperature limit for the tree life form, 5 – 8 °C.

5.3.4 Analysis

I was interested in both the effect of distance from treeline and microsite characteristic, defined in terms of neighbouring object (type, height, direction) on growth and survival of the two species. Analysis was limited to seedlings planted above treeline because microsite characteristics below treeline were highly correlated (Pearson's correlation, correlation = 0.98, $p < 0.05$).

5.3.4.1 Growth

Growth was measured in terms of the monthly rate of change in the relative annual basal area increment (g) where basal area is square of the diameter divided by two and then multiplied by pi. The relative basal area increment is then calculated as the difference in basal area at the beginning and end of the period divided by the basal area at the beginning of the period, divided by the length of the period (in months)

I first compared growth between *N. solandri* and *P. contorta* seedlings (species analysis). This analysis was limited to the eight unwarmed microsites in transects 3 and 4 in which both *N. solandri* and *P. contorta* seedlings survived the growing season. Analysis was conducted in a paired t-test.

The second analysis (the full growth model) evaluated the effect of distance beyond treeline, microsite neighbouring object type and microsite neighbour height on growth. Microsites neighbouring object direction was not included because only three individuals in eastern microsites survived the growing season. This model utilizes data from the first three transects.

Both *N. solandri* and *P. contorta* were included in this model. Inclusion of a species variable depended upon results from the species analysis whereby I included a species variable only if the species analysis was significant. Growth was modelled in linear mixed effects model, stipulating a Gaussian error distribution with distance from treeline, microsite neighbour object type (not vegetated, vegetated), microsite neighbour height, and species, if significant, as fixed effects and whether or not keas affected plant height as a random effect. In the 2007-2008 growing season, keas snapped the top off ten of the 45 nursery obtained seedlings planted above treeline and none of the seedlings obtained from below the treeline. The kea random effect was included because the reduction in height by keas could have affected subsequent growth. I used Akaike's Information Criterion with correction for small sample size (AICc; Burnham & Anderson 1998), to determine the best model out of all possible models containing distance, microsite height, microsite type, and their interactions. The best model was selected as the simplest model with the lowest AICc (Bohanec & Moder 1997). I retained any variables and interactions in the final model if they were significant. Analyses were conducted with the lme4 package (Bates & Maechler 2009) in R v. 2.10 (R Development Core Team 2008) with AICc and the number of parameters calculated directly using the AICcmodavg package (Mazerolle 2010).

In the final analysis, I evaluated the effect of treatment on growth (treatment model). As with the full growth model, a species fixed effect was included only if the species model was significant. This model included data only from the fourth transect. The effect of treatment (OTC, control), and distance from treeline on growth were evaluated with repeated measures ANOVA with an index of microsite location (1 to 15) to take into account the paired nature of treatments. An interaction between distance and treatment was considered but was not included in the final treatment model because it was not significant.

5.3.4.2 Mortality

Mortality was assessed separately for the two species and periods (growing season, dormant period). Seedlings were considered to have survived if at least one leaf or needle was alive at time of re-measurement and to be dead if missing for two consecutive census periods. The mortality probability was calculated for each time interval (December – March, April – November) to account for replacement of missing and dead seedlings throughout the study. The probability of mortality was considered a Bernoulli process in which the probability of each seedling not surviving to time t is a monthly probability, given t is in months. Mortality was modelled in a logistic regression model within a Bayesian framework. The mortality probability was linked to explanatory variables using a logit link function. Distance beyond treeline was standardized by dividing the variable by two times its standard deviation (Gelman & Hill 2007). This method allowed us to put the variable on the same scale as other variables but retain the original structure of the data. Categorical variables (treatment, microsite neighbour direction) were included by coding them as dummy variables and choosing one of the classes as a reference class with the coefficient set to zero (Gelman & Hill 2007). The effect of keas snipping off portions of seedlings was included within the variable seedling height because the kea would have affected survival through changes in height rather than directly killing the plant. This variable was more informative than including a kea random effect because it takes into account how change in height affect survival. Further details of the mortality model development are provided in Chapter 4.

The model was fitted using OpenBugs called from the BRugs library (Thomas *et al.* 2006) in R v. 2.10 (R Development Core Team 2008). I used non-informative prior distributions to reflect a lack of prior information about the model parameters, specifying a normal prior with variance 1000 for regression coefficients and a uniform prior in the interval 0-10 for variance parameters. I ran three chains each with a burn-in of 5000 iterations, which was sufficient to ensure convergence as judged by inspection of the chain histories, and then sampled the posterior distributions from a further 10 000 iterations of each chain. The importance of explanatory variables was assessed using 95% Bayesian credibility intervals on these posterior distributions. Further background on Bayesian hierarchical modelling is provided in Appendix C.

5.4 Results

The mean growing season (1st December 2007 - 31st March 2008) temperature 10 cm belowground at the treeline edge was 9.05 °C, which is well above expectations based on global patterns (Körner & Paulsen 2004). Above the treeline, the OTC were effective in increasing the mean daily temperature during the 2008-09 growing season. The mean daily soil temperature was significantly greater inside the OTC than outside (repeated measures ANOVA, $p < 0.05$) by, on average, 0.65 °C (Table 5.1). Mean growing season temperature decreased with distance beyond the treeline at a lower rate in control treatments (0.013 °C m^{-1}) than in OTC treatments (0.026 °C m^{-1}) although the difference in rate was not significant (repeated measures ANOVA, $p = 0.45$).

	Control	Warming (OTC)	Statistical significance of difference
	(n = 13)	(n = 14)	
Average temperatures (°C) December 1 2008 – April 9 2009			
Daily mean	9.88 ± 0.17 SE	10.53 ± 0.31 SE	F = 2.37†
Daily max	13.58 ± 0.13 SE	15.54 ± 0.04 SE	F = 13.36†
Daily minimum	7.38 ± 0.01 SE	7.48 ± 0.02 SE	F = 1.3
	Control	Warming (OTC)	Statistical significance of difference
	(n = 5)	(n = 4)	
Average temperatures (°C) June 3 – October 31 2009			
Daily mean	0.05 ± 0.01	0.51 ± 0.01	F = 56.51†
Daily max	4.29 ± 0.03	7.29 ± 0.02	F = 97.09†
Daily minimum	-2.18 ± 0.01	-2.34 ± 0.02	F= 9.94†
Absolute minimum	-9.0	-9.0	

Table 5.1: Mean iButton® Thermochron® data (01/12/08–09/04/09 and 03/06/09–31/10/09) for seedlings in control and OTC treatments. † indicate difference significant to $p < 0.05$

5.4.1 Growth

Differences in growth between species were evaluated for the eight unwarmed microsites in transects 3 and 4 in which both *N. solandri* and *P. contorta* seedlings survived. Growth, determined by relative basal area increment, varied minimally between species in 2008-2009 growing season (1.77 for *N. solandri* and 1.92 for *P. contorta*) but was more variable between 2009-2010 (2.63, 6.40 respectively). Overall, growth did not significantly differ between species (Paired t-test, t = -1.3119, df = 16, p = 0.208). Further growth analyses do not differentiate between species. In terms of height, which may be a better indicator of ability to reach tree height, results were more variable between species. *N. solandri* height decreased by, on average, 0.17 cm per month in 2008-2009 growing season and by 1.43 cm per month, on average, in the 2009-10 growing season. *P. contorta* seedling height during the same periods increased by 0.07 and 3.38 cm per month, on average. Vertical height growth was not retained in 83% (33/40) of *N. solandri* seedlings in the 2008 dormant period and 40% (12/30) of *P. contorta* seedlings.

Keas decreased the height of 10 of the 45 nursery obtained seedlings by, on average, 17 cm (12 - 30 cm) or 33% (17 - 60%) of the seedling starting height. No locally sourced seedlings were affected. The effect of the kea did not have a lingering effect; in the 2008-09 growing season, seedlings that had been snapped lost 0.47 cm on average, which is less than the average 0.7 cm lost by the rest of the seedlings in the same period.

Model	Log(L)	AICc	Δ AICc	k
BAI n = 114				
micHeight* micType	-187.38	366.95	0	5
distance+ **micHeight*micType**	-191.93	369.08	2.13	6
micHeight	-188.76	372.55	5.6	3
distance + micType + micHeight	-191.96	373.55	6.6	5
distance + micHeight	-193.27	374.50	7.55	4
micHeight* distance	-199.99	374.69	7.74	5
micType	-195.45	394.27	27.32	3
distance + micType	-200.40	396.41	29.46	4
micType* distance	-202.15	396.41	29.46	4
distance	-201.69	397.42	30.47	3

Table 5.2: Comparison of linear mixed effect models for growth. Log(L) is the log-likelihood. AICc is the Akaike Information Criterion with correction for small sample size and ΔAICc shows the difference between the model AICc and the lowest AICc for the model set. K, the number of parameters, is calculated directly using the R package AICcmodavg. Explanatory variables included are distance from treeline (distance), microsite neighbour height (micHeight), microsite neighbour type (micType; bare ground, vegetated). Whether or not seedling height had been lowered by keas was included as a random effect.

The best model for growth included an interaction between microsite height and microsite type (Tables 5.2, 5.3). Growth increased at a slower rate with microsite height for vegetated microsites compared with non-vegetated microsites (Fig. 5.2).

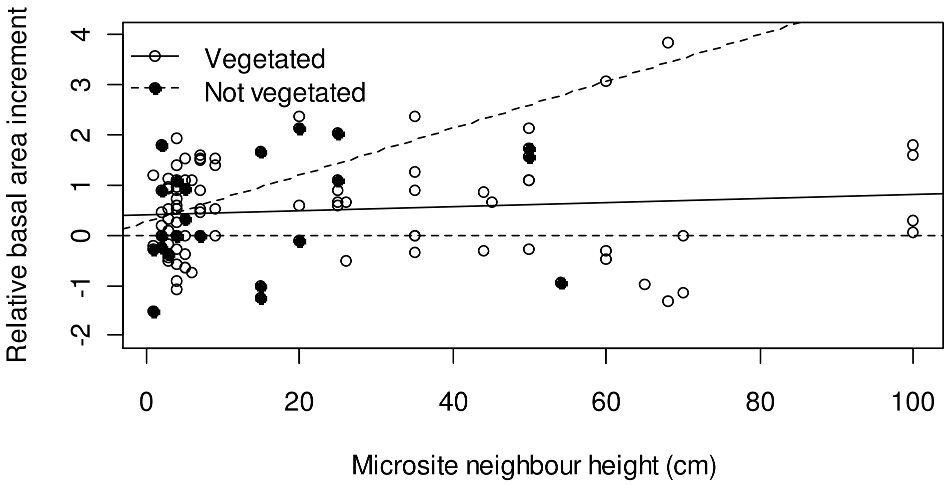

Figure 5.2: The relationship between basal area increment and microsite height for seedlings in vegetated (open circles, solid line) and not vegetated (filled circles, dashed line) microsites. Relationship was determined by regressing growth against microsite neighbour height.

Growth	Coefficient	SE	t-value
micHeight	0.0465	0.0152	3.068
micType	0.1377	0.4095	0.336
MicHeight*micType	-0.4256	0.0161	2.645

Table 5.3: Model coefficients and associated standard errors for the best model identified in Table 5.2. Explanatory variables included are distance from treeline (distance) and microsite neighbour height (MicHeight). † indicates that the variable was significant in the final model.

The treatment model uses growth from both species and does not include a species variable because growth did not significantly differ between species (Paired t-test, p = 0.208). Treatment and distance from treeline, whether included alone or as an interaction, were not significant in explaining growth (Table 5.4; p > 0.05).

	Temperature			Growth		
	Treatment	Distance	Residuals	Treatment	Distance	Residuals
df	1	1	2346	1	1	60
f- value	63.2	26.3		1.12	8.76	
p-value	0.001	0.001		0.293	0.635	

Table 5.4: P-values from the repeated-measures ANOVA of treatment and distance from treeline on temperature and growth. An index of microsite location (1 - 15) is the repeated factor.

5.4.2 Mortality

Analysis of mortality was limited to the 2008-2009 and 2009-2010 growing seasons because of perceived negative effects of transplanting. Mortality in the reciprocal transplanting experiment was 50% in the 2007-08 growing season, which is slightly lower than the 58% that died above treeline in the same period. No further mortality occurred in the reciprocal transplanting seedlings following the 2007-08 growing season. After the 2007-2008 growing season, seedling mortality in the growing season (2008-2009, 2009-2010) and dormant periods (2008, 2009) contrasted between species. *N. solandri* seedling mortality was greater in the growing season than the dormant period and *P. contorta* seedling mortality did not differ between seasons (Table 5.5). Between species, *P. contorta* seedlings were less likely to survive in the growing season and just as likely to survive the dormant period relative to *N. solandri* seedlings (Table 5.5).

N. solandri						
	Growing season			Dormant period		
	mortality probability	Sample size	number surviving	mortality probability	sample size	number surviving
Overall	0.677	81	64	0.891	123	74
Control	0.583	26	23	0.753	29	26
OTC	0.522	27	25	0.799	30	25
P. contorta						
	Growing season			Dormant period		
	mortality probability	Sample size	number surviving	mortality probability	sample size	number surviving
Overall	0.891	38	14	0.849	37	27
Control	0.880	20	8	0.692	22	17
OTC	0.819	20	11	0.831	19	18

Posterior estimates of the mean and credible intervals (CI) between species		
Mean	1.5710	-0.460
CI	0.8925 – 2.285	-1.217 – 0.202

Table 5.5: *N. solandri* and *P. contorta* seedling mortality probabilities for the 2008-09 and 2009-10 growing seasons and the 2008 and 2009 dormant periods along transects one to three (overall) and in the control and OTC treatments in transect four. Also shown is the posterior estimate of the mean and credible interval of the difference in mortality between species in unwarmed microsites in the growing season and dormant period. The results of this analysis are for the *P. contorta* seedlings relative to *N. solandri* seedlings; positive values indicate greater mortality in *P. contorta* relative to *N. solandri* seedlings. All values calculated directly from the data.

Microsite conditions influenced *N. solandri* mortality more than *P. contorta* mortality. In the growing season, *N. solandri* seedlings were less likely to survive in the eastern microsite direction relative to northern microsite direction (Fig. 5.3a). In the dormant period, seedling mortality was more likely to occur in taller microsites (Fig. 5.3a). No microsite conditions were significantly related to *P. contorta* mortality in the growing season and dormant period (Fig. 5.3b).

Distance from the treeline did not significantly affect *N. solandri* survival in either the growing season or the dormant period and exerted a positive effect on *P. contorta* survival in the growing season, whereby *P. contorta* seedling mortality decreased with distance beyond treeline in the growing season but did not have an effect in the dormant period. In the growing season, mortality was less likely to occur for taller *N. solandri* seedlings and, during the dormant period, mortality was less likely to occur for taller *N. solandri* seedlings and more likely to occur in taller *P. contorta* seedlings (Fig. 5.3).

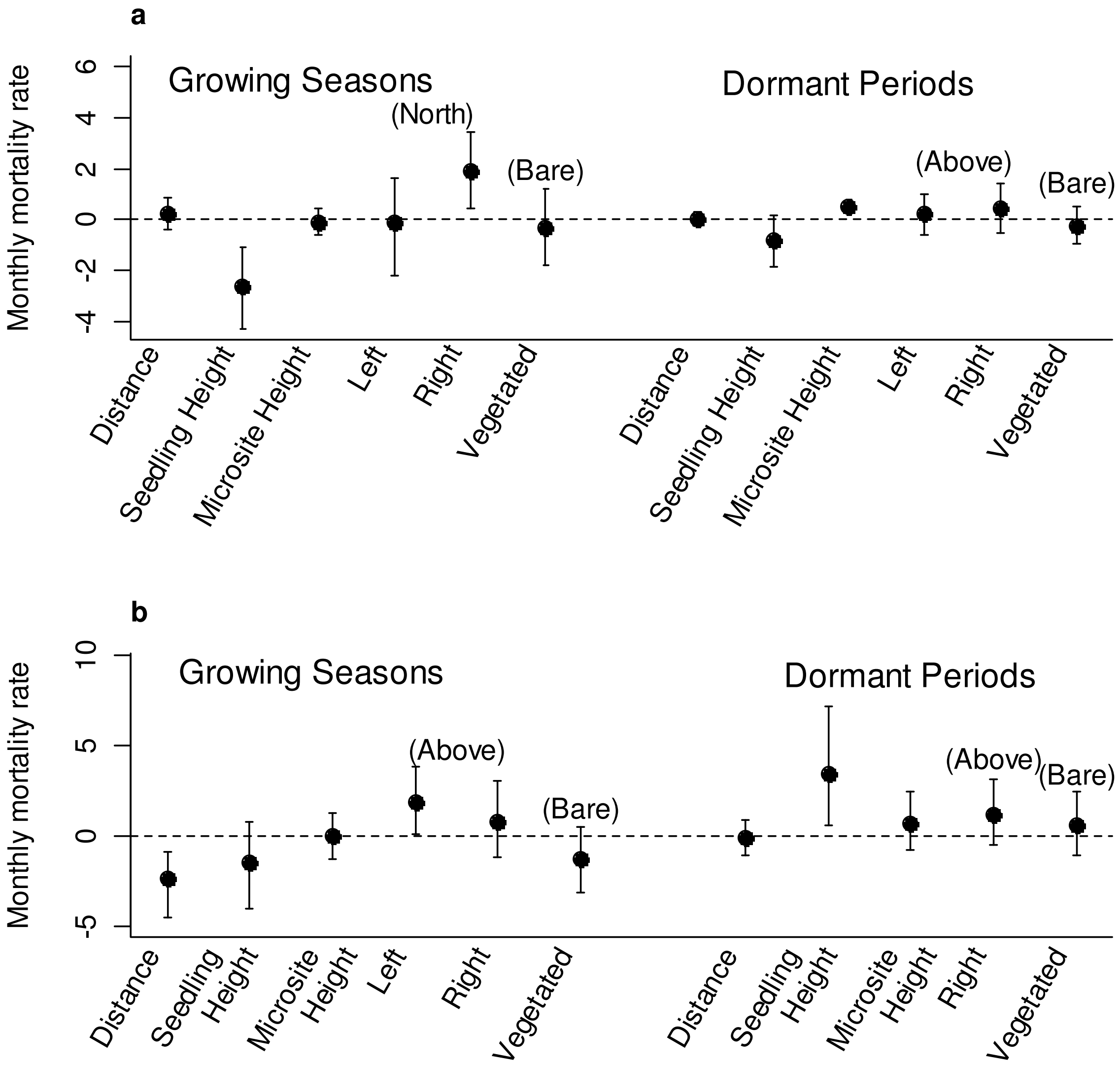

Figure 5.3: The mean and 95% credible intervals for the parameter estimates describing the effect of each explanatory variable on mortality for *N. solandri* (a) and *P. contorta* (b) seedlings in transects one-three (all microsites unwarmed). The parameter estimates for the levels of the factor variables are with regard to a reference class (shown in parentheses), which is set to zero. Credible intervals crossing the zero line (dashed) are not significant.

The interaction between distance and treatment was not significant in the treatment model. Results are shown for the model without interaction. Survival did not differ between control and OTC treatments for either *N. solandri* or *P. contorta* seedlings in either season although *P. contorta* mortality tended to decrease with further distance from the treeline edge in the growing season and in the OTC treatment relative to the control treatment in the dormant period (Table 5.5, Fig. 5.4).

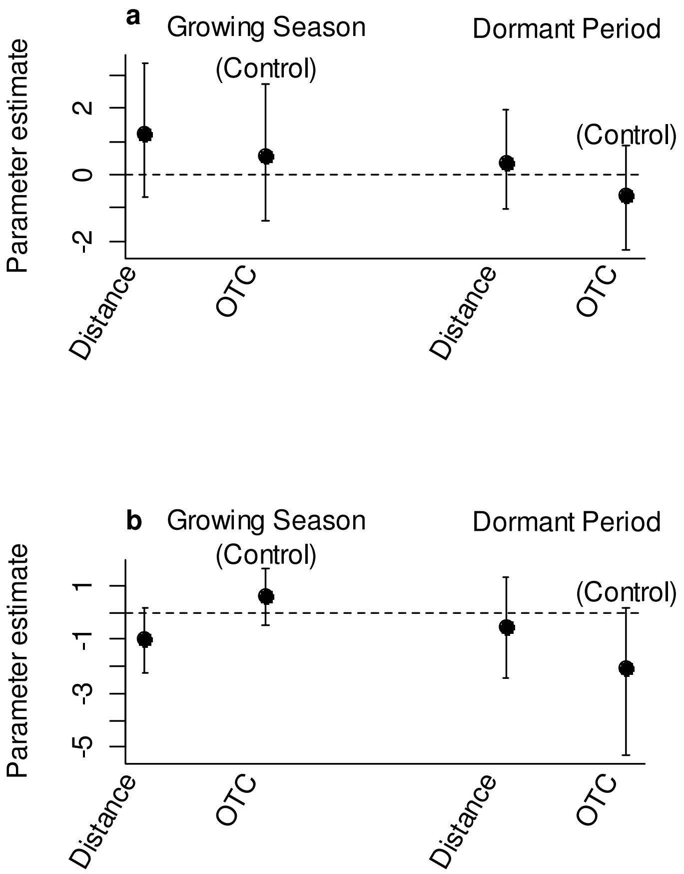

Figure 5.4: The mean and 95% credible intervals for the parameter estimates describing the effect of each explanatory variable on mortality for *N. solandri* (a) and *P. contorta* (b) seedlings in OTC and control treatments (transect four). The parameter estimates for the levels of the factor variables are with regard to a reference class (shown in parentheses), which is set to zero. Credible intervals crossing the zero line (dashed) are not significant.

N. solandri survival was lower in this study than in the 1968 multi-species trial. Between the beginning of December 2007 and the end of November 2009, 22 of 49 *N. solandri* seedlings survived in the first three transects. The annual survival probably of *N. solandri* survival was 0.67. In the 1968 trial, 8 of 9 seedlings transplanted at 1600 m in 27% light exposure survived the first two years of the experiment and 5 of the original 9 seedlings were surviving after four years. In the first two years, the annual survival probability was 0.943 and over the last four years the annual survival probability was 0.863. *P. contorta* survival was not reported.

5.5 Discussion

The *Nothofagus* treeline occurs at a mean growing season temperature of 9.05 °C, which is above the identified global tree life form mean growing season temperature limit (5 – 8 °C) (Körner & Paulsen 2004). The results of this study, however, indicate that low growing season temperature is not limiting seedling growth or survival; growth and survival did not decline with elevation or improve with passive warming. Prior trials of growth along elevation gradients exhibit no indication that growth significantly decreases with elevation (Norton 1984). Cold-temperature tolerance is also an insufficient explanation of low *Nothofagus* treeline position, *N. solandri* was just as likely to survive the dormant period as *P. contorta*.

The difference in performance between the two species must, therefore, relate to microsite conditions in the growing season, in which *N. solandri* was less tolerant of microsites with neighbouring objects to the right of the seedling and *P. contorta* was less tolerant of microsites with neighbouring objects to the left of the seedlings. Microsite with neighbours to the right are less effective in providing shelter from early morning sky exposure than neighbours above or to the right (Ball *et al.* 1991). Although both species are shade intolerant as trees, at the seedling stage, *N. solandri* is intolerant of high light exposure and *P. contorta* is tolerant of light exposure (Pfister & Daubenmire 1975; Wardle 1985b; Despain 2001). At high elevations, *N. solandri* intolerance to high light exposure may persist beyond the first few years of growth (Wardle 2008). The difference in tolerance to light exposure between species most likely relates to stem development. *N. solandri* stems and leaves extend rapidly and are less developed than slower growing *P. contorta* needles (Benecke & Havranek 1980), conferring a greater sensitivity for new *N. solandri* growth than *P. contorta* growth to frosts and desiccation during the growing season.

If *N. solandri* intolerance to light exposure at the seedling stage is limiting treeline position, then taxon-specific limitation should be evident as a lower overall survival probability for *N. solandri* than for *P. contorta* seedlings. However, *N. solandri* seedlings were just as likely to survive the dormant period as *P. contorta* seedlings and exhibited a lower growing season mortality probability than *P. contorta* (Table 5.5). The contrasting results of *N. solandri* and *P. contorta* seedling mortality in this trial with expectations of taxon-specific limitation and with the 1968 multi-species trial may have resulted because climatic conditions were too warm for *P. contorta*, because of natural microsite conditions, or because the presented results are ephemeral. *P. contorta* can survive in growing season temperatures > 20 ^{o}C (Thompson *et al.* 1999) and passive warming did not result in lower survival (Fig. 5.4b; Table 5.5), indicating that the relationship with distance was not due to changes in temperature. Planting *P. contorta* seedlings in microsites with neighbouring objects is not a sufficient explanation of initial survival rates, pine seedlings were able to grow beyond the confines of shelter in the 1968 study. Most likely, the high *N. solandri* survival relative to *P. contorta* survival during the growing season represents ephemeral patterns. Survival was positively related to *N.*

solandri stem size, which, in general, indicates greater resource reserves (Fig. 5.3). *N. solandri* seedling height decreased in both the growing seasons and the dormant periods, suggesting that resource reserves are being depleted and that survival should decline with time, as resource reserves accumulated prior to planting are lost or that *N. solandri* height is limited to the height of neighbouring vegetation (Table 5.3). Similar results were observed in the 1968 trial in which nursery obtained *N. solandri* seedlings grew faster than seedlings germinated *in situ* but growth converged as resource reserves of nursery obtained seedlings were depleted (Wardle 1985b). The absence of mycorrhizae above treeline may also affect *N. solandri* growth and survival above treeline. The presence of mycorrhizae was a significant factor in the long-term (> 4 years) survival of beech seedling planted above treeline in the 1968 trial (Wardle 1985b). It is possible that the low vertical growth rates and mortality are related, in part, to whether or not mycorrhizae are present. Seedlings obtained from below the treeline are likely to have mycorrhizal associations before transplanting and are unlikely to have been limited by an absence of mycorrhizae above treeline, however, naturally occurring recruitment may be (Baylis 1980).

The biggest difference between species in both the 1968 and this trial was their ability to grow. In both trials, *N. solandri* responded negatively to limited shelter and *P. contorta* responded positively. *N. solandri* seedlings planted in 1968 had still not grown beyond the confines of their shelter after 35 years whereas, after 6 years, *P. contorta* seedlings had grown beyond their shelter and reached over 2 m in height (Wardle 1985b, 2008). Taxon-specific tolerances may not limit survival at treeline but does influence which species could form a new treeline.

The greatest difference between *N. solandri* and *P. contorta* in survival occurred in the growing season. Growing season conditions were also important in limiting *P. engelmannii, Fagus sylvatica, Larix decidua*, and *Abies lasiocarpa* survival in the 1986 trial (Wardle 1985b). These four treeline forming species, plus *N. solandri*, all exhibited signs of damage following early season frosts (Wardle 1985b). Further damage and dieback from winter desiccation was also associated with early season frosts (McCracken *et al.* 1985). The only tree-forming species that was not affected by early season frosts, *P. contorta*, is infrequent at treeline within its native range (Despain 2001).

5.6 Conclusions

Globally, the treeline conforms to a single predictable temperature parameter, growing season temperature (Körner & Paulsen 2004). This is because the best adapted species to both summer and winter condition occur at the treeline (Jobbagy & Jackson 2000). Whether or not the treeline occurs below the expected thermal limit because better adapted species are not present has rarely been assessed. Introduced treeline forming species were planted above *Nothofagus* treelines in New Zealand and Patagonia. The introduced species survived and grew but the band of survival beyond treeline is not much greater than the maximum distance that the native *Nothofagus* species could survive (Wardle 1985b; Instituto Forestal 1986; Richardson & Higgins 1998; Wardle 2008). The greater difference between species occurred in vertical growth. If the definition of the treeline is the upper limit in which tree species will survive and grow to at least 2 m in height, then the *N. solandri* is unlikely to form a treeline at the expected thermal limit.

This study evaluated growth and survival of seedlings in natural microsites. Seedlings, however, do not naturally occur more than 20 m from the treeline edge and most seedlings occur within 5 m of the treeline edge (Table 4.5). Whether taxon-specific traits related to seed dispersal ability limit the *N. solandri* treeline below the expected elevation based on global patterns requires further evaluation. In Chile, *N. pumilio* is limited by seed dispersal and seedling emergence (Cuevas 2000). In Australia, *E. pauciflora* is limited by seedling establishment (Green 2009). Both treelines are considered to be below their potential thermal limit. In New Zealand, where two *Nothofagus* species can form treeline, the position of the treeline is limited by taxon-specific tolerances and the lack of species that can more readily establish and grow above treeline.

Chapter 6

Interspecific neighbour interactions influence *Nothofagus* seedling survival at treeline in New Zealand

6.1 Abstract

Interspecific plant interactions influence plant species' distributions and ability to respond to climatic change. The role of interspecific interactions in shaping the transition zone between forest and alpine zones (treeline) was assessed in New Zealand through observations of naturally occurring *N. solandri* seedlings above treeline and seedlings planted in experimentally manipulated microsite conditions (vegetation removal and passive warming). Naturally occurring seedlings occurred more often than expected based on microsite availability in microsites with shelter but less than expected in microsites with dense aboveground vegetation. I therefore expected survival of seedlings to be negatively affected by competitive interactions. However, seedling survival in manipulated microsites was greatest when neighbouring vegetation was retained. Experimental warming did not affect survival irrespective of whether vegetation was removed or retained. The results of the experimental work indicate that interspecific plant interactions are primarily facilitative and that climate warming should not alter interactions. The deviation in observed patterns in experimental manipulation of microsite conditions from naturally regenerating seedlings indicates that shelter is necessary for seedling survival but recruitment into sheltering microsites, possible during germination, may be limiting.

6.2 Introduction

Understanding the processes that limit plant species distributions is of long standing importance in ecology (MacArthur 1972; Gaston 2009). The relationship between climate and species' distribution is well established (del Barrio *et al.* 2006; Engler & Guisan 2009) and is frequently used to predict invasion success (Duncan *et al.* 2009) and future distributions in light of climate change (Hijmans & Graham 2006). The role of other factors, including physiological adaptations to abiotic stress (Chown & Gaston 1999) and interspecific plant interactions (Dullinger *et al.* 2005; Araújo & Luoto 2007), that could, at least partly, determine species' limits and explain why some species are responding to climatic changes but not others (leRoux & McGeoch 2008; Harsch *et al.* 2009), are insufficiently described.

Plant-plant interactions have significant influences on the ability of species to respond to changing climatic conditions. For example, facilitative interactions will facilitate expansion and competitive interactions will impede expansion of a plant species' distribution (Morin 1999; Suttle *et al.* 2007). Thus, as plant-plant interactions act along a continuum, bounded on either end by negative (competition) and positive (facilitation) interactions, that can fluctuate in time and space depending upon abiotic stress (climatic, resource), life stage and predation (Menge & Sutherland 1987), it is important to consider interspecific interactions in terms of abiotic stress along with climate when assessing the processes controlling current and future plant species' distributions.

Plant-plant interactions are rarely exclusively competitive or facilitative; the interacting plants may simultaneously experience competition and facilitation (Bertness & Callaway 1994). Here, I define the interactions by the net outcome of the interactions, focusing on the effect of the plant of interest. Facilitative interactions result in a net positive effect and competitive interactions in a net negative effect on the plant of interest. In both interactions, the effect of the interactions on the other plant is assumed to be negligible or positive.

Observed interspecific interactions do not always match expectations of the stress gradient hypothesis, in which plant interactions should be facilitative at high environmental stress and competitive at low environmental stress (Menge & Sutherland 1987; Callaway *et al.* 2002; Eränen & Kozlov 2008). There are several reasons for this. First, at extremely high levels of stress, the positive effects diminish and neighbouring plants may not be able to sufficiently modify microsite conditions for facilitation to occur (Michalet *et al.* 2006). Second, facilitative interactions are more likely to occur when the interacting species are at different life history stages (Schiffers & Tielbörger 2006; Sthultz *et al.* 2007; Leger & Espeland 2009). Species characteristics and resource needs differ throughout the developing stages of the species' life history such that species either need different resources or their means of resource acquisition are physically separated (Terradas *et al.* 2009). For example, in old-fields of North Carolina, herbaceous cover facilitated germination of woody species (De Steven 1991a) but also reduced survival and growth of woody seedlings (De Steven 1991b). The difference occurs presumably because germinating seeds are not competing with tussocks for soil resources but seedlings are (Breshears & Barnes 1999; McCarron & Knapp 2001). Third, interspecific interactions are more likely to be facilitative when species are dissimilar in competitive or stress-tolerance life histories (Maestre *et al.* 2009). For example, interactions between *Stipa tenacissima* and *Pistacia lentiscus*, both stress tolerant species, are competitive at both low and high rainfall regimes (Maestre & Cortina 2004) whereas the stress tolerant plant, *Taraxacum officinale*, facilitates the survival of the stress intolerant plant, *Cerastium arvense*, at the upper end of a temperature stress gradient (Badano *et al.* 2007). Finally, whether observed interspecific interactions are facilitative or competitive will depend upon the measure of plant performance. For example, interactions between the same two plants may be facilitative when measuring reproduction but competitive when measuring mortality (Travis *et al.* 2005). Careful consideration of the limiting life history stage is imperative when evaluating the role of interspecific interactions in controlling species distributions.

Here, I evaluated the role of plant-plant interactions in terms of treeline advance. Treelines are temperature sensitive boundaries of tree distribution (Daubenmire 1954; Cabrera 1996; Körner & Paulsen 2004). Therefore, treeline position is expected to shift to higher elevations or latitudes in response to climate warming (improved climatic conditions). Despite climate warming over the past century, upward shifts in treeline distributions are not ubiquitous (Harsch *et al.* 2009). Sufficient recruitment at or just below the treeline has been observed to suggest that recruitment above the treeline is ultimately limiting treeline expansion (Chapter 4; Camarero *et al.* 2000; Cuevas 2000; Ninot *et al.* 2008; Smith *et al.* 2009), with most emphasis being on seedling establishment rather than germination.

In this study, I evaluate the role of interspecific interactions on *Nothofagus solandri* var. *cliffortioides* seedling recruitment above treeline by characterizing patterns of natural recruitment and by modifying one form of climatic stress, low temperature. I focus on changes in temperature stress, the assumed primary limiting climatic factor. I assume that other abiotic and biotic stressors are either negligible, constant across the field sites or are indirectly related to changes in temperature. In discussing the role of plant-plant interactions, I focus on interspecific interactions, although the arguments also apply to intraspecific interactions.

The role of competition and facilitation in limiting *N. solandri* distribution has not been assessed nor has whether climate warming can be expected to decrease abiotic stress (e.g. low temperature, frost, desiccation) or not. To address these issues, I analyzed growth and mortality of seedlings in experimentally manipulated microsites and compare expected recruitment patterns based on experimental results with observed recruitment patterns of naturally recruited seedlings above treeline. Microsites were manipulated by removing vegetation and by passive warming. If competitive interspecific interactions limit treeline position and recruitment above treeline, then mortality should be lower in microsite where vegetation was retained than where removed and the reverse if interactions were facilitative. If interactions are facilitative under current temperatures, I expected that passive warming would shift interactions from facilitative to competitive if warming is the primary abiotic stress agent and sufficient warming occurs to decrease abiotic stress. Of course, a change in interactions may not be evident with climate warming if the degree of warming achieved is not sufficient to decrease temperature stress or low temperature is not limiting (directly or indirectly).

6.3 Methods

6.3.1 Field sites

Natural recruitment patterns above treeline were assessed across seven transects in five regions of the South Island, New Zealand, which differed distinctly in climate regime, soil parent material and alpine vegetation (Fig. 4.2, Table 6.1). Transects were chosen based on representativeness of the region and ease of access (Wardle *et al.* 2006). The treeline is composed of either *Nothofagus solandri* var. *cliffortioides* (four transects) or *Nothofagus menziesii* (one transect) or a mixture of both species (two transects). Dominant vegetation patterns above treeline vary from dense tussock-shrub mosaics with no bare soil to a mixture of tussock, shrub and bare soil. Areas of bare soil above treeline result from avalanche, frost heave or scree disturbance. Further description of the transects are provided in Chapter 4.

Mean annual temperature is warmest and recruitment greatest at the most easterly located of the seven transects, Craigieburn, so a shift in treeline position is most likely to occur at this transect. As a clear shift in treeline position has thus far not occurred (Chapter 4), Craigieburn is the best of the seven transects to determine if interspecific interactions are limiting recruitment beyond treeline. Direct testing of interspecific biotic interactions was conducted close to the existing long-term research transect in Craigieburn Forest Park (43°11' S, -171° 71' E). All experiments were conducted on a southeast facing aspect 10 m before the start of the long-term research transect. The treeline at Craigieburn is composed solely of *N. solandri*. Further description of the field site is provided in Chapter 5.

Site	Elevation (m)	Aspect	Mean annual temperature (°C)	Total annual precipitation (mm)	Dominant vegetation
Haast East	1220	e	4.67	1794.7	Dense scrub
Haast West	1240	s	4.53	1794.7	Rocky outcrop, soil
Faust	1328	ssw	5.18	2137.9	Shrub-tussock- soil mosaic
Craigieburn	1350	se-sw	5.72	1866.8	Interrupted by scree fields
Maori Saddle	1082	sw	4.80	3920	Dense scrub and tussocks
Takahe East	1100	ne	4.11	1744.6	Fern
Takahe West	1106	ssw	4.11	1744.6	Grassland with scrub

Table 6.1: The mean annual temperature and total annual precipitation in Haast East, Haast West, Faust, Craigieburn, Maori Saddle, Takahe East and Takahe West based on monthly mean climate records from the nearest temperature station to each transect. Temperature stations are not located at treeline and vary in elevation and distance from the treeline transects. The effect of difference in elevation on temperature was corrected for by using the lapse rate 0.66 °C/100 masl (Norton 1985). Precipitation could not be corrected for and is likely to be underestimated, especially at Takahe East and West.

6.3.2 Natural regeneration

The area between the treeline edge and 10 m above treeline were searched along all seven transects (86 - 549 m in length) in 2007 for all seedlings (< 1 cm diameter). Observation error (seedlings missed at time of census) was estimated to be less than 10%, based on the number of individuals greater than 50 cm observed in 2007 that were not recorded in 2002 and, therefore, most likely having established prior to 2002. Microsite was also described for at least half of the seedlings found along each transect in 2007. Full microsite sampling was not accomplished because this portion of data collection was irregularly overlooked. Evaluation of the location of seedlings in which microsites were overlooked revealed that missing data were most common in transects with the greatest number of recruits: Craigieburn, Faust and Haast West. Within a transect, microsite data were recorded for at least half of all seedlings found within a sector except at two of nine Craigieburn sectors, two of 13 Faust sectors, two of seven Haast West sectors, one of five Haast East sectors and one of 11 Maori Saddle sectors. At the sectors in Faust, Haast East and Maori Saddle with missing data, only one seedling was observed within the sector. These sectors were removed from subsequent analyses. There was no difference in the distance along the transects and from the treeline of seedlings for which microsites were described and not described. I, therefore, did not remove sectors in which missing data was present if microsite conditions were described for at least half of the seedlings present.

Microsites were defined as the 10 cm radius surrounding a seedling and were grouped into seven classes: 1) exposed -in soil without a sheltering object such as a rock, bank, or rocky outcrop; 2) eroded bank -including eroded banks and below rocky outcrops; 3) rock or boulder -directly next to a large rock or boulder of at least 20 cm in height, does not include rock scree; 4) *Nothofagus* tree -seedling or sapling located under the canopy of a tree of at least 2 m in height located above treeline edge; 5) shrubs -seedling located within the cover of low-statured shrubs; 6) tussock -seedling located directly within the cover of *Chionochloa* species; 7) other -including ferns, alpine mat vegetation, and rock scree.

Microsite availability along a transect was described for the first 10 m above the treeline edge because prior analysis indicated that the majority (90%) of recruitment occurs within 10 m of the treeline edge (Table 4.4). I visually assessed the percentage of microsites along each transect that were exposed, eroded bank, tussock, shrub, rock, *Nothofagus* trees above treeline, or other.

Microsite preference was assessed for each transect by comparing observed patterns in microsite occupancy with estimated microsite availability. Occupancy within a transect was calculated for each microsite type as the percent of all seedlings found along the transect occurring within the microsite type. Microsite availability was calculated for each transect as the average estimated percentage of microsites within each microsite type. Microsite preference was then determined as the ratio of occupancy to availability. Microsite type was considered preferred if percent occupancy was greater than percent availability, evaluated using chi-square tests (Alldredge & Ratti 1992).

6.3.3 Experimental observations

The type of interspecific interactions were evaluated by transplanting 40 *Nothofagus solandri* var. *cliffortioides* seedlings from below the forest canopy into specific vegetated microsites within 5 m of the treeline edge. Experimental manipulation was conducted within 5 m of the treeline edge because 90% (281/311) of naturally occurring seedlings at the long-term Craigieburn transect occurred within 5 m of the treeline edge (Chapter 4). Seedlings were chosen from below treeline because an insufficient number of naturally seeded seedlings were found above treeline. Neighbouring vegetation was limited to the three most common alpine plants, a tussock (*Chionochloa pallens*) and two common short-statured shrub species

(*Dracophyllum uniflorum*; *Podocarpus nivalis*). Seedlings were transplanted in January 2008 and monitored through March 2010.

N. solandri seedling response (growth, mortality) to interspecific interactions with the three common alpine species and temperature stress were tested by manipulating neighbouring vegetation (*C. pallens*, *D. uniflorum*, *P. nivalis*) cover and temperature within microsites. Vegetation was removed by clipping all aboveground growth at the start of the experiment. Reclipping of vegetation was not necessary over the duration of the study. Belowground vegetation was retained in order to minimize soil disturbance and because *N. solandri* seedlings are more often limited by competition for space than resources (Wardle 1984) and facilitation is primarily an aboveground effect (Germino *et al.* 2002). Temperature was warmed passively using open top chambers (OTC). OTC were constructed from three 2 mm thick acrylic sheets. Each sheet was 0.5 m in length along the bottom edge, 0.33 m along top edge and cut at a 60° angle at each side. The open top design of the OTC allows precipitation to reach seedlings but has the side effect of decreasing wind-exposure and possibly providing shelter from early-morning solar radiation. Further details of OTC design and construction are provided in Chapter 5.

Four treatment conditions were established: control (vegetation intact, not warmed), control+OTC (vegetation intact, passive warming), vegetation removal (vegetation clipped, not warmed), and vegetation removal+OTC (vegetation clipped, passive warming). Treatments were grouped in ten experimental blocks with one replicate of each treatment in each block. Slope and vegetation were controlled for within each block. Vegetation was *C. pallens* in four treatment blocks and *D. uniflorum* and *P. nivalis* in three treatment blocks each. In total, 40 seedlings were transplanted, four treatments per experimental block and ten experimental blocks.

Seedlings were obtained from just below the treeline edge and transplanted in January 2008 into one of four treatment conditions. In the control and control+OTC treatments, seedlings were transplanted as close to the tussock rootmat or shrub main stem as possible. In vegetation removal and vegetation removal+OTC treatments, seedlings were planted as close to the centre of the now removed vegetation as possible. Transplantation stress was minimized by retaining as much of the root mat and soil surrounding the seedlings as possible.

Height and diameter of seedlings were recorded at time of transplanting and subsequently at the beginning of each season (December, April) through March 2010. Height was measured with a metre-ruler to the nearest 1 mm and diameter was measured with callipers to the nearest 0.1 mm. Survivorship was assessed at the beginning of each season (December, April). Dead seedlings were replaced in April and December 2008, following the first growing season and dormant period.

Effectiveness of chambers in warming temperature were monitored with iButton® Thermochron® temperature loggers (Dallas Semiconductor Corporation, Dallas, TX, USA) between the first of January 2009 and the 31st of March 2009. Dataloggers were placed 10 cm belowground in each microsite of five treatment blocks during the growing season. Temperature was logged hourly. During the dormant period, temperature differences between treatments were monitored aboveground to assess stress related to snow cover duration. Warmer treatments were expected to exhibit lower snow cover and therefore expose seedlings to colder temperatures. Further details on OTC and dataloggers are provided in Chapter 5.

To identify difference in the number of days with snow cover at least 10 cm aboveground, iButton® Thermochron® dataloggers were placed 10 cm above soil surface between the 3rd of June 2009 and 31st of October 2009 in a control and a control+OTC treatment. Dataloggers were installed after the first snowfall (early May 2009) and were not present throughout the entire snow period. Snow cover at least 10 cm aboveground was determined by the degree of temperature variation aboveground, where temperature variation of less than 1 ºC over a 24 hour period indicates snow cover (Jones *et al.* 2001).

6.3.4 Analysis

The effect of treatment (control, vegetation removal, control+OTC, vegetation removal+OTC) on temperature during the growing season was evaluated using analysis of variance with temperature as the response function, treatment as the predictor and experimental block as a random effect. Treatment was included as categorical variable with four categories: control, control+OTC, vegetation removal, vegetation removal+OTC. Significant treatment differences were further evaluated using Tukey's honest significant difference test (TukeyHSD).

An insufficient number of seedlings in the control+OTC and vegetation removal treatments survived for comparison of growth so analysis is limited to survival. Survival was evaluated for each time interval and included the 2008 and 2009 dormant periods and the 2008-2009 and 2009-2010 growing seasons. This allowed me to take into account replacement of dead seedlings in November 2008. Seedlings were considered to have survived if at least one leaf was alive at time of re-measurement.

For each period, seedlings were coded as being alive (1) or dead (0). These data were then modelled as if they represented draws from a Bernoulli distribution in which the outcome, S (whether a seedling was alive or dead), after t months was related to the monthly probability of mortality, m, during that period:

$$S \sim Bernoulli(1-m)^t \qquad \text{eqn 6.1}$$

The monthly probability of mortality was then related to explanatory variables using a logit link function to constrain the probabilities to between 0 and 1. Mortality was modelled in relation to the categorical variable treatment (control, control+OTC, vegetation removal, vegetation removal+OTC) and the categorical variable microsite vegetation type (tussock, shrub). Categorical variables were included by coding them as dummy files and choosing one of the classes as a reference class (control treatment, tussock vegetation) with the coefficient set to zero. I also included an experimental block random effect (included as an index of experimental block from 1 to 10) to take into account that replicates were grouped in blocks. The effect of each experimental block was assumed to be drawn from a normal distribution with a mean of zero and a standard deviation estimated from the data (Gelman & Hill 2007). Interactions between treatment and vegetation type were not evaluated because there were insufficient replicates of each treatment within a vegetation type to evaluate interactions. The theoretical underpinnings of the mortality analysis and model formulation are provided in Chapter 4.

The model was fitted using OpenBugs called from the BRugs library (Thomas *et al.* 2006) in R v. 2.10 (R Development Core Team 2008). I used non-informative prior distributions to reflect a lack of prior information about the model parameters, specifying a normal prior with variance 1000 for regression coefficients and a uniform prior in the interval 0-10 for variance parameters. I ran three chains each with a burn-in of 5000 iterations, which was sufficient to ensure convergence as judged by inspection of the chain histories, and then sampled the posterior distributions from a further 10 000 iterations of each chain. The importance of explanatory variables was assessed using 95% Bayesian credibility intervals on these posterior distributions. Further information on model development and interpretation are detailed in Chapter 4 and Appendix C.

6.4 Results

6.4.1 Natural regeneration

Seedling occupancy in eroded banks was greater than availability at all transects except Takahe East, the only transect in which no eroded bank microsites were available (Fig. 6.1,

Table 6.2) and greater than expected in *Nothofagus* tree microsites, where available, except at Haast West. Occupancy was below availability in the bare soil microsite at all transects and was variable, relative to availability, for all other microsites classes. Across all transects, the eroded bank microsite represented 4% of the available microsites yet, overall, 43% of the seedlings were found in eroded banks. Occupancy in shrub and tussock microsites, although high, was still below expectations based on availability. Occupancy in exposed and rock microsites was also below availability (Fig. 6.1). Occupancy in the "other" microsite class is not shown as no seedlings occupied this microsite class.

	No seedlings	χ^2	df
Site			
Haast West	55	1088.7	5
Haast East	20	101.1	5
Faust	7	1312.3	5
Craigieburn	104	251.9	5
Maori Saddle	8	1938.9	5
Takahe West	38	199.7	5
Takahe East	6	54.5	5
Overall			
Exposed	13	23.26*	6
Eroded bank	129	$3487^{\dagger}$	6
N. solandri tree	18	$55.96^{\dagger}$	6
Rock	17	31.06*	6
Shrub	70	243.8*	6
Tussock	54	106.1*	6

Table 6.2: Comparison of microsite availability and microsite seedling occupancy along each transect based on chi-square tests. *Indicates that microsite occupancy is significantly underrepresented and †indicates that microsite occupancy is significantly overrepresented based on chi-square tests.

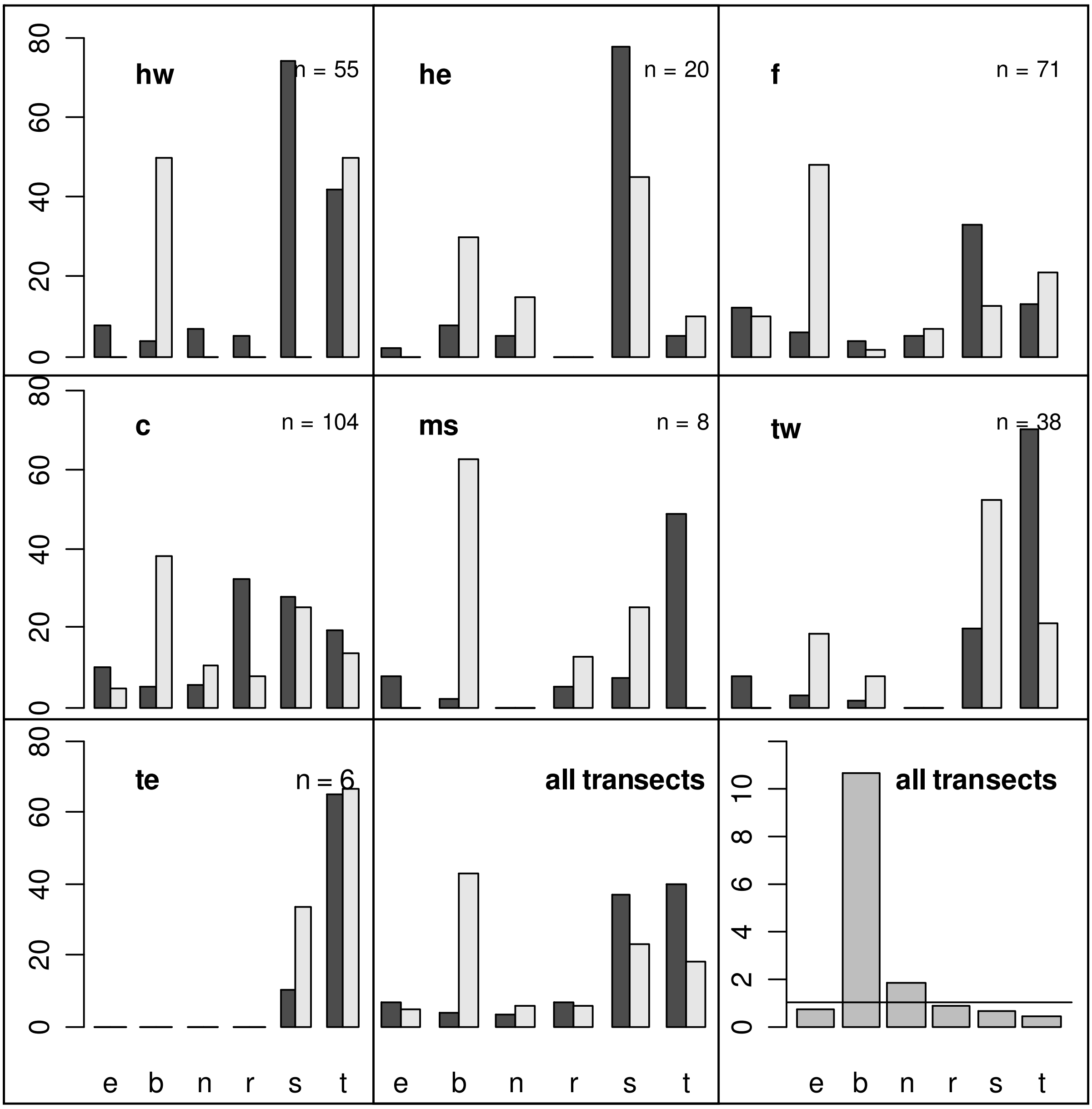

Figure 6.1: Seedling microsite availability (dark grey bars) and microsite occupancy (light grey lines) within each of the six microsite types for each transect and across all transects. Within each transect, microsite occupancy is considered over represented if occupancy is greater than availability. The lower right graph shows the ratio of seedling microsite occupancy:microsite availability. Transect codes are: Haast West (hw), Haast East (he), Faust (f), (Craigieburn (c), Maori Saddle (ms), Takahe West (tw), Takahe East (te). Microsite type codes are: exposed (e), eroded bank (b), *N. solandri* tree above treeline (n), rock/boulder (r); shrub (s); tussock (t). The "other" microsite class is not shown because of its low occurrence within and between transects.

6.4.2 Experimental observations

Temperature differences between the vegetation removal and vegetation removal+OTC treatments and the control and control+OTC treatments were most pronounced late afternoon to early evening and weakest late morning (Table 6.3). The warmest temperatures were in the vegetation removal+OTC treatment and the coldest temperature in the vegetation removal treatment (Table 6.3). The mean daily temperature between December 2008 and April 2009 differed significantly between treatments (ANOVA, F = 24. 9, $p < 0.05$). The mean daily temperature was significantly warmer in the vegetation removal+OTC treatment than all other treatments (TukeyHSD, $p < 0.05$; Fig. 6.2). The vegetation removal treatment was warmer than the control and control+OTC treatments during the daylight hours (Table 6.3) but the additional warmth was not retained through the night (TukeyHSD, $p > 0.05$, Fig. 6.2).

	Control	Control+OTC	Vegetation removal	Vegetation removal+OTC
	(n = 5)	(n = 5)	(n = 5)	(n = 5)
Average temperatures (°C) January 1, 2001 – March 31, 2009				
Daily mean	10.55 ± 0.21 SE	10.31 ± 0.22 SE	11.00 ± 0.26 SE	12.59 ± 0.22 SE
Daily max	13.58 ± 0.29 SE	14.35 ± 0.30 SE	16.38 ± 0.41 SE	19.03 ± 0.48 SE
Daily minimum	8.43 ± 0.15 SE	7.58 ± 0.15 SE	8.09 ± 0.20 SE	8.88 ± 0.20 SE
	Control	Control+OTC		
	(n = 1)	(n = 1)		
Average temperatures (°C) June 3 – October 31, 2009				
Daily mean	0.28 ± 0.21 SE	0.67 ± 0.24 SE		
Daily max	3.65 ± 0.52 SE	5.09 ± 0.58 SE		
Daily minimum	-1.73 ± 0.14	-1.91 ± 0.18		
Snow period				
Mean snow-off date	October 10th	September 30th		
Snow occurrence (days)	39	46		
Snow melt events	5	6		

Table 6.3: Average daily mean, max and minimum temperature (°C) in each treatment during the growing season and the average daily temperature and snow occurrence in control and control+OTC treatment in the dormant period. Temperature measurements determined using data collected from Thermochron ibutton dataloggers.

Snow cover at 10 cm aboveground ended on October 10th 2009 in the control treatment and September 30th 2009 in the control+OTC treatment. Intermittent periods of decreased snow cover (less than 10 cm) were evident throughout the dormant period. During the recorded time period in which snow was present 10 cm aboveground (June 3rd – October 15th), removal of snow to below 10 cm by snowmelt or wind redistribution was observed five times in the control treatment and six times in the control+OTC treatment. Snow cover to 10 cm aboveground occurred on 39 days in the control treatment and 46 days in the control+OTC treatment (Table 6.3).

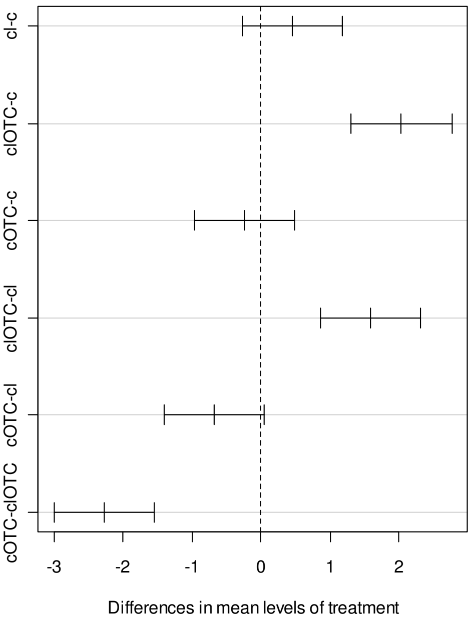

Figure 6.2: 95% confidence intervals of differences in mean daily temperature for December 2008 through March 2009 between treatments. Confidence intervals that do not overlap zero are considered significantly different. Legend symbols are: control (c); control+OTC (cOTC); vegetation removal (cl); vegetation removal+OTC (clOTC).

Treatment significantly influenced seedling mortality. In both the growing season and dormant period, seedling mortality was greater in the vegetation removal and vegetation removal+OTC treatments relative to the control treatment (Fig. 6.3a; Table 6.4). There was no difference in mortality between the control and control+OTC treatments in either season (Fig. 6.3; Table 6.4). Seedling mortality did not differ in *D. uniflorum* and *P. nivalis* microsites relative to C. *pallens* microsites in either the growing season or dormant period (Fig. 6.3; Table 6.4). Seedling mortality in was lowest in the control treatment in the dormant period (0.331) and growing season (0.047).

	Growing season			Dormant Period		
	Mortality probability	Number of seedlings transplanted	surviving	Mortality probability	Number of seedlings transplanted	surviving
Control	0.331	16	10	0.047	16	12
Removal	0.610	15	4	0.180	18	6
Removal+OTC	0.803	11	1	0.410	13	1
Control+OTC	0.518	14	6	0.082	13	8

Table 6.4: Monthly mortality probability for transplanted seedlings in each treatment in the growing seasons (2008-09 and 2009-10) and dormant periods (2008 and 2009). Monthly mortality probabilities are calculated from the models used to generate Figure 6.4.

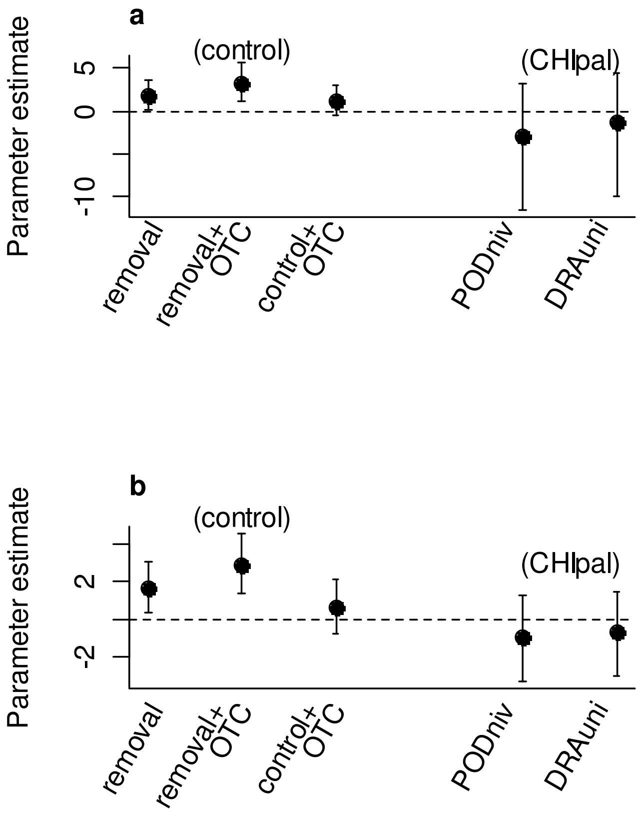

Figure 6.3: The mean and 95% credible intervals for the parameter estimates describing the effect of each explanatory variable on the monthly probability of mortality during the growing season (a) and the dormant period (b). The parameter estimates for the levels of the factor variables are with regard to a reference class (shown in parentheses), which is set to zero. Credible intervals crossing the zero line (dashed) are not significant.

6.5 Discussion

The results of the transplantation experiment indicate that tree seedling interactions with three common alpine plants, *D. uniflorum, P. nivalis* and *C. pallens*, tended to be facilitative in both the growing season and dormant period. Passive warming did not significantly affect survival rates beyond the effect of vegetation removal. The abiotic stressor limiting seedling survival to facilitative microsites is not clear but most likely relates, during the growing season, to seedling intolerance to direct day or night sky exposure (Wardle 1985b). Newly emerged *N. solandri* seedlings are sensitive to desiccation and older stems to frosts (Wardle 1974; Wardle 1985b). Cold induced photoinhibition limits seedling survival at treeline in Wyoming, USA, and the Yukon, Canada and high solar radiation induced photoinhibition limits survival in Ecuador (Germino & Smith 1999; Bader *et al.* 2007b; Danby & Hik 2007a). Tussock provides *Eucalyptus pauciflora* seedlings shelter against frosts in Australia (Ball *et al.* 1997) and shrubs provide *Pinus ponderosa* seedlings protection from desiccation in the Cascade Range, USA (Keyes *et al.* 2009).

Interspecific interactions are considered to be less important during the winter months than the growing season because plants are not competing for resources and snow cover provides shelter but, in New Zealand, where snow cover can be quite variable (Table 6.3), interspecific interaction may be critical for survival (Fig. 6.3b). In the Yukon, Canada, seedlings at treeline sites with low snow cover experience high winter desiccation whereas seedlings with high snow cover do not (Danby & Hik 2007b). In windblown sites of the Rocky Mountains, USA, and the Spanish Pyrenees, seedling recruitment occurs most often within the shelter of Krummholz (short, twisted trees; Weisberg Baker 1995; Camarero *et al.* 2000; Batllori *et al.* 2009), presumably because Krummholz provide shelter from the negative effects of wind (Cairns 2001).

The importance of facilitative interspecific interactions for seedling survival is confirmed in naturally recruiting populations, *N. solandri* seedlings exhibit clear preferences for microsites providing shelter; seedling occupancy was underrepresented in the exposed microsites, amongst rock scree or vegetation with sparse canopy ("other" microsite class). However, seedling occupancy was below availability in tussock and shrub microsites, indicating that seedlings are not getting into potentially suitable and readily available microsite classes. The lower than expected occurrence in tussock and shrubs is unlikely to result from competitive interactions at the seedling stage; root traits of tussocks and trees native to New Zealand make them less likely to compete (Meurk *et al.* 2002; Walker *et al.* 2003) and experimental manipulation indicates that shrubs and tussocks facilitate seedling survival (Fig. 6.3).

The prevalence in bare soil microsites and underutilization of tussock and shrub microsite types may indicate that germination or seedling emergence may be limiting seedling occupancy in potentially suitable microsites. In New Zealand, *N. solandri* seeds will germinate 300 m above treeline in sheltered bare soil microsites (Wardle 1985b), so germination ability above treeline is not limiting. However, germination in the most vegetated microsites (e.g. tussock, shrub) has only been assessed below treeline, where germination is poor in dense litter (Wardle 1984). This is because seed stores are insufficient for cotyledons to extend past dense aboveground vegetation or for germination radicles to penetrate through dense organic matter or root masses (Wardle 1984). Similarly, in the Alaskan tundra, removal of belowground competition was critical for recruitment to occur (Hobbie & Chapin 1998).

6.6 Conclusions

The discrepancy between naturally occurring seedling microsite occupancy and survival in modified microsites raises two important considerations when evaluating the role of interspecific interactions in species distributions. First, interactions are life-stage dependent. Germination in tussock and scrub microsites has not been tested above treeline but, from trials below the canopy, there are strong indications that these microsites classes are unlikely to be suitable. Thus, although the microsites are suitable or even favourable for seedlings they are unlikely to promote forest expansion.

Second, the availability of suitable microsites from seed germination to tree establishment will have a strong influence on tree species distributions and recruitment patterns (Šrůtek *et al.* 2002; Resler *et al.* 2005; Anschlag *et al.* 2008). For example, recruitment is limited to boulders and terrace risers in the Glacier National Park (Resler *et al.* 2005) and to Krummholz in the Rocky Mountains (Bekker & Malanson 2008). Given the low occurrence of preferred microsites, those with bare soil and shelter, treeline expansion may be strongly limited by the lack of suitable microsites. If limitation occurs at the germination stage and the interspecific interaction is competitive, as it appears to be based on trials below the canopy (Wardle 1984), then decreases in climatic stress or abiotic stress are unlikely to result in greater recruitment rates (Menge & Sutherland 1987). Disturbances that create sheltered bare soil microsites, such as frost heave or debris slides, may be more critical for *Nothofagus* treeline advance than climate warming.

Chapter 7
General Discussion

The aim of this PhD study was to evaluate current and future treeline position relative to climatic conditions by 1) using global patterns to assess the mechanisms controlling treeline dynamics and pattern, 2) investigating the role of the identified mechanisms in controlling treeline form and processes at an abrupt treeline, and 3) evaluating the appropriateness of using treeline form to indicate the mechanisms causing and maintaining treeline formation and position. Although the effects of land-use, natural disturbance and orographic and edaphic features are important, these factors tend to limit treelines below the potential climatic limit, mask potential response to climate change and hinder identifying how species traits and plant-plant interactions affect the ability of plant species to track changing climatic conditions. Thus, I have focused on climatic limits and largely ignored the effect of land-use, natural disturbance and local orographic and edaphic factors.

7.1 Treeline dynamics

Change in treeline position was assessed globally to determine the mechanisms causing treeline formation and controlling treeline dynamics (Chapter 2). As expected based on previous assessments of global patterns (Körner & Paulsen 2004), global treeline dynamics are controlled by temperature. In contrast to expectations, recruit ment beyond the treeline was influenced more by winter temperature than summer temperature. The discrepancy is due, in part, to the definition of the treeline. Prior assessments of the relationship between treeline position and elevation have focused on the upper limits of single-stemmed trees, thereby excluding tree species exhibiting a Krummholz growth form. Abrupt treelines are either rare or are not included because they were deemed to be disturbed or taxon-specific. If only diffuse treelines are considered, then treeline response is closely linked to annual warming. However, if all possible minimally disturbed treeline forms are considered, then the effect of temperature on treeline dynamics is more complex. The discrepancy may also result from an inherent publication bias whereby treeline advance is more likely to be published than non-advance. The meta-analysis potentially overcame this limitation by including papers that did not explicitly study advance.

By considering treeline form, I was able to evaluate why treeline response to climate warming differed from expectations. In particular, I was able to identify which processes limit tree species ability to respond to climatic change and identify potential causal mechanisms (Chapter 3). As expected from previous research, diffuse treelines appear to be limited by ability to grow, abrupt treelines by seedling mortality and Krummholz by dieback (Wiegand *et al.* 2006). Growth, by definition, is limited by growing season conditions whereas mortality and dieback can be limited year-round. These results are consistent with expectations from Chapter 2, in which diffuse treelines responded to annual warming and abrupt, island and Krummholz to winter warming. These results indicate that the mechanisms shaping the structure and position of current treeline distributions may also be indicative of the tree species' ability to respond to climatic changes. The framework developed in Chapter 3 provides a series of testable hypotheses regarding the mechanisms controlling treeline formation and treeline dynamics. In the next few paragraphs, I use the abrupt *Nothofagus* treeline in New Zealand to demonstrate the applicability of the framework in understanding tree formation and dynamics and in developing testable hypotheses.

Testable hypotheses relate to the potential for treeline position to track climatic change, what mechanism affecting plant performance is controlling current and potential treeline position, which climatic conditions are limiting, which species traits are critical in determining potential position and how plant-plant interactions influence potential position. Based on the framework, I hypothesize that the abrupt *Nothofagus* treeline in New Zealand will be 1) relatively stable in position, 2) limited at the first-level (tree performance) by seedling mortality, although growth limitation and dieback will also be evident but to a lesser extent than seedling mortality, 3) the primary second-level mechanism (stresser) is unlikely to be related to low temperature and ability to grow (negative carbon balance, slow biosynthesis) or stem lost (breakage), 4) *Nothofagus solandri* var. *cliffortioides* and *Nothofagus menziesii* should be shade dependent or at least shade tolerant during the early stages of development but not necessarily as trees, and 5) the third-level mechanism (neighbour interactions) should be facilitative, with positive feedback being evident.

Results from the seven permanent transects indicate that the *Nothofagus* treeline, even if initiating treeline advance, has been relatively stable (Chapter 4). Recruitment is occurring above treeline but recruitment is limited to within 5-10 m of the treeline edge and, after 15 years of monitoring and a century of climate warming, it is still not clear if the treeline is advancing. In terms of the first-level mechanism limiting tree performance, this study indicated that recruitment, not growth or mortality, were limiting treeline position and dynamics. Because of the intermittent nature in which the treeline was monitored, I could not readily measure seedling mortality, especially during the stage when the majority of mortality occurs, the first couple of years. In this study, mortality referred to mortality across all size classes, with mortality most likely to occur in smaller stems, and calculated recruitment rates encompass seed production, germination and seedling mortality up to the point of the census year. Given the high rates of recruitment, especially at the treeline edge, I assume that seed production and germination ability are not limited, although germination may be a limiting factor, especially when tussock density is dense, such as at Maori Saddle and Takahe East (Chapter 6). Similarly, at the *Nothofagus pumilio* treeline is Chile, seedling emergence is a critical limiting stage in treeline dynamics (Cuevas 2000). However, the poor occupancy in potentially suitable microsites and hypothesized limitation to germination, point to the importance of positive feedback for recruitment. Here, facilitation is important for seedling survival (Chapter 6) but establishment is limited to microsites that are suitable for both germination and seedling survival, those with bare soil and shelter. Suitable microsites are created by either disturbance or, more often, by microsite modifications by *Nothofagus* trees, thus creating ideal conditions for germination and seedling establishment. Given that suitable microsites with bare soil and shelter are infrequent, the forest edge and positive feedback are critical for seedling establishment.

The climatic stressor limiting *Nothofagus* treeline position and dynamics is unlikely to be related to low temperature. Planting seedlings 150 m above treeline and adding passive warming did not affect growth, at least in terms of basal area increment (Chapter 5). Vertical growth was affected but, even then, *N. solandri* and *N. menziesii* do not form Krummholz, even if they are multi-stemmed (Norton & Schöenberger 1984). Krummholz do form at the *N. pumilio* treeline in South America, but the treeline is still abrupt and limited by seedling establishment (Daniels & Veblen 2004). Finally, *N. solandri* and *N. menziesii* are both shade tolerant, at least at the seedling stage (Wardle 1984). Other abrupt treelines across the world also fit within expectations based on the framework. In the Spanish Pyrenees, abrupt treelines reflect high age-dependent mortality and strong positive feedback whereas the diffuse treeline reflects growth inhibition (Camarero & Gutierrez 2002). In the tropics and Australia, recruitment beyond the treeline is limited by sky exposure (Ball *et al.* 1991; Bader *et al.* 2007b).

The framework can be evaluated using observations (Chapter 4) or experiments (Chapters 5 and 6). Long-term observations are valuable, especially in determining treeline dynamics and the first-level mechanism (growth, seedling mortality, dieback) but, as observed in Chapter 6, experiments are also necessary to test hypotheses formulated under the proposed framework and eliminate alternative mechanisms. This study, along with studies in the Spanish Pyrenees (Batllori *et al.* 2009) and tropics (Bader *et al.* 2007a; Bader *et al.* 2007b) has the benefit of utilizing both observations and experimental manipulation of microsite conditions, either by planting seedlings in different microsites or modifying microsite conditions, to specifically test for facilitation.

7.2 Implications for other treeline sites and predictions

The results from Chapters 2 and 3 confirm that treelines globally are controlled, at least in part, by growing season temperature but winter conditions are also important. Exposure to strong winds, frosts and desiccation will affect survival (Ball *et al.* 1991; Cuevas 2000; Germino *et al.* 2002; Bader *et al.* 2007b; Batllori *et al.* 2009). Predicting whether a treeline site will respond to climate warming depends upon the climatic conditions and taxon-specific traits present at treeline (Chapter 2). Diffuse treelines are limited by growing season conditions and are the most responsive to climate warming. Krummholz, island and abrupt treelines are limited by conditions in both the growing season and the winter and have been less responsive to climate warming. In New Zealand, the treeline position and relative inertia to climate warming reflects the importance of facilitative interactions and insignificance of low temperature on survival (Chapters 5 and 6). The importance of shelter in limiting more widespread rapid treeline expansion has rarely been assessed but is likely to be as important as seed dispersal rates. Predictions of future treeline position and subsequent effects on alpine or arctic vegetation based on growing season temperature would not be expected to be valid at treelines not limited by growing season temperature (abrupt, island and Krummholz forms).

7.3 Implications beyond treeline

Treelines are commonly monitored because they are considered early indicators of vegetative response to climate warming. The results of this thesis indicate that species at the margins of their distribution should shift to higher altitudes or latitudes if limited by growth due to low temperatures in the growing season. Response is more variable if limited by seedling mortality or dieback. Ability to respond will be influenced by taxon-specific tolerances and site-specific climatic conditions. For example, sites in the Spanish Pyrenees limited by low temperature are advancing but sites limited by wind are not (Camarero & Gutierrez 2004) and, in New Zealand, vertical height growth and survival rates differ between conifers and angiosperms (Wardle 1985b). Taxon-specific tolerances are important in determining species distributions and ability to respond to climate change (leRoux & McGeoch 2008) but may be less important than local climate, at least when only contrasting a single life-stage (Chapter 5).

Species ability to respond to changing climatic conditions significantly influences the species' extinction risk. For example, under a moderate climate change scenario, extinction risk for plants in Europe and South Africa increased from 3.6 – 15.6%, respectively, if plants disperse at the rate of warming to 11.5 – 21.4%, respectively, if plants are unable to disperse (Thomas *et al.* 2004). Based on treeline response globally and in New Zealand, the extinction rate can be expected to be closer to the no-dispersal estimate (Chapter 4; Cuevas 2000; Bader *et al.* 2007b; Green 2009).

The applicability of observations made under current climatic conditions to inform future plant distributions raises critical concerns. First, projections based on correlating current species distributions with current climatic conditions (e.g. bio-climatic envelope models) may be inaccurate because the current species distribution is not in equilibrium with current climatic conditions. Second, the importance of species interactions, especially at different life stages, is often not taken into account. Third, current and past climatic conditions from which inferences on potential distributions and community compositions are made do not necessarily reflect the entire environmental conditions within which the species can survival (i.e. no-analog climate). Thus, ability to predict future distributions and the effects of shifting distributions may be significantly hindered if an appropriate reference climate does not exist either currently or historically to future conditions (Williams & Jackson 2007). The proposed framework overcomes these limitations in projecting future distributions by taking into account species traits and plant-plant interactions when identifying critical limiting mechanisms rather than forecasting future distributions based on past relationships with climatic conditions. Thus, I do not make predictions of how far or rapidly the treeline will shift upward but what aspect of climatic change will affect the local treeline. For example, at abrupt treelines, climate warming during the summer would not result in an increase in treeline position.

7.4 Recommendations for future research

The *Nothofagus* treeline provides an excellent system to evaluate the causes of treeline formation and the mechanisms limiting plant species response to climate change. Further work identifying the life history stage limiting *Nothofagus* recruitment beyond treeline is necessary. That *Nothofagus* are less tolerant of climatic conditions at treeline is not substantiated. *Nothofagus pumilio*, a deciduous broadleaved species, which should be more cold tolerant than the evergreen broadleaved species, *N. solandri* and *N. menziesii*, also exhibits recruitment limitation. Further, *N. solandri* does not exhibit a lower tolerance to high elevation conditions than *P. contorta*, at least not in terms of survival and general ability to grow at the seedling stage. Any limitation to *Nothofagus* treeline expansion is speculated to occur prior to seedling establishment. Germination trials above treeline indicate that seed can germinate above treeline (Wardle 1985b) but trials under the canopy forest indicate that germination is limited to microsites with limited aboveground vegetation. Germination trials will elucidate whether ability to germinate in dense vegetation or dispersal ability limit *N. solandri* and *N. menziesii* occurrence in seemingly suitable microsites (tussocks, shrubs). Another critical step is seedling development into a tree (2 m high). Trials above treeline also indicate that height growth is limiting and may hinder development of a new treeline. Monitoring seed production, dispersal, germination, and survival through several life history stages will provide sufficient detail to identify bottlenecks to treeline expansion.

Treeline patterns observed globally result from processes acting at fine spatial scales. For example, treeline advance is ultimately a function of recruitment which is best explained in terms of macro- and micro-climate along with microsite conditions (Holtmeier & Broll 2005). Linking pattern to process at a global scale requires fine scale data collected using standardized methods from sites globally. Recording temperature at multiple treeline sites over extended durations in different microsites will provide insight into the variability in treeline response to climate warming and the effects of temperature on recruitment. Global comparisons of germination and recruitment patterns will provide insight into the causes of variability in ability to respond to climate warming. Expanding the paired plantings conducted in Chapter 5 to several other sites globally will further elucidate the role of taxon-specific and site-specific factors in limiting treeline position and ability to respond to climate warming.

Linking form to the mechanisms proposed in Chapter 3 will also require extensive taxonomic data collected globally, including fecundity, mortality, recruitment and growth. Assessing taxon-specific tolerances to treeline conditions at different life-history stages is necessary to identify the critical life-stage and related climatic factors limiting treeline advance. Treeline advance is limited either by ability to grow to tree height, seedling survival, germination or seed production. Each life-history stage may be limited by different mechanisms (Daniels & Veblen 2004) so observing the limiting stage is critical. Climatic variables other than temperature also need to be monitored globally but at a scale relevant to individual tree performance.

This thesis, along with numerous published papers, assert the importance of facilitation in enabling growth and survival in otherwise unfavourable climatic conditions but does not identify the stressors. Accurately predicting plant species response to climatic change will require identifying the stressors limiting recruitment and microsite properties enabling recruitment.

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Appendix A
Database of treeline response

Study ID	Advance	Study Duration	Methodology	Treeline Type	Treeline Form	Disturbance	Family
1	yes	80	field based	alpine	diffuse	none	Pinaceae
1	yes	80	remotely sensed	alpine	Krummholz	none	Pinaceae
2	yes	94	field based	alpine	diffuse	human	Pinaceae
3	no	4	remotely sensed	alpine	Krummholz	none	Mixed
3	yes	4	remotely sensed	alpine	Krummholz	none	Mixed
4	no	1	field based	alpine	abrupt	natural	Loranthaceae
5	no	5	remotely sensed	alpine	Krummholz	none	Pinaceae
5	no	5	remotely sensed	alpine	Krummholz	none	Pinaceae
6	yes	40	remotely sensed	alpine	abrupt	human	Pinaceae
7	yes	43	remotely sensed	alpine	diffuse	none	Mixed
7	yes	43	remotely sensed	alpine	diffuse	none	Mixed
8	yes	80	field based	alpine	Krummholz	natural	Pinaceae
9	no	81	field based	alpine	Krummholz	none	Pinaceae
10	no	40	field based	alpine	Krummholz	none	Pinaceae
11	yes	10	field based	alpine	diffuse	none	Pinaceae
12	yes	55	remotely sensed	alpine	diffuse	natural	Pinaceae
13	no	58	remotely sensed	alpine	abrupt	human	Rosaceae
14	no	10	field based	arctic	Krummholz	none	Pinaceae
14	no	10	field based	arctic	Krummholz	none	Pinaceae
14	no	10	field based	arctic	Krummholz	none	Pinaceae
14	no	10	field based	arctic	Krummholz	none	Pinaceae
15	yes	95	field based	alpine		human	Pinaceae
15	yes	95	field based	alpine	diffuse	none	Pinaceae
15	no	95	field based	alpine	Krummholz	none	Pinaceae
16	yes	48	field based	alpine	diffuse	human	Pinaceae
17	no	1	field based	alpine	abrupt	human	Salicaceae
17	no	1	field based	alpine	abrupt	human	Salicaceae
18	no	100	field based	alpine		natural	Pinaceae
19	yes	61	remotely sensed	alpine	diffuse	human	Pinaceae
20	yes	7	field based	alpine	diffuse		Pinaceae
21	no	96	field based	alpine	Krummholz	natural	Nothofagaceae
22	no	96	field based	alpine	Krummholz	natural	Nothofagaceae
22	no	2	field based	alpine	abrupt	none	Nothofagaceae
23	no	10	field based	alpine	abrupt	natural	Nothofagaceae
24	no	100	field based	alpine	Krummholz	human	Betulaceae
24	no	100	field based	alpine	Krummholz	none	Betulaceae
24	no	100	field based	alpine	Krummholz	none	Betulaceae
24	no	100	field based	alpine	Krummholz	human	Betulaceae
24	no	100	field based	alpine	Krummholz	human	Betulaceae
24	no	100	field based	alpine	Krummholz	none	Betulaceae
24	no	100	field based	alpine	Krummholz	none	Betulaceae
24	no	100	field based	alpine	Krummholz	none	Betulaceae
24	no	100	field based	alpine	Krummholz	none	Betulaceae
24	no	100	field based	alpine	Krummholz	human	Betulaceae
24	no	100	field based	alpine	Krummholz	none	Betulaceae

Study ID	Advance	Study Duration	Methodology	Treeline Type	Treeline Form	Disturbance	Family
24	no	100	field based	alpine	Krummholz	none	Betulaceae
25	yes	1	field based	alpine	Krummholz	none	Pinaceae
26	yes	42	remotely sensed	alpine	diffuse	none	Pinaceae
27	no	10	field based	alpine	diffuse	none	Pinaceae
27	yes	10	field based	alpine	diffuse	none	Pinaceae
28	no	18	field based	alpine	Krummholz	none	Nothofagaceae
28	no	18	field based	alpine	Krummholz	none	Nothofagaceae
29	yes	39	field based	alpine	Krummholz	none	Nothofagaceae
29	no	39	field based	alpine	Krummholz	none	Nothofagaceae
30	no	51	field based	alpine	diffuse	human	Pinaceae
31	yes	50	field based	alpine	Krummholz	human	Pinaceae
32	yes	93	remotely sensed	alpine	diffuse	human	Salicaceae
33	yes	1	field based	arctic	Krummholz	none	Betulaceae
34	yes	100	field based	arctic	Krummholz	natural	Pinaceae
34	yes	100	field based	arctic	Krummholz	none	Pinaceae
34	yes	100	field based	arctic	Krummholz	none	Pinaceae
35	no	100	field based	arctic	Krummholz	natural	Pinaceae
36	no	45	field based	arctic	diffuse	none	Pinaceae
36	no	93	field based	arctic	diffuse	none	Pinaceae
36	no	92	field based	arctic	diffuse	none	Pinaceae
37	yes	12	remotely sensed	alpine	diffuse		Pinaceae
38	yes	107	field based	arctic			Pinaceae
39	no	85	field based	alpine	Krummholz	none	Pinaceae
40	no	55	field based	alpine	Krummholz	none	Pinaceae
41	yes	29	field based	alpine	diffuse	human	Betulaceae
42	no	35	field based	alpine	Krummholz	human	Pinaceae
43	no	80	field based	arctic	Krummholz	none	Betulaceae
44	yes	16	field based	alpine	diffuse	none	Pinaceae
44	no	16	field based	alpine	diffuse	none	Pinaceae
44	no	16	field based	alpine	diffuse	none	Pinaceae
44	yes	16	field based	alpine	diffuse	none	Pinaceae
45	yes	49	remotely sensed	alpine	Krummholz		Betulaceae
46	yes	96	field based	alpine	Krummholz	none	Pinaceae
47	no	2	field based	alpine	diffuse	human	Salicaceae
47	no	2	field based	alpine	diffuse	human	Salicaceae
48	yes	55	field based	alpine	diffuse	none	Betulaceae
48	yes	55	field based	alpine	diffuse	none	Betulaceae
48	yes	55	field based	alpine	diffuse	none	Betulaceae
48	yes	55	field based	alpine	diffuse	none	Betulaceae
49	no	52	remotely sensed	alpine	Krummholz	human	Pinaceae
50	no	1	field based	alpine	Krummholz	none	Salicaceae
51	yes	8	field based	alpine	diffuse	none	Betulaceae
51	yes	8	field based	alpine	diffuse	none	Pinaceae
52	yes	15	field based	alpine	diffuse	none	Pinaceae
52	no	15	field based	alpine	diffuse	none	Pinaceae
52	yes	15	field based	alpine	diffuse	none	Pinaceae
53	yes	20	field based	alpine	diffuse	none	Betulaceae
54	yes	9	field based	alpine	diffuse	none	Pinaceae
55	yes	56	field based	alpine	diffuse	none	Pinaceae
55	yes	56	field based	alpine	diffuse	none	Betulaceae
56	yes	93	field based	alpine	diffuse	none	Betulaceae

Study ID	Advance	Study Duration	Methodology	Treeline Type	Treeline Form	Disturbance	Family
57	yes	50	field based	alpine	diffuse	none	Pinaceae
58	no	3	field based	alpine	Krummholz	none	Nothofagaceae
59	yes	96	field based	alpine	diffuse	none	Pinaceae
60	no	92	field based	arctic	Krummholz	none	Pinaceae
61	yes	92	field based	arctic	Krummholz	none	Pinaceae
62	no	96	field based	alpine	diffuse	none	Pinaceae
63	yes	100	field based	arctic	diffuse	natural	Pinaceae
63	yes	50	field based	arctic	diffuse	natural	Pinaceae
63	yes	80	field based	arctic	diffuse	natural	Pinaceae
64	yes	100	field based	arctic	diffuse	none	Pinaceae
65	yes	1	field based	alpine		none	Pinaceae
66	yes	100	field based	arctic			Pinaceae
67	no	51	field based	arctic	Krummholz	none	Pinaceae
68	yes	1	field based	alpine	diffuse		Pinaceae
68	yes	1	field based	alpine	diffuse		Pinaceae
69	no	25	remotely sensed	arctic	Krummholz	none	Pinaceae
69	no	25	remotely sensed	arctic	diffuse	none	Pinaceae
70	yes	95	field based	alpine	diffuse	human	Pinaceae
71	no	40	field based	arctic	Krummholz	none	Pinaceae
72	no	38	field based	alpine	Krummholz	human	Pinaceae
73	yes	43	field based	alpine	diffuse	none	Pinaceae
74	yes	102	field based	alpine	diffuse	none	Pinaceae
75	no	102	field based	alpine	Krummholz	none	Pinaceae
75	yes	102	field based	alpine	abrupt	none	Pinaceae
76	yes	60	field based	alpine	diffuse	none	Pinaceae
77	yes	100	field based	alpine	diffuse	human	Salicaceae
77	yes	100	field based	alpine	diffuse	human	Salicaceae
78	yes	90	field based	alpine	diffuse	human	Pinaceae
79	yes	94	field based	alpine	diffuse	human	Pinaceae
79	no	94	field based	alpine	diffuse	natural	Pinaceae
80	no	96	field based	alpine	Krummholz	none	Pinaceae
80	no	96	field based	alpine	Krummholz	none	Pinaceae
80	no	96	field based	alpine	Krummholz	none	Pinaceae
81	yes	100	field based	arctic	diffuse	natural	Pinaceae
81	no	100	field based	arctic	diffuse	natural	Pinaceae
81	yes	100	field based	arctic	diffuse	none	Pinaceae
82	yes	7	field based	alpine	diffuse	human	Pinaceae
82	no	7	field based	alpine	Krummholz	none	Pinaceae
83	no	60	field based	arctic	Krummholz	none	Pinaceae
84	yes	95	field based	arctic	diffuse	none	Pinaceae
85	yes	90	remotely sensed	arctic	diffuse	none	Pinaceae
86	yes	90	remotely sensed	arctic	diffuse	none	Pinaceae
87	yes	1	field based	alpine	diffuse	human	Betulaceae
88	no	1	field based	alpine	diffuse	human	Pinaceae
89	yes	50	remotely sensed	arctic	Krummholz	none	Betulaceae
90	yes	80	field based	arctic	diffuse	none	Pinaceae
91	no	90	field based	arctic	abrupt	none	Pinaceae
91	yes	90	field based	arctic	diffuse	none	Pinaceae
91	yes	90	field based	arctic	diffuse	none	Pinaceae
91	no	90	field based	arctic	Krummholz	none	Pinaceae
92	yes	58	field based	alpine	diffuse	none	Pinaceae

Study ID	**Advance**	**Study Duration**	**Methodology**	**Treeline Type**	**Treeline Form**	**Disturbance**	**Family**
92	yes	58	field based	alpine	diffuse	none	Pinaceae
92	yes	58	field based	alpine	diffuse	none	Pinaceae
92	yes	58	field based	alpine	diffuse	none	Pinaceae
93	yes	30	remotely sensed	arctic	diffuse	none	Pinaceae
94	no	108	field based	alpine	Krummholz	human	Pinaceae
94	yes	108	field based	alpine	Krummholz	human	Pinaceae
95	yes	1	field based	alpine	diffuse	none	Betulaceae
96	no	78	remotely sensed	alpine	Krummholz	natural	Pinaceae
96	no	78	remotely sensed	alpine	Krummholz	none	Pinaceae
97	no	100	field based	arctic	Krummholz	none	Pinaceae
98	yes	95	field based	alpine	diffuse	none	Pinaceae
98	yes	95	field based	alpine	diffuse	human	Pinaceae
99	no	252	field based	alpine	Krummholz	none	Pinaceae
100	no	10	field based	alpine	abrupt	none	Nothofagaceae
101	no	1	field based	alpine	diffuse	none	Mixed
101	no	1	field based	alpine	Krummholz	none	Mixed
102	yes	29	remotely sensed	alpine	diffuse	none	Pinaceae
103	yes	104	remotely sensed	alpine	diffuse	human	Pinaceae
103	no	104	remotely sensed	alpine	Krummholz	none	Pinaceae

Study ID	**Lat °**	**Long °**	**Elevation (masl)**	**Aspect**	**Distance to Ocean (km)**	**Climate station distance**	**Climate station elevation difference**
1	42.36	-114.35	2100	cold	828	18.13	721
1	42.36	-114.35	2100	cold	828	18.13	721
2	43.15	-108.18	2900	cold	1300	25.19	1216
3	67.5	27.04	450	cold	450	22.07	294
3	67.5	27.04	473	warm	450	22.07	271
4	0.36	-77.42	3700		291	130.95	888
5	40.23	-105.31	500	cold	1603	25.83	-1171
5	40.23	-105.31	450	neutral	1603	25.83	-1221
6	28.15	98.46	4300	cold	930	337.32	2651
7	44.19	-72.53	846		204	12.33	455
7	44.19	-72.53	884		204	12.33	417
8	42.36	-114.35	2300	cold	828	18.13	921
9	40.02	-105.35	3450	cold	1603	7.18	1779
10	49.92	-123.03	2438	neutral	66	59.43	2215
11	36.3	-118.3	3300	neutral	240	56.38	2097
12	48	-114.35		cold	757	33.92	
13	-8.35	-77.05	4330	neutral	189	417.50	4193
14	56.07	-76.46	3.5		13.9	283.15	-2.5
14	56.09	-76.44	10		13.8	262.58	-1.2
14	56.3	-76.32	4.8		14.6	281.49	4
14	56.4	-76.4	60		19	250.39	54
15	42.28	-1.38	2430		126	280.28	2410
15	42.36	-1.03	2360		128	213.32	2015
15	42.37	-0.02	2110		174	278.14	2340
16	42.01	2.44	2040	neutral	259	70.78	1945
17	-0.2	-78.16	4100		250	36.06	1288
17	-0.19	-78.15	3700	cold	250	37.01	888
18	35.19	-111.36	3500	warm	595	34.80	1261
19	35.43	-106.31	3200		1304	50.54	1292
20	68	-154	760	warm	431	160.15	564
21	-54.13	-68.41	600	cold	62	93.12	686
22	-54.13	-68.41	700	neutral	62	74.81	586
22	-54	-68.74	700	neutral	62	74.81	686
23	-42.19	172.07	1200	neutral	60.5	107.22	1160
24	62.1	9.23	700	cold	165	3.43	-274
24	62.1	9.23	1121	neutral	165	3.43	140
24	62.1	9.23	1210	neutral	165	3.43	147
24	62.1	9.23	1114	warm	165	3.43	236
24	68.1	18.85	740	cold	198	155.97	687
24	68.1	18.85	1156	cold	198	155.97	729
24	68.1	18.85	698	warm	198	155.97	1145
24	68.1	18.85	1140	warm	198	155.97	1129
24	69.4	23.58	772	cold	182	75.42	658
24	69.4	23.58	460	neutral	182	75.48	639
24	69.4	23.58	791	neutral	182	75.48	327
24	69.4	23.58	423	warm	182	75.48	290
25	40.04	-105.35	3540	neutral	1603	8.15	1869
26	61	-138	1300	neutral	212	188.80	1291
27	60.45	-137.3	1336	cold	220	167.72	1327
27	60.45	-137.3	1432	warm	220	167.72	1423
28	-41.15	-71.18	1600	neutral	230	0.84	760

Study ID	Lat °	Long °	Elevation (masl)	Aspect	Distance to Ocean (km)	Climate station distance	Climate station elevation difference
28	-40.47	-72.12	1340	neutral	138	110.17	500
29	-40.44	-71.04	1400	cold	230	79.79	460
29	-40.44	-71.04	1300	warm	230	79.79	560
30	45.16	6.48	1500	warm	610	68.49	-960
31	47.4	15.5	1900	neutral	1090	114.81	1691
32	37.13	-106.3	3500	neutral	1325	31.37	1157
33	68.5	-155.7	200		291	249.08	4
34	61.26	59.43	950	warm	870	233.81	319
34	69.57	97.37	590	warm	752	162.55	187
34	70.52	102.53	220	cold	788	84.88	855
35	58.04	-75.3	200	neutral	830	171.39	194
36	55.3	-75.36	210	neutral	160	309.94	319
36	56.13	-75.27	325	warm	97.2	225.48	273
36	57.07	-75.34	279	cold	838	388.72	204
37	46.12	7.3	2450	neutral	680	56.09	-10
38	68.24	35.16	300	warm	139	118.08	249
39	57.08	-3.5	600	neutral	171	10.77	261
40	64.4	15.5	650	neutral	201	45.17	196
41	62.3	8.5	1170	neutral	123	201.23	
42	39.63	-105.81	3500	warm	1550	18.86	737
43	65	-18			140	75.79	
44	66.13	28.33	410	neutral	550	156.53	231
44	67.34	24.11	465	warm	410	108.91	286
44	68.02	24.05	420	neutral	380	131.53	241
44	69.4	26.58	275	cold	182	42.94	142
45	59.15	59.1	900	neutral	1116	71.59	437
46	46.47	25.06	1880	cold	1000	102.42	1436
47	-15.22	-66.02	2100	cold	585	575.18	2742
47	-15.22	-66.02	2800	warm	585	575.18	2042
48	63	13	895	cold	225	95.36	265
48	63	13	920	neutral	225	95.36	318
48	63	13	920	neutral	225	95.36	290
48	63	13	948	warm	225	95.36	290
49	48.43	-113.65	2160	warm	826	48.09	1254
50	4.35	-75.1	3700	neutral	251	626.32	888
51	63.14	12.27	900	neutral	155	77.91	270
51	63.14	12.27	900	neutral	155	77.91	270
52	63.2	12.2	685	cold	155	81.55	
52	63.2	12.2		neutral	155	81.55	230
52	63.2	12.2	860	warm	155	81.55	55
53	63.1	12.21	915	neutral	155	72.53	285
54	63.15	12.26	891	neutral	155	78.52	261
55	63.14	12.26	850	neutral	155	114.67	340
55	63.26	13.06	970	warm	183	77.61	220
56	63.13	12.23	880	warm	155	75.83	250
57	63.14	12.25	670	warm	155	77.32	40
58	-35.45	-71.2	1115	neutral	100	354.17	287
59	49.02	-124.19	1300	neutral	66	28.31	1292
60	52.03	-89.45	3500		2023	82.72	3114
61	59.4	-73.2			275	301.75	
62	63.1	13.05	700	cold	200	103.36	70

Study ID	Lat °	Long °	Elevation (masl)	Aspect	Distance to Ocean (km)	Climate station distance	Climate station elevation difference
63	64	-150	945	neutral	865	59.36	314
63	66	-148	700	neutral	485	143.77	155
63	68	-161	160	neutral	170	128.16	555
64	66	-148	950	cold	485	128.16	805
65	51.11	-115.34	2350	cold	851	17.85	966
66	44.07	-72.56			190	5.84	
67	62	-98.5			355	424.04	
68	43	-110	2900		1350	28.06	1167
68	45	-109	2950		1300	17.94	714
69	55	-75			160	428.63	
69	63	-110			1616	278.88	
70	36.1	-111.9	1570	neutral	600	23.17	-498
71	66.48	65.34	190		385	59.29	174
72	66.49	65.32	500	warm	385	60.07	484
73	42.45	24.24	2100	neutral	275	62.09	-827
74	36.5	-118.16	3000	neutral	240	33.59	1797
75	37.5	-119.12	3500	warm	248	49.19	2292
75	38.03	-119.16	3100	cold	325	48.30	1892
76	53.5	89.01	1600	neutral	2230	179.08	1346
77	37.19	-111.8	3200	warm	800	39.81	2222
77	39.19	-111.8	2500	cold	954	16.11	751
78	44.37	7.05	1800	neutral	642	148.53	-660
79	46.17	11.44	1980	cold	987	125.83	1398
79	46.17	11.45	1890	cold	987	125.85	1308
80	46.12	7.3	2370	cold	680	56.09	-360
80	46.12	7.3	2510	neutral	680	56.09	50
80	46.12	7.3	2100	warm	680	56.09	-90
81	57.22	-62.52			65	182.44	594
81	57.51	-65.53	630		240	361.96	319
81	57.55	-62.38	355		58	363.48	
82	57.06	-3.49	490	neutral	171	8.62	301
82	57.06	-3.49	640	neutral	171	8.62	151
83	57.45	-76.2	150		198	158.91	144
84	66.5	65.5	350		398	52.01	334
85	66.46	65.22	410		385	64.85	394
86	66.46	65.22	410	neutral	385	64.85	394
87	28.37	84.01	4200		890	308.14	4151
88	28.3	-16.6	2020	warm	407	33.32	1403
89	68.06	-161.31		neutral	205	143.94	
90	67.28	-162.14	150	neutral	203	50.35	145
91	64	-125	900	cold	2082	106.01	882
91	64	-125	980	cold	2082	106.01	802
91	64	-140	1250	cold	2082	42.78	880
91	64	-125	1010	warm	1356	106.01	912
92	40.26	-121.31	1250	neutral	224	44.52	1562
92	40.26	-121.31	2600	neutral	224	44.52	212
92	40.26	-121.31	2400	warm	224	44.52	-188
92	40.26	-121.31	850		224	44.52	1362
93	65	-120			726	262.51	
94	46.1	9.43	2455	neutral	890	109.70	2267
94	46.14	10.26	2370	neutral	922.5	72.09	360

Study ID	Lat °	Long °	Elevation (masl)	Aspect	Distance to Ocean (km)	Climate station distance	Climate station elevation difference
95	62	15	750	neutral	280	197.84	120
96	37.45	-119.35	3400	neutral	230	39.08	2292
96	37.45	-119.35	3500	neutral	230	39.08	2192
97	57.43	-76.5	140		925	148.51	134
98	46.11	7.51	2580	neutral	680	60.84	-996
98	46.15	7.47	2350	neutral	680	59.32	-1226
99	44.5	88.1	2800	neutral	2883	88.85	1881
100	-42.19	172.07	1350	neutral	60.5	107.22	1310
101	40.31	-105.38	2900	neutral	1580	35.76	1229
101	40.31	-105.38	3850	neutral	1580	35.76	2179
102	39.38	-116.48	2500	neutral	580	53.29	487
103	37.13	-106.3	3500	cold	1325	31.37	1157
103	37.13	-106.3	3500	neutral	1325	31.37	1157

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Appendix B

Assessment of how differences among GHCN stations in the rate of temperature change varied as a function of distance apart and differences in elevation

To determine whether sites located further away from climate stations might differ systematically in estimates of their rate of temperature change, I used the data from all 2651 climate stations in the GHCN database that had at least 50 years of complete annual data since 1900 AD. For each station, I calculated the rate of mean annual temperature change since 1900 AD as the slope of the least squares regression line for the relationship between mean annual temperature and year. I then calculated the difference in slope between each pair of stations, and the great circle distance between stations, and plotted these for stations located up to 650 km apart (Fig. C2a). A regression line fitted to these data had a slope close to zero (0.000018), which suggests there is no systematic bias in how the rate of mean annual temperature change differs among stations located further apart, although the variance increases with distance.

I also examined the difference in the slope of the temperature change for pairs of stations and their difference in elevation, for those stations located within 650 km of each other (Fig. C2b). A regression line fitted to these data also had a slope close to zero (-0.0000011), which suggests there is no systematic bias in how the rate of mean annual temperature change differs among stations located at varying elevations.

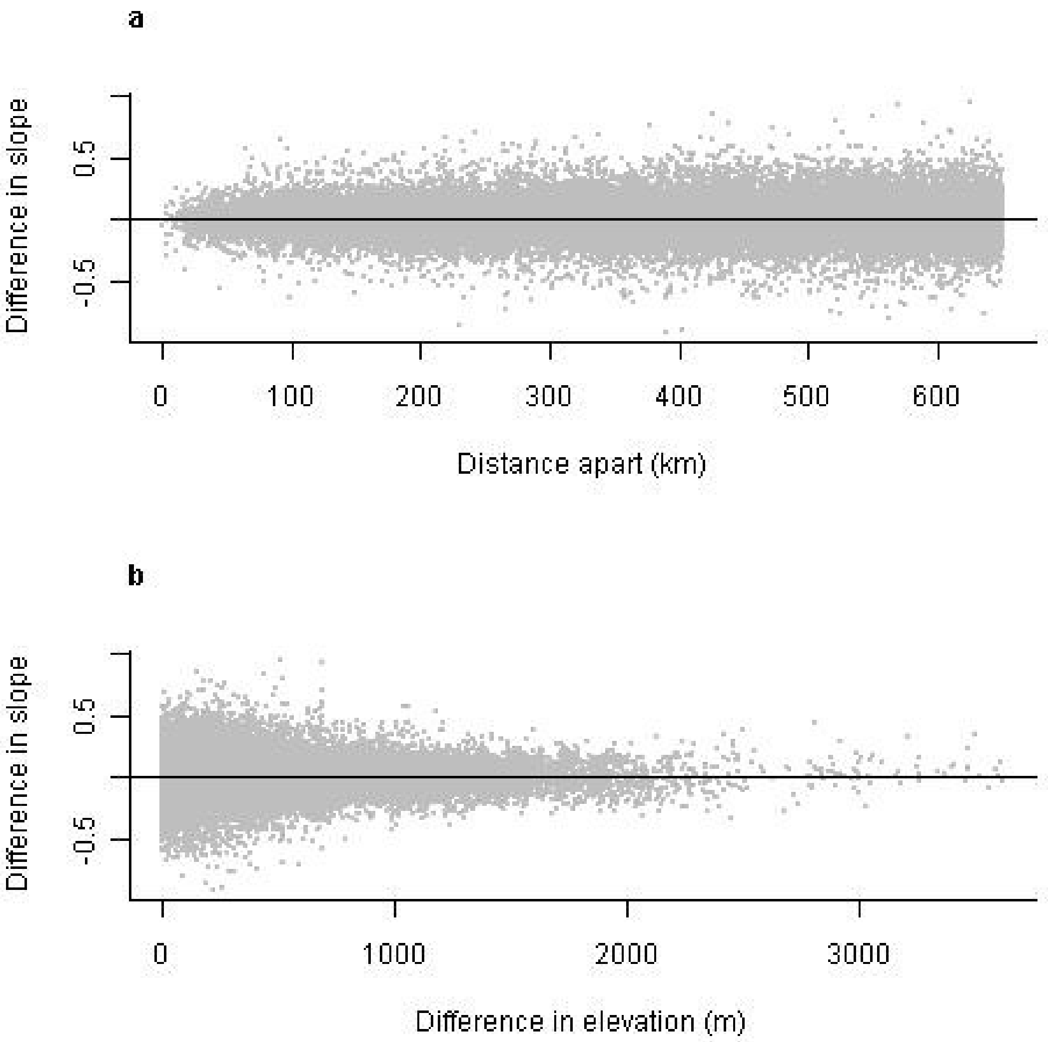

Figure C2: a Scatterplot of the relationship between difference in rate of mean annual temperature change (measured as the slope of the regression line between mean annual temperature and year) and great circle distance apart, for climate stations in the GHCN database that are less than 650 km apart. b Scatterplot of the relationship between difference in rate of mean annual temperature change (measured as the slope of the regression line between mean annual temperature and year) and difference in elevation, for climate stations in the GHCN database that are less than 650 km apart.

Appendix C
Bayesian hierarchical modelling

I chose to use Hierarchical Bayesian modelling (HB) for three primary reasons. First, the HB framework can easily accommodate complex data in which measured variables are collected at different scales (Clark 2005). For example, height relative growth rate was measured for individual trees but potential solar radiation was calculated for sections along transects. Downscaling height growth to the same scale that potential solar radiation was estimated would result in a loss of data whereas upscaling potential solar radiation data to the individual tree scale would result in inferences beyond what is feasible by the data. The flexibility also allowed us to take into account that the length of time between census periods varied. Second, the HB framework allows for incorporation of missing values (Gelman & Hill 2007; Cressie *et al.* 2009). For example, diameter was not measured for all trees because I could not always reach the base of the tree. Rather than excluding all data for trees in which diameter was not recorded, the HB framework allows missing data to be included by first modelling the missing data as if missing at random (Gelman *et al.* 2004). The missing data can then be inferred from the measured data based on specified mean and variance (Cressie *et al.* 2009). Third, the framework of the analysis in which separate models are developed for the data, the process, and the parameters allows for accounting in uncertainty/variability due to insufficient sampling and uncertainty at each level (Gelman & Hill 2007). In other words, I can account for where variability or uncertainty occur and incorporate this variability in parameters that might otherwise be unrealistically treated as fixed (Cressie *et al.* 2009). Thus, results offer more realistic interpretations than classical statistical approaches.

The model is composed of three levels, the data, process and parameter models. I illustrate the model development using the survival model in its most basic state, with one parameter, tree height. The data model (likelihood) is the status of survival as a vector of ones and zeros describing whether the individual survived or not as a Bernoulli sample:

$$a_i \sim \mathrm{bern}(s_i) \qquad \text{(eqn D.1)}$$

In the process model, I then model survival (s) as a function of parameters describing individual effects (e.g. height) and includes an uncorrelated random effect (ϵ_i):

$$\mathrm{logit}(s_i) = \beta * \mathrm{height}_i + \epsilon_i \qquad \text{(eqn D.2)}$$

Finally, the parameter model for β is a normal distribution with mean (α) and standard deviation (σ):

$$\beta \sim N(\alpha, \sigma) \qquad \text{(eqn D.3)}$$

After the model is built prior values for parameters have to be set. Here I used non-informative priors so that the likelihood informs the posterior probability. The analysis is then accomplished by a sampling-based approach. In this case I used Gibbs sampling, a Markov change Monte Carlo (MCMC) technique (Gelman *et al.* 2004; Gelman & Hill 2007).

The posterior probability distribution is simply the prior probability distribution updated by the data where the "updating" process is accomplished through the MCMC simulations. In the simplest case, in which the model is not hierarchical and priors are non-informative, the credible intervals calculated from the posterior distribution are near identical to classical confidence intervals (Huber & Train 2001; Clark 2005).

In many cases the difference between using Bayesian and classical approaches is in the philosophical development rather than the numerical estimates (Huber & Train 2001; Clark 2005). This is because classical and Bayesian analyses can return similar results, especially when the Bayesian model is simple and priors are non-informative. Thus, the mean of the posterior probability distribution is similar to the mean of data and the 95% Bayesian credible interval is similar to the 95% confidence interval.

Interpretation is similar between Bayesian and classical statistics. The parameter estimates are the best estimate of the posterior probability distribution given the observed data and prior knowledge of the distribution. Parameter estimates reflect the mean of the posterior probability distribution and the 95% credible intervals. A negative parameter estimate indicates an inverse association, e.g. the rate of height growth is inversely related to potential solar radiation and indicates that height growth is slower at sites with higher potential solar radiation. The 95% Bayesian credibility intervals shown are the range in which 95% of the parameter probability, calculated using MCMC methods, fall. If this interval does not overlap with 0, I have a strong belief, in the Bayesian sense of the word, that the value really is not 0, which is comparable, in concept, to a significance with $p < 0.05$.

Appendix D

Database methodology for treeline form, life form and disturbance

The database included 195 treeline sites described in 119 published treeline studies. Treeline studies published prior to March 2009 were identified using journal search tools (Web of Science, BIOSIS, JSTOR, Proquest Dissertations and Theses search), internet web searches, and by direct communication with the authors of studies. I analyzed 243 published treelines studies and included only those in which form for an alpine or arctic treeline could be distinguished based on the author's explicit description. I was limited to descriptive classifications because of the limited number of studies that reported quantitative changes in height and canopy cover. I therefore (re-)classified all treelines ourselves based on descriptions of tree shapes (single-, multi- stemmed, deformed or twisted) and changes in height and density along the treeline ecotone. When necessary, the information necessary for classification was also derived from photographs or direct communication with authors. Treelines were classed into one of the three forms described above: diffuse, abrupt, or Krummholz. When more than one treeline form was recorded at a study site, I used the form recorded at the uppermost alpine or arctic treeline limit. In the case where both Krummholz and upright trees occur at the upper limit, the treeline was classed as Krummholz. I included data on disturbance (natural, anthropogenic, or undisturbed) as outlined in Harsch *et al.* (2009). I classed the dominant species at each site as needle-leaf, evergreen broadleaf or deciduous broadleaf.

Appendix E

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Appendix F

Description of long-term treeline monitoring field sites

Mt Faust–13 sectors: Mt Faust is the second highest treeline site in this study, at 1328 masl. The first 3 sectors are on a broad, gentle ridge where tall trees form the forest limit. The vegetation above is mainly a shrub-tussock mosaic of *Dracophyllum uniflorum, Podocarpus nivalis, Chionochloa australis* and *Chionochloa pallens*. Open areas are mostly *Racomitrium lanuginosum*, lichen crust and bare ground formed by local erosion form microsites for seedling establishment. As Sector 4 crosses on to a steep concave slope dominated by *C. pallens,* the forest limit dips steeply. Sector 5 crosses a narrow spur, with vegetation at first similar to Sectors 1-3, but towards the southern end the forest margin drops into the next steep, concave slope with *C. pallens* grassland. The sector ends on a small spur with *D. uniflorum* bushes. Sector 6 rises steeply across an eroded gully with a stream, and thence through dense scrub of *D. uniflorum* and *P. nivalis*, ending where the forest edge rises up the gully side.

Sector 7 continues through dense scrub across the broad slope to the south. Sectors 8 and 9 are similar to 1-3. Sector 10 is transitional in character to Sectors 11-13, where forest ascending a steep slope ends abruptly at the lower edge of a bench as low, windshorn trees. On the bench, shrubs are shorter than other crests, and there is more *C. australis* and bare ground.

Mt Haast–12 sectors (5 east facing, 7 west facing): The eastern part of the transect begins on a prominent ridge, and the first 4 sectors follow the forest limit descending its northern side, through dense scrub of *D. uniflorum* with taller *D. longiflorum, Phyllocladus alpinus*, and *Coprosma pseudocuneata*. Sector 5 crosses a very steep slope of outcropping bedrock subject to slipping of soil and vegetation; the base tape here crosses a ledge with *D. uniflorum* scrub, and below it there is largely bare soil and rock extending down to the forest edge.

The western part of the transect at first runs horizontally, 20 m below bluffs, across a colluvial slope with open *C. pallens* grassland with patches of *C. australis* and *Pentachondra pumila*. Sector 2 continues steeply up the colluvial slope through dense *C. pallens* with some *C. rubra*, and clumps of *Olearia colensoi*. Sector 3 crosses a rocky slope with a mosaic of *C. pallens* and *C. australis*. Sector 4 crosses a 40° slope below a small bluff, then a colluvial slope with mainly *C. pallens*, and ends on a boulder field. Sector 5 occupies a rocky slope with *C. pallens* grassland with 20% bare ground. The first part of Sector 6 has *C. australis* dominant, and also 20% bare, whereas the distal part is rock outcrops with *C. australis* and *P. nivalis*. Sector 7 begins with large boulders, shrubs and *C. rubra*, and then crosses a 5° slope with *C. australis, Chionochloa rubra* and *C. pallens.* The forest limit throughout the transect consists of tall trees, with *N. solandri* being most numerous on the eastern part and *N. menziesii* on the western part.

Craigieburn–9 sectors: This site represents the highest treeline in this study at 1350 masl. The transect begins on an east-facing slope, in a mosaic of *Chionochloa macra* grassland and *P. nivalis* low scrub, and crosses between high points of the forest limit that separate deeply-descending strips of scree, to the stony crest of a broad spur where, in Sector 3, the aspect changes to south. The remainder of the transect alternates between high points of the forest limit occupying slight spurs, and steep concave slopes occupied by *C. macra*, patches of scree, and avalanche-damaged *N. solandri*.

Maori Saddle– 11 sectors: the transect begins in dense scrub of *D. longifolium* and *Olearia lacunosa*, but this changes to a more open mosaic of *D. longifolium, Chionochloa rigida* and *Phormium cookianum* which continues to the end of Sector 3. From here the transect follows the forest edge steeply down-slope through tall *D. longifolium* in Sector 4 and tall *Olearia colensoi* and *O. lacunosa* through Sector 5. At the beginning of Sector 6 the slope levels out in an opening of *C. rigida* tussocks. Sectors 7 to 9 cross a mosaic of tall *Olearia-Dracophyllum* scrub and *C. rigida* tussocks. From pegs 10 to 12 is mainly open *C. rigida*, with patches of *C. crassiuscula* and isolated shrubs. In sector 1-3 the dominant shrubs appear relatively young, and in sector 6. *C. rigida* tussocks have been suppressed beneath a tall shrub canopy, suggesting that successional processes may be occurring. However, there is no evidence of slope instability, and a search revealed no evidence of past fire (Philip Knightsbridge, pers. comm.).

Takahe Valley– 12 sectors (4 east facing, 9 west facing): Over most of the eastern part of the transect the main cover is *Gleichenia circinata*, with about 5% *D. uniflorum.* On steeper slopes *D. uniflorum, C. crassiuscula* and *Chionochloa teretifolia* co-dominate. These species and the others present, including *Carpha alpina, Lepidothamnus laxifolius, Lycopodium fastigiatum, Oreobolus* spp. and *Schoenus pauciflorus*, indicate leached, poorly drained soil. The western part has grassland of *C. pallens* and *C. teretifolia*, with shrubs of *D. uniflorum* and *Coprosma fowerakeri* which are taller and denser at the forest edge.