Original Article

Southern Hemisphere temperate tree lines are not climatically depressed

Ellen Cieraad[1,2*], Matt S. McGlone[1] and Brian Huntley[2]

[1] *Landcare Research, PO Box 69040, Lincoln 7640, New Zealand,* [2] *School of Biological and Biomedical Sciences, Durham University, Durham DH1 3LE, UK*

***Correspondence:** Ellen Cieraad, Landcare Research, PO Box 69040, Lincoln 7640, New Zealand.

E-mail: cieraade@landcareresearch.co.nz

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ABSTRACT

Aim Southern temperate tree lines are found at low elevations compared with their Northern Hemisphere counterparts. They are also regarded as forming at warm temperatures, which has been attributed to taxon-specific limitations. Using New Zealand tree lines as an example, we assess whether these tree lines are anomalously warm compared with the global mean.

Location New Zealand.

Methods Soil and air temperatures were measured over two years at six New Zealand tree line sites, and compared with other local and global growing season temperature data. In New Zealand and other oceanic regions, the long, variable seasonal transitions make calculations of mean growing season temperatures highly sensitive to how the growing season is defined. We used both the conventional (wide) definition (from when mean weekly root-zone temperature exceeds 3.2 °C in spring, to when it first falls below 3.2 °C in autumn) and a narrow definition (the period during which temperatures are continuously above 3.2 °C). Application of these criteria leads to similar mean growing season temperatures in continental regions, but different ones in oceanic regions. We tested whether growing season temperatures differ between northern and southern temperate tree lines.

Results New Zealand tree lines had a mean root-zone temperature during the wide growing season of 7.0 °C ± 0.4 SD, not significantly different from those at northern temperate tree lines. The mean temperature of the narrow growing season was 7.8 °C, warmer than tree lines elsewhere, but still within the range reported for temperate tree lines (7–8 °C).

Main conclusions Whilst they are found at lower elevations, New Zealand tree lines form at temperatures similar to those at Northern Hemisphere temperate tree lines. Together with similar recent evidence from Chile, these results refute the previously postulated taxon-specific limitation hypothesis, and suggest these southern temperate tree lines are not climatically depressed, but are governed by the same thermal threshold as other tree lines worldwide.

Keywords

Chile, conifers, New Zealand, *Nothofagus*, Southern Hemisphere, taxon-specific limitation, temperate forests, temperature, timberline, tree line microclimate.

INTRODUCTION

The biophysical controls on the upper elevational limit of trees have been much debated and, although the exact mechanisms remain elusive, it is clear that at most tree lines thermal limitation to growth during the summer is critical (see e.g. Holtmeier & Broll, 2005; Holtmeier, 2009; Körner, 2012). At equivalent latitudes, summers in the Southern Hemisphere are less warm than those in the Northern Hemisphere owing to the oceanic influence on the relatively small landmasses, compared with the more intense heating of the large northern landmasses (Veblen *et al.*, 1996; Körner, 1998; Han *et al.*, 2012). Hence it is no surprise that at the same latitude, tree lines in the Southern Hemisphere form at lower elevations than in the Northern Hemisphere (Fig. 1). However, it has been suggested that they are also climatically depressed (form at warmer temperatures) compared with their northern counterparts (e.g. Wardle, 1998). In a global study of tree line temperatures that showed a remarkable convergence of growing season temperatures across biomes worldwide, south temperate tree lines in Chile and New Zealand were significantly warmer than the northern temperate tree lines and the global mean (Körner & Paulsen, 2004). To explain these results, it has been suggested that these warm southern tree lines, formed by the genus *Nothofagus* (the southern beeches; Nothofagaceae), are ‘taxon-specific’ boundaries that do not represent climatic tree lines (Körner & Paulsen, 2004; Hoch & Körner, 2012; Körner, 2012). Such a taxon-specific limitation implies that the local flora either lacked the genetic potential or time to evolve cold-hardy alpine trees (Sakai *et al.*, 1981; Wardle, 1998; Körner & Paulsen, 2004; Wardle, 2008).

These explanations seem improbable. To take the New Zealand example, tree species in the tree line ecotone are not just from *Nothofagus*; at least 35 tree species (in 14 families and 17 genera; see Appendix S1 & S2 in Supporting Information) occur in the tree line ecotone and they share a common elevational limit at any given mountain site where they are present (Wardle, 2008). Close relatives to these species form high-elevation, cool-temperature tree lines elsewhere (Wardle, 2008), and it is thus unlikely that the genetic potential is lacking. In addition, there has been at least 2.5 million years during which alpine tree lines have been present (Heenan & McGlone, 2013). On similarly young mountains, such as Mount Wilhelm (Papua New Guinea), locally evolved trees form tree lines with growing season temperatures close to or lower than the global norm (Körner, 2012). It is thus unlikely that the lack of suitable lineages or the recent formation of the alpine zone left insufficient time for the evolution of cool, high elevation tree species, at least in New Zealand.

Furthermore, in contrast to earlier results, recent studies have found growing season temperatures close to the global mean at two sites in Chile with *Nothofagus* tree lines (Hoch & Körner, 2012; A. Fajardo & F. Piper, Research Center of Patagonian Ecosystems, Coyhaique, Chile, unpublished) and at one site in New Zealand (Mark *et al*., 2008, recalculated in Körner, 2012). The discrepancy between the earlier and recent results challenges the representativeness of the earlier temperature records. A possible explanation for this discrepancy is that the earlier sites were not spatially representative of the regional tree line. Additionally, as interannual variation in temperature is a feature of most temperate locations, and this variability increases with elevation (Fig. 1 in Giorgi *et al.*, 1997), tree line temperature datasets from a short period (e.g. one year) may not capture temperatures that are representative of the long-term climate (Körner & Paulsen, 2004). Comparisons with longer term datasets or averaging multi-year data may allow assessment of the magnitude of such anomalies.

In this study we aim to establish whether New Zealand tree lines, as an example of southern temperate tree lines, are significantly warmer than the global range proposed elsewhere (Körner & Paulsen, 2004; Hoch & Körner, 2012; Körner, 2012), or whether they are close to the global norm, as suggested by recent findings at a single New Zealand site (Mark *et al.*, 2008, as recalculated in Körner, 2012). We use soil and air temperatures recorded at six New Zealand tree line sites for over two years and compare these data with previously published temperature records from tree lines in New Zealand and globally. We discuss the representativeness of the previous and new temperature records and the appropriateness of the notion of taxon-specific limitations in the formation of temperate tree lines in the Southern Hemisphere.

MATERIALS AND METHODS

Site selection

New Zealand tree lines are of two main forms: abrupt *Nothofagus* tree lines mostly in the eastern rain-shadow districts; and gradual or diffuse tree lines of diverse composition in oceanic, western districts. Tree line elevation varies from *c.* 1500 m in the North Island to *c.* 900 m close to the southern tip of the South Island (Wardle, 1985), similar declines in tree line elevation with latitude are found in the southern Andes (Fajardo *et al.*, 2011). At similar latitudes in New Zealand, eastern abrupt tree lines are about 200 m higher than the strongly oceanic gradual tree lines on western coastal mountains (Fig. 1).

Our six field sites span 10° of latitude. Four gradual mixed conifer–broad-leaved tree line sites (Mt Fox, Mikonui, Camp Creek and Kelly Creek) were located west of the Southern

Alps in Westland (referred to below as ‘gradual tree line’ sites). One abrupt *Nothofagus solandri* var. *cliffortioides* (Hook.f.) Poole tree line site was located in the North Island and one in the South Island (‘abrupt tree line’ sites Kaweka and Rainbow, respectively; Fig. 2, Table 1). All sites faced from north-east to north-west and were moderately steep (20–40°). At the gradual tree lines, continuous snow cover is present for only about 2 weeks every year, whereas at the abrupt sites snow cover may last 1–2 months. A more detailed description of the sites and climatic conditions can be found in Cieraad & McGlone (2014). Tree lines at all locations represent the local natural climatic tree limit and have been largely free of anthropogenic disturbances (e.g. grazing, fire, forest clearance) (Wardle, 2008).

Data collection

We defined elevational tree line as the line connecting uppermost groups of trees > 3 m tall (following Körner & Paulsen, 2004). Although it has been suggested a 2 m cut-off may be more appropriate for a global comparison of tree lines (Holtmeier, 2009), we followed the 3 m convention to maintain comparability with existing studies of temperatures at tree line. Along the tree line at each of the six field sites, three loggers were established on parallel ridges about 100 m horizontally apart. Tinytag Plus2 data loggers (precision ± 0·2 °C, Gemini, Chichester, UK) recorded air and soil temperatures hourly (T_{air} and T_{soil}). The protocol for soil logger placement followed Körner & Paulsen (2004): loggers were buried with the temperature sensor 10 cm below the soil surface in a location screened throughout the day by the forest tree canopy. In addition, at one location at each field site, an air temperature logger (shielded from direct sunlight by an aerated white plastic screen) was fixed to a metal pole at 1.3 m above the ground surface (following standard New Zealand protocol; New Zealand Meteorological Service, 1973) and placed under the open canopy of gradual tree lines and in the immediately adjacent tussock grassland at abrupt tree lines.

All data loggers were checked for stability and accuracy in an ice-water bath and at several higher temperatures prior to 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 soil temperature data showed daily amplitudes lower than 5.5 °C, confirming that the loggers had remained under full shade (Körner & Paulsen, 2004). Measurements were obtained between November 2008 and May 2011, and at least 2 years of continuous data were available for each site, except at the Kaweka site, where air temperature was only recorded for one year (Table 1).

Data analyses

The replicated soil temperature data at each site were condensed by averaging hourly readings from the three loggers. For soil and air temperatures from each site, daily T_{min}, T_{max} and the arithmetic T_{mean} were then calculated, as well as monthly and annual summaries.

Air temperatures at the six New Zealand sites (Cieraad & McGlone, 2014) were compared with data from tree line sites in major biomes around the world. The air temperature data were provided by: Robert Baxter (Durham University, Durham, UK), a co-principal investigator of Arctic Biosphere–Atmosphere Coupling at multiple scales (ABACUS) project (boreal: Abisko field site, Sweden; data from 1 July 2007 to 4 September 2009); Gerhard Wieser (Federal Research and Training Centre for Forests, Natural Hazards and Landscape, Vienna, Austria; northern temperate: Mt Patscherkoffel, Austria; data from 1 January 2007 to 31 December 2010); Günter Hoch (University of Basel, Basel, Switzerland; tropics: Nevado Sajama, Bolivia; 24 August 1999 to 31 August 2000); Nick Pepin (University of Portsmouth, Portsmouth, UK; tropics: Kilimanjaro, Kenya; 1 October 2008 to 9 September 2010); Lohengrin Cavieres (Universidad de Concepción, Concepción, Chile; southern temperate/mediterranean: Farellones, Chile; 23 October 2004 to 26 March 2005);

and the Australian Meteorological Bureau (http://www.bom.gov.au/climate/data; southern temperate/Mediterranean: Thredbo, Australia; 1 January 2001 to 31 December 2010).

Growing season comparisons with global tree lines

As air temperature data are available from only a few tree line sites, and the global study by Körner & Paulsen (2004) has set a strong precedent to use soil temperature for systematic and consistent comparisons of growing seasons at tree line, we use soil temperatures and follow Körner & Paulsen (2004) in defining the growing season as the main basis for comparison in this study. The growing season starts when the mean weekly soil temperature at 10 cm depth first exceeds 3.2 °C in spring, and ends when this falls below 3.2°C for the first time in autumn. This threshold soil temperature correlated with a concurrent weekly mean canopy air temperature of 0 °C, below which biological activity is minimal (Körner & Paulsen, 2004). The protocol included a case-by-case examination to prevent biologically unrealistic growing seasons (Jens Paulsen, University of Basel, Basel, Switzerland, pers. comm.). For example, the growing season could not start in the three mid-winter months (June–August, in the Southern Hemisphere).

Growing season calculations for the New Zealand sites were performed on the soil temperature measurements of the one year which spanned a full Southern Hemisphere growing season (July 2009 and June 2010). To assess whether that year was representative of the whole dataset (up to 2.5 years), we also condensed the soil temperature data for each site to a 365-day dataset by averaging any data obtained for the same day in multiple years (Körner & Paulsen, 2004). Growing season statistics for these averaged data are similar to those of year 2009–10, and are provided in Appendix S3 (Table S2). To further assess whether the data were representative of the long-term mean, we assessed the temperature anomalies during the study period. Almost all records included data from the entire period from 2009–2010 (Table 1). The first year in this study (2009) was slightly colder (−0.22 °C) than the long-term national mean (1971–2000, Mullan *et al.*, 2010). Temperatures in the first 6 months of 2010 were close to their respective long-term means, but owing to a warm August−December, the year 2010 was the fifth warmest on record (+0.53 °C; records began in 1909).

Körner & Paulsen (2004) report that a sensitivity test, in which a few doubtful days at the transition into or out of the growing season were either included or excluded, affected season means by less than 0.1 °C. However, our study shows that long, highly variable seasonal transitions at the oceanic New Zealand tree lines may affect seasonal means by up to 1 °C depending on whether brief excursions of temperature below the threshold are included in its calculation. Without data on the actual local growing season (e.g. shoot extension, cambium activity), decisions to include or exclude such excursions are arbitrary. Yet in these oceanic climates these decisions will greatly affect the calculated seasonal mean, and therefore the comparison with global data.

We therefore report two calculations of growing season temperature: a ‘wide’ and a ‘narrow’ growing season. First, the ‘wide’ calculation follows the Körner & Paulsen (2004) protocol described above. Second, we calculate the ‘narrow’ growing season mean, which only included that part of the year when mean daily temperatures continuously remained above the 3.2 °C threshold. The narrow growing season is thus shorter and warmer than the wide growing season. This measure represents the warmest growing season possible given the 3.2 °C threshold, and thus the warmest, most conservative, estimate for challenging the notion that the southern temperate tree lines are anomalously warm. Soil temperature data from previously documented tree line sites in New Zealand were provided by Alan Mark (Otago University, Dunedin, New Zealand; Mt Burns; see also Mark *et al.*, 2008), Christian

Körner and Jens Paulsen (University of Basel, Basel, Switzerland; Mt Haast and Kaimanawa, Körner & Paulsen, 2004; Mt Burns, recalculated from Mark *et al*., 2008, Körner, 2012). The mean (narrow and wide, see below) growing season temperatures at these three *Nothofagus* sites were calculated using the protocols described below to enable direct comparison with the six tree line sites, including two formed by *Nothofagus*, of the current study.

One-sided *t*-tests (assuming unequal variance) were performed to test whether mean soil temperature in the narrow and wide growing season at New Zealand tree lines were significantly different than those at Northern Hemisphere temperate tree lines (Körner & Paulsen, 2004; Körner, 2012). Data analyses were performed in R 2.12.2 (R Development Core Team, 2011).

RESULTS

Mean annual air temperatures at the six tree line sites ranged from 5.5 to 6.3 °C. The mean monthly air temperatures ranged from 1.1 °C for the coldest month to 10.4 °C for the warmest month (Fig. 3). At the gradual tree lines, soils scarcely froze at 10 cm depth (up to a total of three nights at any site across all years), while those under an abrupt tree line canopy froze an average of 34 days per year, mainly in association with snow cover (Fig. 4). The temperature data from the six sites are discussed in more detail in Cieraad & McGlone (2014; see also Table S1 in Appendix S3).

Growing season temperature

Mean soil temperature during the growing season was calculated following Körner & Paulsen (2004) for comparison with global tree lines (the ‘wide’ growing season). Mean soil temperatures at the six New Zealand tree line sites in this study ranged from 6.6 to 7.8 °C (Table 2). Growing season length was shorter and mean soil temperature was warmer at abrupt (195 days, 7.6 °C) than at gradual (270 days, 6.8 °C) tree lines (Fig. 4). Growing season temperatures at the six sites in this study were colder than the two New Zealand sites (Mt Haast 8.2 °C and Kaimanawas 10.7 °C) reported by Körner & Paulsen (2004), and similar to the recalculated growing season at Mt Burns (6.7 °C, Mark *et al*. 2008, recalculated in Körner 2012). Calculations of the narrow and wide growing season for these sites with earlier data showed some inconsistencies and indicated problems with representativeness of the recorded periods, which are further detailed in the Discussion section. Based on these results, growing season temperature calculations for New Zealand reported below include the six sites described in this study and the recalculated Mt Haast site.

The mean soil temperature for the wide growing season at New Zealand tree lines ($n = 7$, mean 7.0 °C ± 0.4 SD) was not significantly different from those at northern temperate tree lines ($n = 15$, 7.1 °C ± 0.5 SD) (*t*-test, $\text{d.f.}_{\text{Welch}} = 14$, $t = 0.21$, $P_{\text{one-tail}} = 0.42$). If the more strict narrow growing season definition was applied, New Zealand’s tree lines (7.8 °C ± 0.4 SD) are significantly warmer than tree lines elsewhere (*t*-test, $\text{d.f.}_{\text{Welch}} = 15$, $t = -3.5$, $P_{\text{one-tail}} < 0.01$), but still within the range reported for temperate tree lines (7–8 °C).

DISCUSSION

The often-reported correlation of alpine tree line position with the mean air temperature isotherm of *c*. 10 °C in the warmest month holds for temperate regions (Körner, 2012), including New Zealand (mean across the six sites in this study: 10.4 °C, Fig. 3). Winter temperatures are highly variable between sites worldwide, but relatively warm in New Zealand and Australia compared with other temperate sites (Fig. 3). The Chilean tree line site presented here (formed by *Kageneckia angustifolia*, Rosaceae, at 33 °S, at 2200 m a.s.l.) was warmer than all other sites. This is attributed to the strong Mediterranean climate at the site (Piper *et al*., 2006), which may have resulted in a drought-induced climatically depressed tree line (A. Fajardo, Research Center of Patagonian Ecosystems, Coyhaique, Chile, pers. comm.), as shown for a *Nothofagus* mediterranean Chilean site (Fajardo *et al*., 2011).

As mean growing season warmth based on soil temperatures are now available for many more tree line sites compared with air temperatures (e.g. 40 sites worldwide presented in Körner, 2012), we used this metric from seven New Zealand tree line sites (six recorded as part of this study and one previous record, see below) to compare growing season warmth. Using the wide growing season definition (Körner & Paulsen, 2004), mean growing season temperature at New Zealand tree lines was 7.0 °C ± 0.4 SD (individual sites were up to 1 °C colder, Fig. 4, Table 2). This puts New Zealand tree lines at the cool end of the reported mean temperature range for temperate tree lines worldwide (7–8 °C; Körner & Paulsen, 2004), and close to the global mean of 6.4 °C ± 0.7 SD (Körner, 2012). Similar mean soil temperatures for the growing season have recently been reported for *Nothofagus pumilio* tree lines in southern Chile (Hoch & Körner, 2012; Fajardo & Piper, in review).

Growing seasons at the eastern abrupt tree lines were approximately 6 months long, which is consistent with phenological data from such sites (e.g. Benecke & Havranek, 1980; Benecke *et al.*, 1981). The more oceanic gradual tree lines in the west had growing seasons of almost 9 months, much longer than temperate seasons reported elsewhere (Körner, 2012). Although few phenological data are available to confirm this, there are indications that opportunistic growth of New Zealand's evergreen tree line trees is possible during warmer spells for much of the year. For example, growth of *Metrosideros umbellata* (Myrtaceae) near the Camp Creek tree line occurred intermittently over an 8-month period (September–May, Payton, 1989), and a small subalpine tree (*Olearia ilicifolia*, Asteraceae) can continue growing through winter in the tree line ecotone (Haase, 1986).

Although using a single growing season definition is necessary when comparing multiple sites, care is required when applying these definitions and interpreting the resulting means (Gehrig-Fasel *et al.*, 2008). The variability in season transitions at oceanic sites makes it difficult to apply growing season concepts developed primarily for use in more continental northern temperate and boreal regions, which have much more clear-cut seasonal transitions. For example, the inclusion into the growing season calculation of (multiple) short excursions below the temperature threshold lowered the resulting growing season mean temperature at the six New Zealand sites by as much as 1 °C. A similar fall in mean temperature was found if 2 weeks of daily $T_{\mathrm{mean}} > 5$ °C from late September were included into the growing season at the two earlier published New Zealand sites (rather than starting mid-October, Fig. 5 in Körner & Paulsen, 2004).

Because the application of the threshold temperature in these variable seasonal transitions is rather subjective, we also calculated the mean temperature over a growing season that was consistently warmer than the 3.2 °C threshold. By definition, the mean soil temperature of this 'narrow' growing season is warmer than the 'wide' growing season (see Materials and Methods). However, this mean narrow growing season temperature for the seven New Zealand sites (7.8 °C ± 0.4 SD) still sits within the range reported for Northern Hemisphere temperate tree lines (7–8 °C, Körner & Paulsen, 2004). Although we suspect that this narrow growing season underestimates the length of the actual growing season at these sites, the mean temperature at New Zealand tree line sites is in the range of previously reported northern temperate sites, and not anomalously warm.

Körner & Paulsen (2004) suggest that by focusing on the spatial replication across tree lines around the world, they minimized 'any bias introduced by local climatic peculiarities of a given year'. However, in the case of the three tree line locations in New Zealand and Chile, they may have been unlucky with their space-for-time approach. The two Chilean sites in Körner & Paulsen (2004) were at the same location, albeit different aspects in the same valley; thus the generalization of a warm tree line in the southern Andes was based on data from one, pseudoreplicated, location, as pointed out by Fajardo *et al.* (2011). Moreover, it has been shown that the tree line at this exact location is strongly affected by drought, as well as temperature, and may represent a drought-depressed tree line (Fajardo *et al.*, 2011), rather than being representative of temperate Andean tree lines.

Relatively short-term datasets, such as those described here (2–2.5 years) and elsewhere (1–3 years, Körner & Paulsen, 2004), may not accurately represent the long-term conditions at the given site because of interannual variability (Körner & Paulsen, 2004). The earlier record for the two New Zealand tree lines (Körner & Paulsen 2004; December 1998 – March 2000) included the warmest (1998) and second warmest (1999) years on record since 1909; in central North Island 1998, 1999 and 2000 were 0.81, 0.72 and 0.30 °C warmer, respectively, than the 1971–2000 mean (Mullan *et al*., 2010). Inspection of their raw data showed that the use of only records from the calendar year 1999 in the calculated means of the sites resulted in a strong (warm) bias. If all records were included, by averaging each calendar day that was available for both 1999 and 2000 (January–March), the growing season temperature dropped by more than 1 °C for both sites. In addition, one could argue that the growing season may have started some 3 weeks earlier (see above). Taking these two factors into account, the recalculation from their raw hourly data yielded a growing season soil temperature of 7.1 °C for Mt Haast (cf. 8.2 °C, Körner & Paulsen 2004), and 8.6 °C for the Kaimanawa site (cf. 10.7 °C, Körner & Paulsen 2004); the latter still standing out from all other New Zealand sites as much warmer. As the diurnal temperature record indicates that the logger was correctly placed in full shade (Körner & Paulsen 2004), and there is no reason to suspect that the Kaimanawa tree line site has been lowered by disturbance, we suggest that this site may be affected by a local factor (e.g. nutrient limitation or drought).

Our recalculations of the two growing season means for Mt Burns failed to reproduce the growing season means published either originally (Mark *et al.*, 2008) or the recalculation presented in Körner (2012) (8.7 and 6.4 °C, respectively, compared with our recalculation based on the raw data of 7.1 °C). An assessment of the dataset shows that Mark *et al.* (2008) started the growing season when an *hourly* value crossed the 3.2 °C threshold, whereas in the original global and subsequent studies, a *weekly* mean temperature was the determining factor (our wide growing season, equivalent to Körner & Paulsen, 2004; Körner, 2012). While the reanalysis presented in Körner (2012) was based on a weekly threshold, it appears a correction to the hourly data of –2.17 °C compared with the original dataset was also applied. Although no reason for this correction was provided, we presume it was to account for possible calibration errors in the original dataset. Over the 3.5 year record (Mark *et al.*, 2008), an absolute minimum soil temperature of 1.97 °C, which is unusually warm for tree lines in all but (sub-)tropical biomes (Körner & Paulsen, 2004) and may indicate calibration errors. However, since the accuracy of the data logger used in this study was never tested (Alan Mark, pers. comm.), the exact magnitude of such errors cannot be verified or corrected. Given the above uncertainties, we excluded the Kaimanawa and Mt Burns sites from the summary statistics for New Zealand tree line sites, but included the recalculated values from the Mt Haast site (Table 2). The 2009–10 growing season available in the current study covered a year with temperatures close to the long-term mean (see Materials and Methods), and calculations based on the one fully covered growing season provided similar results to data averaged for 2.5 years (see Table S2). This suggests that the records in this study are fairly representative of longer-term temperatures.

As southern temperate tree lines are not solely formed by *Nothofagus* species (e.g. see Appendix S2 for the long list of tree species that occur in the New Zealand tree line ecotone), the three locations in this biome used by Körner & Paulsen (2004) are not fully representative of the New Zealand tree lines. The four gradual tree lines formed by diverse conifer–broad-leaved forest included in this study are located at temperatures (6.8 °C ± 0.1) close to the global tree line norm (6.4 °C ± 0.7; Körner, 2012). These growing seasons are longer and their mean temperature cooler than their more continental *Nothofagus* counterparts (Table 2). As air temperatures at New Zealand and Australian tree lines are also similar (Fig. 3), the assumption that oceanic tree lines are lower as well as warmer than more continental sites at the same latitude (e.g. Leuschner, 1996; Han *et al.*, 2012) does not hold. This is explained, at least partially, by the effect of the length of the growing season on the resulting temperature mean (Gehrig-Fasel *et al.*, 2008; Cieraad, 2012). Moreover, the sensitivity of these means to the application of the thresholds (as described above) suggests that the growing season at oceanic and continental tree lines perhaps cannot be fully captured by this same metric (Cieraad, 2012).

In the light of the apparent problems of temporal and spatial representativeness of these earlier results and the growing number of recent findings of New Zealand and Chilean tree lines with temperatures close to the global norm (this study; Hoch & Körner, 2012; Fajardo & Piper, unpublished), we suggest that southern temperate tree lines are not caused by a taxon-specific limitation (Körner & Paulsen, 2004), but instead are influenced by the same thermal threshold as are other tree line sites worldwide.

The unassisted spread of the naturalized conifer *Pinus contorta* above abrupt New Zealand tree lines (Ledgard, 2001; Wardle, 2008) poses a challenge to our conclusion that New Zealand tree lines form at similar growing season temperatures to those elsewhere. Abrupt *Nothofagus* tree lines would be some 150 m higher if they reached the elevational limit of *Pinus* spp. While temperature records at the *Pinus* limit in New Zealand are not available, the mean growing season temperature of such sites is likely to be c. 0.9 °C lower (assuming a standard lapse rate of 0.6 °C 100 m^{-1}) and thus falls inside the variability range of the New Zealand tree line sites described here. This phenomenon has been taken as evidence that indigenous trees lack the capacity to grow at cool temperatures (Lee, 1998). However, the fact that these abrupt *Nothofagus solandri* var. *cliffortioides* tree lines tend to be tall (c. 6 m high) suggests that it is not growth limitation per se, but rather that they are prevented from extending higher by exposure-related stresses including photoinhibition, wind and drought (Wilson & Agnew, 1992; Smith *et al.*, 2003; Bekker, 2005; Bader *et al.*, 2007). *Pinus contorta* does not occur in the western Southern Alps and it is doubtful that it would have a similar advantage over indigenous trees in the much less stressed oceanic gradual conifer–broad-leaved tree lines there. Our general conclusion that New Zealand indigenous trees are capable of growing to the thermal limits that trees achieve elsewhere is therefore still valid.

CONCLUSIONS

Although lower in elevation than tree lines at similar latitudes in the Northern Hemisphere, New Zealand and Chilean temperate tree lines are not climatically depressed compared with their northern counterparts. Instead of being governed by taxon-specific limitations, these Southern Hemisphere temperate tree lines are influenced by similar thermal thresholds as are other tree line sites worldwide. While temperature is an important driver of tree line position globally, there is considerable variability at smaller spatial (regional and local) scales, which is affected by additional factors (such as drought, exposure and micro-topography; see e.g. Holtmeier, 2009; Fajardo *et al.*, 2011; Körner, 2012). Nonetheless, at larger scales, the coincidence of mean temperature in the growing season at tree lines all around the world is suggestive of a common set of biological causes. Importantly, however, the exact mechanisms remain elusive (Körner, 2012).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Images from selected New Zealand tree line sites.

Appendix S2 Woody taxa forming the tree line ecotone.

Appendix S3 Summary of air and soil temperatures recorded (Table S1) and growing season (Table S2) for the six New Zealand tree line sites used in this study.

BIOSKETCHES

Ellen Cieraad is a plant ecologist. Her research focuses on the distribution and functioning of plants along environmental gradients. She has a special interest in elevational gradients and the drivers of tree line form and position.

Matt McGlone is a palaeoecologist with a research focus on vegetation and climate change in the New Zealand region. Recent projects have involved the study of Holocene tree line changes on the New Zealand mainland and the subantarctic islands.

Brian Huntley is a palaeoecologist, ecologist and biogeographer whose research addresses interactions between species, ecosystems and their changing environment. His work spans a range of taxonomic groups and ecosystems, from tree line trees of the Arctic and Southern Alps, to southern African birds and extinct Pleistocene mammals of Eurasia.

Editor: Peter Linder

TABLES

Table 1 Details of the tree line locations studied in New Zealand, and length of soil and air temperature records. Within region, sites are ordered by increasing latitude. Tree species indicated with * form only shrub-statured individuals (< 3 m tall) at that site.

Tree line site name	Long. (°E)	Lat. (°S)	Elevation (m a.s.l.)	Main woody species in the ecotone[1]	Temperature recorded (d/m/y–d/m/y)
Gradual					
Camp Creek	171.57	42.71	1160	*Halocarpus biformis* (Podocarpaceae), *Libocedrus bidwillii* (Cupressaceae), *Olearia* spp.[2] (Asteraceae), *Dracophyllum* spp.[3] (Ericaceae)	31/01/2009–27/04/2011
Kelly Creek	171.58	42.78	1150		13/05/2009–28/04/2011
Mikonui	170.87	43.06	1210		17/01/2009–20/03/2011
Mt Fox	170.01	43.50	1185		06/01/2010–22/03/2011
Abrupt					
Kaweka	176.36	39.29	1460	*Nothofagus solandri* var. *cliffortioides* (Nothofagaceae), *Phyllocladus alpinus** (Podocarpaceae)	26/11/2008–06/06/2011
Rainbow	172.86	41.89	1530	*Nothofagus solandri* var. *cliffortioides* (Nothofagaceae)	11/04/2009–09/04/2011

[1] Plant names follow Allan Herbarium (2000)

[2] *Dracophyllum* spp. comprises *Dracophyllum longifolium* and *Dracophyllum traversii.*

[3] *Olearia* spp. comprises *Olearia arborescens, Olearia avicenniifolia, Olearia colensoi, Olearia ilicifolia, Olearia lacunosa* and *Olearia paniculata.*

Table 2 Means, extremes and sums of growing-season of 10 cm soil temperatures from nine New Zealand tree line sites (for details of the six sites in this study, see Table 1). Units are °C unless indicated.

	Annual						Growing season Narrow (warm)		Growing season Wide (cold)	
Tree line site name	T_{mean} (T_{median})	Extr T_{min}[5]	Extr T_{max}[6]	Warmest month T_{mean}	GDD0[7]	GDD5[8]	T_{mean} (T_{median})	Length (d)	T_{mean} (T_{median})	Length (d)
Mt Burns[2,4]	6.4 (6.5)	2.0	16.9	10.0	2307	721	7.6 (7.5)	262	7.1 (7.2)	298
Mt Fox[1]	6.1 (5.9)	0.2	15.1	10.4	2235	692	7.5 (7.2)	245	7.1 (6.9)	274
Mikonui[1]	5.5 (5.1)	−0.2	14.0	10.2	2002	610	7.7 (7.5)	201	6.6 (6.5)	270
Kelly Creek[1]	5.7 (5.4)	0.0	15.3	11.0	2090	695	8.2 (7.7)	189	6.8 (6.8)	268
Camp Creek[1]	5.8 (5.3)	0.1	14.8	10.3	2106	655	8.1 (7.7)	189	6.8 (6.8)	268
Mt Haast[3]	4.2 (3.8)	0.7	12.8	9.6	2058	567	7.1 (6.7)	265	6.9 (6.5)	278
Rainbow[1]	4.6 (4.4)	−0.9	13.9	10.5	1637	557	7.7 (7.7)	169	7.4 (7.5)	186
Kaweka[1]	5.8 (5.3)	0.3	15.2	11.2	1929	656	8.0 (7.9)	192	7.8 (7.5)	204
Kaimanawa[3,4]	8.1 (8.3)	1.2	16.0	12.7	2969	1216	8.6 (8.8)	336	8.6 (8.8)	336
Mean	5.5 (5.2)	0.3	14.8	10.4	2046	644	7.8 (7.5)	207	7.0 (6.9)	250
S.D.	0.7 (0.8)	0.8	1.2	0.5	204	61	0.4 (0.4)	35	0.4 (0.4)	38
Range	2.2 (2.7)	2.9	4.1	1.6	670	164	0.8 (1.6)	96	1.2 (1.1)	92

[1] Sites measured as part of this study

[2] Values are recalculated from Mark *et al*. (2008) raw data, see Results and Discussion.

[3] Values are recalculated from Körner & Paulsen (2004) raw data, see Results and Discussion.

[4] Data are excluded from summary statistics at the bottom of the table because of probable calibration and placement errors, respectively, see Results and Discussion.

[5] Extreme minimum hourly temperature recorded

[6] Extreme maximum hourly temperature recorded

[7] Growing degree days with a base temperature of 0℃ (sum of the daily T_{mean} above the base temperature)

[8] Growing degree days with a base temperature of 5℃ (sum of the daily T_{mean} above the base temperature)

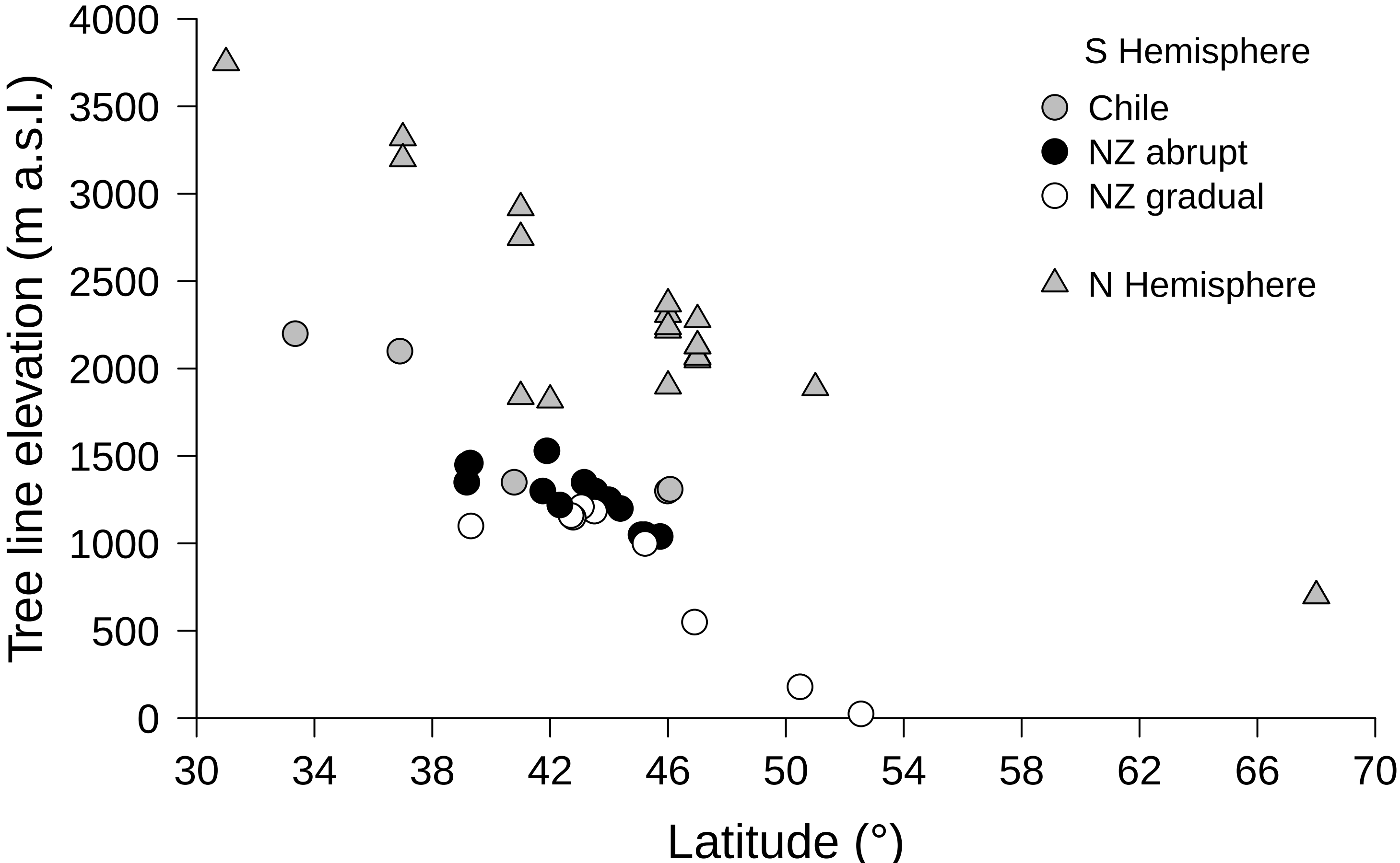
FIGURE LEGENDS

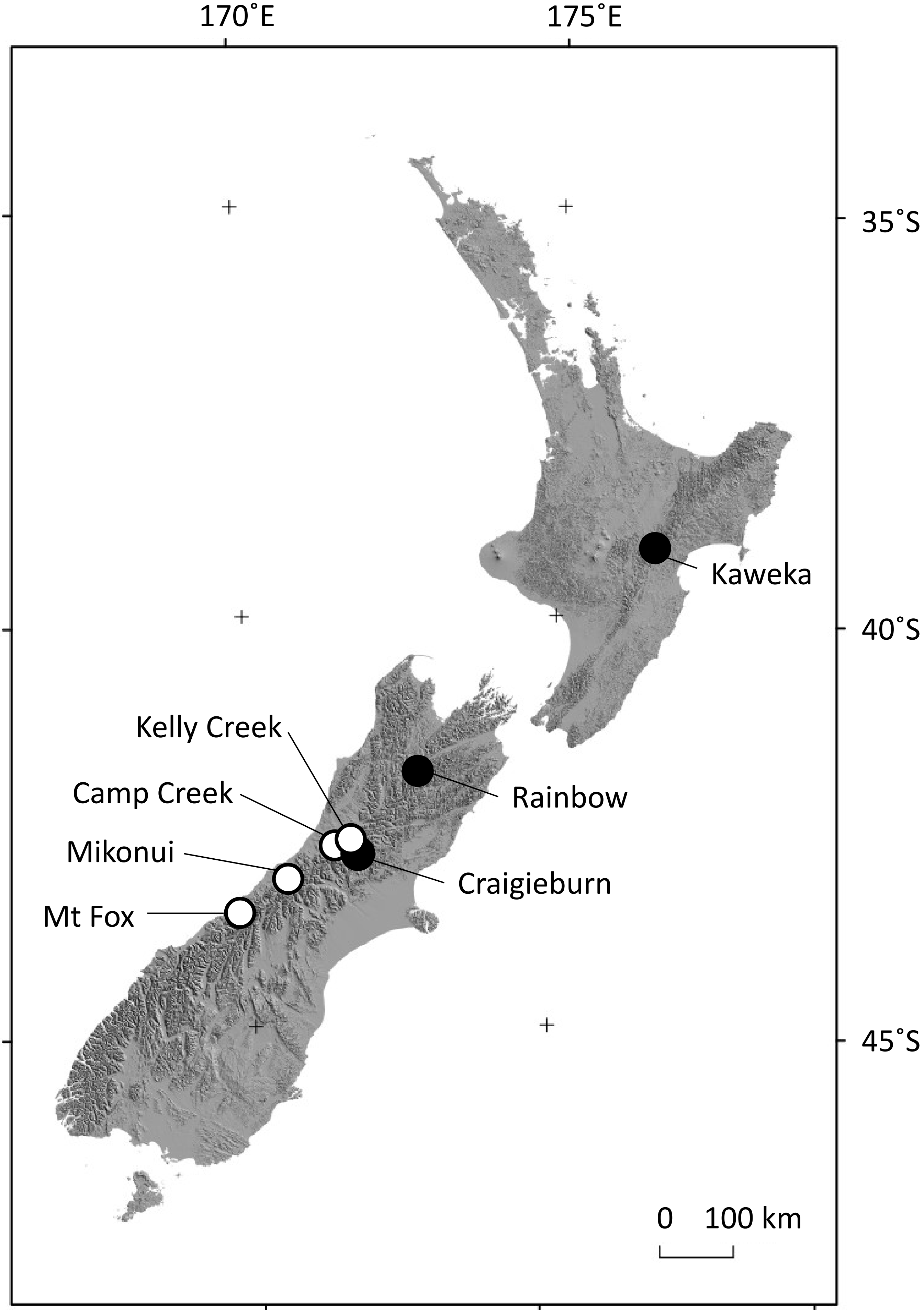
Figure 1 Latitudinal trend of tree line elevation in the Northern and Southern Hemispheres. Northern Hemisphere data is from Körner & Paulsen (2004); Chile from Piper *et al.* (2006) and Fajardo *et al.* (2011, 2013); and New Zealand from Cieraad (2012). At the same latitude, southern temperate tree lines are at lower elevations than their more continental northern counterparts. At the same latitude in New Zealand (NZ), the highly oceanic gradual tree lines (open circles) form at lower elevations than abrupt tree lines (black circles).

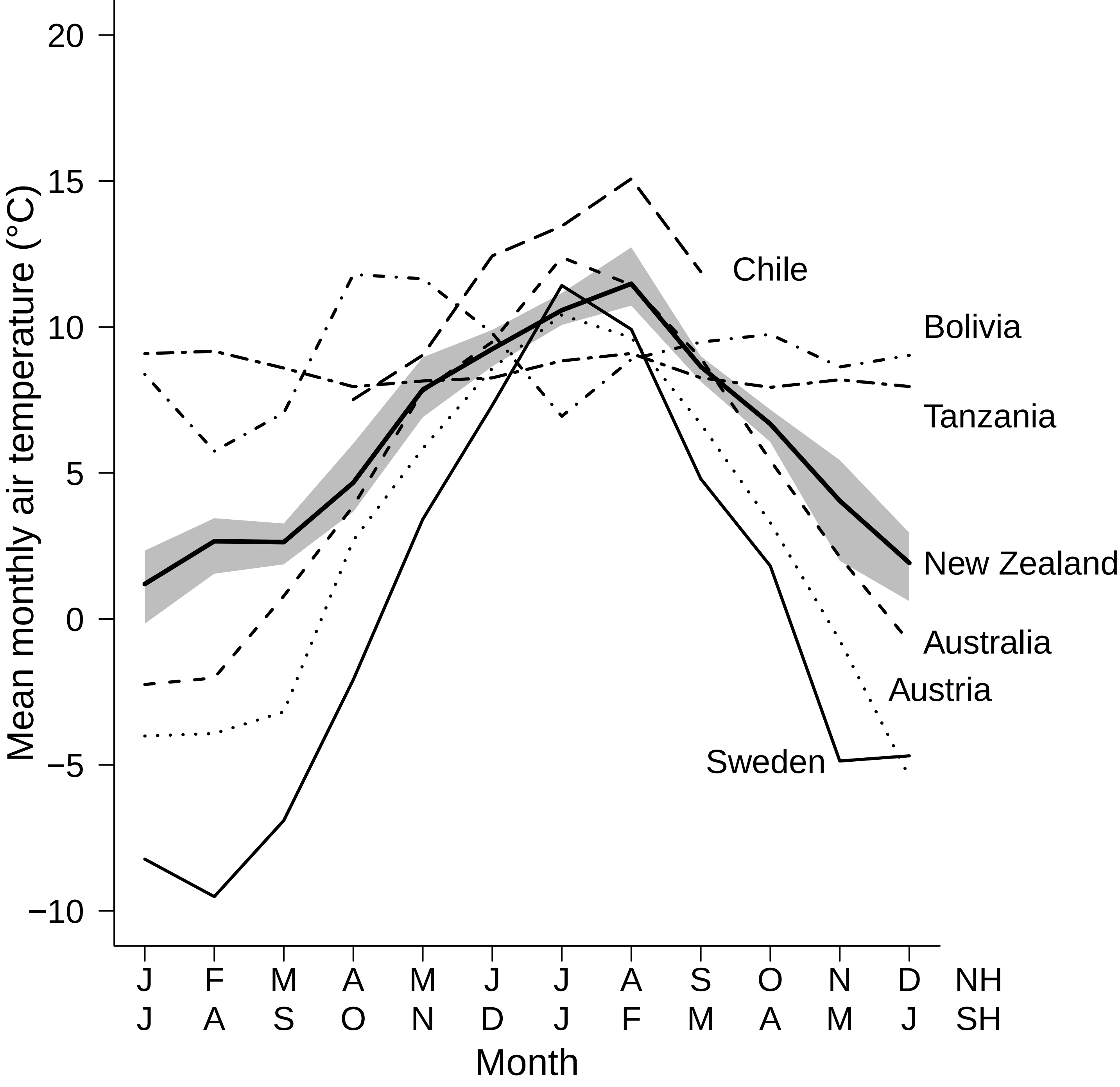
Figure 2 Location of New Zealand tree line study sites. White circles indicate gradual tree line sites; black circles indicate abrupt tree line sites. See Table 1 for site details.

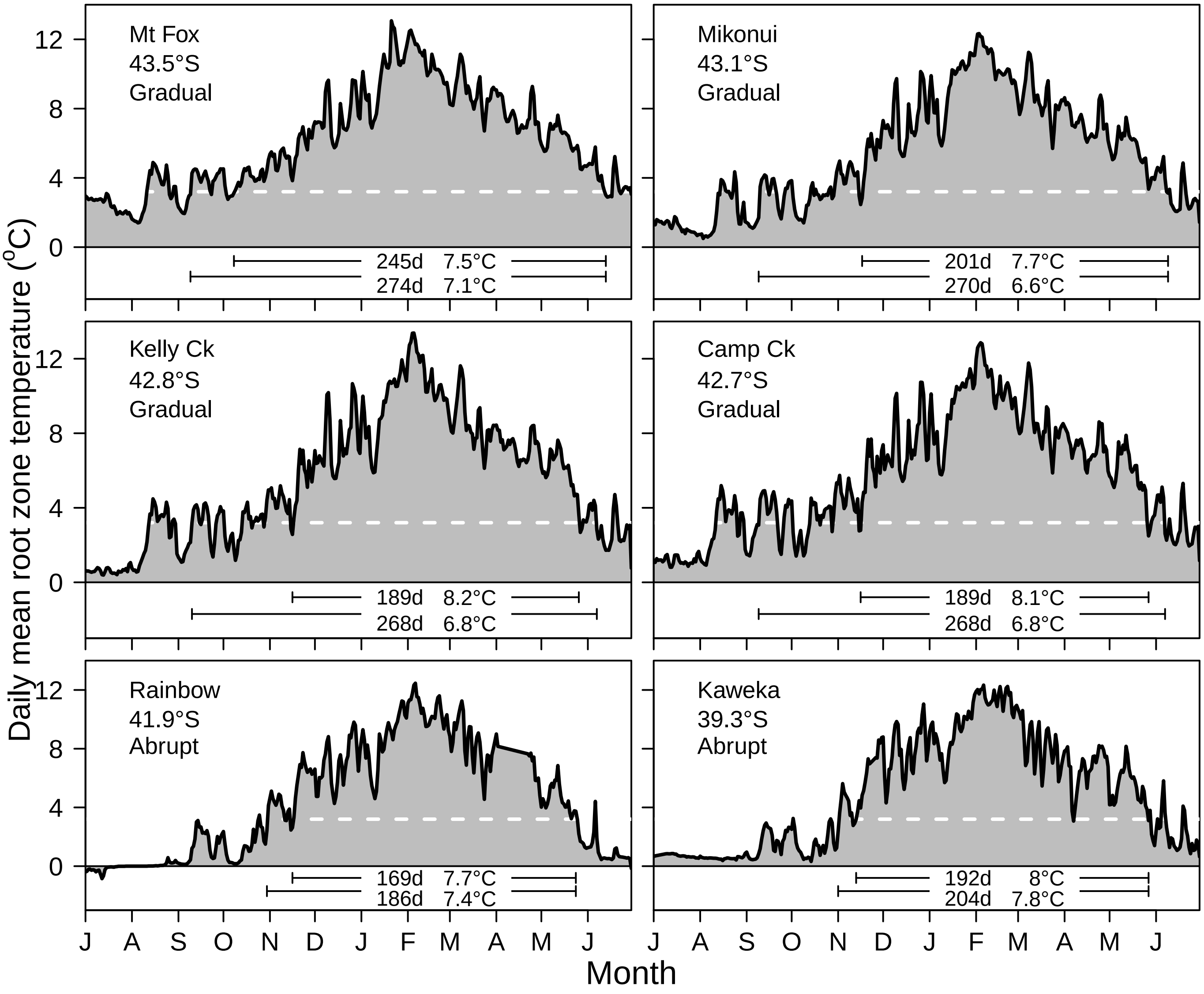
Figure 3 Mean monthly air temperature at the New Zealand tree line (grey shading shows minimum and maximum mean monthly temperature across the six locations in this study, with the solid line indicating the average) compared with different tree line sites around the world. See text for more details. Northern and Southern Hemisphere months (NH and SH, respectively) have been portrayed such that the growing season is in the middle of the graph. The Chilean tree line corresponds to a *Kageneckia angustifolia* tree line which is under strong mediterranean influence, and drought-depressed (Piper *et al.*, 2006), as was the Chilean locality included in Körner & Paulsen (2004). The tree line at Thredbo (Australia) is approximately 60 m above the weather station – data have not been corrected, but could be *c.* 0.4 °C colder than displayed, if a standard lapse rate of 0.6 °C per 100 m was applied.

Figure 4 The annual course of soil (10 cm) temperature and growing season details at six New Zealand tree line sites. The growing season is defined by a 3.2 °C thermal threshold (white dashed line), either at first crossing of the threshold in spring and autumn (wide growing season), or as a continuous period above the threshold (narrow growing season, see Materials and Methods). The length (in days; d) and mean temperature (°C) of the growing season are shown at the bottom of each graph (top is narrow growing season; bottom, wide growing season).


Tree line elevation (m a.s.l.)
4000
3500
3000
2500
2000
1500
1000
500
0
30
34
38
42
46
50
54
58
62
66
70
Latitude (°)
S Hemisphere
● Chile
● NZ abrupt
○ NZ gradual
▲ N Hemisphere


170˚E
175˚E
35˚S
40˚S
45˚S
Kaweka
Rainbow
Kelly Creek
Camp Creek
Mikonui
Craigieburn
Mt Fox
0
100 km


Mean monthly air temperature (°C)
20
15
10
5
0
−5
−10
Chile
Bolivia
Tanzania
New Zealand
Australia
Austria
Sweden
J F M A M J J A S O N D NH
J A S O N D J F M A M J SH
Month


Mt Fox
43.5°S
Gradual
245d 7.5°C
274d 7.1°C
Mikonui
43.1°S
Gradual
201d 7.7°C
270d 6.6°C
Kelly Ck
42.8°S
Gradual
189d 8.2°C
268d 6.8°C
Camp Ck
42.7°S
Gradual
189d 8.1°C
268d 6.8°C
Rainbow
41.9°S
Abrupt
169d 7.7°C
186d 7.4°C
Kaweka
39.3°S
Abrupt
192d 8°C
204d 7.8°C
Daily mean root zone temperature (°C)
0
4
8
12
J
A
S
O
N
D
J
F
M
A
M
J
Month

SUPPORTING INFORMATION

Southern Hemisphere temperate tree lines are not climatically depressed

Ellen Cieraad, Matt S. McGlone and Brian Huntley

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Appendix S1 Tree line ecotones of contrasting forms in New Zealand. Top (left and right): diffuse mixed conifer–broad-leaved tree line ecotone at Camp Creek, Westland; bottom: abrupt *Nothofagus solandri* var. *cliffortioides* tree line on the St Arnaud Range (left) and at Craigieburn (right). Images first appeared in Cieraad & McGlone (2014); they are reprinted here with permission from the *New Zealand Journal of Ecology*.

Reference: Cieraad, E. & McGlone, M.S. (2014) Thermal environment of New Zealand's gradual and abrupt treeline ecotones. *New Zealand Journal of Ecology*, **38**, 12-25.

SUPPORTING INFORMATION

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Appendix S2 Woody taxa forming trees in the tree line ecotone in New Zealand

	Family	**Genus**	**Species**
Pinophyta (conifers)	Cupressaceae	*Libocedrus*	*bidwillii*
	Podocarpaceae	*Halocarpus*	*biformis*
		Podocarpus	*cunninghamii*
		Phyllocladus	*alpinus*
Magnoliophyta (angiosperms)	Araliaceae	*Pseudopanax*	*colensoi*
			crassifolius
			linearis
			simplex
	Asteraceae	*Brachyglottis*	*eleagnifolia*
		Olearia	*arborescens*
			avicenniifolia
			colensoi
			crosby-smithiana
			ilicifolia
			lacunosa
			moschata
			paniculata
	Cornaceae	*Griselinia*	*littoralis*
	Cunoniaceae	*Weinmannia*	*racemosa*
	Elaeocarpaceae	*Aristotelia*	*serrata*
	Ericaceae	*Archeria*	*traversii*
		Dracophyllum	*fiordense*
			longifolium
			scoparium
			townsonii
			traversii
	Fabaceae	*Carmichaelia*	*arborea*
			stevensonii
	Malvaceae	*Hoheria*	*glabrata*
			lyalli
	Myrtaceae	*Leptospermum*	*scoparium*
		Metrosideros	*umbellata*
		Neomyrtus	*pedunculata*
	Myrsinaceae	*Myrsine*	*divaricata*
	Nothofagaceae	*Nothofagus*	*fusca*
			menziesii
			solandri var. *cliffortioides*
	Onagraceae	*Fuchsia*	*excorticata*
	Pittosporaceae	*Pittosporum*	*colensoi*
			divaricatum
			patulum
			rigidum

	Rubiaceae	*Coprosma*	*tenuifolia*
	Winteraceae	▨ *Pseudowintera*	▨ *colorata*

[1] Species listed are those observed by the authors, and/or by the late Peter Wardle, reaching a height of > 3 m in the tree line ecotone, as well as those identified by various authors as occurring in timberline forests (Wardle 1977, 1984, 1991; Wardle *et al*., 2001; Williams 1989, 1991). Grey shading indicates taxa that only infrequently reach tree line at a stature of > 3 m (Peter Wardle, pers. comm.).

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SUPPORTING INFORMATION

Southern Hemisphere temperate tree lines are not climatically depressed

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Appendix S3 Summary of air and soil temperatures recorded (Table S1) and growing season (Table S2) for the six New Zealand tree line sites used in this study.

Table S1 Summary of air and soil temperatures recorded at the six New Zealand tree line (TL) locations in this study. Soil temperatures were recorded under the tree line forest canopy. Air temperature was recorded in the open canopy (gradual tree line) or in the grassland within 10 m distance from the forest/tree line margin (abrupt tree line). For location details, see Table 1; for more detail about the study set-up and an in-depth discussion of results, see Cieraad & McGlone (2014).

Location (type)	Annual			Warmest months					Extremes		Growing degree-days		
	Avg. T_{mean}	Avg. T_{min}	Avg. T_{max}	1 month T_{mean}	3 months T_{mean}	6 months T_{mean}	Coldest month T_{mean}	Frost days	Extr. T_{min}	Extr. T_{max}	GDD 0	GDD 5	GDD 10
Camp Creek (gradual)													
Soil	5.8	5.2	6.5	10.3	9.5	8.5	1.9	0	0.1	14.8	2106	655	49
Air	5.8	2.5	10.7	10.7	9.9	8.6	1.6	103	-6.4	27.6	2139	769	146
Kelly Creek (gradual)													
Soil	5.7	5.2	6.3	11.0	9.9	8.6	1.2	0	0.0	15.3	2090	695	66
Air	6.1	2.7	11.5	11.6	10.3	8.9	1.7	96	-6.0	31.8	2242	833	186
Mikonui (gradual)													
Soil	5.5	5.1	5.9	10.2	9.4	8.3	1.9	0	-0.2	14.0	2002	610	30
Air	6.2	2.2	12.8	11.2	10.5	9.2	1.6	119	-6.3	34.2	2260	857	189
Mt Fox (gradual)													
Soil	6.1	5.8	6.6	10.4	9.8	8.7	2.8	0	0.2	15.1	2235	692	41
Air	6.3	2.6	12.0	10.9	10.4	9.2	1.9	108	-6.1	30.6	2334	892	190
Kaweka (abrupt)													
Soil	5.3	4.8	5.8	11.2	9.7	8.3	0.8	0	0.0	15.2	1929	656	64
Air	5.5	2.5	9.4	11.8	10.6	9.0	-0.2	126	-6.5	25.1	2077	844	174
Rainbow (abrupt)													
Soil	4.5	4.0	5.1	10.5	9.4	8.1	0.0	34	-1.5	13.9	1488	543	32
Air	5.6	1.7	11.4	12.7	11.0	9.6	0.1	145	-9.1	26.6	2145	925	233

Table S2 Growing season summary for the six New Zealand tree line sites in this study, using a dataset based on growing season compared with averaged 365-day datasets. Any data obtained for the same day in multiple years (between 2008 and 2011, see Table 1) were averaged, before calculating the length and mean (median) temperature for the ‘wide’ growing season following Körner & Paulsen (2004), and the ‘narrow’ growing season (see Materials and Methods). The 2009–10 growing season data is also presented in Table 2.

	Growing season Narrow (warm)				Growing season Wide (cold)			
	2009-‘10 growing season		averaged 365-day (2008-‘11)		2009-‘10 growing season		averaged 365-day (2008-‘11)	
Tree line site name	T_{mean} (T_{median})	Length	T_{mean} (T_{median})	Length	T_{mean} (T_{median})	Length	T_{mean} (T_{median})	Length
Mt Fox	7.5 (7.2)	245	7.8 (8.3)	236	7.1 (6.9)	274	6.9 (7.4)	292
Mikonui	7.7 (7.5)	201	7.5 (7.9)	232	6.6 (6.5)	270	6.6 (7.3)	275
Kelly Creek	8.2 (7.7)	189	7.9 (8.3)	242	6.8 (6.8)	268	7.0 (7.6)	265
Camp Creek	8.1 (7.7)	189	7.8 (8.0)	245	6.8 (6.8)	268	6.8 (7.4)	279
Rainbow	7.7 (7.7)	169	7.6 (7.9)	197	7.4 (7.5)	186	7.6 (7.9)	197
Kaweka	8.0 (7.9)	192	7.9 (7.9)	218	7.8 (7.5)	204	7.1 (7.4)	245

References

Cieraad, E. & McGlone, M.S. (2014) Thermal environment of New Zealand’s gradual and abrupt treeline ecotones. *New Zealand Journal of Ecology*, **38**, 12-25.

Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, **31**, 713-732.