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Authors: Cieraad, Ellen, McGlone, Matt, Barbour, Margaret M., and Huntley, Brian

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Seasonal Frost Tolerance of Trees in the New Zealand Treeline Ecotone

Ellen Cieraad†§*
*Matt McGlone**
Margaret M. Barbour‡ and*
Brian Huntley†

*Landcare Research, PO Box 40, Lincoln 7640, New Zealand
†School of Biological and Biomedical Sciences, Durham University, South Road, Durham, DH1 3LE, U.K.
‡Faculty of Agriculture, Food and Natural Resources, University of Sydney, Private Bag 4011, Narellan, NSW 2567, Australia
§Corresponding author: cieraade@landcareresearch.co.nz

Abstract

New Zealand treeline species have low frost tolerance compared to their northern hemisphere counterparts, and appear susceptible to out-of-season frosts. However, foliage from high altitude trees is rarely directly measured. This study compares seasonal frost tolerance of mature treeline trees with local temperatures to assess whether frost affects their performance. Photosystem efficiency and seasonal frost tolerance (temperatures causing 10% and 50% foliage mortality, LT_{10} and LT_{50}, respectively) were measured on foliage from four native and one exotic species across the treeline ecotone. For all species, photosystem efficiency and frost tolerance were lower in spring and summer than in autumn. Frost tolerance changed with altitude only for exotic *Pinus contorta* in spring. Spring frosts regularly exceeded LT_{10} for all species. In all seasons over the last 20 years, the minimum temperature experienced was at least 4 °C warmer than the LT_{50}; however, east of the Main Divide, a 1-in-40 year extreme minimum temperature in summer reached LT_{50} levels. This study suggests frosts may cause some foliar damage, especially in spring, but the effects of frosts on mature trees are unlikely to control the position of the New Zealand treeline.

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Introduction

New Zealand treelines are lower in altitude than treelines at similar latitudes in the northern hemisphere (Körner 1998), and are anomalously warm compared to their northern counterparts (Körner and Paulsen, 2004). Most species forming northern hemisphere treelines are extremely frost tolerant, whereas their equivalents in the southern hemisphere are not (Bannister and Neuner, 2001). As several northern hemisphere treeline conifers grow above the native New Zealand treeline and are capable of aggressive spread (Wardle 1985a, 2008), there can be no doubt that they can overcome some aspect(s) of the environment that prevent(s) upward expansion of native trees. Frost has been argued to be the most likely candidate (Wardle, 2008) as growing season warmth is sufficient for exotic trees to reach at least 200 m higher in altitude than the natives.

The New Zealand treeline climatic regime is highly oceanic and, compared with northern temperate areas with similar mean annual temperatures at treeline, the growing season tends to be longer but not as warm at its peak, and winters shorter and milder (Mark et al., 2000). Growing seasons (estimated by phenology) at New Zealand treelines may be nearly twice as long as those in Europe (Benecke et al., 1981). Although winters are not severe, spring and early summer temperatures tend to be highly variable. Introductions and experimental plantings at and above the native New Zealand treeline have shown that several exotic treeline species generally considered to tolerate low winter temperatures, including *Picea engelmannii* and *Larix decidua*, are highly susceptible to summer frosts (Benecke et al., 1981; Wardle, 1985a). Wardle (2008) argued that, because of the low frost resistance of New Zealand trees, occasional severe frosts in spring and autumn killed unhardened tissue, and frost-related dieback over winter prevented permanent height gains of trees. He argued that this low frost resistance was a consequence of the short time available for its evolution in New Zealand, a view supported by Körner and Paulsen (2004).

The hypothesis that the native trees are limited by frost at their upper altitudinal limit has been supported by transplant experiments in the Craigieburn Range, New Zealand, in which frost-sheltered *Nothofagus* seedlings and saplings were shown to grow 150 m above the natural treeline (Wardle 1985a). However, old, well-established plants were incapable of extending branches outside of the 30 cm high shelters without suffering dieback.

Despite the clear importance of frost in New Zealand treeline studies, little research has been done on this subject since Peter Wardle's pioneering studies in the 1970s and 1980s. Frost tolerance has been measured on most of the major treeline species (Wardle, 1991), but often using material not sourced at treeline. Techniques used to assess frost damage have varied from study to study, and it is difficult to compare results. The temporal variation of frost tolerance reduces comparability and is poorly studied (Bannister, 2007), even though it is known that seasonality greatly affects frost tolerance (foliage is most resistant in winter and de-hardens towards summer; e.g., Alberdi et al., 1985; Bannister and Neuner, 2001). Additionally, it may not be solely frost that affects foliage: if combinations of frost and other environmental factors, such as high radiation or strong winds, damage tree foliage. The severity of such combinations increases with altitude, and one would expect an altitudinal trend of decreasing performance, as well as a decrease in performance in the seasons in which the environmental conditions are most adverse. This can be quantified by chlorophyll fluorescence measurements that indicate changes in photosystem efficiency (Richardson et al., 2001).

In this paper, we critically examine the suggestion that frost affects tree performance at New Zealand treelines and that this in turn is a significant factor in determining treeline altitude. We use two contrasting treelines. On the eastern side of the Southern Alps,

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Nothofagus solandri var. *cliffortioides* dominates at treeline, with a subdominant coniferous tree, *Phyllocladus alpinus*. These treelines are typically abrupt and abut alpine tussock grassland. Exotic *Pinus contorta* is invading above these treelines. In the central western districts of the Southern Alps, a diverse, diffuse tree line forms, in which the conifers *Halocarpus biformis* and *Libocedrus bidwillii* are dominant. If frost is a determinant of treeline position, we hypothesize that the treeline species should extend close to the minimum isotherm at which frost damage occurs, and that foliage becomes more tolerant to frost as treeline is approached. If this is not the case, then other factors must be more important in limiting tree performance. If foliage is progressively more stressed by environmental conditions closer to treeline, chlorophyll fluorescence values should decrease with altitude. Periods of low photosystem efficiency, as indicated by fluorescence measurements across seasons and altitudes, will hence provide information regarding the timing and candidate processes involved in foliar damage.

Methods

SITES AND PLANT MATERIAL

Altitudinal gradients through the treeline ecotone were selected at two sites in New Zealand, one on the east and one on the western slopes of the Southern Alps (Fig. 1). Treelines at both sites have not been depressed by human activities or avalanches, and they represent the local natural climatic tree limit (Wardle, 2008). The sites experience similar thermal conditions during the growing season, but the eastern site has markedly lower winter temperatures and longer lasting snow cover than the more oceanic western site (Cieraad, 2011). Five species were sampled at different altitudes depending on their altitudinal distribution and the local treeline altitude (Table 1). Foliage of the evergreen broadleaf species, *Nothofagus solandri* var. *cliffortioides* (Hook.f.) Poole (Nothofagaceae), and of two evergreen conifers, *Phyllocladus alpinus* Hook.f. (Podocarpaceae) and the exotic *Pinus contorta* Loudon subsp. *contorta* (Pinaceae), was collected from Craigieburn on the east side of the Southern Alps. *N. solandri* dominates treeline forests on the eastern sides of the North and South Islands (Wardle, 2008). This species forms a clear abrupt treeline, where the closed canopy forest (ca. 5 m tall) is abruptly replaced by alpine tussock grassland (Wardle, 2008). Although *N. solandri* is the main tree species at the site, some shrubs are also present (including *P. alpinus*), and exotic species are spreading from nearby plantations. Most notably, *Pinus contorta* subsp. *contorta* has successfully established as tree-sized individuals (Ledgard, 2001) some 150 altitudinal meters above the

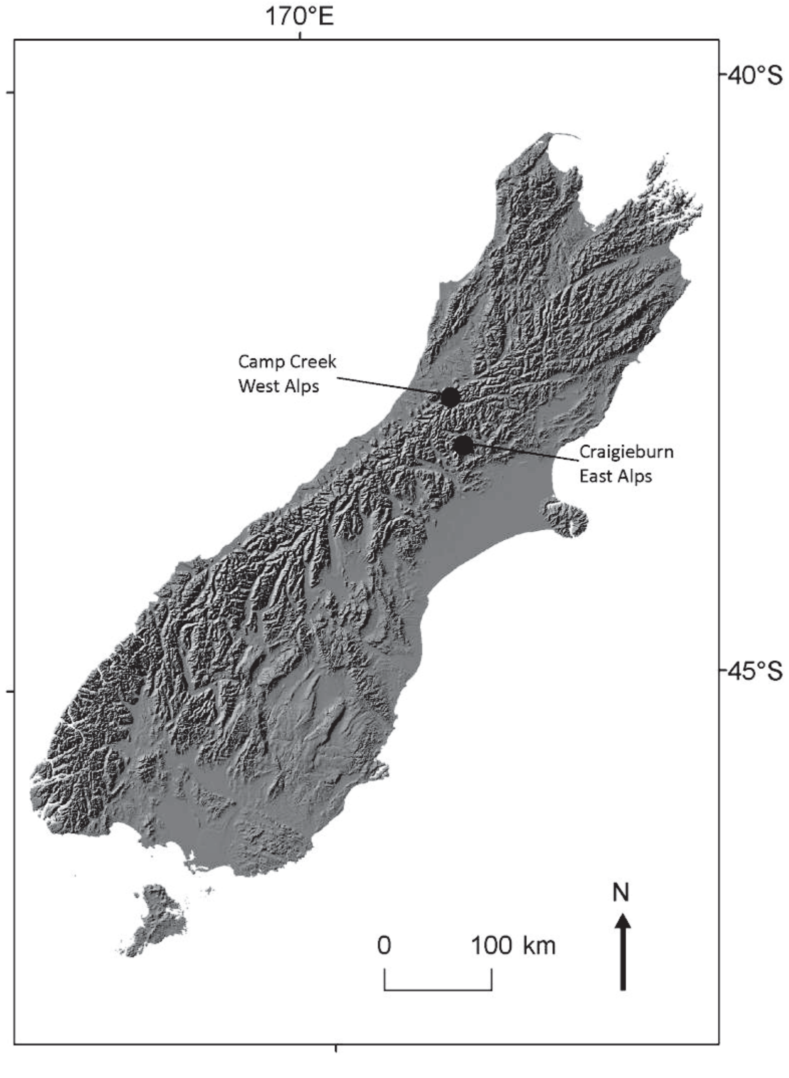

FIGURE 1. Location of sample sites in the South Island of New Zealand.

TABLE 1

Details of sites and species sampled.

Site	Species	Altitudinal range sampled (m a.s.l.)	Highest altitude attained by trees (>3 m) (m a.s.l.)
East Alps: Craigieburn (43.12°S, 171.70°E)	*Nothofagus solandri* var. *cliffortioides*	1250–1450	1350
	Phyllocladus alpinus	1250–1480	NA (only shrubs; no trees >3 m present)
	Pinus contorta	1250–1550	1450
West Alps: Camp Creek (42.72°S, 171.57°E)	*Halocarpus biformis*	850–1250	1150
	Libocedrus bidwillii	850–1120	1120

highest *N. solandri* trees, and *P. contorta* seedlings can be found for an additional 200 m (Wardle, 2008).

Foliage of *Halocarpus biformis* (Hook.) Quinn (Podocarpaceae) and *Libocedrus bidwillii* Hook.f. (Cupressaceae) was collected at Camp Creek on the west side of the Southern Alps. These co-existing conifer species are evergreen and long-lived (Wardle, 1991) and often form the tallest trees in the mixed conifer-broadleaved hardwood treeline ecotone communities that dominate in western areas where *Nothofagus* species are absent (Reif and Allen, 1988). The species will hereafter be referred to by their generic name only, and the sites as West Alps and East Alps, respectively. Trees were sampled at 100 m vertical intervals over the whole treeline ecotone, i.e., the gradient from tall closed canopy forest stands to the treeline (uppermost limit of >3-m-tall trees) (Table 1). Where the species were present above the treeline (<3 m tall), samples were also taken. In the case of *Phyllocladus*, no trees >3 m were present, so shrubs were sampled along the whole gradient.

Material was collected from the sites three times during the year: at the end of the growing season when hardening had started (autumn: 4 and 11 April 2010 for West Alps and East Alps, respectively); in spring, before leaves had flushed (30 and 31 October 2010); and in early summer (9 and 15 January 2011). A mid-winter collection at the sites was not feasible because of difficulties with access. On a northwest-facing slope of ca. 30° inclination, at each altitude, five mature individuals were selected (different trees each season). From each individual, a sample was taken consisting of eight short shoots with the most recent, fully expanded foliage. Foliage was consistently collected from fully sunlit branches in the top half of the crown (shotgun sampling where necessary), as frost tolerance and stress levels may differ between sun and shade leaves (e.g., Stecher et al., 1999). Samples were kept in polythene bags in an insulated container during transport to the laboratory where they were held in a refrigerator at ca. 4 °C overnight. Shoots were then allocated randomly to eight frost treatments (see below).

FREEZING TREATMENTS

Freezing treatments followed Bannister et al. (2005). Small shoots (ca. 5 cm) with foliage were placed on damp paper towel inside polythene bags and cooled to seven treatment temperatures (0, −3, −6, −9, −12, −15, and −18 °C) at a rate of 5 °C h^{-1}. Control samples were held in a refrigerator at +4 °C. The range of target temperatures was selected so that the least severe treatment was likely to inflict no damage, whereas the most severe treatment would be at a temperature lower than those experienced in the field. The target temperature was held for 4 h (Taschler et al., 2004); the combination of this length of time and a damp towel with the sample prevented supercooling (Bannister and Lord, 2006). Diurnal temperature records at New Zealand treeline show daily extreme minimum temperatures are generally attained in the early morning and remain at similar values for 2–4 h before dawn (Cieraad, 2011). The material was then thawed to +4 °C at a rate of ca. 5 °C h^{-1} before being placed at room temperature (ca. 20 °C) in the dark. Freezer air temperatures were measured using a calibrated thermocouple (type T) and logged at one-second intervals using a data logger (CR10X, Campbell Scientific Inc., Logan, Utah, U.S.A.). An on/off control relay, activated by the data logger, was used to keep two freezers within 0.3 °C of their respective target temperatures. Cold air stratification inside the freezers was eliminated by the use of a small fan. The seven frost treatments were allocated randomly to the two freezers, and were conducted over 2 d.

DAMAGE ASSESSMENT

Foliage damage was assessed by chlorophyll-*a* fluorescence measurements 3 d after frost treatments. The ratio of variable to maximum fluorescence of the sample (F_v/F_m) of dark-adapted photosynthetic systems (>30 min) (Maxwell and Johnson, 2000) was determined using a portable infrared gas analyzer with chlorophyll fluorescence attachment (Li6400 and Li6400-40 LCF, Lincoln, Nebraska, U.S.A.). As dead material effectively has an F_v/F_m of zero, the degree of damage was calculated as the photoinactivation ratio (*PhI*) as described by Larcher (2003):

$$PhI = (1 - F_{fT}/F_{max}) \tag{1}$$

where F_{fT} is the F_v/F_m of the sample exposed to a freezing temperature T, and F_{max} is the maximum value of F_v/F_m for all samples of each tested species.

The temperature producing 50% damage (LT$_{50}$) was determined by linear interpolation using the temperature causing the highest *PhI* of <50% and the temperature causing the lowest *PhI* of >50% (Bannister et al., 1995, 2005; Sierra-Almeida et al., 2009). Extrapolation was used only if the F_v/F_m from the coldest treatment approached 50% of F_{max}. In cases where the lowest temperature treatment (−18 °C) caused less than 50% damage to a sample, that temperature was taken as the best estimate of freezing tolerance.

Alternative methods of frost damage assessments include electrolyte leakage and visual estimates. Electrolyte methods have been tried on New Zealand subalpine plant species, but with limited success, as a number of the species tested (including *Phyllocladus alpinus*, also in this study) showed no perceptible electrolyte release, probably due to their thick cuticle (Reitsma, 1994). Although chlorophyll fluorescence measurements may overestimate the degree of frost resistance, particularly if readings of F_v/F_m are taken soon after thawing, they are similar to visual estimates when leaves are allowed to develop damage over several days after thawing (see review in Bannister, 2007).

PHOTOSYSTEM EFFICIENCY

The F_v/F_m of control (unfrozen) dark-adapted samples measured the day after collection provided a measure of the efficiency of photosystem II. F_v/F_m values for healthy plants are typically around 0.83 (Bjorkman and Demmig, 1987), and lower values indicate damaged photosystems, for example through photoinhibition (Maxwell and Johnson, 2000).

CLIMATIC DATA

Frost tolerance (LT_{10} and LT_{50}) data were compared with temperatures experienced at treeline to assess if (and if so, how frequently) these temperatures exceed the frost tolerance and can thus result in lethal foliar damage. As no long-term climatic data are available from New Zealand treeline sites, data from nearby weather stations were used to construct models predicting the temperature at higher altitudes. Data from lower altitude stations and a generic lapse rate of 6 °C km^{-1} have been used in the past to estimate temperatures experienced at treeline (e.g., Wardle, 2008). However, treeline temperature estimates so calculated can deviate markedly from actual treeline temperatures. Reasons for this include the positioning of stations in inland basins with more extreme conditions (due to cold air drainage and pooling), as well as lapse rates that differ dramatically throughout the year (e.g., Blandford et al., 2008). Therefore, instead of using a generic lapse rate, models of daily minimum temperature (T_{min}) at treeline were constructed using long-term, low altitude climate data and overlapping shorter-term treeline data, and including factors such as temperature, rainfall, atmospheric pressure, insolation, wind-speed, and wind-direction. These models were then used to predict treeline temperature for longer time series for which measured treeline data were not available. Climatic data were downloaded from the National Institute of Water and Atmosphere website (http://cliflo.niwa.co.nz).

For the East Alps site, frost tolerance data were compared with temperature data from a weather station at Craigieburn (less than 1 km from the collection site, at 914 m a.s.l.). From 1967 to 1986 there was another station directly uphill (at Ski Basin, 1554 m a.s.l.). T_{min} at treeline (at 1350 m, lying between the two stations on the same slope) was interpolated from the 20 years of data when these stations were both operating. Interpolated treeline T_{min} were then used to construct a model predicting treeline T_{min} from data at the lower (Craigieburn) station during this time, using a linear modeling approach. Average monthly lapse rates of T_{min} varied from 0.5 to 6.1 °C km^{-1}, and a model consisting only of Craigieburn T_{min} explained 90% of the variation in interpolated treeline T_{min}. This was improved (as indicated by Akaike's Information Criterion [AIC]; see Burnham and Anderson, 2002) by adding the following parameters: insolation, mean daily wind speed, and month (as a factor). This best model explained 91% of the variation. Craigieburn weather station data from the last 40 years (1971–2010) and this model were used to estimate treeline T_{min}, which was then summarized by month.

For the West Alps site, a similar approach was adopted: temperature data were collected at a weather station at the Camp Creek treeline (ca. 100 m from the treeline collection site in this study) between March 1978 and April 1984 (Ian Payton, unpublished data; Payton, 1989). These data were modeled using data recorded by the Hokitika weather station (ca. 40 km to the west, 39 m a.s.l.). Average monthly lapse rates of T_{min} varied from 1.2 to 5.6 °C km^{-1}. A model only containing Hokitika T_{min} explained only 54% of the variation in treeline T_{min}, whereas a more comprehensive model (selected using AIC) explained 71% of the variation. The latter model included the following significant parameters: Hokitika T_{min}, wind direction (included as a combination of cosine and sine to account for the circularity of this variable), wind speed, atmospheric pressure, and month (as a factor). This model was used to predict T_{min} at the Camp Creek treeline from the Hokitika data for the period 1971–2010, and the results again summarized by month.

STATISTICAL ANALYSES

The effects of altitude and time of sampling (season) on frost tolerance and photosystem efficiency were assessed in a linear model in R v. 2.12.2 (R Core Development Team, 2011). Following Crawley (2002), models were simplified by progressively removing non-significant terms and selecting the minimum adequate model. At each step of this backward selection procedure, the non-significant term with the smallest associated effect size was eliminated. Main effects were removed only after relevant interactions had been eliminated. Differences in photosystem efficiency and frost tolerance between treeline individuals and short-statured individuals occurring above the treeline were assessed using *t*-tests.

Results

FROST TOLERANCE

At the East Alps site, all species were more tolerant of frosts in autumn than in spring or summer (Fig. 2). Altitude did not affect the frost tolerance of *Nothofagus* or *Phyllocladus*, although both species showed significant seasonal variation in frost tolerance (autumn LT_{50} was −11.2 °C and −15.6 °C for *Nothofagus* and *Phyllocladus*, respectively, compared to −10.8 °C and −12.9 °C in spring, and −5.5 °C and −5.7 °C in summer) (Fig. 2). *Pinus* had a frost tolerance of −18 °C at most altitudes in autumn (i.e. no sign of damage at the lowest temperature tested), although decreased tolerance at the highest altitude site resulted in a slight but significant positive altitudinal trend. In summer, altitude did not affect frost tolerance of *Pinus* (−6.8 °C), whereas in spring tolerance increased significantly with altitude, from −10.5 °C to −16.5 °C

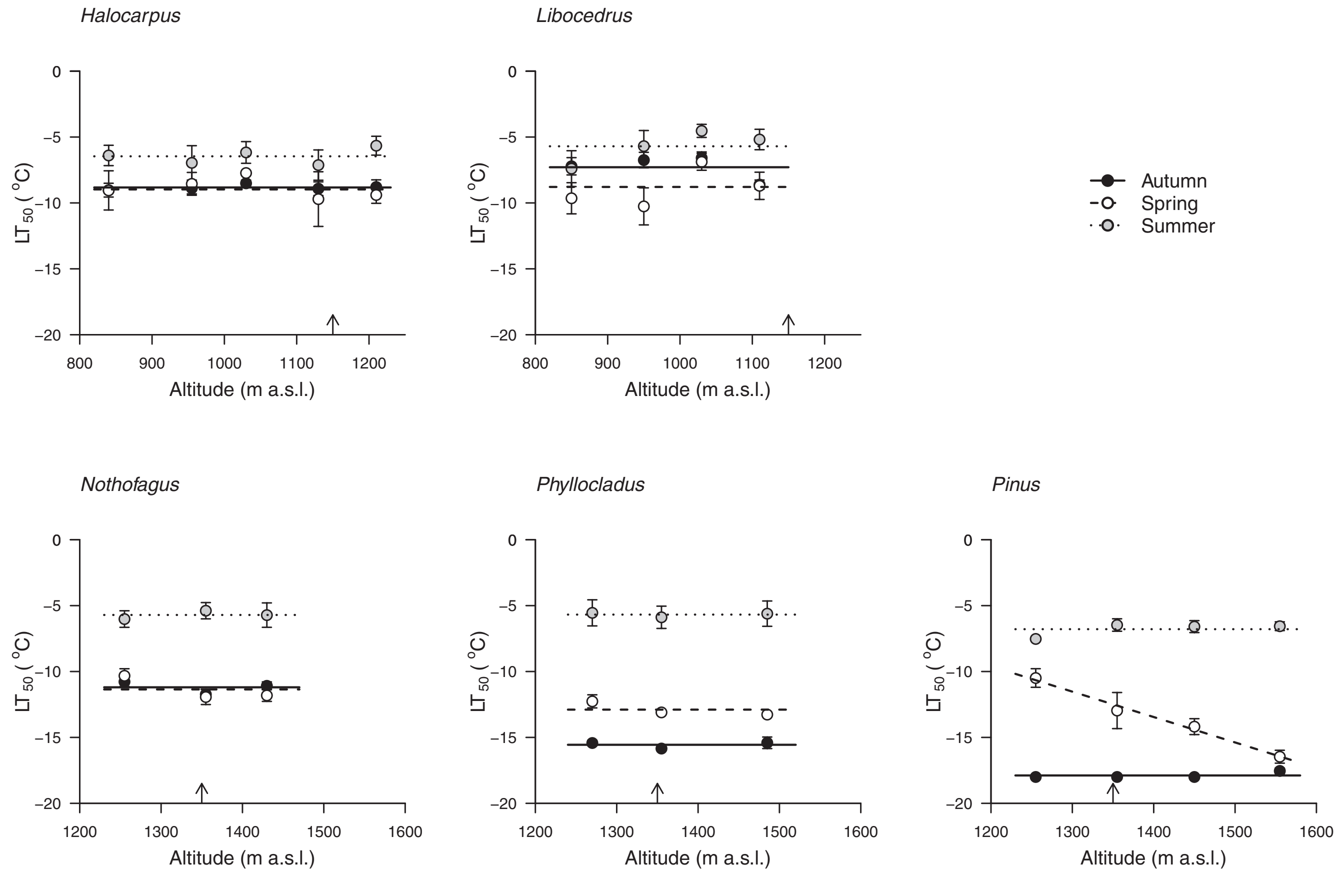

FIGURE 2. Effect of altitude and season on the frost tolerance (mean LT_{50}, temperature that causes 50% lethal damage to the photosystem, ± 1 standard error) of treeline species at the West Alps (top row) and East Alps (bottom row) sites. Arrows indicate the local native treeline altitude. All species are more tolerant of frosts in autumn than in spring and summer. Frost tolerance only differs with altitude for *Pinus* in spring.

(Table 2, Fig. 2). For all species and sites, the temperature at which foliage damage was initiated (10% damage, LT_{10}) followed the same trends with altitude and season as described for LT_{50} (data shown only for treeline altitude in Fig. 3).

At the West Alps site, altitude did not affect LT_{50} of either conifer species (Fig. 2). However, there was a seasonal effect: frost tolerance was highest in spring and lowest in summer. *Halocarpus* could withstand frosts down to −8.7 and −9.0 °C in autumn and spring, respectively, but only −6.6 °C in summer. Frost tolerance of *Libocedrus* was also lowest in summer (−5.7 °C), while withstanding frosts of −7.3 and −8.8 °C, in autumn and spring, respectively (Table 2, Fig. 2).

The LT_{50} of all species was substantially below the extreme minimum monthly air temperatures experienced at the treeline in all seasons in the last 20 years (Fig. 3). However, at the East Alps treeline, a rare (1 in 40 year) extreme frost event in January (−4.8 °C) was very close to temperatures causing 50% foliar damage. At the same site, regular frost events in spring, and perhaps also summer, approach the LT_{10} for all species. At the West Alps site, temperatures causing 10% damage at the treeline were encountered in the last 20 years only for *Libocedrus* in spring.

PHOTOSYSTEM EFFICIENCY

For two species (*Halocarpus* at West Alps and *Nothofagus* at East Alps), there was a significant negative trend of photosystem efficiency (F_v/F_m) with altitude. For *Halocarpus*, the time of sampling affected this trend, with no significant altitudinal trend in autumn (Fig. 4, Table 3). All species showed decreasing F_v/F_m in spring compared to autumn, and an intermediate level in summer (Fig. 4, Table 3). For *Pinus*, F_v/F_m did not differ significantly over the entire altitudinal range. However, if the highest site (where individuals were <3 m tall) was excluded, F_v/F_m decreased significantly with altitude in all seasons (data not shown). Only in spring was F_v/F_m of low-statured *Pinus* at the highest altitude site significantly different from F_v/F_m at the treeline site (t-test: mean F_v/F_m at treeline $= 0.586$, mean 100 m above treeline 0.670; $t = -3.70$, df $= 5.62$, $p = 0.01$). Photosystem efficiency did not differ between treeline individuals and low-statured *Halocarpus* 100 m above treeline in any season.

DISCUSSION

All five New Zealand treeline species in this study were least frost tolerant in early summer, which is the most intensive growth period (Benecke and Havranek, 1980), as has been described by others (Tranquillini, 1979; Bannister and Neuner, 2001; Larcher, 2005). Although exact comparisons with previous frost tolerance studies are difficult because of different damage assessment techniques, collection location, and timing, LT_{50} values generally concurred with those from previous studies. The maximum frost toler-

TABLE 2

Linear model results for frost tolerance (LT_{50}) for each species.

	df	Sum of Squares	Mean Squares	F	*p*
West Alps					
Halocarpus					
Season	2	93.7	46.8	12.6	<0.001
Residuals	70	260.2	3.9		
Libocedrus					
Season	2	90.3	45.2	10.0	<0.001
Residuals	55	248.1	4.5		
East Alps					
Nothofagus					
Season	2	310.3	155.1	96.2	<0.001
Residuals	42	67.7	1.6		
Phyllocladus					
Season	2	785.5	392.7	251.2	<0.001
Residuals	43	67.22	1.6		
Pinus					
Altitude	1	43.8	43.8	31.1	<0.001
Season	2	1229.6	614.8	436.8	<0.001
Altitude:Season	2	80.1	40.1	28.5	<0.001
Residuals	55	77.4	1.4		

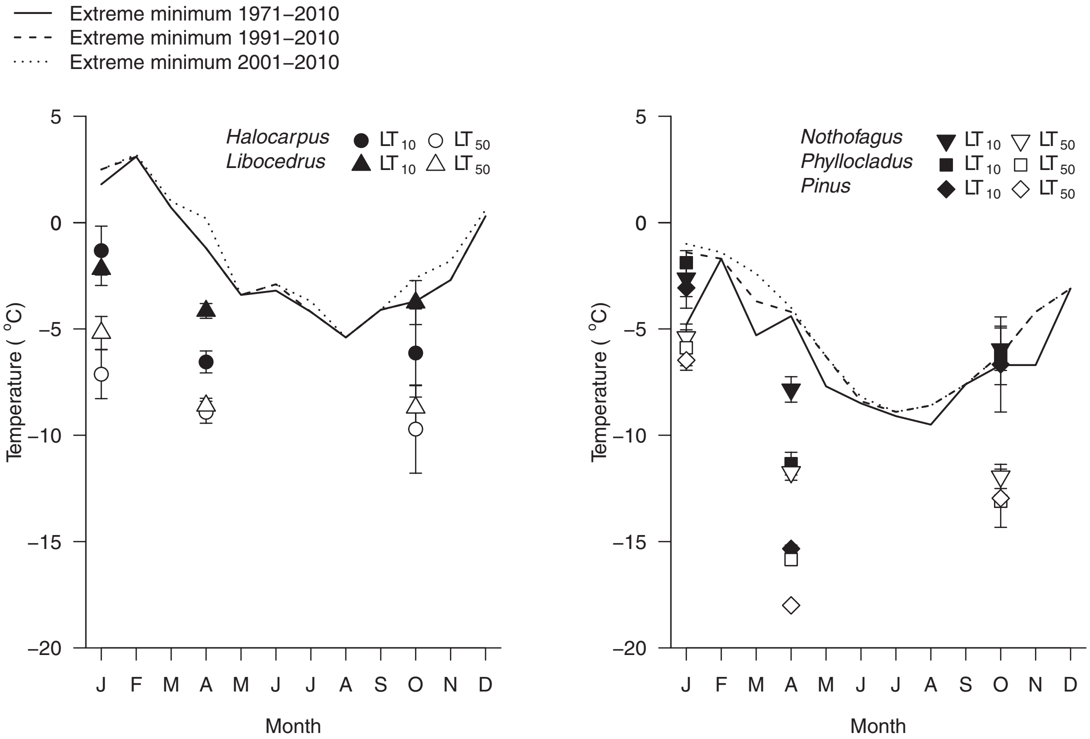

FIGURE 3. Frost tolerance temperature (mean temperature at which 10% and 50% of the foliage is damaged, LT_{10} and LT_{50}, respectively, ±1 standard error) of trees of five species at treeline in relation to estimated monthly extreme minimum air temperatures at the West Alps (left) and East Alps (right) sites for the last 10, 20, and 40 years.

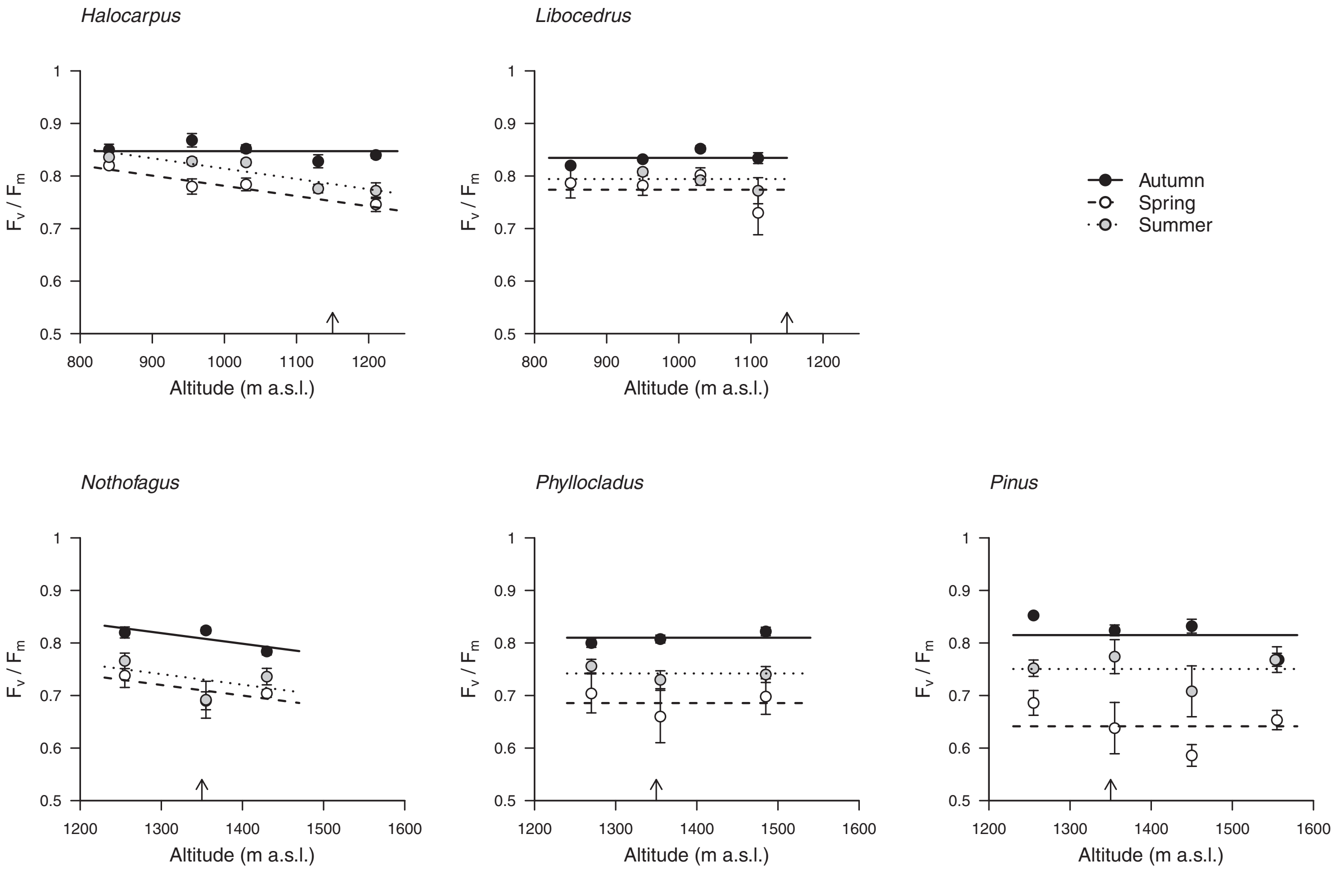

FIGURE 4. Effect of season and altitude on photosystem efficiency (F_v/F_m, mean ± 1 standard error) of treeline species at the West Alps (top) and East Alps (bottom) sites. Efficiency is highest for all species in autumn and lowest in spring. *Nothofagus* and *Halocarpus* show a significant decline in efficiency with altitude.

TABLE 3

Linear model results for photosynthetic efficiency (F_v/F_m) for each species.

	df	Sum of Squares	Mean Squares	F	*p*
West Alps					
Halocarpus					
Altitude	1	0.0290	0.0290	47.58	<0.0001
Season:Altitude	2	0.0634	0.0317	51.98	<0.0001
	2	0.0047	0.0024	3.86	0.026
Season					
Residuals	66	0.0403	0.0006		
Libocedrus					
Season	2	0.0365	0.0183	10.93	0.0001
Residuals	54	0.0902	0.0017		
East Alps					
Nothofagus					
Altitude	1	0.0094	0.0094	5.47	0.024
Season	2	0.0812	0.0406	23.66	<0.0001
Residuals	41	0.0704	0.0017		
Phyllocladus					
Season	2	0.11553	0.0578	16.042	<0.0001
Residuals	42	0.1512	0.0036		
Pinus					
Season	2	0.31662	0.158312	38.767	<0.0001
Residuals	58	0.2369	0.0040		

ance for *Nothofagus solandri* var. *cliffortioides* in this study (−11.2 °C) fell within the range of −10 to −13 °C reported by previous studies (Wardle and Campbell, 1976; Sakai and Wardle, 1978; Sakai et al., 1981; Greer et al., 1989). The summer tolerance of ca. −5.5 °C fell between −3.5 and −7 °C, previously reported for seedlings (Greer et al., 1989) and mature trees (Wardle and Campbell, 1976), respectively. *Phyllocladus alpinus* tolerated temperatures down to −15.6 °C in autumn, close to −16.3 °C reported by Reitsma (1994), but not as extreme as the −18 to −20 °C recorded by Sakai and Wardle (1978). Foliage of closely related *Phyllocladus aspleniifolius* near the treeline in Tasmania tolerated frosts down to −14 °C (Read and Hill, 1988). In its native range, *Pinus contorta* can withstand temperatures down to −35 °C in winter and −9 °C in summer (Bigras et al., 2001); in this study, the species showed no damage in autumn at the lowest temperature measured (−18 °C), but LT_{50} increased up to ca. −7 °C in summer.

The maximum frost tolerance values in this study for the West Alps conifers, *Halocarpus biformis* and *Libocedrus bidwillii*, were ca. 4 °C warmer (−9.0 °C and −8.8 °C, respectively) than the −13 °C recorded for both species by Sakai and Wardle (1978). Collection locations are likely to explain this difference, as their material came from east of the Main Divide, and thus was exposed to more extreme winter conditions, likely resulting in increased hardening. Additionally, the maximum frost tolerance in this current study was determined in autumn, whereas the species may continue to harden further into the winter (Sakai and Wardle's samples were collected mid-winter).

The frost tolerance of native species in this current study did not vary with altitude. Alberdi et al. (1985) found *Nothofagus* spp. from lower altitudes in southern Chile had only a slightly lower tolerance than those near treeline. In contrast, exotic *Pinus contorta* showed a significant altitudinal trend in frost tolerance, but only in spring. At this time of sampling, the de-hardening process had begun at the lower altitudes, with frost tolerance values approaching summer values. In contrast, at higher altitudes, lower temperature postponed de-hardening, resulting in similar spring and autumn values of ca. −16 °C for the shrub-statured individuals 200 m above the native treeline.

Frost tolerance of *N. solandri* var. *cliffortioides* in this study is similar to that of related species at treeline in other southern hemisphere regions. Its foliage can withstand frosts of similar severity as foliage of *N. dombeyi* (−8.5 to −12.8 °C), and is much more tolerant than *N. nitida* (−6.2 to −8.5 °C) (Alberdi et al., 1989; Reyes-Díaz et al., 2005; Bannister, 2007). Both these evergreen species are common in upper montane forests in Chile, but do not reach the local treeline. In Tasmania, evergreen *N. cunninghammii* at treeline is frost tolerant to similar levels (−11 °C) (Feild and Brodribb, 2001). In contrast, in South America, buds of deciduous treeline-forming *N. antarctica* and *N. pumilio* can withstand much colder temperatures (−20 to −22 °C) (Sakai et al., 1981; Alberdi et al., 1985). The reduced frost tolerance of New Zealand compared to South American treeline *Nothofagus* had led Wardle (1998, 2008) to suggest that frost is an important factor in the formation of the lower local treelines in New Zealand (Wardle, 1998, 2008).

However, this study shows that, at all times, the average LT_{50} of all species far exceeded (by at least 4 °C) minimum air temperatures that trees would have experienced at the respective treeline locations over the past 20 years (Fig. 3). Of course, onset of damage (indicated by LT_{10}) occurs at higher temperatures, closer to the air temperatures experienced at treeline. Such minor frost damage may be expected regularly for all species at the East Alps site in spring (when LT_{10} are within 0.5 °C of T_{min}) and less regularly in summer (when LT_{10} is between 0.6 °C and 1.8 °C lower than T_{min} for these species). This concurs with our field observations and damage descriptions (e.g., Wardle and Campbell, 1976; Wardle, 1985a). Additionally, a minimum of −5 °C occurred once in the summer months in a longer time series of 40 years at East Alps; such a frost would result in foliar damage approaching 50% for all species at this site (Fig. 3). The canopy, however, has a buffering effect and only the small proportion of foliage in the outer canopy will be exposed to these temperatures (McGlone et al., 2004). Hence, the risk of a severely damaging frost during summer is low, and even extreme episodic frosts are unlikely to kill adult trees of the five species at either location.

Lack of frost tolerance has been implicated as a driver of treeline altitudes in tropical regions, where trees cannot avoid the harsh environment of high elevation tropical nights by becoming dormant (Cordell et al., 2000; Rada et al., 2001). Outside the tropics, it remains unclear whether frost is a mechanism that can actually determine temperate treelines. It has been suggested that the limitation of tree growth with increasing altitude may be due primarily to the inability of trees to complete summer growth, with subsequent death because of winter desiccation and frost damage of immature growth (Tranquillini, 1979). Others have suggested that trees at temperate treeline are dormant during seasonally harsh episodes, and that temperate treeline position is rarely determined by freezing temperatures causing injury (Jobbágy and Jackson, 2000; Körner, 2003). This study concurs with the latter proposition, and suggests that, although some damage may occur, it is unlikely that such occasional frosts control the temperate New Zealand treeline position through dieback of adult trees.

Wardle (1973, 1985b) suggested that limiting factors for treeline may be met in the seedling stage. Indeed, in a recent study, Piper et al. (2006) found that *Kageneckia angustifolia* seedlings at treeline in temperate Chile are less tolerant than the temperatures often encountered at this site, suggesting that the lack of frost tolerance will affect treeline formation in this area (Piper et al., 2006). In New Zealand, no direct comparisons of frost tolerance of seedling and mature foliage exist for any treeline species. However, one study of seedlings (Greer et al., 1989) found LT_{50} comparable to tolerance of mature tree foliage reported in Wardle and Campbell (1976), and suggested that, at least for *Nothofagus solandri*, age does not affect frost tolerance. In Chile, similar adult and seedling of two *Nothofagus* species also had similar levels of frost tolerance (Reyes-Díaz et al., 2005). Even so, seedlings occupy space closer to the ground surface, and may be exposed to colder (potentially 3 °C lower) temperatures compared to those in the canopy, especially on calm clear nights (Wilson et al., 1987, Wardle, 1985b). Given the 4 °C window between absolute minimum temperatures experienced and frost tolerance values, and the short-lived nature of the seedling stage, we suggest that frost sensitivity during the seedling stage cannot alone be the determining factor of treeline position.

Overall, it appears that the New Zealand treeline species, at least in winter, have excess frost tolerance relative to the risk of damaging frosts at treeline. In winter, the differences in LT_{50} between the five species are largest (-18 to -8.6 °C). In summer, despite the very different leaf and tree structures, biogeographic and ecological distributions of the species, they show a much narrower range in LT_{50} (-7.1 to -5.2 °C). This suggests that a minimal level of tissue adaptation secures protection down to -7 to -5 °C, which apparently is relatively easily achieved by most trees capable of growing in the alpine zone. Almost 80% of the 58 New Zealand trees assessed for winter freezing resistance of their leaves can tolerate -5 °C or colder (Wardle, 1991). *Phyllocladus alpinus* is the only native species in this study whose range extends out to the drier, eastern basins where, in winter, daily minimum temperatures colder than -10 °C are commonly experienced. The ability to achieve such levels of winter tolerance, as in *Phyllocladus alpinus* and *Pinus contorta*, may be linked to the permanent structural protection provided by the robust anatomical features of these conifers, as has been suggested for other conifers and winter cereals (Savitch et al., 2002; Öquist and Huner, 2003).

This study does not take into account exacerbating factors, for example frost desiccation or cold-induced photoinhibition. In other locations, these processes affect trees near treeline (e.g., Hadley and Smith, 1986; Bader et al., 2007). If combinations of frost and other environmental factors, such as high radiation or strong winds, are damaging to tree foliage, and the severity of such combinations increases with altitude, one would expect an altitudinal trend of decreasing performance. This can be measured by fluorescence measurements that indicate changes in photosystem efficiency, F_v/F_m (Richardson et al., 2001). In this study, photosystem efficiency decreased towards treeline for some species: *Nothofagus* in all seasons and *Halocarpus* in autumn and spring (Fig. 4). In contrast, *Phyllocladus* and *Libocedrus* showed no change in F_v/F_m with altitude. In the Himalayas, De Lillis et al. (2004) also found that fluorescence measurements of trees in the treeline ecotone were more strongly related to species than to altitude. In the current study, exotic *Pinus contorta* showed a pattern of decreasing photosystem efficiency towards treeline in spring (or slower recovery after winter), but individuals at the highest site had higher photosystem efficiency than at the treeline site (overall resulting in a non-significant linear altitude effect). A similar pattern has been reported in the U.S.A., where *Picea* and *Abies* showed decreasing photosystem efficiency with altitude towards treeline, although at the highest altitude site efficiency was increased, probably related to the prostrate plant architecture and/or stress-tolerant physiology at this site (Richardson et al., 2001). As the trees at the highest site in this study were not more sheltered, nor prostrate, it seems likely that a more stress-tolerant physiology of *Pinus contorta* may explain this increase in F_v/F_m measurements at the highest site.

F_v/F_m measurements were low (0.65–0.8) in spring and highest (0.8–0.85) in autumn for all species. Although frost alone is not sufficient to kill foliage, these results suggest that adverse environmental conditions in winter and/or spring do cause some foliar damage. The seasonal course of F_v/F_m suggests that over-wintering leaves have accumulated damage through adverse conditions (e.g., a combination of cold temperatures, and high light and wind conditions), whereas the photosynthetic efficiency of newly flushed foliage (first measured in early summer) continued to improve towards autumn. These seasonal differences are particularly visible in the East Alps species (Fig. 4), which occupy an environment with a more seasonal climate than the West Alps species. Similarly, in a study of photosynthetic capacity of five conifers along near treeline in the U.S.A., Koh et al. (2009) found that lower temperatures in autumn were initially correlated with increases in maximal photosynthetic capacity, ''as long as the declining temperatures remained in a range that should likely permit further net carbon gain'' (p. 320). However, when winter encroached and freezing events became common, strong photosynthetic down-regulation followed (Koh et al., 2009). Stecher et al. (1999) also found an extreme reduction in fluorescence in *Picea abies* and *Pinus cembra* near treeline in winter (down to 10%), and a slow recovery towards summer.

The question of the ability of *Pinus* to grow at higher altitudes than the native treeline species remains to be answered. The results of this study suggest that frost tolerance cannot explain the difference in performance between it and native trees. *Phyllocladus* can endure -16 °C frosts, almost 5 °C colder than *Nothofagus*, yet it barely reaches tree height in the alpine ecotone and grows as a low (<2.0 m in height), layering shrub (Wardle 1969). It is a very slow growing tree, in contrast to *Nothofagus*, and it is possible its high level of frost resistance comes at the price of less rapid growth (e.g., Koehler et al., 2012; Molina-Montenegro et al., 2011). Additionally, the collapse of tissue under moderate water stress, common to Podocarpaceae, may limit the success of *Phyllocladus* in this summer-dry alpine environment (Brodribb, 2011).

As *Nothofagus solandri* seedlings transplanted above the species' natural treeline (Wardle 1985a, 2008) survived as long as they were kept under shelter, insufficient warmth during the growing season is not the reason for the species' failure to match the performance of *Pinus contorta*. Instead, we suggest the main difference between these species is the superior ability of *Pinus* to counter a range of exposure-related factors, such as high light, wind, and dryness, whilst continuing growth. At the seedling stage, *Pinus contorta* performs best in full sunlight (Despain, 2001), while *Nothofagus* seedlings are intolerant of high light, and occur only a few meters upslope from the abrupt treeline, where the parent canopy provides shade or shelter (Wardle, 2008). Cold-induced photo-inhibition has been suggested to affect *Nothofagus* at treeline (Ball, 1994), but this has not yet been quantified. In addition, dry conditions (high vapor pressure deficits) strongly reduce stomatal conductance and carbon accumulation of *Nothofagus* (Benecke and Havranek, 1980). In contrast, *P. contorta* subsp. *contorta* favors harsh, dry, high radiation sites in its native habitat (Despain, 2001) and the relative lack of such habitats in New Zealand may have restricted the opportunities for such a specialist to evolve here. On the other hand, it is highly unlikely that *P. contorta* could invade under the intensely oceanic conditions (milder, wetter, cloudier) above the gradual west coast or sub-Antarctic treelines. Here, the New Zealand treeline may not be anomalously low, but reflect a universal limit to tree growth governed by the warmth of the growing season (Körner and Paulsen, 2004).

CONCLUSION

Frost tolerance did not show a trend with altitude along the gradient studied here for four New Zealand native trees, and an altitudinal decrease of photosystem efficiency was found only for some species. There was a significant trend in frost tolerance of the exotic *Pinus* with altitude, but only in spring. The results of this study suggest that frost is not a major factor limiting the performance of adult trees near treeline in New Zealand. Although occasional frosts, especially in spring, may damage some of the adult foliage, we suggest only a small portion of the tree's foliage is affected, and that such frosts are unlikely to control treeline position through dieback of adult trees. In the last 20 years, the window of at least 4 °C between extreme minimum temperatures and the LT_{50} of mature foliage suggests that, even if seedlings were significantly more frost sensitive, they would not suffer seriously damaging effects.

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