



Global controls of forest line elevation in the northern and southern hemispheres

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ABSTRACT

1. We explored whether the independent evolutionary history of extratropical forests in the southern and northern hemispheres affects the temperature–elevation relationship of mountain forest lines. We compiled 115 forest line descriptions from the literature, covering the major extratropical mountain ranges of the world. We related forest line elevation to thermal regimes using mean annual temperature adjusted to sea level (MAT) and seasonal thermal amplitude (STA, mean of the warmest month minus the mean of the coldest) obtained from a global climate database.

2. Thermal variables explained 79% of the global variability of forest line elevation, which increased approximately 130 m for every 1 K of MAT and for every 2 K of STA. After considering STA, there was no significant effect of ‘hemisphere’ on forest line elevation. MAT–elevation relationships for sites with STA < 15 K were the same between hemispheres.

3. Sites dominated by different tree life forms

had similar mean temperatures for the warmest month (differences < 3 K), but contrasting mean temperatures for the coldest (differences > 30 K). Along a gradient of increasing STA and decreasing winter temperatures, forest lines were first dominated by evergreen broadleaf trees, followed by deciduous broadleaf species, evergreen conifers, and finally deciduous conifers.

4. Our results suggest that temperatures during the warm part of the year are the main control of forest line elevation in extratropical regions while temperatures during the cold part of the year affect the dominant life form of trees. There is a high degree of convergence in adaptation to mountain climates between trees species of both hemispheres. This convergence suggests that there is not a wide vacant altitudinal belt for introduced forest line species of the northern hemisphere into the southern hemisphere.

Key words alpine ecosystems, convergent evolution, forest distribution, mountain ecosystems, seasonality, temperature, thermal amplitude, timberline, treeline.

INTRODUCTION

High mountain forests often display a characteristic discontinuity in their distribution — the forest line. This boundary represents the upper limit of forest canopies and is associated with temperature decrease along elevational gradients. The elevation of forest lines can be viewed as the outcome of a confrontation of abiotic and biotic factors (Scuderi, 1987) in which the climate of higher elevations becomes increasingly less favourable and interacts with the tolerance of

tree species, determining their upper limit. Most of the previous research on forest line elevation at global and regional scales has focused on abiotic factors, usually considering latitude as a surrogate of temperature (Hermes, 1955; Cogbill & White, 1991; Körner, 1998). Despite the phylogenetic independence of forest line species at the global scale, their tolerance to low temperature was assumed to be constant globally in previous studies. In this paper we compare the elevation–temperature relationship between the extratropical zones of the northern and

southern hemispheres, where forest line species evolved independently. As a necessary background for this comparison we establish a quantitative global relationship between forest line elevation and temperature using a global climate database (Leemans & Cramer, 1990).

In temperate and boreal regions, forest line elevation is negatively associated with latitude. This relationship has been statistically confirmed in mountain ranges of Asia, Europe, and North America (e.g. Oshawa, 1990; Cogbill & White, 1991; Malyshev, 1993). The most obvious mechanism underlying this association is the decrease in temperature from the tropics to the poles. However, the association between forest line elevation and latitude does not display a strict correlation globally (Körner, 1998). Between 70°N and 30°N, forest line elevation increases with decreasing latitude, from 30°N to 20°S there is a slight decrease of altitude, and from 20°S to the southern extreme of America and New Zealand, forest line elevation drops dramatically again. At the same latitude, forest line elevation is 1000–1500 m higher in the northern hemisphere than in the southern hemisphere (Körner, 1998). Regional analyses reveal an increase of forest line elevation from oceanic to continental climates (Ellenberg, 1966; Faegri, 1972; Malyshev, 1993; Fang *et al.*, 1996; Malyshev & Nimis, 1997). At equal latitudes, the forest lines of oceanic islands are 1000–2000 m lower than those in the closest continental areas (Leuschner, 1996). The control of forest line elevation by warm season temperature rather than by year round or cold season temperatures has been suggested as the cause of higher forest lines in continental climates (e.g. Troll, 1973; Walter, 1973; Wardle, 1974). In relation to this trend, Troll (1973) and Walter (1973) noticed an increasing presence of broadleaf tree species in the forest line of the most oceanic mountain ranges of the northern hemisphere.

Körner (1998) reviewed five hypotheses concerning the control of forest lines, which included frost-related stress, mechanical disturbance and herbivory, reproductive constraints, insufficient net carbon uptake, and growth limitation by low temperature. Direct physiological evidence supports growth limitation by low temperatures during the active season as the most robust explanation of forest line position (Körner, 1998). The fact that growth limitation rather than

stress is the major constraint for trees at forest lines gives mechanistic support to the notion that growing season temperature is the major control of forest line elevation, and suggests that winter temperatures may be relatively unimportant. Temperatures during the warm season can be viewed as the result of two components of thermal regimes: mean annual temperature and seasonal thermal amplitude. We define seasonal thermal amplitude as the difference between the mean monthly temperature of the warmest and the coldest months of the year. Previous global analyses of forest line elevation have focused on mean annual temperature, using latitude as a surrogate (Hermes, 1955; Körner, 1998). Latitude can be gathered easily for any forest line point, but it has an imperfect correlation with mean annual temperature at the global scale. As extreme examples of this mismatch, mean annual temperatures in Scandinavia and northern Siberia or the Appalachians and the central Rockies differ by more than 15 K at the same latitude and elevation (Leemans & Cramer, 1990). To our knowledge, no attempts to relate global patterns of forest line elevation with both mean annual temperature and seasonal thermal amplitude in a quantitative fashion have been performed.

Cold forests of the northern and southern hemispheres had their evolutionary origins at high latitudes long after the break up of Pangea (200 million years ago), resulting in an extended history of isolation and independent evolution of their tree species (Dettman *et al.*, 1990; Francis, 1991; Manos, 1997). In the coldest forests of the northern hemisphere, those forming mountain forest lines and bordering arctic tundra, the dominant trees are usually conifers of the pine family (Pinaceae). In the southern hemisphere, the coldest forests are dominated by broadleaf species of the genus *Nothofagus* (Nothofagaceae). Conifers in the temperate forests of the southern hemisphere belong to the Araucariaceae, Cupressaceae, and Taxodiaceae families and are rarely found at forest lines (Beadle, 1981; Hart, 1987; Veblen *et al.*, 1996).

Is the disparate history and evolution of cold forest tree species the cause of lower forest lines in the southern hemisphere compared to the northern hemisphere? Concomitantly, is there a vacant altitudinal belt or niche for northern Pinaceae species in the alpine regions of the southern

hemisphere? We hypothesized that the lack of high elevation conifers of the pine family lowers forest lines in the southern hemisphere. We addressed this hypothesis by comparing the major mountain systems of the world based on forest line descriptions, compiled from the literature and climate data from a global climate database. We focused on extratropical systems in order to simplify the comparison of forest line communities with independent evolutionary origins.

METHODS

We compiled a database of forest line sites in mountain ranges located above 30° latitude in the northern and the southern hemispheres, and combined it with information from a global climate database (Leemans & Cramer, 1990). A strict definition of forest line was used — the upper limit of the continuous tree canopy. Scrub formations or 'krummholz' were not considered. For each site we obtained values for forest line elevation and coordinates for latitude and longitude as given by the authors. In a few cases we obtained geographical coordinates from maps. Where available, we also recorded the list of dominant tree species at each site. Sites were discarded if: 1) there was any indication in the literature of a change in forest line elevation due to human disturbance (a common situation in several mountain ranges of Europe); 2) the forest line was less than 200 m below the mountain top, where very local climatic effects can depress forest lines close to summits (Troll, 1973; Barry, 1992); 3) there was no clear definition of what the authors considered to be the forest line; and 4) the precipitation was low enough to constrain the development of closed forests (e.g. mountain ranges in central Asia). When more than one site was described for the same mountain peak or group of peaks (e.g. Wardle & Coleman, 1992) we averaged their elevation. After imposing these criteria, we obtained data for 115 forest line sites from 31 publications covering the most important mountain systems of extratropical regions globally (Appendix 1). We followed species nomenclature from Farjon (1993) for Pinaceae, Manos (1997) for Nothofagaceae, and the Integrated Taxonomy Information System (USDA, 1999) for the remaining families.

We gathered temperature data for forest line sites from a global climate database developed at the International Institute of Applied Systems Analyses (IIASA; Laxenburg, Austria) (Leemans & Cramer, 1990). This global database has mean monthly values of temperature, precipitation, and cloudiness for a grid of 0.5° latitude by 0.5° longitude. The temperature data set was based on more than 6000 weather stations (Leemans & Cramer, 1990).

We extracted from the IIASA database values of mean annual temperature and seasonal thermal amplitude for each forest line site. Mean annual temperature (MAT) was calculated as the 12-month average for the site and seasonal thermal amplitude (STA) was calculated as the difference between the mean monthly temperature for the warmest and coldest months. To explore the relationship between MAT and forest line elevation it was important to use temperature values that corresponded to the same elevation. The temperature values in the IIASA database represent the spatial average of grid squares adjusted according to their average elevation (Leemans & Cramer, 1990). We removed the effect of the elevation of individual grid squares by recalculating temperature at sea level with the aid of a global topographic database containing average elevation values for a 0.5° latitude by 0.5° longitude grid. The location of weather stations globally is usually biased to lower elevations (Barry, 1992). For this reason we adjusted MAT values from the database to a common sea-level basis rather than extrapolating values to forest line elevation, resulting in small elevation corrections. Mean annual temperature at sea level was calculated as follows:

$$\text{MAT} = \text{MAT}_{\text{grid}} + \text{elevation} \times 0.006$$

MAT and *MAT_{grid}* are mean annual temperature at sea level and mean annual temperature in the IIASA database for the grid square (degrees C), *elevation* is the average altitude above sea level (m) for the grid square, and *0.006* is the lapse rate of temperature change with elevation (K/m). This lapse rate is appropriate for cold and temperate regions (Barry, 1992). We evaluated the sensitivity of temperature corrections to local elevation changes among grid squares in two ways. We first considered

only the grid square corresponding to the forest line site, and we then included that same grid square plus its contiguous terrestrial neighbours (because forest line sites are in mountain areas, neighbouring grid squares encompass important elevation changes). Both estimates of MAT were quite similar ($r^2 = 0.97$, $P < 0.0001$; slope nonsignificantly different from one, $P = 0.61$; intercept not-significantly different from zero, $P = 0.78$). No elevation corrections were applied for STA assuming that it is not affected by elevation. We evaluated this assumption by computing the variability of STA among the forest line site grid square and its contiguous terrestrial neighbours; in all the cases the coefficient of variation among contiguous grid squares was $< 12\%$. We preferred the use of MAT and STA as opposed to growing season mean temperature or degree days sums because these alternative independent variables require an arbitrary definition of fixed growing season start and end dates, or fixed base temperatures. MAT and STA are able to capture most of the geographical variation of thermal regimes as the shape of the annual temperature cycle displays little variation across extratropical regions (Schneider 1996).

To quantify the role of annual temperature and its seasonal range on forest line elevation, we performed a stepwise regression analysis with forest line elevation as the dependent variable and MAT and STA as the independent variables. Northern and southern hemisphere data were first analysed independently. We tested linear and nonlinear models and included a term for the interaction between variables.

To evaluate the hypothesis that the independent evolutionary origin of forest line species affects the temperature–elevation relationship in the northern and southern hemispheres, we performed two analyses. At a coarse scale we pooled data from both hemispheres and included hemisphere as a binary variable in the multiple regression (south = 0, north = 1). At a more detailed scale, we selected those sites from the northern hemisphere that were within the range of STA of southern hemisphere sites and directly compared their regression models between forest line elevation and MAT.

Besides hemisphere contrasts, we were interested in potential associations between life forms of

forest line trees and thermal regimes. For this analysis, we grouped forest lines according to the dominance of evergreen broadleaf, deciduous broadleaf, evergreen conifer, and deciduous conifer species. We compared MAT, STA, and mean monthly temperature for the coldest and warmest month at the forest line position with a standard *t*-test. The temperatures at the forest line position were calculated using the elevation difference between the grid square and the forest line and the same lapse rate used for sea level temperature corrections. We evaluated the sensitivity of this analysis to changes in the lapse rate by recalculating the temperatures at the forest line position considering extreme lapse rates of 0.004 and 0.008 K/m (Barry, 1992).

RESULTS

Forest line elevation showed a linear increase with mean annual temperature (MAT) in both hemispheres (Fig. 1, Table 1). MAT explained 50% of the variability of forest line elevation in the northern hemisphere and 83% in the southern hemisphere ($P < 0.0001$ in both cases). MAT for northern hemisphere forest lines covered more than 35 K, ranging from -17.3°C in northern Siberia to 18.4°C in the south central Rockies. In the southern hemisphere the range of MAT was less than 10 K, from 3.7°C in Tierra del Fuego to 13.1°C in northern Patagonia (Appendix 1, Fig. 2a).

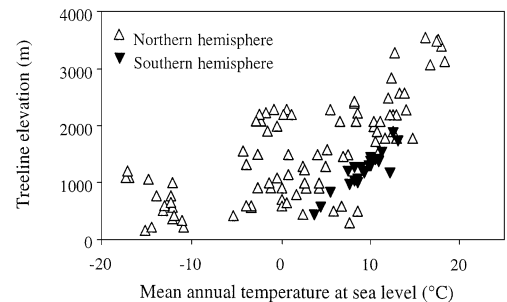


Fig. 1 Forest line elevation as a function of mean annual temperature at sea level for all sites of this study. Forest line elevation values were obtained from the literature review and temperature was calculated using global databases of temperature and elevation.

Table 1 Regression models of forest line elevation. Models include 93 sites for the northern hemisphere, 22 for the southern hemisphere, and 115 globally. Independent climatic variables are mean annual temperature at sea level (MAT) and seasonal thermal amplitude (STA). Slope coefficients are in m/K and intercepts are in m. Hemisphere was included as an independent binary variable in the global model and was not significantly related to forest line elevation ($P = 0.15$). In all cases, MAT had a stronger association with elevation than did STA. Interactions between variables and logarithmic transformations of data did not improve the models significantly

Model	Variable	Coefficients	<i>P</i> -values	R ²
Northern hemisphere	MAT	64	< 0.0001	0.50
	Intercept	1392	< 0.0001	
Northern hemisphere	MAT	134	< 0.0001	0.79
	STA	70	< 0.0001	
	Intercept	-847	< 0.0001	
Southern hemisphere	MAT	126	< 0.0001	0.83
	Intercept	90	= 0.4491	
Southern hemisphere	MAT	110	< 0.0001	0.88
	STA	42	= 0.0157	
	Intercept	-164	= 0.2565	
Globe	MAT	128	< 0.0001	0.79
	STA	63	< 0.0001	
	Intercept	-613	< 0.0001	

Seasonal thermal amplitude (STA) was positively associated with forest line elevation in both hemispheres, but its range of variation and explanatory power were higher in the northern than in the southern hemisphere (Table 1). In the northern hemisphere STA ranged from 10 K in Scotland to 60 K in Northern Siberia, while in the southern hemisphere it only ranged from 7 K for the islands of Tasmania and Tierra del Fuego to 13 K in northern Patagonia (Appendix 1, Fig. 2a). The inclusion of STA in the regression models explained an additional 29% ($P < 0.0001$) and 5% ($P = 0.016$) of forest line elevation in the northern and southern hemispheres, respectively (Table 1), and no significant interactions between MAT and STA were found. Non-linear functions did not improve the models. The slopes of the multiple regression models revealed that the effect of 1 K of STA was equivalent to approximately 0.5 °C of MAT in both hemispheres (Table 1, Fig. 2b).

We hypothesized that forest lines would be lower in the southern hemisphere than in the northern hemisphere because of phylogenetic constraints (i.e. lack of Pinaceae species). In

fact, there were no differences in the forest line elevation–temperature relationship. We first pooled both hemispheres into a common multiple regression model in which MAT and STA explained 79% of forest line variability ($P < 0.0001$) (Table 1). As in the previous multiple regressions, the interaction between the two thermal variables was nonsignificant. A hemisphere effect, introduced as a binary variable in the multiple regression model, was also not significant ($P = 0.15$).

We also compared the relationship between MAT and forest line elevation, considering sites with similar STA values in both hemispheres. Because of the narrow range of STA in the southern hemisphere, only northern hemisphere sites with $STA < 15$ K were included in this analysis. Independent regressions of MAT and forest line elevation for each hemisphere did not show significant slope or intercept differences ($P > 0.1$; Fig. 3). Some forest lines in the northern hemisphere were occupied by broad-leaf species of the genera *Betula* and *Fagus* (Appendix 1). These species dominated forest lines of Scotland, western Scandinavia, and the Spanish mountains, which had some of the

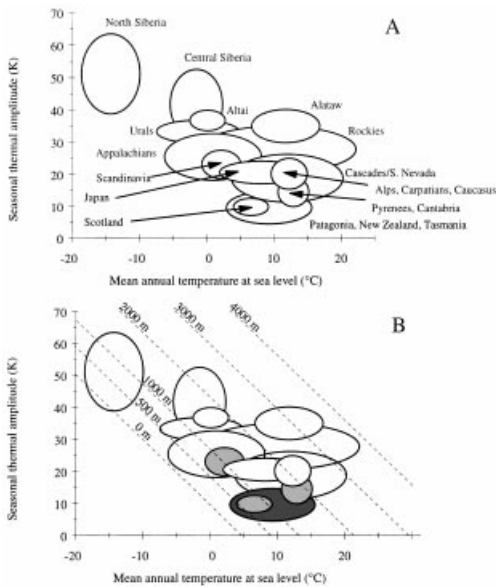


Fig. 2 A) Ranges of mean annual temperature at sea level and seasonal thermal amplitude for the mountain systems and regions covered by this study. Each ellipse indicates a mountain range or region and includes all of its sites. Width and height of the ellipses represent the maximum and minimum values of each region. Some of the mountain ranges are pooled into a single ellipse because of their similarity. Alaska and North-east Asia are not presented because they included few sites with a very large range for both thermal variables (see values in Appendix 1); B) Isolines of forest line elevation based on the multiple regression model for both hemispheres (Table 1). White ellipses indicate regions where all forest line sites are dominated by conifers; grey ellipses, regions where some sites are dominated by broadleaf species and some by conifer species; and black ellipses, regions where all sites are dominated by broadleaf species.

lowest STA values for northern hemisphere sites (Fig. 2a).

Dominant tree life forms were not randomly associated with thermal regimes. Along a gradient of decreasing MAT and increasing seasonality, evergreen broadleaf trees occupied warmer and less seasonal extremes, followed by deciduous broadleaf species, then evergreen conifers, and finally deciduous conifers, which occupied the coldest and most seasonal habitats (Table 2).

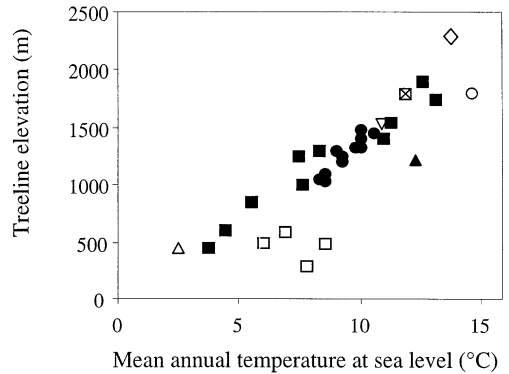


Fig. 3 Forest line elevation as a function of mean annual temperature at sea level for all sites with a seasonal thermal amplitude < 15 K. Forest line elevation values were obtained from the literature review and temperature was calculated using global databases of temperature and elevation. Linear regressions for each hemisphere are significant and their slopes and intercepts are not significantly different ($P > 0.1$). All sites in Patagonia, three sites in Scotland, and the site in Cantabria are occupied by broadleaf deciduous trees. Sites in New Zealand and Tasmania are dominated by broadleaf evergreen forests. All North American sites, the sites in the Pyrenees and the Alps, and one site in Scotland, are dominated by evergreen conifers.

These changes resulted in extremely contrasting winter temperatures, but similar summer temperatures at forest line. The mean temperature of the coldest month at forest line ranged from $-32\text{ }^{\circ}\text{C}$ in deciduous conifer forests to $-1.9\text{ }^{\circ}\text{C}$ in evergreen broadleaf forests; in contrast, mean temperature for the warmest month did not differ between these two vegetation types ($P = 0.06$) and was slightly higher in deciduous broadleaf and evergreen conifer forests (Table 2). Across all sites, the standard deviations of the mean monthly temperature of the coldest and warmest month of the year at the forest line were ± 13.6 and ± 2.8 K, respectively.

Table 2 Temperature regimes for forest line sites according to the life history of the dominant species. Average values of mean annual temperature at sea level (MAT), seasonal thermal amplitude (STA), and mean monthly temperature for the coldest and warmest month at forest line elevation are indicated. Temperature data were extracted from a global database (Leemans & Cramer, 1990). Sea level and forest line temperatures were calculated using a lapse rate of 0.006 K/m (see text). Values between brackets show standard deviations and letters indicate significant differences (*t*-test, $P < 0.05$). The last column indicates the distribution of each species life form

Life Form	MAT (°C)	STA (K)	Cold month (°C)	Warm month (°C)	Distribution
Broadleaf evergreen	10.0 (0.7) ^a	8.8 (0.6) ^a	-1.9 (0.5) ^a	6.8 (0.5) ^a	New Zealand, Tasmania
Broadleaf deciduous	9.2 (3.9) ^a	12.9 (5.0) ^b	-4.3 (4.1) ^b	8.5 (2.2) ^b	Patagonia, Scotland, Spain, Scandinavia
Conifer evergreen	5.9 (9.5) ^b	27.3 (11.3) ^c	-18.0 (11.3) ^c	9.3 (2.3) ^b	Northern hemisphere
Conifer deciduous	-4.0 (8.5) ^c	39.2 (4.9) ^d	-32.3 (6.4) ^d	6.9 (3.6) ^a	North-Central Rockies, Central Asia

Changes in the lapse rate used for forest line temperature calculations had a slight effect on our results. After an extreme change of ± 0.002 K/m in lapse rate, estimated temperatures at the forest line changed on average ± 1.6 K. This was smaller than the standard deviation of the mean temperature of the warmest month. As lapse rates tend to increase from oceanic to continental climates, we could expect mean temperature for the coldest and warmest months in Table 2 to be slightly higher in broadleaf forest lines and lower in conifer forest lines.

DISCUSSION

Our analysis confirmed the effects of mean temperature and seasonality as controls of forest line elevation globally. Previous descriptions of mountain forest lines at regional and global scales identified a strong association between latitudinal gradients of temperature and forest line elevation (Troll, 1973; Oshawa, 1990; Cogbill & White, 1991; Malyshev, 1993), but at the global scale an important part of the variation in cold and temperate zones remained unexplained (Körner, 1998). Several authors pointed to the continentality of climate or seasonal thermal amplitude, as a cause of the elevation–latitude mismatch (Troll, 1973; Wardle, 1974). By considering mean annual temperature and seasonal thermal amplitude explicitly in our analysis, we were

able to explain almost 80% of forest line elevation variation in extratropical regions of the globe (Table 1).

The positive effect of thermal amplitude on forest line elevation indicates that the warm, rather than cold, part of the year determines the limit of tree growth, suggesting that before trees are able to reach zones where lethal winter temperatures kill them they are constrained by the lack of temperatures warm enough for establishment or growth. The global association between forest line elevation and temperature regimes does not provide the ultimate mechanism of temperature control, but our results point to the warm portion of the year as the key for further experimentation. Summer temperature can affect forest lines through its effect on the net fixation of carbon and growth rate of trees (Schulze *et al.*, 1967; Tranquillini, 1979; Häsler, 1982; Stevens & Fox, 1991). It can also affect forest line through more episodic events, such as summer frosts that damage trees when tissues are more sensitive or through exceptionally warm growing seasons that allow tree establishment (Kearny, 1982; Wardle, 1985). Any of these factors individually, or in combination, may be responsible for the global patterns presented here. Körner, (1998) suggested that the reduction of growth rates with temperature is the key mechanism, as opposed to net carbon fixation, because under low temperatures plants stop producing new cells and

differentiating functional tissues before they experience a shortage of photoassimilates. This suggestion is supported by dramatic reductions of growth with increasing elevation in the forest line zone that are not accompanied by similar declines in photosynthetic rates (Tranquillini, 1979; Häslér, 1982; Körner *et al.*, 1986; Körner, 1998). Along elevation gradients, tree communities are limited at lower levels than shrub or forb communities because tree meristems do not benefit from the radiant warming commonly observed in low canopies (Körner 1998).

Our hypothesis that the lack of Pinaceae conifers in the southern hemisphere results in lower forest lines was rejected. Two different comparisons of forest line elevation between hemispheres supported the conclusion that under similar thermal conditions there are no altitudinal differences between the forest lines of the two hemispheres. Several sites in Europe under the same type of oceanic climates that occur in the southern hemisphere had forest lines occupied by broadleaf species, even when Pinaceae species were present in the region (Fig. 3). Forest lines tended to be dominated by broadleaf species, then by evergreen conifers, and finally by deciduous conifers as thermal seasonality increased. This result agrees with the observation that the tundra-taiga ecotone in the arctic is occupied by *Betula* spp. (broadleaf deciduous trees) in the most oceanic portion of the arctic belt (Iceland, Greenland, and western Scandinavia) and by conifers in the rest of the area (Hustich, 1983).

The fact that forest line species have high convergence in their adaptation to thermal constraints has important implications for forestry and conservation of alpine and subalpine systems in the southern hemisphere. At first glance the elevation contrast between forest lines of northern regions, like the Rockies, and the mountain ranges of the southern hemisphere suggests that the introduction of northern hemisphere forest line species into the mountain ranges of Patagonia or New Zealand might raise the forest limit by at least several hundred meters. This is appealing from a forestry perspective because new areas may produce timber, but worrisome from a conservation standpoint because both forest line and alpine communities might be easily invaded by the introduced species. Many forest line conifers of the northern hemisphere have been successfully

introduced to Patagonia and New Zealand at lower elevations (Scott, 1970; Instituto Forestal, 1986; Richardson & Higgins, 1998). However, the results of this work suggest that there is not a wide vacant altitudinal belt for introduced species when thermal seasonality is taken into account.

Across temperate and colder zones of the globe, forest lines had similar summer temperatures but contrasting winter temperatures (Table 2). This pattern agrees with conservative temperature requirements for growth and contrasting tolerances to low temperatures measured among species from continental and oceanic forest lines. Forest line species from both oceanic and continental climates show similar temperature thresholds for growth, which typically fall within the 5–8 °C range (Hellmers *et al.*, 1970; James *et al.*, 1994; see Körner, 1998 for review). On the other hand, species from continental forest lines, such as *Picea engelmannii* or *Pinus pumila*, tolerate extremes of –70 °C, while species from oceanic forest lines, such as *Nothofagus antarctica* or *N. solandri*, only resist temperatures to –22 °C and –17 °C, respectively (Sakai *et al.*, 1981).

The adaptation to grow at low temperatures appears to be the most important biotic factor controlling forest line elevation, and our results suggest convergent adaptations among tree species of different phylogenetic origins. The evidence of convergent evolution exposed by forest line distributions agrees with a general pattern of structural and functional convergence among grassland and shrubland ecosystems with equivalent climates and independent evolutionary histories in South and North America (Puelo *et al.*, 1998). The broad range of tolerance of perennial tissues to experimental low temperatures observed among species from oceanic and continental forest lines indicates a high potential for adaptive adjustment to local minimum winter temperatures. When necessary, tree species are able to tolerate temperatures below –70°, but in areas where these extremes never occur, tolerance is significantly reduced. We propose that the tolerance to absolute minimum temperature rarely operates as a control of tree survival in natural forest line conditions.

The combined effect of MAT and STA helps explain globally why forest lines have relatively constant elevation from subtropical to equatorial regions — increases in MAT towards the equator

are counterbalanced by a dramatic decrease of STA (Oshawa, 1990; Körner, 1998). In North America, Africa, and Asia, STA is more than 16 K at 30 °N, decreases to less than 3 K at 10 °N, stays constant to 10°S, and increases to less than 13 K at 30 °S in South America and Africa (calculated from Leemans & Cramer, 1990; see also Oshawa, 1990). However, the extrapolation of our regression model into the tropics underestimates forest line elevation by ≈ 500 m. Examples are Mt Wilhelm in New Guinea, where predicted and observed elevations are 3400 and 3900 m, respectively (Oshawa, 1990), or central Mexico where these values are 3450 and 4000 m, respectively (Lauer, 1978). Subtropical Andean forest lines dominated by trees of the genus *Polylepis* show even greater differences (Wardle, 1974). Different environmental variables or ways to characterize thermal regimes are probably needed to explain forest line elevation patterns in tropical regions where temperature seasonality is low.

Some important limitations of both the forest line elevation and the temperature datasets used in this work could have contributed to part of the unexplained variation in the regression analysis. Even though we defined forest line as the upper limit of continuous tree canopies, some discrepancies in the often implicit definition of tree (e.g. minimum height) or closed canopy (e.g. minimum area covered by trees) among the references could also have added to this variation. We tried to eliminate errors associated with human disturbance and deforestation by considering observations in which the authors explicitly described the forest line as natural. However, this characterization can be questionable in some mountain ranges of the Old World where deforestation was widespread in the past. In some sites, the presence of krummholz formation above the forest line confirmed a natural elevational limit of forest canopies. As an example, in Scotland krummholz formations are contiguous to the forest line at 600 m at 57 °N, but in warmer mountain ranges at 55.5 °N the forest line is at 500 m and no krummholz zone has been described, suggesting a possible imprint of human activities (see Kelletat, 1972; Grace & Norton, 1990). In addition to these sources of error, some inaccuracies in the temperature data can be expected as a result of the coarse spatial resolution of the climate database and the

fixed lapse rates used in this work. Despite these limitations, the global datasets provide a useful opportunity to identify associations between forest line elevation and thermal regime across a broad range of climates.

The dramatic floristic and physiognomic shifts observed above and below forest lines make them a useful ecotone to study the effects of present and past climate changes on vegetation distribution (e.g. Rochefort *et al.*, 1994). Our global quantification of temperature effects on forest line elevation may help interpretations of past fluctuations of mountain forest lines and prediction of their future position. Although describing global vegetation patterns does not reveal the basic mechanisms that control plant distributions, it is a useful approach to eliminate factors that plot-based studies may be unable to unmask. In this paper, the combination of broad climatic ranges that occur at continental scales and the effect of independent floristic realms, which occur at global scales, showed that annual and seasonal climate are important determinants of montane forest distribution; phylogenetic constraints apparently are not.

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Appendix I List of the forest line sites used in this study. Sites are grouped by mountain system or region. Latitude and longitude are indicated in degrees and decimal fraction, elevation above sea level is indicated in meters. Mean annual temperature at sea level (MAT, degrees C) and seasonal thermal amplitude (STA, K) are shown. The physiognomy or life form of the forest that occupies the forest line (LF) is classified as conifer deciduous (CD), conifer evergreen (CE), broadleaf evergreen (BE), and broadleaf deciduous (BD) according to the dominant species (NA indicates that no species information was available). The three most abundant tree species of each site are indicated, unless the forest is dominated by only one or two species

North America and Europe

Area	Site	Lat (degrees)	Lon (degrees)	Elev (m)	MAT (°C)	STA (K)	LF	Dominant species	Reference
Alaska	Alatna	67.5	-155.0	550	-12.1	40.7	NA	NA	Hermes (1955)
	Mt McKinley	62.5	-150.0	720	0.2	28.3	NA	NA	Hermes (1955)
	St Elias	59.5	-140.0	450	2.5	13.4	NA	NA	Hermes (1955)
	Heines	59.2	-135.8	900	3.0	16.0	CE	<i>Picea sitchensis</i>	Daubenmire (1953)
Central Rockies	Churchill Peak	58.0	-125.0	1500	0.8	33.8	NA	NA	Hermes (1955)
	Jasper	53.1	-120.1	2300	5.6	22.8	CE	NA	Griggs (1938)
	Banff	50.9	-115.2	2250	8.7	23.2	CD	<i>Larix lyallii</i> <i>Abies lasiocarpa</i>	Richards & Bliss (1986)
	Glacier NP	48.9	-113.8	2100	8.4	22.8	CE	<i>Abies lasiocarpa</i> <i>Picea engelmannii</i>	Brown (1994)
	Grand Teton	43.6	-110.9	3300	12.8	24.7	NA	NA	Griggs (1938)
	Niwot Ridge	40.1	-105.6	3406	17.9	26.2	NA	NA	Komarkova & Webber (1978)
	San Juan Mountains	37.5	-108.1	3540	17.5	22.8	CE	<i>Picea engelmannii</i>	Petersen & Mehlinger (1976)
Cascades	Mt Baker	48.8	-121.7	1600	5.2	21.6	CE	<i>Tsuga mertensiana</i>	Heikkinen (1985)
	Mt Olympus	47.8	-123.5	1550	10.9	12.9	NA	NA	Hermes (1955)
	Mt Rainier	46.9	-121.7	2000	10.4	21.7	NA	NA	Griggs (1938)
	Mt Hood	45.3	-121.7	2200	12.6	19.8	NA	NA	Griggs (1938)
Sierra Nevada	Mt Shasta	41.3	-122.1	2600	13.2	23.3	NA	NA	Hermes (1955)
	Yosemite NP	37.9	-119.3	3100	16.8	19.8	CE	<i>Pinus contorta</i> <i>Pinus albicaulis</i>	Parker (1994)
	Sequoia NP	36.5	-118.4	3500	17.5	23.1	CE	<i>Pinus balfouriana</i>	Lloyd & Graumlich (1997)
	Mt Whitney	35.5	-118.2	3550	16.2	20.3	CE	<i>Pinus balfouriana</i>	Scuderi (1987)
Appalachians	San Bernardino Mts	34.1	-116.8	3150	18.4	19.0	CE	<i>Pinus contorta</i> <i>Pinus flexilis</i>	Minnich (1984)
	Gerin	55.0	-68.0	550	-3.2	30.6	CE	<i>Picea mariana</i> <i>Picea glauca</i>	Cogbill & White (1991)
	Menihek	54.7	-68.0	590	-3.2	31.4	CE	<i>Picea mariana</i> <i>Picea glauca</i>	Cogbill & White (1991)
	Mealy	53.6	-58.0	580	0.2	21.8	CE	<i>Picea mariana</i> <i>Picea glauca</i>	Cogbill & White (1991)
	Labrador	53.0	-62.0	780	1.8	28.8	CE	<i>Picea mariana</i> <i>Picea glauca</i>	Cogbill & White (1991)
	Otish	52.2	-71.0	900	-1.1	31.4	CE	<i>Picea mariana</i> <i>Picea glauca</i>	Cogbill & White (1991)
	Groulx	51.6	-68.0	990	-1.3	27.8	CE	<i>Picea mariana</i> <i>Picea glauca</i>	Cogbill & White (1991)
	Shickshock	48.9	-66.5	1160	0.9	25.3	CE	<i>Picea mariana</i> <i>Picea glauca</i>	Cogbill & White (1991)
	Katahdin	45.9	-69.1	1280	5.0	24.1	CE	<i>Picea rubens</i> <i>Abies balsamea</i>	Cogbill & White (1991)
	White	44.3	-71.3	1490	7.5	23.9	CE	<i>Picea rubens</i> <i>Abies balsamea</i>	Cogbill & White (1991)
	Adirondack	44.1	-74.0	1480	6.9	25.2	CE	<i>Picea rubens</i> <i>Abies balsamea</i>	Cogbill & White (1991)

Appendix I *continued.*

Area	Site	Lat (degrees)	Lon (degrees)	Elev (m)	MAT (°C)	STA (K)	LF	Dominant species			Reference
Scandinavia	Mt Noulja	67.0	20.0	650	0.7	26.9	BD	<i>Betula pubescens</i>	<i>Pinus sylvestris</i>		Sveinbjornsson (1983)
	Handolan	63.1	12.5	900	4.3	21.3	BD	<i>Betula pubescens</i>	<i>Pinus sylvestris</i>	<i>Picea abies</i>	Kullman (1983)
	Harjedalen	62.9	12.3	1000	4.2	21.0	BD	<i>Betula pubescens</i>			Kilander (1965)
Scotland	Ben Klikberg	58.3	-4.0	300	7.8	10.0	BD	<i>Betula pubescens</i>			Kelletat (1972)
	Monadliath Mts	57.2	-3.5	600	6.9	10.3	BD	<i>Betula pubescens</i>			Kelletat (1972)
	Ben Nevis	56.8	-5.0	500	6.0	11.2	BD	<i>Betula pubescens</i>	<i>Alnus</i> sp.		Kelletat (1972)
Alps	Southern uplands	55.5	-2.5	500	8.6	11.3	CE	<i>Pinus sylvestris</i>			Kelletat (1972)
	Davos	46.7	10.2	2100	10.5	19.2	CE	<i>Picea abies</i>			Karrasch (1973)
	Tarantaise	45.5	7.0	2100	11.2	20.7	CE	<i>Picea abies</i>	<i>Pinus uncinata</i>		Bravard (1972)
Pyrenees	Glarus	47.0	9.1	1900	10.8	18.0	CE	<i>Pinus cembra</i>	<i>Picea abies</i>		Schimper (1903)
	Mt Ventoux	44.2	5.2	1800	11.6	14.0	CE	<i>Pinus uncinata</i>	<i>Abies alba</i>		Schimper (1903)
	Neouvielle Group	42.6	-1.0	1800	13.0	17.0	BD	<i>Fagus sylvatica</i>			Hollermann (1972)
Cantabria	Mt Perdu	42.5	-0.5	2200	13.0	16.8	CE	<i>Pinus uncinata</i>			Hollermann (1972)
	Sierra Guara	42.4	2.0	2300	13.9	13.3	CE	<i>Pinus uncinata</i>			Hollermann (1972)
	Picos de Europa	43.5	-4.8	1800	14.8	14.0	BD	<i>Betula pendula</i>	<i>Fagus sylvatica</i>		Ern (1966)
Carpathians	West Tatra	49.3	20.0	1730	10.7	19.6	CE	<i>Picea abies</i>	<i>Pinus cembra</i>	<i>Larix decidua</i>	Plesnik (1973)
Caucasus	West Caucasus	43.5	42.5	1900	12.6	23.1	CE	<i>Picea</i> spp.			Zimina (1973)
Urals	Khulga	65.7	59.5	400	-5.2	33.9	CE	<i>Picea obovata</i>	<i>Pinus sibirica</i>	<i>Betula pubescens</i>	Malyshev (1993)
	Chugar	64.0	59.0	600	-3.8	33.2	CE	<i>Picea obovata</i>	<i>Pinus sibirica</i>	<i>Betula pubescens</i>	Malyshev (1993)
	Pavdinsky	59.3	58.5	900	0.2	34.3	CE	<i>Picea obovata</i>	<i>Pinus sibirica</i>	<i>Betula pubescens</i>	Malyshev (1993)
	Taganay	55.9	59.0	1000	2.8	32.1	CE	<i>Picea obovata</i>	<i>Pinus sibirica</i>	<i>Betula pubescens</i>	Malyshev (1993)
	Bolshoy Iremel	54.5	59.0	1300	2.4	32.0	CE	<i>Picea obovata</i>	<i>Pinus sibirica</i>	<i>Betula pubescens</i>	Malyshev (1993)
	Yaman Tow	54.3	59.0	1250	2.8	32.0	CE	<i>Picea obovata</i>	<i>Pinus sibirica</i>	<i>Betula pubescens</i>	Malyshev (1993)
Asia											
Area	Site	Lat (degrees)	Lon (degrees)	Elev (m)	MAT (°C)	STA (K)	LF	Dominant species			Reference
Alataw	Lepsy	45.3	80.7	2400	8.2	35.6	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Kapal	45.1	81.1	2450	8.2	38.0	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Tian Shan	42.5	80.0	2600	13.8	33.4	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
Altai	Chibit	50.4	87.6	2100	-2.2	36.8	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Kuray	50.3	89.5	2240	-1.7	37.9	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Sailugem	50.1	89.0	2200	-2.3	38.8	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Kucherla	50.1	86.2	2280	0.8	39.2	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)

North Siberia	Lena I	71.5	131.0	150	-15.1	42.7	CD	<i>Larix gmelinii</i>	<i>Larix gmelinii</i>	<i>Larix sibirica</i>	Malyshev (1993)
	Bulun	70.6	127.0	195	-14.4	46.1	CD	<i>Larix gmelinii</i>	<i>Larix gmelinii</i>	<i>Larix sibirica</i>	Malyshev (1993)
	Talnakh	69.5	88.4	200	-10.9	40.6	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Kapchuk	69.4	90.9	350	-12.0	40.9	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Imangda	69.1	89.7	325	-11.0	41.0	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Kutaramkan	68.8	92.0	500	-13.2	41.4	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Khantaysoke	68.4	90.8	400	-11.9	41.9	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Khakoma	67.9	97.9	770	-13.9	43.4	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Beldunchana	67.8	95.8	765	-13.9	42.9	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Ende	67.6	91.7	575	-12.9	42.7	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Verkhnee Tembenchi	67.2	94.1	775	-12.2	42.9	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Nyakshingda	67.0	93.6	660	-12.2	42.8	CE	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
	Bytantay	67.0	132.0	1100	-16.9	60.2	CD	<i>Abies sibirica</i>	<i>Picea obovata</i>	<i>Pinus sibirica</i>	Malyshev (1993)
	Sartang	64.9	133.2	1100	-17.3	57.7	CD	<i>Abies sibirica</i>	<i>Picea obovata</i>	<i>Pinus sibirica</i>	Malyshev (1993)
	Lena II	64.5	131.0	1200	-17.2	58.8	CD	<i>Abies sibirica</i>	<i>Picea obovata</i>	<i>Pinus sibirica</i>	Malyshev (1993)
	Suntar	63.0	141.5	1050	-14.8	59.6	CD	<i>Abies sibirica</i>	<i>Picea obovata</i>	<i>Pinus sibirica</i>	Malyshev (1993)
	Central Siberia	Stanovoye	56.0	114.0	1550	-4.1	47.9	CD	<i>Larix gmelinii</i>	<i>Larix gmelinii</i>	<i>Larix sibirica</i>
Baikalsky		54.0	108.0	1500	-2.6	35.7	CD	<i>Larix gmelinii</i>	<i>Larix gmelinii</i>	<i>Larix sibirica</i>	Malyshev (1993)
Tungir		54.0	120.0	1325	-3.8	46.8	CD	<i>Larix gmelinii</i>	<i>Larix gmelinii</i>	<i>Larix sibirica</i>	Malyshev (1993)
East Sayan		52.0	98.0	2100	-2.7	34.7	CD	<i>Larix gmelinii</i>	<i>Larix gmelinii</i>	<i>Larix sibirica</i>	Malyshev (1993)
West Sayan		52.0	88.0	2200	0.4	34.8	CD	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
Kurtushibinsky		52.0	90.0	2000	-0.4	35.2	CD	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
Tsagan Shibetu		50.6	87.0	2200	1.2	37.4	CD	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
Sangilen		50.5	96.5	1900	-1.4	33.8	CD	<i>Larix gmelinii</i>	<i>Larix gmelinii</i>	<i>Larix sibirica</i>	Malyshev (1993)
Mongun Taiga		50.2	87.0	2300	-0.7	38.4	CD	<i>Larix sibirica</i>	<i>Larix gmelinii</i>	<i>Picea shrenkiana</i>	Malyshev (1993)
North-east Asia	Chersky	65.2	161.0	1000	-12.0	40.1	CE	<i>Abies sibirica</i>	<i>Picea obovata</i>	<i>Pinus sibirica</i>	Ohsawa (1990)
	Kamtshatka	55.0	160.0	900	-2.5	22.3	CE	<i>Picea jezoënsis</i>	<i>Betula ermanii</i>	<i>Larix gmelinii</i>	Ohsawa (1990)
	Shikhote Alin	49.0	138.0	1100	-0.4	39.8	CE	<i>Picea jezoënsis</i>	<i>Abies nephrolepis</i>	<i>Betula ermanii</i>	Ohsawa (1990)
	Mount Changbaishan	41.3	128.1	2100	6.6	30.0	CE	<i>Abies spp.</i>	<i>Betula ermanii</i>		Ohsawa (1990)
Japan	Mount Horoshiri	42.7	142.4	1500	4.2	22.7	CE	<i>Picea jezoënsis</i>	<i>Betula ermanii</i>		Ohsawa (1990)
	Mount Hiuchidake	36.6	139.2	2200	12.3	20.7	CE	<i>Abies mariesii</i>	<i>Betula ermanii</i>		Ohsawa (1990)
	Mount Yakushidake	36.0	138.3	2500	12.1	19.9	CE	<i>Abies mariesii</i>	<i>Betula ermanii</i>		Ohsawa (1990)
	Mount Fuji	35.1	138.4	2850	12.4	19.0	CE	<i>Abies veitchii</i>	<i>Betula ermanii</i>		Ohsawa (1990)

Appendix I *continued.*

South America and Oceania

Area	Site	Lat (degrees)	Lon (degrees)	Elev (m)	MAT (°C)	STA (K)	LF	Dominant species	Reference
Patagonian Andes	Hermite Island	-56.8	-67.7	450	3.7	6.7	BD	<i>Nothofagus pumilio</i>	Hueck (1966)
	Ushuaia	-54.8	-68.0	600	4.4	6.7	BD	<i>Nothofagus pumilio</i>	Tuhkanen (1990)
	Lago Argentino	-50.0	-73.0	850	5.5	10.6	BD	<i>Nothofagus pumilio</i>	Dimitri (1972)
	Lago Belgrano	-47.8	-72.0	1000	8.1	11.1	BD	<i>Nothofagus pumilio</i>	Dimitri (1972)
	Lago La Plata	-45.5	-71.5	1300	8.3	11.0	BD	<i>Nothofagus pumilio</i>	Observation by the authors
	Puerto Aysen	-45.3	-72.7	1250	7.5	10.0	BD	<i>Nothofagus pumilio</i>	Observation by the authors
	El Bolsón	-42.0	-72.0	1400	10.4	11.8	BD	<i>Nothofagus pumilio</i>	Dimitri (1972)
	Bariloche	-41.0	-72.0	1550	11.3	11.8	BD	<i>Nothofagus pumilio</i>	Dimitri (1972)
	Lanin	-39.5	-71.3	1750	13.1	13.1	BD	<i>Nothofagus pumilio</i>	Dimitri (1972)
	Bio-Bio river sources	-38.3	-71.7	1900	12.6	13.4	BD	<i>Nothofagus pumilio</i>	Hueck (1966)
Tasmania	Mount Field	-42.4	146.5	1220	12.3	7.3	BE	<i>Nothofagus cunninghamii</i> <i>Eucalyptus coccifera</i>	Ogden & Powell (1979)
New Zealand	Eglington	-45.0	168.0	1040	8.5	8.7	BE	<i>Nothofagus menziesii</i>	Wardle & Coleman (1992)
	Hollyford	-44.7	168.3	1100	8.5	8.8	BE	<i>Nothofagus menziesii</i>	Wardle & Coleman (1992)
	Mataketake	-43.8	169.5	1050	8.3	9.0	BE	<i>Nothofagus menziesii</i>	Wardle & Coleman (1992)
	Andrews	-43.2	172.5	1450	10.6	8.0	BE	<i>Nothofagus solandri</i>	Wardle & Coleman (1992)
	Avalanche	-43.2	171.7	1320	9.8	8.9	BE	<i>Nothofagus solandri</i>	Wardle & Coleman (1992)
	Libretto	-42.3	172.7	1330	10.1	8.3	BE	<i>Nothofagus solandri</i>	Wardle & Coleman (1992)
	Croesus Tk	-42.1	171.6	1200	9.3	9.7	BE	<i>Nothofagus menziesii</i>	Wardle & Coleman (1992)
	Rahu	-42.1	172.1	1250	9.3	9.1	BE	<i>Nothofagus menziesii</i>	Wardle & Coleman (1992)
	St Arnaud W	-41.8	172.9	1480	10.1	7.7	BE	<i>Nothofagus solandri</i>	Wardle & Coleman (1992)
	St Arnaud E	-41.8	172.6	1400	10.1	8.5	BE	<i>Nothofagus solandri</i>	Wardle & Coleman (1992)
	Mt Arthur	-41.3	171.7	1300	9.0	9.8	BE	<i>Nothofagus menziesii</i>	Wardle & Coleman (1992)