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New Zealand Forest to Alpine Transitions in Global Context

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Abstract

New Zealand high-altitude tree limits are formed either abruptly by evergreen *Nothofagus* or by low forest of more frost-tolerant small trees reaching similar maximum altitudes. Whereas most tree limits are contiguous with low-growing alpine vegetation, in New Zealand a belt dominated by tussock grasses intervenes that is vulnerable to invasion by hardy introduced trees and seems ecologically equivalent to fire-maintained high-altitude tropical grasslands. New Zealand tree limits coincide with warmer growing-season temperatures than other tree limits, including deciduous *Nothofagus* in the southern Andes. They also correlate with coldest-month mean temperatures around 0°C, in accordance with the limits of broadleaved evergreen trees globally, unlike north temperate subalpine trees that withstand extreme winter cold. Adverse environments lead to krummholz that in temperate regions can form an attenuated belt above the forest limit, but in New Zealand *Nothofagus* krummholz develops only at or below the forest limit, in accordance with absence of *Nothofagus* seedlings beyond a few meters above the forest limit. The relatively low altitudes attained by New Zealand trees are related to isolation and the recent uplift of high mountains, and the differentiation between *Nothofagus* forest and low forest reflects historical and geological events.

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Introduction

Transitions from forest to alpine vegetation on tropical and southern hemisphere mountains are less extensive but floristically more diverse than on northern hemisphere mountains. Among these, New Zealand transitions are the most taxonomically and physiognomically complex and second only to Andean transitions in extent. Separated by 2000 km of ocean from those of Australia, they are among the most isolated, and situated on mountains that began to rise only in the late Pliocene, they are among the most recent in origin. They also have been little affected by human activities, except where destroyed by fire on rain-shadow mountains. In this review I compare the New Zealand situation with others, in respect of taxonomy, physiognomy, ecological dynamics, and limiting environmental factors.

Several components of the forest-alpine transition are considered. *Tree limit* can comprise trees isolated above the *forest limit* or coincide with the latter; cf. *alpine treeline* defined by Körner and Paulsen (2004) as "the connecting line between the uppermost forest patches in an area, with trees upright and at least 3 m in height and growing in groups." The transition often also includes *krummholz*, i.e. trees stunted or deformed by environmental stress. Genetically dwarf forms, in which the most rapid growth occurs in peripheral stems instead of being concentrated in tall, vulnerable, leading shoots, are referred as to *shrubs*. *Inverted forest limits* are formed against treeless valley floors. Limiting altitudes cited refer to the highest elevations reached regionally rather than average positions that are likely to be lower because of local environmental irregularities or disturbances. I refer to the dormant season as *winter*, and to aspects as *sunlit* and *shaded*.

Description of New Zealand Forest-Alpine Transitions

SUBALPINE NOTHOFAGUS FOREST

Most New Zealand tree limits coincide with a forest limit of two *Nothofagus* species with evergreen, broad, coriaceous leaves scarcely 1 cm long. *N. menziesii* usually dominates where annual precipitation exceeds 2000 mm and *N. solandri* var. *cliffortioides* on drier mountains or shallower soils (Wardle, 1991). Altitudes attained on coastal mountains range from 1400 m at lat. 38°S to 900 m at lat. 46°S but are 200–300 m higher in summer-warm inland districts where, at lat. 42°S, they can exceed 1500 m. Locally, altitudes are highest on steep, convex slopes regardless of aspect, but average lower on shaded aspects. The forest is typically close-canopied and composed single-stemmed, erect trees, though the upper fringe can consist of multi-stemmed trees with procumbent lower trunks that can root adventitiously (Norton and Schoenenberger, 1984). At or below the forest limit, *Nothofagus* can be reduced to krummholz on wind-exposed sites and shallow soils. Where snow accumulates in the forest margin, krummholz develops through tipping of trunks and bending and breaking of branches; stems exposed above the snow pack are likely to die back during winter. Shrubs, especially *Coprosma* species, occupy gaps, and outliers of the grassland that predominates above the forest limit can occupy gentle slopes and benches.

Nothofagus limits dip sharply into gullies (Fig. 1), and *Nothofagus* does not enter U-shaped valley heads, except for short distances on mid-slopes. *Nothofagus* also forms inverted forest limits against flat valley floors, especially on recent soils. Finally, large areas completely lack *Nothofagus*, most notably west of the Southern Alps over a distance of >200 km centered on lat. 43°S and in contiguous headwaters of east-flowing rivers; other significant gaps are the dormant volcano Mount Taranaki (39°18′S), mountains on either side of the Manawatu Gorge (40°S), and Stewart Island (47°S).

SUBALPINE LOW FOREST

Where *Nothofagus* is absent, mid slopes support tall forest with *Podocarpus*, *Libocedrus*, *Weinmannia*, *Metrosideros*, etc. At

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FIGURE 1. Sharp forest limit of *Nothofagus menziesii*, rising highest on a convex slope. Above, and towards the foreground, smaller trees and shrubs grade into tall grassland. Mataketake Range, 43°49′S, 169°17′E. Photo by Janet Wilmshurst.

its upper limits, which are 150–200 m below tree limit, this gives way to shorter, often very dense woody vegetation. Thirteen species become trees over 3 m tall on sheltered sites, but on wind-exposed sites and shallow, infertile soils, they become reduced to shrub stature, without dieback occurring. *Dracophyllum longifolium* (Epacrideae) has needle-like leaves, *D. traversii* and *D. fiordense* have strap-like glabrous leaves up to 60 cm long, *Olearia* species (Astereae) have leathery leaves with dorsal tomentum, and *Pseudopanax colensoi* (Araliaceae) leaves are broad and mesomorphic. Podocarpaceae includes the needle-leaved *Podocarpus hallii* × *P. nivalis*, *Phyllocladus alpinus* which has broad cladodes, and the cupressoid *Halocarpus biformis*, which ranges from single-stemmed trees to low, layering colonies. *Hoheria* species (Malvaceae) are fast-growing, dominate on recent or rejuvenated soils and, exceptionally for the New Zealand flora, have soft, deciduous leaves (Haase, 1987). The composition of low forest on drier mountains differs from that on the wetter, cloudier mountains where it is most extensive; for example, *Hoheria lyallii* and *Halocarpus bidwillii* replace *Hoheria glabrata* and *Halocarpus biformis*, respectively, and *Phyllocladus alpinus* is widely dominant.

Shrubs 1–2 m tall fill gaps or contribute to the canopy where this is lower, the most abundant being *Dracophyllum uniflorum* and *Coprosma* spp. generally, *Hebe* spp. where there has been disturbance, *Olearia colensoi* and *Brachyglottis buchananii* in wet, cloudy localities, and *Podocarpus nivalis* on drier mountains. The stems of these shrubs are typically layering and directed downhill, and accommodate pressures from deep or sliding snow and soil movement. *Leptospermum scoparium* and, on drier mountains, *Discaria toumatou* can be small trees at low altitudes, but reach tree limit only as layering shrubs.

The tree species reach altitudinal limits equivalent to those reached by *Nothofagus* but maintain them overall across the slopes of both V- and U-shaped valleys. However, their course is irregular

FIGURE 2. In same locality as Figure 1, showing *Nothofagus menziesii* forest bordered by small trees of *Dracophyllum longifolium* and *Olearia lacunosa*, grading into *Dracophyllum* shrubs, *Chionochloa* grass tussocks, and *Phormium cookianum* in the foreground. Photo by Janet Wilmshurst.

in detail, because gentle slopes with deeper, less rocky soil favor grasses and herbs rather than small trees and large shrubs. Subalpine low forest can also form a narrow belt above *Nothofagus* forest (Fig. 2) and extend to valley floors. Its component species occur sparsely within high-altitude *Nothofagus* forest and share the canopy with *Nothofagus* where the latter is reduced to krummholz, especially on gentle slopes with shallow, leached soils.

VEGETATION ABOVE TREE LIMIT

Above the general tree limit, *Phyllocladus alpinus* and *Olearia colensoi* can extend 50 m higher as low-growing, layering colonies on sheltered slopes, while *Dracophyllum longifolium*, *Olearia ilicifolia*, and *Hoheria glabrata* occur as individuals stunted through dieback. Shrubs, especially *Dracophyllum uniforum, Podocarpus nivalis,* and species of *Brachyglottis, Coprosma*, and *Hebe* ascend nearly 300 m above tree limit, becoming increasingly restricted to sunlit spurs. However, most of the belt above tree limit is occupied by grassland, mainly of tall *Chionochloa* tussocks accompanied by large herbs. In the northwest of the South Island, dense swards of *C. australis* also extend widely. Hardy north-temperate trees can be readily established in this belt, with *Pinus contorta*, *P. mugo*, and *Alnus viridis* now spreading from seed (personal observation).

These grasslands extend below tree limit in gullies subject to avalanche, wetness, or drainage of cold night air, and often link with grasslands below inverted forest limits. At their upper limits they grade into low-growing, patchy vegetation of graminoid and mat-forming plants, similar in appearance to alpine vegetation in other parts of the world.

Comparison with Other Forest-Alpine Transitions

Southern Andean tree limits are formed almost entirely of *Nothofagus*, but whereas all New Zealand *Nothofagus* species are evergreen, the high-altitude Andean species are the deciduous *N. pumilio* and *N. antarctica* (Donoso, 1996; Wardle, 1998). *N. pumilio* can reach its altitudinal limit as trees, but more often forest gives way abruptly to extensive krummholz of *N. pumilio* and/or *N. antarctica* with irregular upper limits. *N. pumilio* krummholz mainly results through stems being bent and broken by snow pressure, which becomes increasingly damaging as diameter growth diminishes with increasing altitude (Barrera et al., 2000), although dieback can be evident towards its upper limit (personal observation).

Shrubby *N. antarctica* can occupy valley floors below an inverted forest limit of *N. pumilio*, and above the western fiords forms a wide belt above forest of the evergreen *N. betuloides*. Just as New Zealand *Nothofagus* limits are about the same as those of smaller trees, the upper limit of Andean evergreen *Nothofagus* approximately coincides with those of the small evergreen trees *Drimys winteri*, *Maytenus magellanicus*, and *Embothrium coccineum*. Between 37°30′ and 40°S, *Araucaria araucana* forms an overstorey above deciduous and evergreen *Nothofagus* and even at the upper limit of *Nothofagus* krummholz is an erect tree up to 7 m tall; it is the only subalpine representative of its family, which includes *Agathis australis* in New Zealand.

In Tasmania, the mountains have subdued topography with severe exposure, resulting in expanses of low forest, moorland, and fellfield, with patches of taller forest in sheltered places. *Nothofagus* is represented by *N. gunnii* which is a small deciduous tree or shrub with far-extending branches, *Podocarpus lawrencei* is similar to *P. nivalis,* and the Asteraceae and Epacrideae share some genera with New Zealand. Other tree and shrub genera include *Eucalyptus*, the podocarps *Microstrobus* and *Microcacrys*, the cypress *Diselma*, *Athrotaxis* (Taxodiaceae) and several Proteaceae; none of these genera are now native to New Zealand though most are represented as Tertiary fossils (e.g. Macphail et al., 1993). On the southeastern mountains of the Australian continent, *Eucalyptus pauciflora* forms a well-defined forest limit, and on frosty plains there are inverted forest limits and eucalypt parklands.

The uppermost continuous forest in the tropics, aptly known as cloud forest, shares some genera with New Zealand mountain forests, notably *Weinmannia* and *Podocarpus* in the Andes, *Podocarpus* in New Guinea and East Africa, and *Metrosideros* in Hawaii. Tussock grasslands extend above cloud forest, except in Hawaii where skeletal volcanic soils prevail, and also occupy valley floors below inverted forest limits. In East Africa and the northern Andean páramo, the grasslands include "megaphytes" with rosettes of large, persistent leaves. Most are giant herbs but *Dendrosenecio keniodendron* in East Africa and some *Espeletia* species in the Andes are fire-tolerant small trees with thick, unbranched trunks. *Cyathea* tree ferns play a similar role in New Guinea.

Polylepis forest within the páramo (Lægaard, 1992; Bendix and Rafiqpoor, 2001), and the highest altitude forest of *Dacrycarpus compactus* and small dicotyledonous trees in Papua-New Guinea (Wade and McVean, 1969; personal observation) occur mainly as patches that escape fires in the surrounding grassland. On East African mountains *Erica* shrubland ascends as high as tussock grassland and megaphytes, and in the absence of fire develops into forest (Miehe and Miehe, 1994).

Tropical high-altitude grasslands have been compared with *Chionochloa* grassland in New Zealand, both being characterized by tussock grasses and large perennial herbs (Mark et al., 2000). They differ, however, in that *Chionochloa* grassland extends some 300 m above the limits of native trees, whereas the tropical grasslands contain forest patches and arborescent megaphytes.

The woody component of north temperate forest-alpine transitions shares no genera with New Zealand, and the tall, narrow crowns of *Abies* and *Picea* present a very different aspect. There are parallels, however, in that severe environments lead to krummholz forms, and in that gaps in the distribution of the predominant trees (i.e., Pinaceae) are filled by trees of different physiognomy, for instance *Betula* in Scandinavia. In contrast to New Zealand, where shrubs below the tree limit experience relatively mild winters, intermittent snow cover and generally little damage, evergreen shrubs at northern continental tree limits either depend on protection by winter snow, with stems extending above this being subject to dieback (Larcher and Siegwolf, 1985) or, like *Pinus pumila*, tolerate extreme cold even without snow cover (Sakai et al., 1981; Okitsu and Ito, 1984).

Ecological Dynamics in the Forest-Alpine Transition

FLOWERING, FRUITING, AND GERMINATION

Wind pollination prevails in *Nothofagus*, *Coprosma,* podocarps, and grasses, whereas most dominants of subalpine low forest are insect pollinated. Only *Phormium cookianum* displays the bird pollination mode evident in tropical transitions. Seed dispersal is via small fleshy fruit in podocarps, *Coprosma*, and understorey Ericaceae, and via hooked fruit in the herbaceous *Acaena* and *Uncinia*, but the prevalent mode, as in other temperate forest-alpine transitions, is via small, wind-dispersed propagules. The nuts of subalpine *Nothofagus*, weighing ca. 3.5 mg, recall those of *Betula* and *Alnus* rather than the much larger nuts of Fagacaeae.

Synchronized flowering and fruiting in one summer, separated by summers with little or none, are frequent in the New Zealand flora, and result from initiation of floral primordia during a preceding summer with anomalously high temperatures (Schauber et al., 2002). The phenomenon is especially evident in the forest-alpine transition (personal observation) and involves *Nothofagus*, *Dracophyllum traversii*, *Olearia colensoi*, large, long-living herbs (*Phormium cookianum* and species of *Aciphylla, Celmisia*, and *Astelia*), and *Chionochloa* grasses. For *Chionochloa* at least, mass fruiting appears to achieve satiation of seed predators (Kelly et al., 2000).

Germination in subalpine *Nothofagus* is practically confined to the early summer following autumn seed fall. Compared with those of subalpine north temperate conifers, especially *Pinus* spp., *Nothofagus* seedlings are small and initially slow-growing, with weakly developed tap roots (Wardle, 1991). Seedlings of other woody species of New Zealand forest-alpine transitions, like those of subalpine *Eucalyptus* species, are as small or smaller.

REGENERATION

New Zealand *Nothofagus* species generally regenerate through release of suppressed seedlings in gaps, which can be large as a result of wind-throw or "cohort senescence" triggered by pathogens (Wardle, 1984). Towards the forest limit, regeneration through seedlings can be less important than production of multiple stems from procumbent limbs of established trees (Cullen et al., 2001). *Hoheria* spp. and *Olearia ilicifolia* regenerate mainly on bare ground exposed by erosion, especially in gullies. Stems of the former may live only 150 years but are renewed by basal coppicing (Haase, 1987). Seedlings of other dominants of low forest and associated shrubs appear in gaps (e.g. Haase, 1986), but renewal through layering of lower branches also occurs, especially in the podocarps.

AVALANCHES AND LANDSLIDES

Subalpine *Nothofagus* forests are subject to severe damage by gales and heavy snow falls except, paradoxically, towards the forest limits where trees develop more resistant architectures. Along the sides of avalanche tracks, strips of multi-stemmed trees with procumbent trunks develop. Where massive avalanches, recurring at intervals of several decades, have destroyed forest, resulting herbaceous and shrubby vegetation is slowly reoccupied by *Nothofagus*. Various shrubs and small trees are more tolerant of avalanches, notably *Phyllocladus alpinus* and *Podocarpus nivalis* because of their flexible, layering stems, and *Hoheria* spp. because of their coppicing ability. Zonations are comparable to those on north temperate mountains where forest grades, through snow-induced krummholz, to plants more tolerant of avalanches, especially *Alnus* and *Salix* species.

Landslides resulting from floods and earthquakes result in massive destruction of forest, and *Nothofagus* is among the early pioneers on resulting mineral surfaces (Mark et al., 1964; Rose, 1985). Extensive rock fields and mobile screes extending far below the forest limit remain almost devoid of vegetation.

EFFECT OF INTRODUCED MAMMALS

Among regions with high-altitude tree limits, only New Zealand and Hawaii have no native mammalian herbivores. Their impacts on native vegetation since their introduction after European settlement in the 19th century have been extensively documented. *Nothofagus* species are not highly palatable, although if herbivores were to remain concentrated beyond the life span of existing canopy trees, collapse of the upper forest could be expected (Wardle, 1984). *Nothofagus* regeneration is also influenced indirectly, through depletion of competing shrubs and herbs. Deer (*Cervus* spp.) are the main herbivores, and areas of dead *Olearia colensoi* have also been tentatively attributed to their browsing (Wardle et al., 1971), but since the 1960s deer numbers have been greatly reduced. Thar (*Hemitragus jemlahicus*) can reduce *Dracophyllum uniflorum* scrub and *Chionochloa* grassland to browse-resistant turf (personal observation). Tree limit vegetation is largely inaccessible to domestic sheep, but feral goats (*Capra hircus*) can be damaging locally. Hares (*Lepus europeus*) browse widely in the transition and occasionally ring-bark *Nothofagus* saplings.

INFLUENCE OF FIRE

Sporadic forest fires occurred throughout the Holocene on mountains east of the South Island Main Divide, which are subject to drying föhn winds and annual rainfall under 2000 mm, and also accompanied eruptions on the North Island Volcanic Plateau. Nevertheless, they were too infrequent for significant fire resistance or tolerance to have evolved among New Zealand subalpine trees, thereby contrasting with the ability of *Eucalyptus* spp. and *Nothofagus antarctica* (Burns, 1993) to recover through coppicing. Nor does the flora include trees that rapidly colonize burnt areas, such as *Pinus contorta* in western North America.

Maori from Polynesia arrived in these hitherto uninhabited islands about A.D. 1300. Evidence from soil charcoal, durable *Podocarpus* logs, and palynology show a huge increase in frequency of fires after this, so that predominantly forested eastern landscapes were reduced to grass-, fern-, and shrubland (McGlone and Moar, 1998; Wardle, 2001). Fires since European settlement began in the 1840s reburned and extended this fire-induced vegetation, though remnants of *Nothofagus* forest including intact forest limits survive, especially in the heads of valleys. Low forest and scrub are more vulnerable because of their content of flammable species, especially grasses, podocarps, and *Dracophyllum*, so that remnants survive mainly among rock outcrops and boulder fields.

In the wetter districts, most low forest remains intact, and fires seldom affect the uppermost *Nothofagus* forest. However, in 1890 a fire traveled 9 km through Arthur's Pass (42°55′S on the Main Divide), burning low forest and *Chionochloa* grassland on the floor and adjacent slopes of the pass and extending into *Nothofagus solandri* forest that extends down-valley to the east. Notes and photographs taken in 1897–1898 and transects set up in 1931–1934 and remeasured in 1965–1966 (Calder and Wardle, 1969) and 2001 (Wardle et al., unpublished) have yielded information about resulting successions. Within the first decade, there was regrowth from burned tussocks of *Chionochloa*, *Phormium*, and *Astelia,* and seedlings of woody plants began to appear, mainly of light-demanding, short-lived *Hebe* species, but also including the original dominants. Despite their early appearance, *Dracophyllum* spp. and subalpine podocarps are recovering their original status only slowly, in accordance with their slow growth rates. By 2001, low forest had recovered its original composition though not its original stature, and young *Nothofagus* trees have reestablished the original *Nothofagus* forest margin.

TABLE 1

Temperatures at representative New Zealand tree limits, extrapolated from mean monthly temperatures at the nearest climate stations (New Zealand Meteorological Service, 1983) using a lapse rate of 0.6°C per 100 m. "Growing season" comprises the five months November to March.

Latitude (S)	Altitude (m a.s.l.)	Mean of warmest month (°C)	Mean of coldest month (°C)	"Growing-season" mean (°C)	Tree limit species
39°18′	1460	10.3	0.4	8.6	*Nothofagus solandri*
40°52′	1220	10.3	0.9	9.2	*Nothofagus menziesii*
41°03′	1440*	10.1	−0.6	8.6	*Nothofagus solandri*
41°50′	1450*	9.9	−1.8	8.4	*Nothofagus solandri*
43°07′	1440*	10.6	−1.2	8.8	*Nothofagus solandri*
43°49′	1120	8.2	0.7	6.9	*Nothofagus menziesii*
45°25′	1130*	9.1	−1.3	6.7	*N. solandri* + *N. menziesii*
52°33′	180	8.3	3.7	7.6	*Dracophyllum longifolium*

* Station in inland valley.

This succession can be extrapolated to older and/or more extensive fires: first weedy pioneers, that today include exotic species such as *Rumex acetosella* and *Hypochoeris radicata*; then grassland, that may have its existence prolonged by further fires; then shrubs, and below the original tree limit, return of subalpine trees. The full succession is likely to take hundreds of years, depending on how completely the original vegetation was destroyed.

Where high-altitude *Nothofagus* forest has been supplanted by fire-induced grassland, shrubland, or low forest, it recovers mainly by slow invasion from forest margins, where *Nothofagus* canopies, by extending over and suppressing competing vegetation, provide a zone in which *Nothofagus* seedlings establish. Occasional *Nothofagus* seedlings become established at greater distances, providing nuclei for further spread. Again, the return of *Nothofagus* forest has been so slow that it has scarcely obscured burn patterns established up to 700 years ago (Wardle, 2001).

RESPONSES TO CLIMATIC WARMING?

Transects in the Southern Alps indicated that seedlings and saplings had become established, though usually sparsely, to some 7–9 m beyond the *Nothofagus* forest limit during the 60 years preceding 1990 (Wardle and Coleman, 1992). Favored sites for establishment were small patches of bare ground or moss with less competition from herbs and shrubs. Permanent transects set up in 1991–1993 and remeasured 11 years later revealed few losses among previously established plants and continuing recruitment. This suggests a continuing trend, as opposed to gains cancelled by losses (Wardle et al., 2005). However, the distances to which seedlings and saplings have established beyond the forest edge represent a far smaller rise of the forest limit than would be expected from commonly cited figures for global warming, i.e. 0.6–1.0°C over the last 100 years. Perhaps seedlings are establishing above the forest edge only where there is adequate seed fall and the prospect of immediate ectomycorrhizal infection from the far-spreading roots of marginal trees. Alternatively, the existing forest limit may have been established during a preceding warmer period and maintained by positive feedback (Wilson and Agnew, 1992). At best, however, the evidence for a temperature-driven rise in *Nothofagus* tree limits remains equivocal (Cullen et al., 2001).

On Campbell Island (52°33′S), *Dracophyllum longifolium* has increased its extent and density since the 1850s but not its altitudinal limits. Though the changes have been attributed to climatic warming, successions after fire provide a more immediate explanation (Bestic et al., 2005). In the southern Andes, records of *Nothofagus* seedlings above forest margins (Wardle, 1998) are perhaps related to increases in radial growth that have been correlated with climatic warming (Villalba et al., 1997). At north temperate tree limits, both modest and large advances have been reported (reviewed in Grace et al., 2002).

Temperatures and Forest-Alpine Transitions

Global comparisons between altitudes of tree limits and climate are usually expressed in terms of mean temperatures. These presumably integrate real climatic variables acting on individual trees through their life span, which is up to 360 years for *Nothofagus solandri* var. *cliffortioides* (Wardle, 1984), 600 years for *N. menziesii* and *Dracophyllum traversii* (Haase, 1986), 1000 years for *Halocarpus biformis* (Wardle, 1991), and potential immortality where renewal is by layering or coppicing.

Where *Nothofagus* forest limits reach maximum altitudes on convex slopes in New Zealand they are so regular and sharp that they must lie close to their potential temperature limit; factors such as increased UV and lower atmospheric pressures are unlikely to be important, as the altitudes are so much lower than the 4000–5000 m altitudes that trees attain in the tropics and on north temperate continents.

GROWING-SEASON TEMPERATURES

Worldwide, including New Zealand (Zotov, 1938), correlations with mean temperatures around 10°C for the warmest month are often claimed, but the relationship is more complex. Around the western Pacific, warmest-month means at forest limits range from 13.9°C at lat. 43°30′N to 6.2°C at 5°45′S (Ohsawa, 1990). Averaging over the whole growing season gives a narrower range, between 7.0 and 5.7°C (Körner, 1998). Table 1 indicates that growing-season means in New Zealand are generally above those of most temperate regions, while confirming warmest-month means around 10°C. Lower temperatures in the south are probably compensated by longer summer days.

Climate stations in the southern Andes and in New Zealand at comparable latitudes, altitudes, and distances from the Pacific Ocean show remarkably similar seasonal temperature ranges but the Andean stations are generally cooler. Despite this, *Nothofagus* limits are about 250 m higher in the Andes than in New Zealand. Consequently, warmest-month and growing-season temperatures at *Nothofagus* limits are 2–3°C lower than in New Zealand (Tuhkanen, 1993; Wardle, 1998). This indicates that *Chionochloa* grasslands above New Zealand forest limits substitute for the belt of deciduous *Nothofagus* forest and krummholz in the southern Andes (Wardle, 1998; Mark et al., 2001).

Körner and Paulsen (2004) measured soil temperatures at 0.1 m depth beneath forest canopies, having demonstrated that they are linearly related to mean temperatures at tree canopy height. They found that altitudes of treeline (see **Introduction**) correlate with mean soil temperatures around 6.7°C over the growing season, defined as the period with soil temperatures >3.2°C . Temperatures at New Zealand and Andean treelines, however, averaged 9.5 and 8.9°C, respectively, i.e. they are anomalously high in *both* regions, in contrast to Wardle's (1998) estimates based on the highest limits of *Nothofagus* whether of krummholz or trees. These results are provisional, as Körner and Paulsen sampled only three localities, and Wardle extrapolated from lower-altitude climate stations, although the margin of error should be small where climate stations are near tree limit, as in southern Patagonia and two New Zealand localities.

Jobbágy and Jackson (2000), extrapolating from a global climatic database, estimated warmest-month temperatures at New Zealand forest limits of only 6.8°C, which are *lower* than those for most other regions. However, their data do not accord with the many long temperature records from New Zealand stations.

WINTER TEMPERATURES

Coldest-month mean temperatures at forest limits around the western Pacific range from −17.9°C at lat. 43°30′N to 5.4°C at 5°45′S; since broadleaved evergreen trees are limited by a coldest-month mean of −1°C, they cannot reach the forest limit in northern latitudes, but do so in the tropics (Ohsawa, 1990). Similar coldest-month means also limit broadleaved evergreen species in Europe (Iversen, 1944). With the exception of extremely oceanic Campbell Island, coldest-month mean temperatures extrapolated to New Zealand tree limits (Table 1) are between −2 and 1°C, although those below 0°C may reflect inversions in inland valleys that are not experienced at tree limit.

LEAF AND SOIL TEMPERATURES

In the open, foliage near the ground and soils attain temperatures far above ambient air temperatures, especially during sunny weather, and at night can be colder than air temperatures, especially during calm weather. However, *Nothofagus* seedlings seem unable to exploit the warmth because of sensitivity to frost and/or photoinhibition.

Tree foliage departs much less from air temperature because of less convection of heat from the ground, greater air movement, and generally small leaves (Wilson et al., 1987). In *Espeletia* (Meinzer and Goldstein, 1985) and *Dendrosenecio* (Schulze et al.,1985), thick tomentum increases the boundary layer, allowing leaf temperatures to rise well above ambient temperature. Their large leaves and parabolic leaf rosettes should also enhance temperature gain. They may be compared with *Olearia colensoi* on the wetter, cloudier mountains of New Zealand. Its leathery leaves are glossy above and tomentose beneath, in rosettes about 0.2 m across that form a hemispheric canopy. Leaf temperatures 11°C above air temperature were recorded under calm, sunny conditions (Wardle, 1991).

In New Zealand, as elsewhere, wet soils, persisting snow, avalanches, and shading by surrounding topography depress forest limits locally, to the advantage of herbs and shrubs. Presumably, low soil temperatures accompany such conditions, but if they inhibit tree growth as indicated by Körner and Hoch (2006), it is perhaps through interfering with hydraulic conductance towards tree canopies, as inhibition of root growth should affect herbs, shrubs, and trees alike.

Ecophysiology of Tree Limit

CARBON ASSIMILATION

Daubenmire (1954) suggested that the upward extension of trees might be limited by a need to fix more carbon than shrubs and herbs. While carbon balance may set the upper limits of *Pinus longaeva* in California (Schulze et al., 1967) and *Espeletia neriifolia* in Venezuela (Cavieres et al., 2000), most results indicate that carbon assimilation exceeds the requirements of growth and survival at tree limit (Tranquillini, 1979; Hoch and Körner, 2003; Rada et al., 1996; Velez et al., 1998). In New Zealand *Nothofagus* at tree limit, biomass increments of 18 t ha^{-1} a^{-1} are achieved (Benecke and Nordmeyer, 1982), widths of annual growth rings show no significant decrease compared with lower altitudes (Norton, 1985), and diameter and terminal growth rates are at least 10 times greater than in *Halocarpus* (Wardle, 1991), suggesting that carbon balance is not critical, at least in *Nothofagus*.

Körner (1998) proposed that, globally, tree limits are set by the ability to turn assimilated carbon gain into growth; and that below about 3°C growth does not occur. However, New Zealand tree limits do not reach this global threshold.

LOW-TEMPERATURE TOLERANCES

Nothofagus solandri buds from the forest limit tolerate ca. −15°C in winter, whereas *Phyllocladus alpinus*, *Podocarpus nivalis*, and *Halocarpus bidwillii* tolerate about −20, −22, and −25°C, respectively (Sakai et al., 1981). The difference between the tolerances of *Nothofagus* and the three podocarps accords with their distribution in relation to patterns of cold air drainage. Cold tolerances of −22 and −18°C were measured in *Nothofagus antarctica* and *N. pumilio*, respectively, near their altitudinal limits, whereas that of *N. betuloides* was −15°C, the same as *N. solandri*. This is consistent with the limit of Andean evergreen *Nothofagus* being comparable to the forest limit set by evergreen *Nothofagus* in New Zealand, and the deciduous species occupying a higher, colder altitudinal belt.

Overwintering shoots of trees forming north-temperate tree limits withstand temperatures below −70°C through tolerating intercellular ice (Sakai et al., 1981), whereas in the forest-alpine transition of the tropical Andes, cold hardiness is expressed through supercooling capacity, which in *Polylepis sericea* reaches −6.0 to −8.0°C (Rada et al., 1985). The mechanism of cold tolerance is not known for New Zealand native species.

THE SEEDLING PHASE

The ability of seedlings to establish at or beyond the upper forest margin influences the structure of forest-alpine transitions and their reaction to climatic change (Smith et al., 2003). In New Zealand, *Nothofagus* shows reduced seed production and viability towards tree limit (Wardle, 1984) and little dispersal beyond the forest margin, though these are unlikely to set absolute altitudinal limits for establishment, as there is occasional successful dispersal to at least 6 km, and seed sown 500 m above the tree limit germinates freely (Wardle, 1985). Nevertheless, as noted above, few *Nothofagus* seedlings establish naturally more than 7–9 m above the forest edge. This compares with an abrupt forest limit of *N. pumilio* in Tierra del Fuego, where various constraints progressively reduce seedlings establishment with increasing altitude and none occur more than 10–20 m beyond the forest limit (Cuevas, 2000).

Growing-season frosts that kill expanding shoots of *Nothofagus* may set back established trees temporarily, whereas seedlings at the upper forest margin or below inverted forest limits, having few apical growing points or metabolic reserves, are vulnerable. Surrounding vegetation can protect seedlings against frost, frost-heave, excessive insolation, and grazing by introduced herbivores and native grasshoppers (Acrididae), while disadvantaging them through competition. Winter snow also protects seedlings, but in New Zealand, in contrast to north temperate and southern Andean localities, seldom persists long enough near tree limit to curtail their growing season.

In open areas below Australian forest limits, low night temperatures, especially unseasonable frosts, and photoinhibition impede growth and competitive ability of *Eucalyptus pauciflora* seedlings and cause direct damage (King and Ball, 1998); cold-induced photoinhibition also affects *Nothofagus solandri* seedlings (Ball, 1994).

THE SAPLING PHASE AND DIEBACK

Saplings occupy a steep temperature gradient; on calm nights below an inverted forest limit in New Zealand, Wardle (1985) measured an increase of nearly 5°C between 0.005 and 0.8 m over vegetation, and 8°C above snow. They therefore become less exposed than seedlings to inversion frosts, but are more exposed to wind and wind-driven particles. If these lead to repeated dieback, krummholz develops (Smith et al., 2003). Dieback results from dehydration and is most evident at the end of winter. It has been explained as "frost drought" that occurs when freezing of sapwood and the upper soil horizons prevents replenishment of water lost through evaporation from foliage (Tranquillini, 1979; Boyce and Lucero, 1999).

Some have argued that vulnerability to dehydration arises because incomplete maturation by the end of the growing season results in poorly developed leaf cuticles (Baig and Tranquillini, 1980), whereas others consider that it results from abrasion of cuticles and wax through leaves rubbing or wind-driven particles during winter (Van Gardingen et al., 1991; Hadley and Smith, 1989). In the sapling phase, leading shoots show faster, indeterminate, and seasonally prolonged growth, and in *Nothofagus* at New Zealand tree limits, the distal portions often have not developed closed overwintering buds by the end of the growing season and are vulnerable to dieback.

Even during the relatively mild New Zealand winter, the upper soil layer and sapwood of *Nothofagus solandri* saplings towards the forest limit can freeze (personal observation). In saplings at the upper forest margin in the Craigieburn Range (43°10′S, 171°40′E), small reductions in water content measured during winter in leeward shoots were replenished before the following summer, whereas windward shoots began drying in autumn (April), and by September most had died back (McCracken et al., 1985). The damage was attributed to an April frost.

When sown 150 m above the local tree limit in the Craigieburn Range with competition removed and shade provided (Wardle, 1985), *N. solandri* seedlings were still surviving after 35 years, but shoots growing beyond the shade screens died as soon as autumn frosts began. At the same altitude, *Eucalyptus pauciflorus* seedlings had exceeded the shade screens, attained heights up to 2.3 m, and were still growing vigorously, while one plant of *Pinus hartwegii* from tree limit at lat. 19°N in Mexico had reached 3.1 m, though with winter drying of windward shoots and needles (personal observation).

Three hundred meters above the local tree limit only *Pinus contorta* and *Picea engelmannii* were surviving after 35 years. The former had reached 1.8 m and was producing cones whereas *P. engelmannii* was subject to spring frosting of young shoots and thriving only in the shade of the pines; when its needles were subjected to artificial freezing toward the end of the summer, they developed patterns of drying that seem identical to patterns that become evident during winter in krummholz *P. engelmannii* in the Rocky Mountains (Wardle, 1981). In contrast, *Sophora chrysophylla* and *Dacrycarpus compactus*, provenanced from tree limit in Hawaii and New Guinea, respectively, died during winter when grown 200 m below the *Nothofagus solandri* limit (Wardle, 1971).

Dieback occurs even on winterless tropical mountains, as described for *Erica trimera* in Ethiopia (Miehe and Miehe, 1994) and several species, including *Dacrycarpus compactus*, on Mount Wilhelm in Papua-New Guinea (Wardle, 1971); a tentative explanation is that it involves actively growing shoots affected by frosts occurring on clear nights.

Conclusions

New Zealand *Nothofagus* forest-alpine transitions have been regarded as genus-specific rather than part of a global treeline phenomenon (Körner and Paulsen, 2004). Nevertheless, *Nothofagus* shows ecophysiological responses similar to those at other temperate tree limits, though to different degrees. The attenuated nature of many north temperate forest-alpine transitions has been ascribed to environmental influences on the sapling phase (Smith et al., 2003). In New Zealand, *Nothofagus* forest is continuous right to upper tree limits, which are remarkably abrupt and concordant in altitude. Like abrupt upper limits of *Nothofagus* in Tierra del Fuego, this relates to paucity of seedling establishment above the forest margin. New Zealand tree limits, like those of *Eucalyptus* in Australia, are also unusual in temperate regions, but similar to those in the tropics, in being formed by evergreen broadleaved trees.

Altitudes of tree limit in New Zealand are constrained by growing-season temperatures higher than those at tree limit in other parts of the world. It can be argued that this is because they are also constrained by a coldest-month mean around 0°C that applies to broadleaved trees elsewhere, because they have not evolved the resistance to extreme winter cold that is found at northern hemisphere tree limits, where only seven genera contribute (four in the Pinaceae, *Juniperus*, and the broadleaved, deciduous *Betula* and *Sorbus*). This indicates more stringent selection for cold hardiness than in New Zealand where nine genera contribute to tree limits (five evergreen broadleaved genera in three families, three genera in the Podocarpaceae, and the deciduous broadleaved *Hoheria*, the other species in this endemic genus being evergreen). The New Zealand mountains were isolated from sources of pre-adapted hardy trees, until some were introduced and now thrive above the native tree limit. Some northern tree limits are also lower than usual because of local absence of hardier species; for example, *Fagus sylvatica* has limited cold tolerance (Tranquillini and Plank, 1989) and can form tree limit at atypically warm isotherms (Körner and Paulsen, 2004). In the Himalayas, the evergreen *Quercus semecarpifolia*, that can form tree limit in the absence of conifers, is subject to the same limitation by winter cold as other broadleaved evergreen trees (Ohsawa, 1990).

It may be asked why deciduous *Nothofagus* capable of growing above the native tree limit, like those forming the uppermost belt of forest and krummholz in the southern Andes, have not evolved in New Zealand, especially since *N. solandri* tends to shed the previous season's leaves within a few months of the new season's leaves appearing (Wardle, 1984). The answer may lie in the short time that conditions conducive to evolution of hardier trees have existed in New Zealand, where mountains high enough with climates cold enough to support glaciers developed only during the last 2 m.y. (Gage, 1980). According to DNA evidence, the extant New Zealand taxa of *Nothofagus* subgenus *Fuscospora*, among which only *N. solandri* var. *cliffortioides* has subalpine ecotypes, differentiated within this interval (Knapp et al., 2005). At similar latitudes in the southern Andes glacial conditions existed >4.6 Ma (Mercer and Sutter, 1982; Thomson, 2002). Moreover, the Andes extend to colder latitudes, are isolated from Antarctica by only 500 km, and the rift from Antarctica did not occur until the Miocene. In Antarctica forests including *Nothofagus* existed through the Miocene, and fossils of deciduous *Nothofagus* have been dated to the Pliocene (Webb and Harwood, 1993), though this is contested (Stroeven and Kleman, 1999). Few parts of New Zealand currently experience the winter cold that, globally, is associated with dominance by deciduous broadleaved trees (McGlone et al., 2004). Appropriate environments may have been further limited during equable climatic episodes that periodically enveloped New Zealand from the late Tertiary to the mid Holocene (McGlone et al., 1996), whereas climates must have been continuously harsher on the Patagonian mountains furthest from western coasts.

Subalpine forest dominated by trees of low stature where *Nothofagus* is absent locally or regionally has its closest analog in the subalpine woody vegetation of Tasmania, though it also recalls high-altitude forests on tropical mountains and Himalayan *Rhododendron* thickets. *Nothofagus* forest and subalpine low forest interrelate at small and large scales. At the smaller scale, *Nothofagus* can be slower than other trees to reoccupy areas denuded by fire from Polynesian settlement onwards. By the time *Nothofagus* arrives, the terrain has already been occupied by grassland and shrubland, and given enough time, by low forest; advance of *Nothofagus* depends on slow marginal spread and chance occupation of bare ground through seed dispersal to greater distances. At the larger scale, the major "*Nothofagus* gaps" exist because *Nothofagus* species have been slower than others to reoccupy areas denuded during tectonic, volcanic, and, especially, glacial events (McGlone et al., 2001; Leathwick, 1998), though their rate of spread and establishment is influenced by location of seed sources, avenues for spread, geology and soils, present and past climates and, possibly, tardy infection by ectomycorrhizae.

At the smaller scale, the upper limit of *Nothofagus* is generally the same as for low forest, but locally depressed in areas of cold-air drainage, where even winter-dormant *Nothofagus* shoots can be killed by severe frosts. There is palynological evidence that during the Holocene, upper forest limits formed by *Nothofagus* did not develop until the second half, probably because equable climates during the first half resulted in less difference between summer and winter temperatures and, therefore, frequent growing-season frosts at this altitude (McGlone et al., 1996). *Nothofagus* species in the New Guinea highlands provide an analogy in that they do not reach tree limit and are extensively damaged by occasional severe frosts (Brown and Powell, 1974).

The belt of large tussock grasses, tall herbs and shrubs *above* the tree limit in New Zealand appears to be without equivalent in north temperate regions and the southern Andes, although enclaves of tall shrubs and herbs occur within forest-alpine transitions. However, on southern Andean volcanoes where eruptions have destroyed the upper belt of deciduous forest and krummholz, shrubland and tussock grassland meet a lowered forest limit dominated by evergreen *Nothofagus* (Wardle, 1998). On tropical mountains, tussock grasslands above cloud forest resemble New Zealand *Chionochloa* grasslands above tree limit, but contain stands of hardier trees that have resisted fires.

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References Cited

Baig, M. N., and Tranquillini, W., 1980: The effects of cuticular transpiration on *Picea abies* and *Pinus cembra* and their significance in desiccation at the alpine treeline. *Oecologia (Berlin)*, 47: 252–256.

Ball, M. C., 1994: The role of photoinhibition during tree seedling establishment at low temperatures. *In* Baker, N. R., and Bowyer, J. R. (eds.), *Photoinhibition of Photosynthesis from Molecular Mechanisms to the Field*. Oxford, U.K.: BIOS Scientific Publishers, 365–376.

Barrera, M. D., Frangi, J. L., Richter, L. L., Perdomo, M. H., and Pinedo, L. B., 2000: Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. *Journal of Vegetation Science*, 11: 179–188.

Bendix, J., and Rafiqpoor, M. D., 2001: Studies on the thermal conditions of soils at the upper tree line in the páramo of Papallacta (eastern cordillera of Ecuador). *Erdkunde*, 55: 257–276.

Benecke, U., and Nordmeyer, A. H., 1982: Carbon uptake by *Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole and *Pinus contorta* Douglas ex Loudon ssp. *contorta* at montane and subalpine altitudes. *In* Waring, R. H. (ed.), *Carbon Uptake and Allocation in Subalpine Ecosystems as a Key to Management.* Oregon State University, Forest research Laboratory, 9–21.

Bestic, K. L., Duncan, R. P., McGlone, M. S., Wilmshurst, J. M., and Meurk, C. D., 2005: Population age structure and recent *Dracophyllum* spread on subantarctic Campbell Island. *New Zealand Journal of Ecology*, 29: 291–297.

Boyce, R. L., and Lucero, S. A., 1999: Role of roots in winter water relations of Engelmann spruce saplings. *Tree Physiology*, 19: 893–898.

Brown, M., and Powell, J. M., 1974: Frost and drought in the highlands of New Guinea. *Journal of Tropical Geography*, 38: 1–6.

Burns, B. R., 1993: Fire-induced dynamics of *Araucaria araucana–Nothofagus antarctica* forest in the southern Andes. *Journal of Biogeography*, 20: 669–685.

Calder, J. W., and Wardle, P., 1969: Succession in subalpine vegetation at Arthurs Pass, New Zealand. *Proceedings of the New Zealand Ecological Society*, 16: 6–47.

Cavieres, L. A., Rada, F., Azócar, B., García-Nuñez, C., and Cabrara, H., 2000: Gas exchange and low temperature resistance in two tropical high mountain tree species from the Venezuelan Andes. *Acta Oecologica*, 21: 203–211.

Cuevas, J. G., 2000: Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. *Journal of Ecology*, 88: 840–855.

Cullen, L. E., Stewart, G. H., Duncan, R. P., and Palmer, J. G., 2001: Disturbance and climate-warming influences on New Zealand *Nothofagus* tree-line population dynamics. *Journal of Ecology*, 89: 1061–1071.

Daubenmire, R., 1954: Alpine timberlines in the Americas and their interpretation. *Butler University Botanical Studies*, 11: 119–136.

Donoso, C., 1996: Ecology of *Nothofagus* forests in central Chile. *In* Veblen, T. T., Hill, R. S., and Read, J. (eds.), *The Ecology and Biogeography of* Nothofagus *Forests*. New Haven: Yale University Press, 271–292.

Gage, M., 1980: *Legends in the Rocks. An Outline of New Zealand Geology*. Christchurch: Whitcoulls, 426 pp.

Grace, J., Berninger, F., and Nagy, L., 2002: Impacts of climatic change on the tree line. *Annals of Botany*, 90: 537–544.

Haase, P., 1986: An ecological study of the subalpine tree *Dracophyllum traversii* (Epacridaceae) at Arthur's Pass, South Island, New Zealand. *New Zealand Journal of Botany*, 24: 69–78.

Haase, P., 1987: Ecological studies on *Hoheria glabrata* (Malvaceae) at Arthur's Pass, South Island, New Zealand. *New Zealand Journal of Botany*, 25: 401–409.

Hadley, J. L., and Smith, W. K., 1989: Wind erosion of leaf surface wax in alpine timberline conifers. *Arctic and Alpine Research*, 21: 392–398.

Hoch, G., and Körner, C., 2003: The carbon charging of pines at the climatic treeline: a global comparison. *Oecologia*, 135: 10–21.

Iversen, J., 1944: *Viscum*, *Hedera* and *Ilex* as climatic indicators. *Geologiska Föreningens i Stockholm Förhandlingor*, 66: 463–483.

Jobbágy, E. G., and Jackson, R. B., 2000: Global controls of forest line elevation in the northern and southern hemispheres. *Global Ecology and Biogeography*, 9: 253–268.

Kelly, D., Harrison, A. L., Lee, W. G., Wilson, P. R., and Schauber, E. M., 2000: Predator satiation and extreme mast seeding in 11 species of *Chionochloa* (Poaceae). *Oikos*, 90: 477–488.

King, D. A., and Ball, M. C., 1998: A model of frost impacts on seasonal photosynthesis of *Eucalyptus pauciflora*. *Australian Journal of Plant Physiology*, 25: 27–37.

Knapp, M., Stöckler, K., Havell, D., Delsuc, F., Sebastiani, F., and Lockhart, P., 2005: Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern beech). *PLoS Biology*, 3(1): e14, doi: 10.1371/journal.pbio.0030014.

Körner, C., 1998: A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115: 445–459.

Körner, C., and Hoch, G., 2006: A test of treeline theory on a montane permafrost island. *Arctic, Antarctic, and Alpine Research*, 38: 113–119.

Körner, C., and Paulsen, J., 2004: A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, 31: 713–732.

Lægaard, S., 1992: Influence of fire in the grass páramo vegetation of Ecuador. *In* Balslev, H., and Luteyn, J. L. (eds.), *Páramo, an Andean Ecosystem under Human Influence*. London, San Diego: Academic Press, 151–166.

Larcher, W., and Siegwolf, R., 1985: Development of acute frost drought in *Rhododendron ferrugineum* at the alpine timberline. *Oecologia (Berlin)*, 67: 298–330.

Leathwick, J. R., 1998: Are New Zealand's *Nothofagus* species in equilibrium with their environment? *Journal of Vegetation Science*, 9: 719–732.

Macphail, M. K., Jordan, G. J., and Hill, R. S., 1993: Key periods in the evolution of the flora and vegetation in western Tasmania. I. The early–middle Pleistocene. *Australian Journal of Botany*, 41: 673–707.

Mark, A. F., Scott, G. A. M., Sanderson, F. R., and James, P. W., 1964: Forest succession on landslides above Lake Thomson, Fiordland. *New Zealand Journal of Botany*, 2: 60–89.

Mark, A. F., Dickinson, K. J. M., and Hofstede, R. G. M., 2000: Alpine vegetation, plant distribution, life forms, and environments in a perhumid New Zealand region: oceanic and tropical high mountain affinities. *Arctic, Antarctic, and Alpine Research*, 32: 240–254.

Mark, A. F., Dickinson, K. J. M., Allen, J., Smith, R., and West, C. J., 2001: Vegetation patterns, plant distribution and life forms across the alpine zone in southern Tierra del Fuego, Argentina. *Austral Ecology*, 26: 423–440.

McCracken, I. J., Wardle, P., Benecke, U., and Buxton, R. P., 1985: Winter water relations of tree foliage at timberline in New Zealand and Switzerland. *In* Turner, H., and Tranquillini, W. (eds.), *Establishment and Tending of Subalpine Forest: Research and Management*. Birmensdorf, Switzerland: Swiss Federal Institute of Forestry, 85–93.

McGlone, M. S., and Moar, N. T., 1998: Dryland Holocene vegetation history, Central Otago and the Mackenzie Basin, South Island, New Zealand. *New Zealand Journal of Botany*, 36: 91–111.

McGlone, M. S., Mildenhall, D. C., and Pole, M. S., 1996: History and paleoecology of New Zealand *Nothofagus* forests. *In* Veblen, T. T., Hill, R. S., and Reed, J. (eds.), *The Ecology and Biology of* Nothofagus *Forests*. New Haven: Yale University Press, 83–130.

McGlone, M. S., Duncan, R. P., and Heenan, P. B., 2001: Endemism, species selection and the origin and distribution of the vascular flora of New Zealand. *Journal of Biogeography*, 28: 199–216.

McGlone, M. S., Dungan, R. J., Hall, G. M., and Allen, R. B., 2004: Winter leaf loss in the New Zealand woody flora. *New Zealand Journal of Botany*, 42: 1–19.

Meinzer, F., and Goldstein, G., 1985: Some consequences of leaf pubescence in the Andean giant rosette plant *Espeletia timotensis*. *Ecology*, 66: 512–520.

Mercer, J. H., and Sutter, J. F., 1982: Late Miocene–earliest Pliocene glaciation in southern Argentina: implications for global ice-sheet history. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 38: 185–206.

Miehe, G., and Miehe, S., 1994: Zur oberen Waldgrenze in tropischen Gebirgen. *Phytocoenologia*, 24: 53–110.

New Zealand Meteorological Service, 1983: *Summaries of climatological observations to 1980*. Wellington: New Zealand Meteorological Service, Miscellaneous Publications 177.

Norton, D. A., 1985: A dendrological study of *Nothofagus solandri* tree growth along an elevational gradient, South Island, New Zealand. *In* Turner, H., and Tranquillini, W. (eds.), *Establishment and Tending of Subalpine Forest: Research and Management*. Birmensdorf, Switzerland: Swiss Federal Institute of Forestry, 159–171.

Norton, D. A., and Schoenenberger, W., 1984: The growth forms and ecology of *Nothofagus solandri* at the alpine timberline, Craigieburn Range, New Zealand. *Arctic and Alpine Research*, 16: 371–370.

Ohsawa, M., 1990: An interpretation of latitudinal patterns of forest limits in south and east Asian mountains. *Journal of Ecology*, 78: 326–339.

Okitsu, S., and Ito, K., 1984: Vegetation dynamics of the Siberian dwarf pine (*Pinus pumila* Regel) in the Taisetsu mountain range, Hokkaido, Japan. *Vegetatio*, 58: 105–113.

Rada, F., Goldstein, G., Azócar, A., and Meinzer, F., 1985: Daily and seasonal osmotic changes in a tropical treeline species. *Journal of Experimental Botany*, 36: 989–1000.

Rada, F., Azócar, A., Briceño, B., González, J., and García-Nuñez, G., 1996: Carbon and water balance in *Polylepis sericea*, a tropical treeline species. *Trees*, 10: 218–222.

Rose, A. B., 1985: The forests. *In* Davis, M. R., and Orwin, J. (eds.), *Report on a Survey of the proposed Wapiti Area, West Nelson*. Christchurch: Forest Research Institute Bulletin 84, 68–109.

Sakai, A., Paton, D. M., and Wardle, P., 1981: Freezing resistance of trees of the South Temperate Zone, especially subalpine species of Australasia. *Ecology*, 62: 563–570.

Schauber, E. M., Kelly, D., Turchin, P., Simon, C., Lee, W. G., Allen, R. B., Payton, I. J., Wilson, P. R., Cowan, P. E., and Brockie, R. E., 2002: Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology*, 83: 1214–1225.

Schulze, E.-D., Beck, E., Scheibe, R., and Ziegler, P., 1985: Carbon dioxide assimilation and stomatal response of afroalpine giant rosette plants. *Oecologia*, 65: 207–213.

Schulze, E.-D., Mooney, H. A., and Dunn, E. L., 1967: Wintertime photosynthesis of bristlecone pine (*Pinus aristata*) in the White Mountains of California. *Ecology*, 48: 1044–1047.

Smith, W. K., Germino, M. J., Hancock, T. E., and Johnson, D. M., 2003: Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23: 1101–1112.

Stroeven, A. P., and Kleman, J., 1999: Age of Sirius Group on Mount Feather, McMurdo Dry Valleys, Antarctica, based on glaciological inferences from the overridden mountain range of Scandinavia. *Global and Planetary Change*, 23: 231–247.

Thomson, S. N., 2002: Late Cenozoic geomorphic and tectonic evolution of the Patagonian Andes between latitudes 42°S and 46°S: an appraisal based on fission-track results from the transpression intra-arc Linquiñe-Ofqui fault zone. *Geological Society of America Bulletin*, 114: 1159–1173.

Tranquillini, W., 1979: *Physiological Ecology of the Alpine Timberline*. Ecological Studies 31. Berlin, New York: Springer-Verlag, 137 pp.

Tranquillini, W., and Plank, A., 1989: Ökophysiologische Untersuchungen an Rotbuchen (*Fagus sylvatica* L.) in verschiedenen Höhenlagen Nord- und Südtirols. *Centralblatt für das gesamte Forstwesen*, 106: 225–246.

Tuhkanen, S., 1992: The climate of Tierra del Fuego from a vegetation geographical point of view and its ecoclimatic counterparts elsewhere. *Acta Botanica Fennica*, 145: 64 pp.

Van Gardingen, P. R., Grace, J., and Jeffree, C. E., 1991: Abrasive damage by wind to the needle surfaces of *Picea sitchensis* (Bong.) Carr. and *Pinus sylvestris* L. *Plant, Cell and Environment*, 14: 185–193.

Velez, V., Cavelier, J., and Devia, B., 1998: Ecological traits of the tropical treeline species *Polylepis quadrijuga* (Rosaceae) in the Andes of Colombia. *Journal of Tropical Ecology*, 15: 771–787.

Villalba, R., Boninsegna, J. A., Veblen, T. T., Schmelter, A., and Rubulis, S., 1997: Recent trends in tree-ring records from high elevation sites in the Andes of northern Patagonia. *Climate Change*, 6: 1–30.

Wade, L. K., and McVean, D. N., 1969: Mt Wilhelm studies. I. The alpine and subalpine vegetation. Canberra: Australian National University, Research School of Pacific Studies, Department of Biogeography and Geomorphology Publication BG/1, 225 pp.

Wardle, J. A., 1984: *The New Zealand Beeches: Ecology, Utilisation and Management*. Wellington: New Zealand Forest Service, 447 pp.

Wardle, P., 1971: An explanation for alpine timberline. *New Zealand Journal of Botany*, 9: 371–402.

Wardle, P., 1981: Winter desiccation of conifer needles simulated by artificial freezing. *Arctic and Alpine Research*, 13: 419–423.

Wardle, P., 1985: New Zealand timberlines. 1. Growth and survival of native and introduced tree species in the Craigieburn Range, Canterbury. 2. A study of forest limits in the Crow Valley near Arthurs Pass, Canterbury. *New Zealand Journal of Botany*, 23: 219–261.

Wardle, P., 1991: *Vegetation of New Zealand*. Cambridge: Cambridge University Press, 672 pp.

Wardle, P., 1998: Comparison of alpine timberlines in New Zealand and the southern Andes. *Miscellaneous Series, Royal Society of New Zealand*, 48: 69–90.

Wardle, P., 2001: Holocene forest fires in the upper Clutha district, Otago, New Zealand. *New Zealand Journal of Botany*, 39: 523–542.

Wardle, P., and Coleman, M. C., 1992: Evidence for rising upper limits of four native forest trees. *New Zealand Journal of Botany*, 30: 303–314.

Wardle, P., Field, T. R. O., and Spain, A. V., 1971: Biological flora of New Zealand 5. *Olearia colensoi* Hook. f. (Compositae). Leatherwood, Tupari. *New Zealand Journal of Botany*, 9: 186–214.

Wardle, P., Coleman, M., Buxton, R., and Wilmshurst, J., 2005: Climatic warming and the upper forest limit. *Canterbury Botanical Society Journal*, 39: 90–98.

Webb, P. N., and Harwood, D. M., 1993: Pliocene fossil *Nothofagus* (southern beech) from Antarctica: phytogeography, dispersal strategies, and survival in high latitude glacial-deglacial environments *In* Alden, J., Mastrantonio, J. L., and Ødum, S. (eds.), *Forest Development in Cold Climates: Proceedings of a NATO Advanced Research Workshop held in Laugarvatn, Iceland, June 18–23, 1991*. NATO Science Series A 244 New York: Plenum Press, 135–166.

Wilson, J. B., and Agnew, A. D. Q., 1992: Positive-feedback switches in plant communities. *Advances in Ecological Research*, 23: 263–336.

Wilson, C., Grace, J., Allen, S., and Slack, F., 1987: Temperature and stature: a study of temperatures in montane vegetation. *Functional Ecology*, 1: 405–413.

Zotov, V. D., 1938: Some correlations between vegetation and climate in New Zealand. *New Zealand Journal of Science and Technology*, 19: 474–487.

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