Thermal environment of New Zealand's gradual and abrupt treeline ecotones

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Published online: 6 December 2013

Abstract: In New Zealand, there are treelines of two main forms: abrupt southern beech treelines and gradual conifer–broadleaved treelines. At similar latitudes, abrupt treelines form at higher elevation than gradual treelines, but it is unclear whether this difference is also reflected in the climatic conditions experienced at the contrasting treeline ecotones. In this study, we measured soil and air temperatures across four gradual and two abrupt treelines ecotones in New Zealand for 2 years, and compared the climatic conditions between the treeline forms. Although gradual treelines form at lower elevations, they experience similar summer temperatures as the higher abrupt treelines. In contrast, temperatures in the shoulder season and during winter differed between sites of contrasting treeline forms. Soil scarcely froze and air temperature did not fall below −6°C at the gradual treeline sites, whereas freezing soils and snow were more common (extreme air frosts down to −9°C) at the abrupt treeline sites. Air and soil temperatures mirror the change in tree stature in the ecotone: with increasing altitude through the gradual treeline ecotone, temperature decreased gradually; whereas abrupt temperature changes were found at the abrupt treeline–grassland interface. These altitudinal patterns provide insights into potential mechanisms that drive treeline form and position, and their response to climatic change.

Keywords: altitudinal gradient; conifer–broadleaved; diffuse; elevational gradient; *Fuscospora*, microclimate; *Nothofagus*; temperature; timberline; treeline form

Introduction

Treelines are relatively discrete elevational boundaries formed in response to a gradual gradient in the physical environment. With increasing elevation, forest stature decreases before forest gives way to isolated trees and stunted individuals and eventually to shrubs or herbaceous communities (Tranquillini 1979; Körner 2003). These differing growth forms are an adaptation to the stresses imposed by increasing altitude, including low temperature, snow accumulation, and wind (Grace 1997; Barrera et al. 2000; Körner 2003). New Zealand treeline ecotones are of two main types: abrupt and gradual. Abrupt mountain beech (*Fuscospora*) treelines dominate in the eastern rain-shadow districts; whereas in western, more oceanic districts, gradual ecotones are often formed by a diverse set of conifer–broadleaved species (Wardle 2008; Fig. S1 Supplementary Information). Such contrasting treeline types suggest that treeline position might be driven by different processes and respond to climatic changes in different ways (Harsch et al. 2009; Harsch & Bader 2011).

At similar latitudes, gradual treelines form at lower elevations than abrupt eastern treelines (Fig. 1). Despite a long history of research at the New Zealand treeline (e.g. Zotov 1938; Wardle 1965, 1973, 1985a, 2008; Benecke & Havranek 1980; Cullen et al. 2001), few climatic measurements are available to compare the treeline ecotones of different forms. Although records are now available from four abrupt southern beech treelines around New Zealand (Mark et al. 2000; Körner & Paulsen 2004; Mark et al. 2008), the climatic data from mixed conifer–hardwood treelines consist of a single study of a broadleaved tree (*Metrosideros umbellata,* Myrtaceae) commonly found in the upper montane forest of the central West Coast, South Island (Payton 1989).

Treelines on the western side of the main axial ranges in New Zealand experience high levels of cloud cover and precipitation compared with eastern slopes as a result of the Southern Alps facing the prevailing westerly winds (McCracken 1980; Wardle 1986; Salinger 1988). Summers in subalpine forests in the high rainfall regions on the West Coast have long been considered shorter and cooler than summers in subalpine forests in the eastern rain-shadow region (e.g. Wardle 1973; Veblen & Stewart 1982), but this has never been quantified.

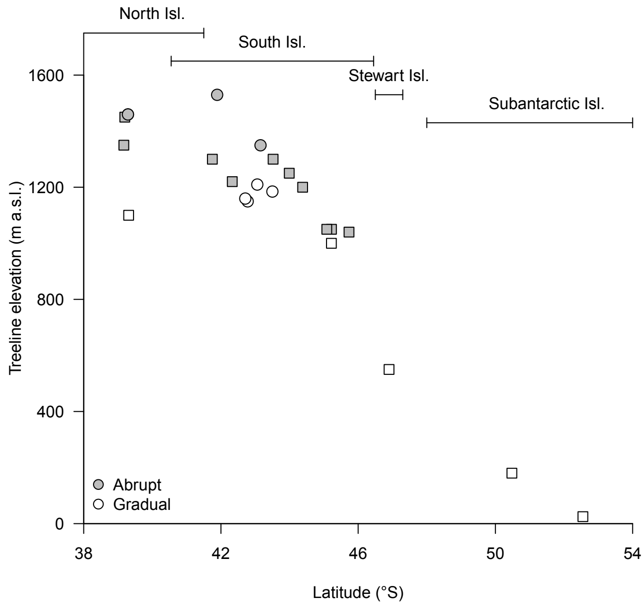

Figure 1. At the same latitude, gradual treelines (white symbols) are at lower elevations than abrupt treelines (grey symbols). Circles indicate treeline sites used in this study; squares are additional treeline sites included for illustration of the latitudinal trend (Cieraad 2012).

Here, we describe the first concurrent temperature measurements across New Zealand treeline ecotones of different forms (abrupt and gradual). We compare climatic conditions across the different ecotones in summer and winter, and discuss how these altitudinal trends in the thermal environment may provide indications of which environmental stressors are limiting tree growth at higher elevations.

Methods

Sites

To characterise the thermal environment of the New Zealand treeline ecotone, six field sites were selected, comprising different treeline types and spanning a large latitudinal range (Table 1; Figs S1 and S2). Four gradual treeline sites of mixed conifer–hardwood (Camp Creek, Kelly Creek, Mikonui, and Mt Fox) were situated west of the Southern Alps in Westland (referred to below as 'gradual treeline' sites). One abrupt beech site was situated in each of the North and South Islands (Kaweka and Rainbow, respectively). Meteorological data from a weather station nearby an additional abrupt treeline site (Craigieburn) were also used (see below). At these latter three sites, the abrupt treeline is formed by mountain beech, *Fuscospora cliffortioides* (previously *Nothofagus solandri* var. *cliffortioides*; Heenan & Smissen 2013), as elsewhere in the rain-shadow region. These sites are referred to below as 'Eastern Alps' or 'abrupt treeline' sites. At Craigieburn, the exotic conifer *Pinus contorta*, introduced to reduce soil erosion in the 1970s, has established and is spreading above the local mountain beech treeline (Ledgard 2001). Treelines at all sites represent the local natural climatic tree limit and have been largely free of human disturbance (such as burning, grazing and forest clearance) or avalanches (Wardle 2008).

Data collection

We defined the elevational treeline as the line connecting uppermost groups of trees > 3 m tall (following Körner & Paulsen 2004). At each of the six field sites, three altitudinal transects were set up on topographically separate units (parallel ridges) about 100 m apart horizontally; each transect consisted of four data-logger sites. In the gradual ecotone, logger sites were established 100 m (vertically) below the treeline, at the treeline, and 100 m and 200 m above the treeline. At the abrupt beech-treelines a pair of data loggers were established, one set within the treeline forest and one in the associated tussock grassland (within 10 m of the treeline canopy); logger sites were also established 100 m below and 100 m above the treeline (see Fig. S2).

Tinytag Plus2 data loggers (precise to ± 0.2°C; Gemini, UK) recorded air and soil temperature (T_{air} and T_{soil}) every hour. The soil logger placement protocol followed Körner & Paulsen (2004) for montane forest and treeline sites: loggers were buried in a location screened by the forest tree canopy throughout the day, with the temperature sensor at 10 cm below the soil surface. At above-treeline sites, loggers were placed at 10 cm depth in the soil on the south side of and beneath the canopy of a shrub or tussock to reduce the effect of direct radiation. Aerial loggers were fixed to a metal pole at 1.3 m above the ground surface and placed outside the closed canopy (in the open canopy at gradual treelines; in the tussock grassland at abrupt treelines). The aerial loggers were screened from direct sunlight by a perforated white plastic screen.

All data loggers were checked for stability and absolute accuracy in an ice-water bath and at several higher temperatures before and after deployment, and the recorded temperatures adjusted accordingly (deviation from zero was < 0.25°C for 95% of loggers; the highest anomaly was 0.6°C). A post hoc verification of treeline soil temperature data showed daily

Table 1. Details of the treeline locations studied, and length of soil and air temperature records (if applicable). Within region, sites are ordered by increasing latitude.

Treeline site name	Long. (°E)	Lat. (°S)	Altitude (m a.s.l.)	Main woody species in the ecotone[1]	Temperature recorded (d/m/y to d/m/y)
Gradual treelines – Western Alps					
Camp Creek	171.57	42.71	1160	*Halocarpus biforme* (Podocarpaceae), *Libocedrus bidwillii* (Cupressaceae), *Olearia* spp.[2] (Asteraceae), *Dracophyllum* spp.[3] (Ericaceae)	31/01/2009 to 27/04/2011
Kelly Creek	171.58	42.78	1150		13/05/2009 to 28/04/2011
Mikonui	170.87	43.06	1210		17/01/2009 to 20/03/2011
Mt Fox	170.01	43.50	1185		06/01/2010 to 22/03/2011
Abrupt treelines – Eastern Alps					
Kaweka	176.36	39.29	1460	*Fuscospora cliffortioides*, *Phyllocladus alpinus* (Podocarpaceae)	26/11/2008 to 06/06/2011
Rainbow	172.86	41.89	1530	*Fuscospora cliffortioides* (Nothofagaceae)	11/04/2009 to 09/04/2011
Craigieburn	171.70	43.12	1350	*Fuscospora cliffortioides* (Nothofagaceae), *Phyllocladus alpinus* (Podocarpaceae), *Pinus contorta* (Pinaceae)	None

[1]The four gradual treeline locations share the main woody components; for the abrupt treeline locations, the main components are identified separately per site.
[2]*Olearia* spp. comprise *O. arborescens*, *O. avicenniifolia*, *O. colensoi*, *O. ilicifolia*, *O. lacunosa* and *O. paniculata*.
[3]*Dracophyllum* spp. comprise *D. longifolium* and *D. traversii*.

amplitudes lower than 5.5°C, confirming that the loggers had remained under full-shade (Körner & Paulsen 2004). Under open canopy or grassland, the daily amplitude was usually larger due to radiative heating of the soil. All measurements were obtained between November 2008 and May 2011, and at least 2 years of continuous data were available for each site (Table 1, except Kaweka *air* temperature, which was only at the treeline; and the highest elevation at Mt Fox, which had only one year of measurements).

Although snow cover was not directly measured, its presence could be inferred. Snow cover strongly dampens the daily amplitude of soil temperatures, because of its insulating effects; at temperatures close to the freezing point, a lack of fluctuations in the temperature trace can thus be used to estimate snow cover duration (Zhang 2005). Compared with more continental treeline sites, continuous snow cover at the studied sites was variable and transient (with durations of less than a month), and thus no in-depth analyses of, for example, melting dates were undertaken (e.g. Green & Venn 2012).

To compare meteorological conditions other than temperature between abrupt and gradual treelines, a Datahog2 (Skye, UK) collected hourly data on relative humidity, wind direction and wind speed at Kelly Creek (May 2009 – April 2011) and additional data were downloaded from the National Institute for Water and Atmospheric Research (NIWA) climate database (cliflo.niwa.co.nz, 2001–2010). Rainfall data were recorded at Inchbonnie (<4 km from the Camp Creek gradual treeline, 116 m a.s.l.); although collected in the lowlands, the yearly rainfall between this site and the treeline (at c. 1200 m a.s.l.) differed less than 10% in 1982–1984 (see Payton 1989). Global radiation data were also available for this lowland site. Temperature and rainfall data for the Eastern Alps were recorded at Craigieburn (914 m a.s.l.). The temperature data were adjusted to treeline elevation (1350 m) using monthly lapse rates calculated from concomitant measurements at 914 m and 1554 m between 1976 and 1986 (monthly lapse rates ranged from 4.8°C per 1000 m altitude in winter to 7.7°C per 1000 m in summer; data not shown, see Cieraad 2012). Monthly averages of relative humidity, global radiation, wind speed, and wind direction were calculated from the Craigieburn station as these variables were not consistently recorded at the higher station.

Data analyses

To condense the temperature data, we averaged the hourly readings at the same elevation on the three altitudinal transects per field site. This resulted in eight datasets per field site; corresponding to the average hourly air and soil temperature at the four altitudes (see Fig. S2b). Daily minimum, maximum, and the arithmetic mean temperature (T_{min}, T_{max} and T_{mean}, respectively) were calculated. The data were also condensed to a 365-day dataset by averaging any data obtained for the same day in multiple years (Körner & Paulsen 2004).

The first year in this study (2009) was cold (−0.22°C) compared with the long-term national mean (as recorded by seven stations from 1971–2000; Mullan et al. 2010), whereas 2010 was the fifth warmest year on record (+0.53°C). The first few months of 2011 (when the last recordings were taken) were near the long-term mean temperature for these months. Temperature data were not adjusted for these anomalies.

To assess whether the seasonal temperature course was significantly different between abrupt and gradual treelines, linear mixed-effects (LME) models for air and soil temperature were used, with field site as a random effect. Models including additive and interactive effects of treeline form (abrupt or gradual) and seasonality (as a sine/cosine function) were compared, as well as the same models with serial correlation incorporated as an autoregressive moving average (ARMA) covariance structure with a lag of 1 or 2 months. Akaike's Information Criterion corrected for small sample sizes (AICc) was used to assess which model was most strongly supported by the data (Anderson 2008).

All analyses in this study were performed in R v. 2.12.2 (R Core Development Team 2011), and included use of the packages *AICcmodavg* (Mazerolle 2011) and *nlme* (Pinheiro et al. 2011).

Results

The best LME models of mean monthly air and soil temperature at the treeline, given the data, included an interaction between time (as a sine/cosine function) and treeline form, and an autocorrelation structure with a lag of 2 months in both models (Fig. 2). In the warm months, mean monthly air and soil temperatures were similar at gradual and abrupt treelines. At the end of summer, temperatures at the abrupt treelines dropped more rapidly than at the gradual treelines, and the colder months were significantly colder at the abrupt treelines (Fig. 2). In addition to the seasonal trend described by the sine/cosine function, the positive autocorrelation of the data shows that observations up to 2 months apart were correlated: for example, if the start of summer is warmer than average, it is likely that the next 2 months are also warm.

Mean annual air and soil temperatures across all altitudes and all sites ranged between 4.7° and 6.4°C, and 4.7° and 5.3°C, respectively. Mean air temperatures during the three warmest months were between 9.9° and 10.5°C at the gradual treelines and between 10.6° and 11.0°C at the abrupt treelines. As expected, temperatures decreased with altitude, but the altitudinal trends differed between air and soil temperatures, and between sites (Supplementary Information Fig. S3; Table S1). The mean annual soil temperature was between 0.5° and 1.6°C colder beneath the abrupt treeline canopy compared with the adjacent tussock grassland, and these differences were even more pronounced during the three warmest months.

Monthly winter temperatures experienced in the abrupt treeline ecotone were colder than those in the gradual ecotones (Table S1; Fig. 2). Absolute minimum air temperature at treeline was between −6.4°C and −6.0°C at the gradual sites, while extremes of −9.1°C and −6.5°C were recorded at the abrupt treelines of Rainbow and Kaweka, respectively. Extreme minima 100 m above the treeline were at least 0.9°C colder than at the treeline, with −10.3°C the lowest recorded (100 m above the Rainbow treeline). Air frosts occurred on around 105 days per year at treeline (although up to 145 at Rainbow), and c. 20 more days 100 m higher. Only the two warmest months were without any air frosts at all six treelines, whereas frosts occurred during most nights in mid-winter. At all sites, 15–20 frosty nights were recorded in each of August, September and October (Fig. S4).

At the treeline in the gradual ecotone, soils very rarely froze. Above the gradual treeline, soils were frozen for up to a week, with an extreme low recorded of −0.2°C (across all altitudes, sites and years; Table S1). In the abrupt treeline ecotones, freezing soil temperatures were recorded more commonly (with an extreme minimum of −2.5°C recorded in the grassland directly adjacent to the Rainbow treeline). Soil

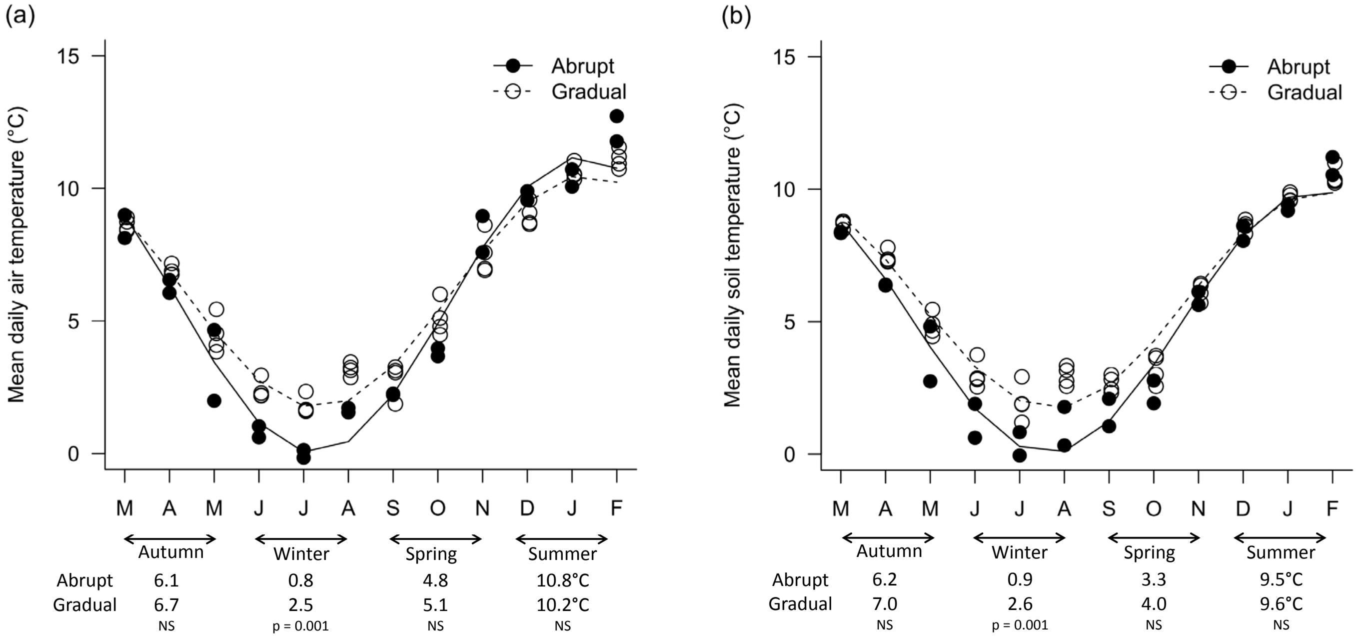

Figure 2. Mean monthly and seasonal air (a) and soil (b) temperatures at the six treeline sites measured in this study. Mean monthly temperatures in spring, summer and autumn do not significantly (NS) differ between treeline forms, but mean winter air and soil temperatures are significantly ($\alpha < 0.5$) colder at abrupt treelines. Lines are predictions from linear mixed-effects models.

100 m below the treeline was frozen for a week at Kaweka, but never at Rainbow. At the treeline, soil beneath the canopy never froze at Kaweka, but freezing temperatures were recorded on average 34 days every year at Rainbow. These soil frosts never fell below −0.5°C and were all associated with snow cover. Soil at sites above both abrupt treelines was frozen for c. 20 days each year (Fig. S4).

Snow cover duration, estimated from non-fluctuating soil temperatures close to 0°C, was almost twice as long in the winter of 2009 than in 2010, but similar patterns along the altitudinal gradient were visible in both years. In the gradual treeline ecotones, the average maximum duration of snow cover over these two measured winters was less than 14 days at all but the very highest altitude. At this highest site (200 m above treeline, or c. 1400 m a.s.l.), there was continuous snow cover for about a month. In contrast, at the abrupt treelines continuous snow cover lasted between 30 and 50 days across the whole ecotone.

Weather stations provided additional meteorological records at gradual and abrupt treeline sites (Fig. 3). Rainfall was evenly distributed throughout the year at both sites, and annual rainfall was approximately three times higher at the gradual than at the abrupt treelines. Average relative humidity was stable at c. 90% throughout the year at the gradual treeline, whereas at the abrupt treeline it was lower, ranging between 70% and 80% with a distinct minimum during the warmer months. At the western gradual treeline, winds most commonly came from a south-to-westerly or a northerly direction. Mean wind run and maximum wind speed were higher in the warm months (220–350 km per day, with mean daily maxima of c. 50 km h^{-1}) than in winter (wind run of < 100 km, mean daily maxima of 10 km h^{-1}). At the abrupt treeline site, a north-east wind direction was most common. Mean maximum wind speed was evenly distributed through the year (c. 20 km h^{-1}), but maximum wind runs of > 200 km occurred in the spring months September, November and December (Fig. 3c–d). Average annual global radiation received was slightly higher at the abrupt treeline (145 MJ) compared with the gradual treeline (133 MJ), with more than half (7 MJ) of the difference attributed to reduced sunshine at the gradual treeline in the months October, November and December.

Discussion

Soil and air temperatures recorded concurrently across six New Zealand treeline ecotones show similar growing season temperatures at all sites, but distinctly different altitudinal and seasonal patterns between abrupt and gradual treelines. These trends provide insights into the mechanisms driving treeline form, and suggest their comparative response to future climatic changes.

Summer temperature

Our temperature data show that the assumption of a marked difference in summer warmth between the different sides of the Southern Alps (e.g. Wardle 1973; Veblen & Stewart 1982) is overstated. Mean air temperature during the three warmest months was 9.9° to 10.5°C at the four gradual treeline sites in this study, only slightly cooler than the 10.6° to 11.0°C of the abrupt mountain beech treelines in the eastern rain-shadow region.

New Zealand treelines have previously been argued to equate with a warmest-month mean air temperature of c. 10°C (Zotov 1938; Wardle 1973, 2008), largely based on extrapolated weather station data. Measured data provided similar means (9.9° to 10.6°C) for the gradual treeline at Camp Creek (Payton 1989) and for two abrupt *Lophozonia menziesii* treelines in the wetter western regions of South Westland and Fiordland (Mark et al. 2000, 2008), but slightly higher at the sites in this study (mean 11.5°C).

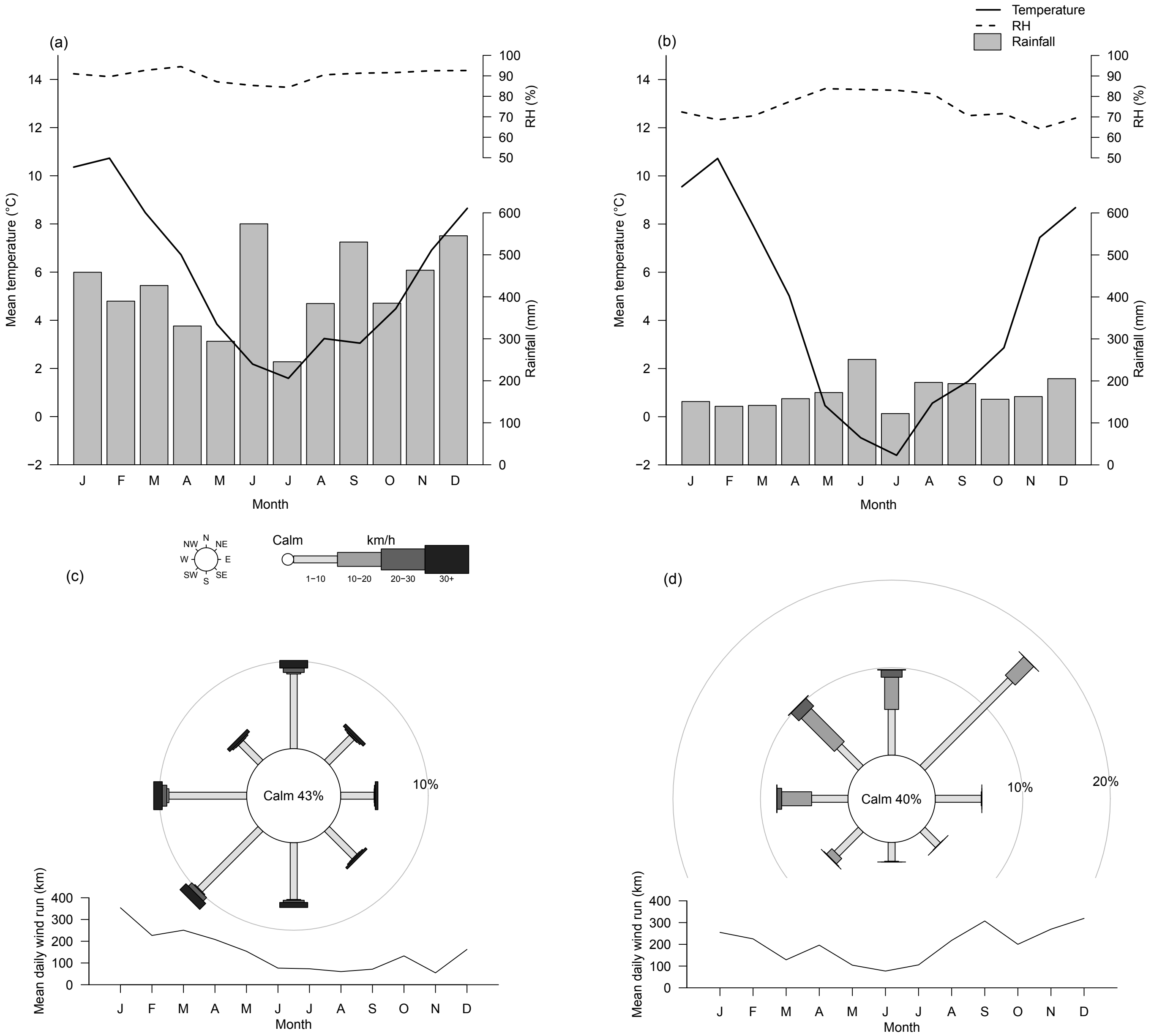

Figure 3. Climatic data from gradual (a and c) and abrupt (b and d) treeline sites. (a, b): Mean monthly temperature, rainfall and relative humidity (RH); (c, d): wind rose and mean daily wind run. Each limb of the wind rose represents a 45° bin of wind directions. The length of each limb represents the amount of time (as a percentage, indicated by the grey circles) that the wind comes from that direction, and the colour and width of the limb indicate the range of wind speeds. Data from a variety of sources (see Methods).

Although the elevation of the western treelines is lower than the eastern treelines, the summer air and soil temperatures experienced at these sites are similar. Moreover, our data show that the growing season at New Zealand treeline, measured by soil temperature, is not anomalously warm compared with treelines elsewhere (Körner & Paulsen 2004), but falls within the global norm (Cieraad 2012). Towards the end of summer, the temperature at abrupt treelines falls more sharply than at gradual treelines, creating a more clearly defined growing season (Fig. 2).

Winter temperature

Climatic differences between the treeline forms are more marked in the winter months. Mean coldest-month air temperature measured at the two abrupt treelines (−0.1°C and +0.2°C) were lower than those at the gradual treelines (1.6° to 1.9°C). Values for the abrupt treelines of this study concurred with Wardle's (2008) correlation of New Zealand beech treelines with a coldest-month mean of 0°C, extrapolated from data collected at low-elevation meteorological stations. These values are slightly warmer than the limits of broadleaved evergreen trees globally at −1°C (Ohsawa 1990). Coldest-month temperatures for the gradual mixed conifer–broadleaved treelines in this study were comparable with the 1.5°C recorded at Camp Creek in 1979–1983 (I.J. Payton, unpubl.).

Although mean monthly temperatures differ between abrupt and gradual treelines in winter, there was no clear difference in the air frost frequency and magnitude at the different treeline forms (Fig. S4). The extreme minimum air temperature recorded at treeline was −9.1°C at Rainbow, whereas all other sites had warmer minima (−6.5° to −6°C). It is unlikely that air frosts of this magnitude play an important role in the position of New Zealand treelines, as the frost tolerance of the trees at treelines of both forms exceed the extreme temperatures experienced there by at least 4°C (Cieraad et al. 2012).

Soil frosts were very rare in the gradual treeline ecotones (the maximum of 3 days per year was attained at 200 m above the Camp Creek treeline; Fig. S4). Continuous snow duration occurred for only about 2 weeks at gradual treelines, and for up to a month 200 m above these treelines, as had been reported for Camp Creek by Payton (1989). Soil frosts and snow cover were more common at the Eastern Alps abrupt treelines: soil frosts occurred around 20 days per year, in association with snow cover (−0.5°C; Fig. S4). With so few and mild soil frosts at 10 cm deep, the hypothesis that reduced uptake of water from frozen soil has a role in the formation of New Zealand treelines (winter desiccation; Wardle 1985c) seems improbable. Rather than soil frosts being a feature of abrupt treelines, this phenomenon is likely to be more related to continentality; similar to the gradual treelines in this study, soil at an abrupt treeline ecotone in the highly oceanic south Westland did not experience freezing until approximately 500 m above the local treeline (c. 1550 m a.s.l.; Mark et al. 2008).

Other weather conditions (wind, sunshine)

In oceanic regions, wind may play an important role in the survival and structure of trees near their elevational limit. Strong winds may affect the growth of treeline trees by cooling their canopy (increased coupling with the atmosphere), increasing mechanical stress, and blasting of wind-blown particles on foliage and bark (Grace 1997). Although slightly less windy overall, the gradual treeline had a higher incidence of strong winds (> 30 km h^{-1}) compared with the abrupt treeline, which experienced more winds with speeds between 10 and 30 km h^{-1} (Fig. 3). At the gradual treeline, winds were also stronger in summer than in winter, whereas the strongest winds at the abrupt treeline occurred in spring (Fig. 3). On exposed sites in the gradual ecotone, tree species can be reduced to shrub-statured individuals without showing contorted growth forms (Wardle 2008), whereas mountain beech in abrupt ecotones can be reduced to krummholz (crippled individuals) due to dieback and deformation at such sites.

Strong winds can also cause considerable snow redistribution (McCracken et al. 1985), and our data suggest that more than 30 additional days with snow cover (up to 124 days, not necessarily continuous) occurred beneath the treeline canopy at Rainbow compared with in the adjacent tussock grassland. These results contradict the suggestion that krummholz beech trees prevail where snow accumulates in the treeline margin (Norton & Schönenberger 1984; Wardle 1985b), since no krummholz occurred at the two mountain beech sites in this study.

The western gradual treeline received more than three times the rainfall of the eastern abrupt treeline; however, the average annual global radiation was similar (average annual global radiation between 2007 and 2010 was 145 MJ at c. 400 m a.s.l., below the abrupt treeline at Craigieburn, and 133 MJ at Inchbonnie at 1000 m a.s.l., below the Camp Creek gradual treeline). Although these data were obtained at lower elevations (c. 450 and 1000 m lower than the local abrupt and gradual treeline, respectively) and they may overstate the actual radiation at treeline if cloud base was often below treeline elevation, previous work using satellite imagery also did not find a clear difference in cloud frequency at gradual and abrupt ecotones (Wardle 1986). Those results may, however, have been confounded as the study years (1982–1984) covered a strong El Niño episode.

Altitudinal patterns

At the gradual treeline sites air temperature during the three warmest months was warmer than the soil temperature, whereas 100 m higher the air was the same temperature or cooler than the soil (Fig. S3a–d). In contrast, soils were warmer than air in the grassland immediately adjacent to the abrupt treeline. We note that the highest altitude site at the gradual Mt Fox treeline (Fig. S3d) was much warmer than lower sites, presumably due to the effect of the very steep (>60° inclination) slope at this site (loggers at all other sites were placed on more or less level surfaces) and lack of vegetation, providing an example of the effect of land surface characteristics (Wardle 1985b) and vegetation stature on temperature (Körner 2007). This may have been exaggerated by the lack of records at this altitude during the cooler year of 2009, biasing the data to the warmer 2010 and 2011 years (see Table 1 and Methods).

The altitudinal temperature trends found in this study correlate with vegetation stature (Körner 2003). In the abrupt-treeline ecotone, abrupt changes in vegetation stature are accompanied by abrupt changes in the temperature regime (Fig. 3e–f; Table S1) (Wilson & Agnew 1992), whereas gradual temperature decreases were found across the gradual ecotone, mirroring the gradual decrease in tree height. Soils supporting mountain beech forest were 1° to 2.5°C cooler than soils of sites less than 10 m away without trees, as has been noted by others (Wardle 1985b; Körner et al. 1986; Mark et al. 2008). These data highlight how the forest canopy creates its own microclimate by shading the soil beneath, preventing soil heat flux and radiative warming from increasing the root zone temperature (Körner 2003). The trees potentially affect their own performance through soil-temperature-mediated feedbacks, since low soil temperatures can limit tree growth, regardless of the air temperature (Körner & Hoch 2006; Hoch 2013).

Although the summer air and soil temperatures are much warmer only just beyond the shade of the canopy, few *Fuscospora* seedlings are found there. Hence this treeline is not limited by growing season warmth. Experimental plantings suggest that seedlings are unable to exploit the summer warmth unless shelter is provided (Wardle 1985a; Harsch 2010). Extreme minimum air temperatures alone are not detrimental, as they do not exceed the species' foliage frost tolerance levels (Cieraad et al. 2012). It is likely that the interaction between exposure-related stresses (e.g. high light, wind, and desiccation) is important in limiting the survival and establishment of seedlings beyond the canopy. While there is considerable support for this notion (e.g. Ball 1994; Wardle 2008), such effects have not yet been quantified.

Short vegetation is warmer than tall vegetation on sunny days with little wind (especially under a continental climate regime), but this type of vegetation may have a reduced thermal advantage in areas of high wind, high humidity and/or where cloud cover reduces insolation with altitude (e.g. oceanic climate) (Grace et al. 1989). However, even at the windy, highly oceanic gradual treeline sites, decoupling of atmospheric temperature from lower-stature vegetation was evident: lapse rates of soil temperatures were lower than air-temperature lapse rates during the three warmest months (slope of the trends in Fig. S3). With increasing altitude across the gradual ecotone, a progressively cooler thermal environment is accompanied by a gradual decrease in tree height, without severely distorting growth forms. This suggests that these gradual treelines represent the ultimate climatic tree limit and that a thermal growth limitation is important at these treelines (Smith et al. 2003; Harsch & Bader 2011).

Climatic change

In a global meta-analysis of treeline responses to climatic change, Harsch et al. (2009) found that gradual treelines were more likely to advance in response to warming than abrupt treelines. This was suggested to be caused by different underlying mechanisms that determine the position of these treelines; temperature may strongly limit growth at gradual treelines and hence they respond more to warming, whereas abrupt treelines are subject to additional constraints that may not have been alleviated by warming (Harsch et al. 2009; Harsch & Bader 2011). Indeed, in contrast to many treelines elsewhere, the abrupt mountain beech treelines appear relatively unresponsive to recent climatic warming (Wardle & Coleman 1992; Harsch & Bader 2011; Harsch et al. 2012). These treelines are limited by recruitment, likely reflecting a lack of microsite availability (Harsch et al. 2012). In contrast, the gradual conifer–broadleaved treelines are more closely linked to summer temperatures and thus theoretically should be more responsive. However, the advance of these treelines has not yet been studied.

Conclusions

Our study shows that gradual and abrupt treelines in New Zealand share similar growing season temperatures, even though gradual treelines form at much lower elevations. The two treeline forms differ markedly in their winter season: the abrupt treeline ecotone experiences colder temperatures, more frosts and a longer lasting snowpack than the gradual treeline ecotone. The exposure and harsh conditions play an important role in limiting recruitment above the abrupt mountain beech treelines, whereas gradual conifer–broadleaved treelines are more closely linked to summer temperatures and thus are also likely to be more responsive to future changes in summer climate.

Acknowledgements

We thank Phillip Cochrane, Simon Burrows, Constantijn Mennes, Veronika Gottstein, Ian Phillips and Benjamin Leutner for their help in the field. We also thank Bill Lee, Sarah Richardson, Susanna Venn and an anonymous reviewer for their comments on earlier versions of this paper, Christine Bezar for editing, and the New Zealand Ecological Society Writer's Workshop 2012 for support. The Department of Conservation gave permission to work at the field sites. Financial support for the first author was provided by a Durham University Doctoral Fellowship. The research was supported by Brian Huntley (Durham University), the Landcare Research Peter Wardle Treeline Research Fellowship, a Canterbury Botanical Society Student Grant and a Royal Forest and Bird Society Stocker Scholarship.

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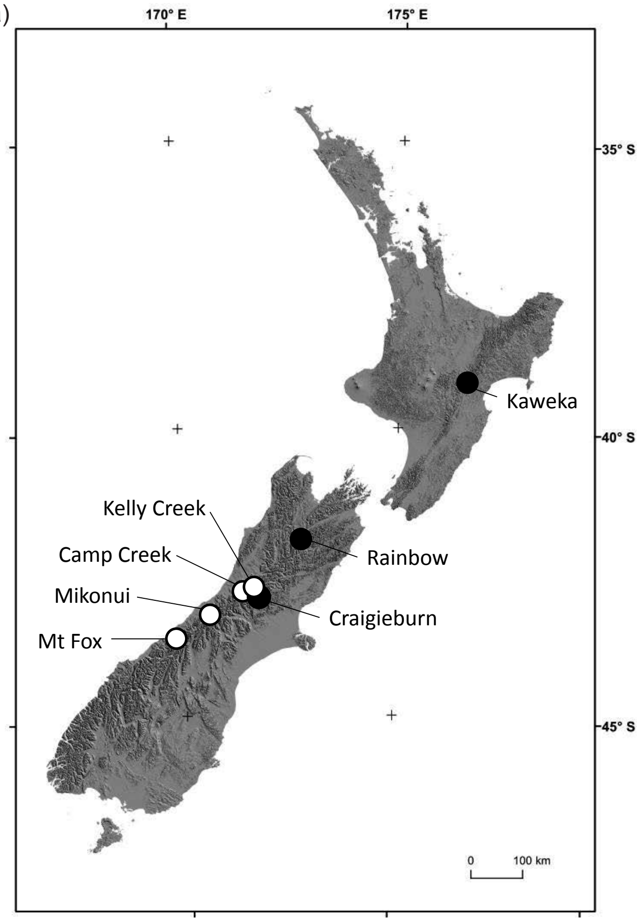
Editorial Board member: Angela Moles
Received 19 May 2013; accepted 16 September 2013

Supplementary Information

Figure S1. Treeline ecotones of contrasting forms in New Zealand. Top (left and right): gradual treeline ecotone at Camp Creek, Westland; bottom: abrupt mountain beech (*Fuscospora cliffortioides*) var. *cliffortioides* treeline on the St Arnaud Range (left) and at Craigieburn (right). (Photo bottom left © Landcare Research; others by Ellen Cieraad).

(a)



(b)

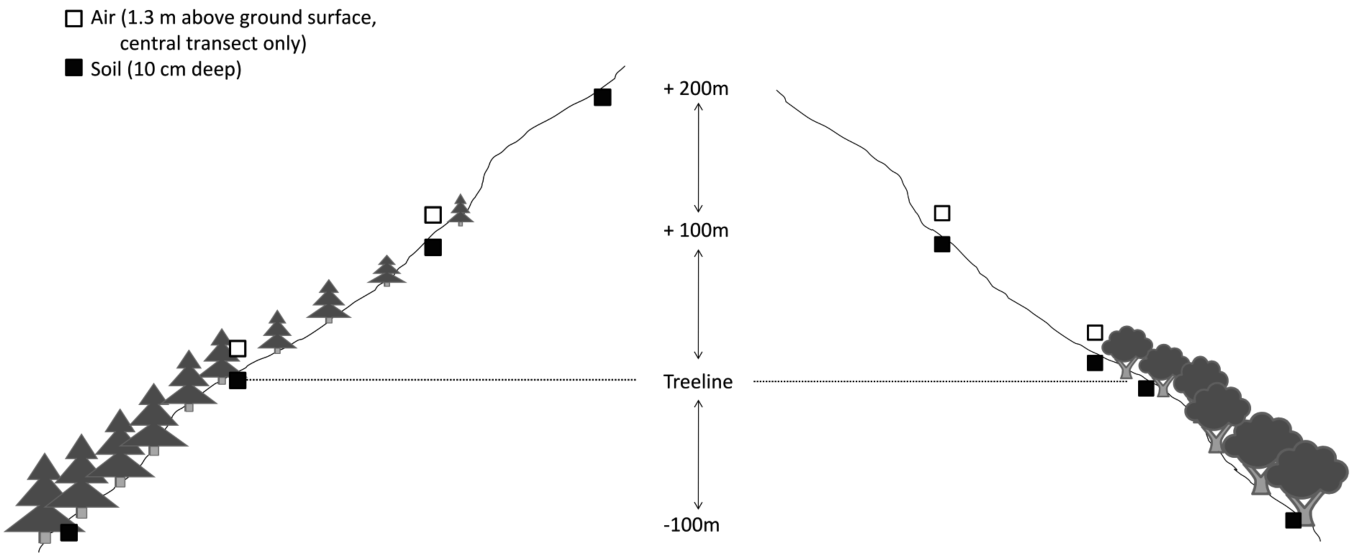


Figure S2. (a) Location of study sites, with white and black circles indicating gradual and abrupt treeline sites, respectively. (b) Schematic set-up of temperature data loggers along an elevational gradient for a gradual treeline (left) and an abrupt treeline (right). Three such transects were laid in parallel at c. 100 m (horizontally) apart. Only the central transect contained air temperature data loggers. Note the paired data loggers at the abrupt treeline (one set beneath the canopy, one set just above – within 10 m – in the tussock grassland).

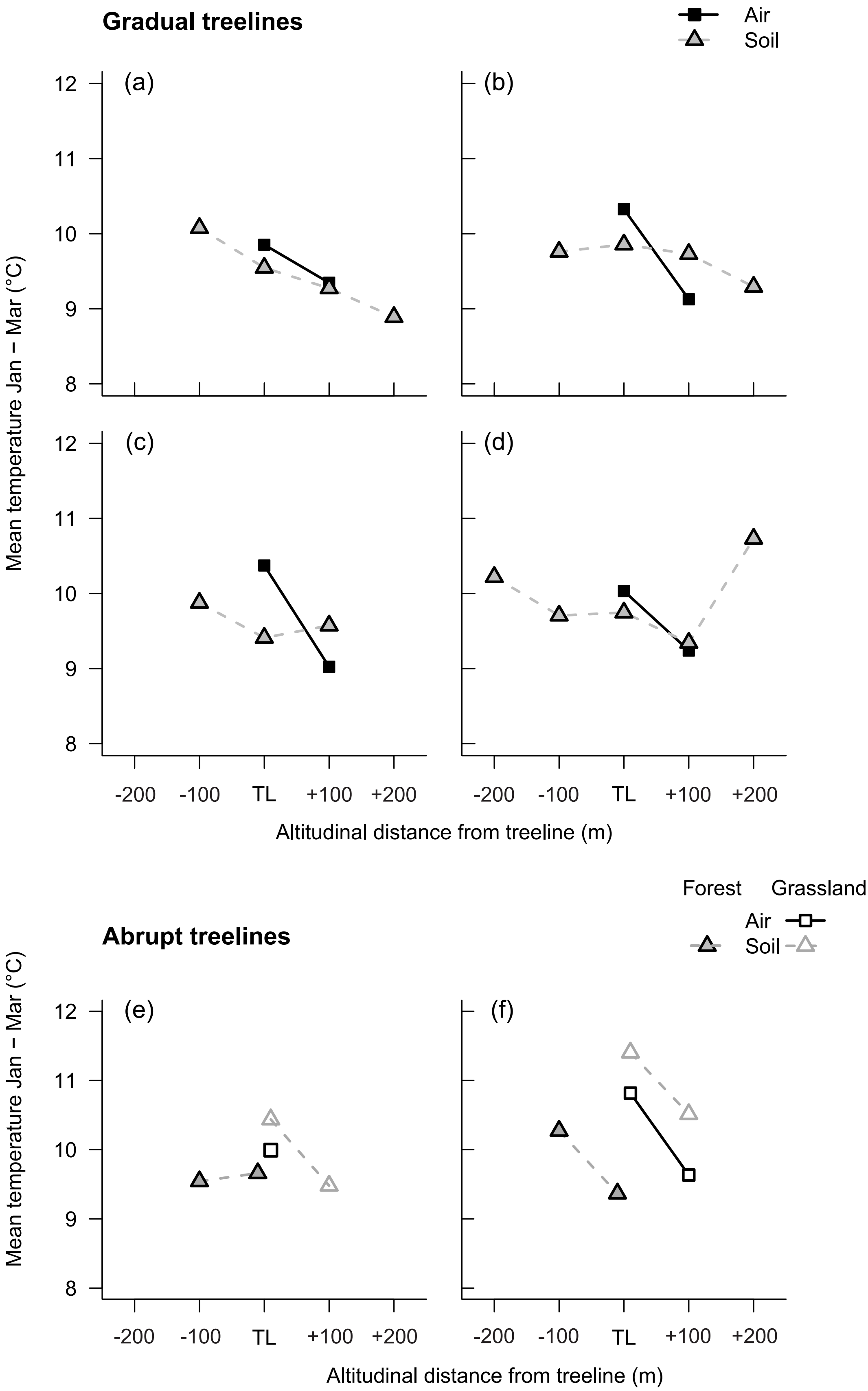


Figure S3. Mean temperature in January–March for the air and soil loggers along an elevational gradient along the four gradual treeline ecotones (a) Camp Creek, (b) Kelly Creek, (c) Mikonui, and (d) Mt Fox, and the abrupt treeline ecotones at (e) Kaweka and (f) Rainbow. Note that at the gradual sites, loggers were set up at 100-m intervals including at the treeline (TL), whereas at the abrupt sites, loggers were set up 100 m above and below the treeline (TL), as well as a pair of logger sites at the treeline itself: one underneath the treeline forest canopy and one in the alpine grassland within 10 m of the treeline (see Methods, and Supplementary Fig. S2).

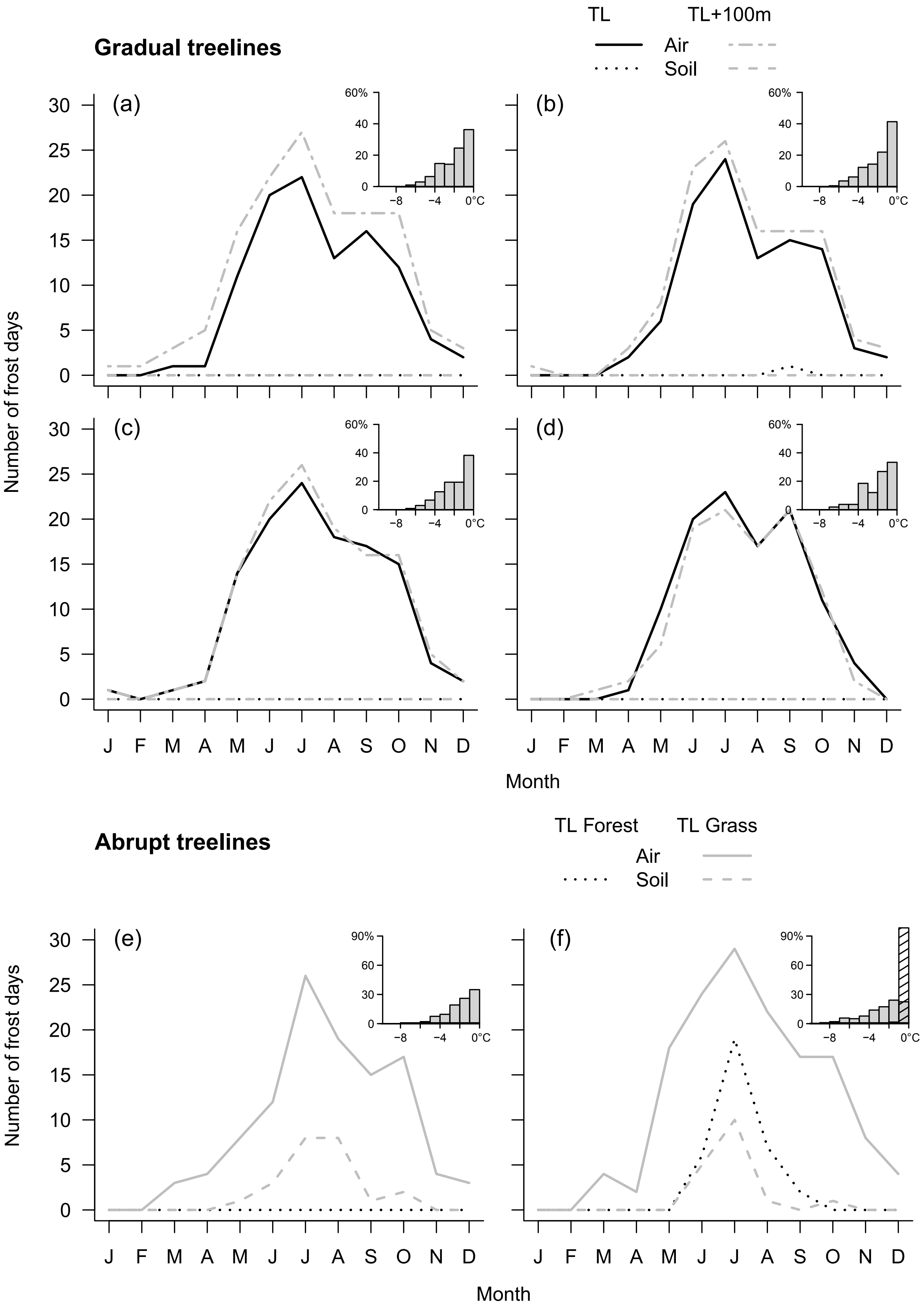


Figure S4. Average number of air and soil frost days per month at the four gradual treeline sites at treeline (TL, black lines) and at 100 m above treeline (grey lines): (a) Camp Creek; (b) Kelly Creek; (c) Mikonui; (d) Mt Fox); and at the two abrupt treeline sites (comparing frosts under the treeline forest canopy – soil only, black line, versus the adjacent grassland, grey lines: (e) Kaweka; (f) Rainbow). Insets show frequency distribution of the intensity of air and soil frosts at the treeline (grey and striped bars, respectively; for the abrupt treeline, soil frosts underneath the forest canopy and air frosts over grass are shown).

Table S1. Temperature summaries for the six treeline sites in this study during 2009–2011. At each site, soil temperature was recorded along an elevational transect through the treeline ecotone, and air temperature was also recorded at a subset of the locations (see Fig. S2, and Methods section for detail). The table shows for each logger altitude the average recorded annual minimum, mean and maximum temperatures (T_{min}, T_{mean}, and T_{max}, respectively), the mean temperature over the warmest 1, 3, and 6 months (mnths) of the year, mean temperature of the coldest month, average number of frost days per year, extreme temperatures (absolute minimum and maximum recorded, Extr. T_{min} and Extr. T_{max}, respectively), and growing degree days (calculated with base temperature of 0°, 5° and 10°C). TL=treeline.

Location		Annual			Warmest months					Extremes		Growing degree days		
Altitude from TL (m)	Logger	Avg. T_{mean}	Avg. T_{min}	Avg. T_{max}	1 month T_{mean}	3 mnths T_{mean}	6 mnths T_{mean}	Coldest month T_{mean}	Frost days	Extr. T_{min}	Extr. T_{max}	GDD 0	GDD 5	GDD 10
Camp Creek (Gradual treeline)														
−100	Soil	6.3	5.8	6.8	10.8	10.1	9.0	2.3	0	0.2	15.4	2285	754	70
TL	Soil	5.8	5.2	6.5	10.3	9.5	8.5	1.9	0	0.1	14.8	2106	655	49
TL	Air	5.8	2.5	10.7	10.7	9.9	8.6	1.6	103	−6.4	27.6	2139	769	146
+100	Soil	5.4	4.9	6.0	9.9	9.3	8.1	1.7	0	0.1	14.1	1984	593	21
+100	Air	5.2	1.7	10.0	10.2	9.4	8.1	0.8	138	−8.2	26.8	1934	665	120
+200	Soil	4.7	4.2	5.2	9.7	8.9	7.6	0.6	3	−0.1	14.7	1704	507	27
Kelly Creek (Gradual treeline)														
−100	Soil	6.0	5.6	6.4	10.8	9.8	8.6	2.1	0	−0.1	15.1	2194	694	44
TL	Soil	5.7	5.2	6.3	11.0	9.9	8.6	1.2	1	0.0	15.3	2090	695	66
TL	Air	6.1	2.7	11.5	11.6	10.3	8.9	1.7	96	−6.0	31.8	2242	833	186
+100	Soil	5.4	4.8	6.1	11.1	9.7	8.3	1.3	0	0.0	17.8	1972	599	47
+100	Air	5.0	2.1	9.1	10.3	9.1	7.8	0.6	112	−6.9	26.3	1874	618	114
+200	Soil	5.1	4.5	6.0	10.5	9.3	8.0	0.9	1	−0.1	17.6	1891	578	50
Mikonui (Gradual treeline)														
−100	Soil	6.2	5.7	6.7	10.6	9.9	8.8	2.6	0	−0.2	15.6	2244	718	48
TL	Soil	5.5	5.1	5.9	10.2	9.4	8.3	1.9	0	−0.2	14.0	2002	610	30
TL	Air	6.2	2.2	12.8	11.2	10.5	9.2	1.6	119	−6.3	34.2	2260	857	189
+100	Soil	5.3	4.9	5.7	10.4	9.6	8.4	1.3	0	0.1	13.8	1929	617	29
+100	Air	5.0	2.0	9.1	9.9	9.2	7.9	0.6	125	−7.8	24.2	1856	611	95
Mt Fox (Gradual treeline)														
−100	Soil	6.1	5.7	6.5	10.6	9.7	8.6	2.5	0	0.0	18.5	2202	676	40
TL	Soil	6.1	5.8	6.6	10.4	9.8	8.7	2.8	0	0.2	15.1	2235	692	41
TL	Air	6.3	2.6	12.0	10.9	10.4	9.2	1.9	108	−6.1	30.6	2334	892	190
+100	Soil	5.5	5.0	6.1	10.1	9.3	8.2	1.8	0	0.4	16.7	1993	600	31
+100	Air	5.6	2.7	9.7	10.2	9.6	8.4	1.0	102	−7.0	25.0	2096	734	133
+200	Soil	6.4	6.0	7.0	11.5	10.9	9.5	2.4	0	0.5	18.2	2345	820	83
Kaweka (Abrupt treeline)														
−100	Soil	5.3	4.8	5.9	11.0	9.7	8.2	0.7	4	−0.5	14.7	1931	642	53
TL Forest	Soil	5.3	4.8	5.8	11.2	9.7	8.3	0.8	0	0.0	15.2	1929	656	64
TL Grass	Soil	5.7	4.9	6.7	12.2	10.4	9.0	0.5	25	−0.8	20.8	2062	784	117
TL Grass	Air	5.5	2.5	9.4	11.8	10.6	9.0	−0.2	126	−6.5	25.1	2077	844	174
+100	Soil	5.1	4.7	5.7	11.0	9.5	8.1	0.6	5	−0.3	15.0	1883	641	53

Location		Annual			Warmest months					Extremes		Growing degree days		
Altitude from TL (m)	Logger	Avg. T_{mean}	Avg. T_{min}	Avg. T_{max}	1 month T_{mean}	3 mnths T_{mean}	6 mnths T_{mean}	Coldest month T_{mean}	Frost days	Extr. T_{min}	Extr. T_{max}	GDD 0	GDD 5	GDD 10
Rainbow (Abrupt treeline)														
−100	Soil	5.5	5.0	6.0	11.4	10.3	9.1	0.7	0.0	0.0	14.6	1808	688	80
TL Forest	Soil	4.5	4.0	5.1	10.5	9.4	8.1	0.0	34	−1.5	13.9	1488	543	32
TL Grass	Soil	5.9	4.8	7.2	13.0	11.7	10.1	0.2	16	−2.5	23.4	1973	888	219
TL Grass	Air	5.6	1.7	11.4	12.7	11.0	9.6	0.1	145	−9.1	26.6	2145	925	233
+100	Soil	5.6	4.3	7.2	11.8	10.5	9.2	0.7	19	−1.5	21.2	1825	721	107
+100	Air	4.7	0.8	10.1	11.3	9.6	8.4	−0.4	163	−10.3	24.6	1849	717	127