FREEZING RESISTANCE OF NEW ZEALAND TREES AND SHRUBS

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SUMMARY: Forty-two native woody species were selected to represent the range of temperature-related ecological gradients in New Zealand. Twigs collected in July (mid-winter) were sent by air to Sapporo, Japan, where they were artificially hardened and then tested for freezing resistance. Although only one plant of each species was sampled from each site in anyone year, results were consistent from year to year.

Freezing resistance of the plants correlates well with their natural distribution; for leaves this ranges from -4°C or warmer for broad-leaved species not extending south of 39°S, to -18°C to -25°C for the hardiest high-altitude shrubby conifers. Ecotypic differences are also apparent. Air temperatures only occasionally reach or exceed the freezing resistance of local native species, but ground frosts are more likely to affect seedlings in frosty depressions.

Other temperate, southern hemisphere, evergreen trees grown at Christchurch, New Zealand, show similar freezing resistances to native species, but two deciduous species of *Nothofagus* are hardier than evergreen *Nothofagus*. Even the hardiest New Zealand trees and shrubs compare only with trees growing in warm temperate, lowland districts of Japan.

INTRODUCTION

Freezing resistance of northern hemisphere trees on both sides of the Pacific Basin has been investigated at Sapporo, Japan, and Minnesota, U.S.A., by the senior author and collaborators. This paper describes an extension of the work to trees and shrubs of New Zealanq, where climates are far more equable than is usual at similar latitudes in the Northern Hemisphere. While horticultural experience is that New Zealand plants show a corresponding low degree of hardiness, there is little quantitative information despite an early experiment on some alpine species (Cockayne, 1897).

Most trees and shrubs growing naturally in New Zealand show well-defined geographic limits along various temperature-related gradients, the main ones being latitude, altitude, distance from the sea (this also coincides with rainfall and humidity gradients), and, as a converse to altitude, topographic inversion.

Tests of freezing resistance were made on 42 native species selected to reflect these gradients, and also on some cultivated trees from other southern hemisphere countries. The study was undertaken to assess the relative hardiness of trees from different parts of New Zealand, and to compare them with trees native to the Northern Hemisphere.

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MATERIALS AND METHODS

The species were collected during July (mid-winter) in three years, mostly from natural habitats near the road which links the west and east coasts of the South Island through Arthurs Pass, but a few were growing wild at Auckland. Cultivated material was collected from Christchurch Botanic Gardens. These localities are shown in Figure 1, and representative climatic data in Table 1.

Sampling of several plants of each species would have been desirable as an indication of variability, but posed several difficulties, including inaccessibility of foliage of tall trees, clonal nature of some species, and difficulty in finding exposed foliage of sub-canopy species. We decided, therefore, that it would be more practical and uniform to take five shoots from a single tree or shrub of each species at each collecting site and date.

Material collected in New Zealand was sent by air from Christchurch, reaching Sapporo the following day. There, five uniform pieces of twig were cut from each sample and enclosed in polyethylene bags. Since the measured hardiness of winter twigs can reflect previous environmental temperature, all twigs were subjected to an artificial hardening regime which consisted of holding samples at 0°C to -1°C for 10 days and -1°C to -3°C for 10 days to induce maximum hardiness and to overcome differences in sites of collection and handling procedures (cf. Sakai, 1970a; Sakai and Weiser, 1973). Hardened twigs were cooled at 2°C increments (or, in some steps, at 1°C or 3°C increments; and

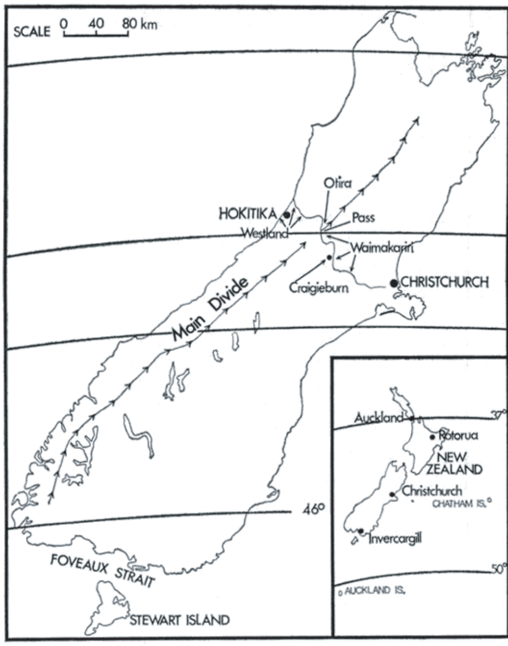

FIGURE 1. *Collection localities for South Island material. The inset shows other localities mentioned in the text or tables.*

the temperatures selected varied from year to year) at 4 hr intervals to successively colder temperatures down to -25°C. After standing at selected test temperatures for either 4 hr or 16 hr, twigs were removed from the freezer and thawed in air at 0°C. To evaluate viability after freezing, thawed evergreen twigs were placed in water in polyethylene bags, and deciduous twigs were placed in water at room temperature, for 20 or 30 days respectively. Thereafter, freezing injury was evaluated visually, using browning as the criterion. Hardiness of the vegetative buds, leaves and living tissues of the twig is expressed as "freezing resistance"-the lowest survival temperatures at which little or no injury was sustained.

DISTRIBUTION OF TESTED NATIVE SPECIES

Latitudinal distribution

The species that grow naturally near sea level may be arranged as follows, according to their southern limits:

North of 39 ° S: *Agathis autralis, A vicennia resinifera. Beilschmiedia tarairi, Metrosideros excelsa. Planchonella novo-zelandica.*

North of 41°20'S: *Knightia excelsa, Libocedrus plumosa. Phyllocladus trichomanoides.*

North of 43°30'S: *Elaeocarpus dentatus, Quintinia acutifolia.*

North of 46 ° 30'S (i.e., Foveaux Strait): *Ascarina lucida, Dacrydium colensoi. Hedycarya arborea. Nothofagus fusca, N. solandri, Phyllocladus alpinus, Pittosporum eugenioides, P. tenuifolium. Podocarpus totara.*

North of 47°20'S (i.e., occurring on Stewart Island): *Coprosma lucida, Dacrydium bidwillii,* D. *cup res sinum. Leptospermum scoparium. Dacrycarpus dacrydioides, Plagianthus betulinus. Podocarpus ferrugineus. P. hallii, Weinmannia racemosa.*

North of 51°S (i.e., occurring in the Auckland Islands): *Dracophyllum longifolium, Metrosideros umbellata.*

Altitudinal distribution

Five altitudinal belts of vegetation may be conveniently recognised in New Zealand, namely lowland, montane, subalpine (extending to the limit of trees and tall shrubs), low-alpine and high~alpine

TABLE 1. *Temperature data* (°C) *at collection localities.*

			1964-73					Long-term	
Locality	Latitude	Altitude (m)	Mean annual air	July mean daily	July mean daily minimum	Lowest screen minimum	Lowest grass minimum	Lowest screen minimum	Length of record (years)
Auckland	36° 51'	49	15.6	11.1	7.7	3.1	-2.4	-0.1	103
Hokitika	42° 43'	4	11.5	7.0	2.1	-1.9	-6.1	-4.2	104
Craigieburn	43° 09'	914	8.1	1.7	-2.7	-7.8	-11.1*	N	N
Craigieburn	43° 08'	1555	4.2	-1.5	-4.4	-11.0	-15.4*	N	N
Christchurch	43° 32'	7	12.0	6.0	1.3	-3.6	-6.5	-7.1	107

* Record incomplete. N = no long-term record.

(Wardle, 1963). Northern species that do not grow *wild* south of latitude 41°20' S can be arranged in two altitudinal groups:

Lowland ouly: *Avicennia resinifera* (estuarine), *Beilschmiedia tarairi, Libocedrus plumosa, Metrosideros excelsa. Planchonella novo-zelandica.*

Extending into lower part of montane belt: *Agathis australis, Knightia excelsa. Phyllocladus trichomanoides.*

Tested species that extend further south can be arranged in five groups according to their altitudinal limits:

Lowland: *Ascarina lucida, Dacrycarpus dacrydioides. Elaeocarpus dentatus. Hedycarya arborea.*

Lower montane: *Coprosma lucida, Dacrydium cupressinum, Pittosporum eugenioides, P. tenuifolium, Podocarpus ferrugineus. P. totara. Quintinia acutifolia.*

Upper montane: *Fuchsia excorticata, Griselinia littoralis, Libocedrus bidwillii. Metrosideros umbellata, Nothofagus fusca, Olearia avicenniaefolia. Plagianthus betulinus, Podocarpus hallii, Weinmannia racemosa.*

Subalpine: *Cassinia fulvida. Dacrydium bidwillii. D. biforme. D. laxifolium, Dracophyllum acerosum,* D. *longifolium. Hebe brachysiphon, Hoheria glabrata. Leptospermum scoparium, Nothofagus solandri, Phyllocladus alpinus. Senecio bennettii. Dacrydium colensoi* was thought to ascend only to lower montane levels when the hardiness tests were carried out, but has since been found in sparse lower-subalpine vegetation on ultramafic rubble.

Low-alpine: *Podocarpus nivalis.*

Distribution along other temperature gradients

Among the northern species, *Avicennia resinifera* is estuarine, and *Metrosideros excelsa* is mainly coastal. *Planchonella novo-zelandica* and *Beilschmiedia tarairi* extend a few kilometres inland. *Agathis australis. Libocedrus plumosa.* and more especially *Knightia excelsa* and *Phyllocladus trichomanoides,* extend to inland districts which have heavy frosts (e.g., the Rotorua district, where a screen minimum of -6.9°C has been recorded).

In the South Island, mild maritime climates extend further inland on the western side than on the east. The most extreme climate is that of intermontane basins east of the main alpine divide, where there are also sharp temperature inversions.

Among lowland and montane species, *Ascarina lucida. Quintinia acutifolia, Elaeocarpus dentatus* and *Hedycarya arborea* extend from the west coast to the western flanks of the Southern Alps; the last two species also grow on the eastern side of the South Island, but only near the sea. *Dacrycarpus dacrydioides, Dacrydium colensoi, D. cupressinum, Metrosideros umbellata, Pittosporum eugenioides, Plagianthus betulin us, Podocarpus ferrugineus. P. totara,* and *Weinmannia racemosa* extend further inland. *Nothofagus fusca* and *Pittosporum tenuifol ium* reach the intermontane basins, but usually grow on slopes rather than the frost-prone valley floors.

Among subalpine and alpine species, the following are mainly restricted to the main divide and the mountains to the west, where the maritime influence is strong: *Dacrydium biforme, D. laxifolium. Hoheria glabrata, Libocedrus bidwillii,* and *Senecio bennettii.*

Dacrydium bidwillii, Phyllocladus alpinus and *Podocarpus nivalis* (all being shrubby podocarps), *Cassinia fulvida, Dracophyllum acerosum, Hebe brachysiphon, Nothofagus solandri* and *Olearia avicenniaefolia* are higher altitude species that extend to the intermontane basins. Among these, the three podocarps, especially *Dacrydium bidwillii,* most successfully occupy the frosty valley floors.

Results and Discussion

Repeatability of results

Measurements of freezing resistance on the native species are shown in Tables 2 and 3. While we cannot claim that these measurements accurately represent the cold tolerance of any population or species, they nevertheless show remarkably good agreement with geographical and ecological distribution; these relationships will be amplified in following sections of the discussion. Table 3 also shows that there is consistency in leaf freezing resistance among trees from similar habitats sampled in different years. Data relating to buds and twigs are not shown in Table 3, as they generally conform to the patterns indicated by the leaf data and Table 2. However, in *Nothofagus solandri* bud and twig resistances of -20°C correspond to the leaf resistance of -5°C measured at 850 m in 1974.

With one exception *(Libocedrus bidwillii)* different plants were tested in different years. Nevertheless, results were consistent for material of anyone species collected at approximately the same altitude and subjected to four hours at the test temperature. In. 1976, when duplicate samples were held at the test temperature for 16 hours and 4 hours respectively, tolerance measured was either the same, or less by 1°C to 2°C at 16 hours (but by 3°C in the case of *Podocarpus nivalis* buds). Hardiness of leaves measured in the rather different experiment of Wardle and Campbell (1976) was also of the same order.

TABLE 2. *Freezing resistance of New Zealand woody plants in °C, graded least to greatest.*

			Twig					Collecting locality				
Evergreen species	Leaf	Bud	Cortex		Xylem	Height	Tier	District	Altitude (m)	Altitude limit (m)	Family	Year
AVICENNIA RESINIFERA	X	X	X		X	3	C	Auckland	0	0	Avicenniaceae	1977
METROSIDEROS EXCELSA	− 3	− 3	− 3		− 3	2	C	Auckland	50	Coastal	Myrtaceae	1977
ASCARINA LUCIDA	− 3	− 3	− 3		− 5	3	U	Westland	50	450	Chloranthaceae	1977
Pittosporum eugenioides	− 3	− 7	− 7		− 7	3	U	Westland	230	700	Pittosporaceae	1977
Planchonella novo-zelandica	− 3	− 8	− 8		− 8	3	C	Auckland	50	Coastal	Sapotaceae	1977
HEDYCARYA ARBOREA	− 3	− 3	− 3		−10	3	U	Westland	90	400	Monimiaceae	1977
BEILSCHMIEDIA TARAIRI	− 4	− 4	− 5		− 5	2	C	Auckland	50	Lowland	Lauraceae	1977
ELAEOCARPUS DENTATUS	− 5	− 5	− 5		− 5	2	C	Westland	90	300	Elaeocarpaceae	1977
KNIGHTIA EXCELSA	− 5	− 8	− 8		− 8	2	C	Chch*	7	Montane	Proteaceae	1977
AGATHIS AUSTRALIS	− 7	− 7		− 7		1	C	Chch*	7	750	Araucariaceae	1976
LIBOCEDRUS PLUMOSA	− 7	− 7		− 7		1	C	Chch*	7	Lowland	Cupressaceae	1976
Dacrycarpus dacrydioides	− 7	− 7		− 7		1	C	Westland	30	200	Podocarpaceae	1976
Podocarpus totara	− 7	− 7		− 7		1	C	Chch*	7	600	Podocarpaceae	1976
Leptospermum scoparium	− 7	− 7		− 7		3	C	Westland	90	1050	Myrtaceae	1976
QUINTINIA ACUTIFOLIA	− 8	− 8	− 8		− 8	2	C	Westland	90	700	Escalloniaceae	1977
Metrosideros umbellata	− 8	− 8	− 8		− 8	2	C	Otira	760	900	Myrtaceae	1977
Weinmannia racemosa	− 8	− 8	− 8		−10	2	C	Otira	760	800	Cunoniaceae	1977
COPROSMA LUCIDA	− 8	− 8	− 8		−10	4	U	Westland	90	650	Rubiaceae	1977
DACRYDIUM CUPRESSINUM	− 8		−10		−10	1	C	Westland	90	600	Podocarpaceae	1977
Griselinia littoralis	− 8	−10	−10		−12	3	C	Otira	900	950	Cornaceae	1977
PITTOSPORUM TENUIFOLIUM	− 8	− 8	−12		−12	3	C	Waim.	610	650	Pittosporaceae	1977
NOTHOFAGUS FUSCA	− 8	−10	−10		−17	1	C	Westland	230	750	Fagaceae	1977
Podocarpus ferrugineus	−10	−7		−10		1	C	Westland	90	600	Podocarpaceae	1976
Cassinia fulvida	−10	−8	−10		−10	4	C	Waim.	790	1200	Compositae	1977
Phyllocladus trichomanoides	−10	−10	−10		−10	1	C	Chch*	7	Montane	Podocarpaceae	1977
Dracophyllum longifolium	−10	−10	−10		−10	3	C	Pass	910	1100	Epacridaceae	1977
SENECIO BENNETTII	−10	−10	−10		−13	4	C	Pass	910	1100	Compositae	1977
NOTHOFAGUS SOLANDRI	−10	−10	−10		−17	2	C	Pass	910	1300	Fagaceae	1977
Olearia avicenniaefolia	−10	−10	−13		−17	3	C	Waim.	760	950	Compositae	1977

DACRYDIUM COLENSOI	−13	−13		−13		2	C	Westland	10	600	Podocarpaceae	1976
PODOCARPUS HALLII	−13	−13		−13		2	C	Otira	450	800	Podocarpaceae	1976
LIBOCEDRUS BIDWILLII	−13	−13		−13		2	C	Otira	900	950	Cupressaceae	1977
HEBE BRACHYSIPHON	(−13)	(−10)		(−15)		4	C	Waim.	610	1200	Scrophulariaceae	1974
DACRYDIUM BIFORME	−13	−13	−13		−15	3	C	Pass	910	1050	Podocarpaceae	1977
DACRYDIUM LAXIFOLIUM	−13		−15		−22	4	U	Pass	910	1050	Podocarpaceae	1977
DRACOPHYLLUM ACEROSUM	−15	−15	−15		−15	4	C	Waim.	930	1200	Epacridaceae	1977
PHYLLOCLADUS ALPINUS	−18 ~ −20		−20		−23	3	C	Pass	910	1300	Podocarpaceae	1977
PODOCARPUS NIVALIS	−22	−20		−22		4	C	Pass	910	1500	Podocarpaceae	1976
DACRYDIUM BIDWILLII	−23 ~ −25		−23		−23	4	C	Waim.	670	1150	Podocarpaceae	1977
Deciduous species												
Fuchsia excorticata	D	(− 5)		(− 5)		3	U	Westland	180	750	Onagraceae	1974
Plagianthus betulinus	D	(− 5)		(− 5)		2	C	Westland	180	750	Malvaceae	1974
HOHERIA GLABRATA	D	(−15)		(−17)		3	C	Pass	900	1050	Malvaceae	1974

Ranking of species according to type face

BEILSCHMIEDIA TARAIRE Freezing resistance correlates very well with position along natural temperature gradients.
Hedycarya arborea Freezing resistance correlates fairly well with position along natural temperature gradients.
Cassinia fulvida Freezing resistance correlates poorly with position along natural temperature gradients.

Freezing resistance assessed from 4 hours exposure to test temperatures, except for bracketed data, which were assessed from 16 hours exposure.
X = fails to survive freezing to −3°C D = deciduous Year = year of collection

Height: 1 = tree > 20 m 2 = tree 10-20 m 3 = shrub or small tree 2-10 m 4 = shrub < 2 m

Tier: C = dominant in canopy U = understorey species

Collecting locality:
Westland = Lowland localities west of Main Divide
Pass = Eastern slope of a Main Divide pass
Chch* = cultivated at Christchurch
Otira = Western slope of a Main Divide pass
Waim. = various inland localities in the catchment of the east-flowing Waimakariri River

Altitud. limit: Approximate altitudinal limit at latitude of collection. Coastal, lowland and montane refer to northern trees, for which more precise information is not available.

TABLE 3. *Freezing resistance of leaves of New Zealand woody plants in* °C, *measured at different sites* or in *different years.*

	Leaf	District	Altitude	Year
Metrosideros excelsa	-3	Auckland	50m	1977
	-4	Japan.	-	1977
Pittosporum eugenioides	-3	Westland	230	1977
	(-5)	Westland	180	1974
Hedycarya arborea	-3	Westland	90	1977
	-3	Westland	30	1976
Leptospermum scoparium	-5	Japan.	-	1977
	-7(-7)	Westland	90	1976
Weinmannia racemosa	-5	Westland	90	1977
	(-5)	Westland	180	1974
	-8	Otira	760	1977
Dacrydium cupressinum	-8	Westland	90	1977
	-5(-5)	Westland	30	1976
Libocedrus bidwillii	-10	Otira	900	1977
	-13(-13)	Otira	900	1976
Nothofagus solandri	(-8)	Waim.	550	1974
	-10	Waim.	800	1977
	-10(-10)	Waim.	800	1976
	[-12]	Waim.	800	1975
	(-15)	Waim.	850	1974Å
	(-12)	Waim.	1200	1974Å
	[-13]	Waim.	1200	1975
	-10	Pass	1000	1977
Dacrydium biforme	-13	Pass	910	1977
	-13(-13)	Pass	910	1976
Dacrydium laxifolium	-13	Pass	910	1974
	-15	Pass	910	1976
Dracophyllum acerosum	-15	Waim.	930	1977
	(-13)	Waim.	930	1974
Phyllocladus alpinus	-10~ -12	Westland	30	1977
	-18~ -20	Pass	910	1977
	-17(-15)	Pass	910	1976
	[-16]	Waim.	1200	1975
Podocarpus nivalis	-18	Waim.	1200	1977
	-22(-20)	Pass	910	1976
	(-20)	Waim.	1200	1974
Dacrydium bidwillii	-23 ~ -25	Waim.	670	1977
	-22(-22)	Waim.	670	1976
	[-23]	Waim.	670	1975

Headings as in Table 2.

( ) indicates 16 hours exposure to test temperature. Other results represent 4 hours exposure.

[ ] indicates data from Wardle & Campbell (1976).

* cultivated plants.

Å measured resistance is inconsistent with altitudes of collection.

Resistance of species in relation to their natural distributions

The measured freezing resistance of species was compared with their natural distribution along the gradients of increasing climatic severity discussed above i.e., in respect to latitude, altitude, distance from the sea and temperature inversions. In Table 2, species have been ranked according to their freezing resistance, and emphasized typographically according to a subjective assessment of the degree of correspondence between measured resistance and natural distribution. Twenty-seven species, ranging from the estuarine mangrove, *Avicennia resinifera*. and the coastal, northern *Metrosideros excelsa*. to the low-alpine *Podocarpus nivalis* and inversion-tolerant *Dacrydium bidwillii*. appear to correspond very well, while nine species conform fairly well. Six species were much less hardy than would be expected; this could be related to choice of material (e.g., from less hardy ecotypes) or, in the case of *Fuchsia excorticata* at least, to a form of frost tolerance that consists of an ability to recover from frequent frost damage by producing epicormic shoots.

Table 2 also indicates that conifers consistently are more resistant than dicotyledonous species. The three shrubby podocarps, *Phyllocladus alpin us*. *Podocarpus nivalis* and *Dacrydium bidwillii* have the greatest resistances, which reflects their success at or above timberline, or on frosty floors of inland valleys.

Ecotypic differences (Table 3).

Ecotypic difference is marked in *Phyllocladus alpinus,* where morphologically and ecologically different lowland and subalpine races were tested (Wardle, 1969). *Weinmannia racemosa* is also hardier in its montane provenance than in the lowland one. *Nothofagus solandri* shows a gradient of increasing freezing resistance according to altitudinal provenance, except for some inconsistency among the highest "Waimakariri" material.

Relationship of freezing resistance to climatic data

Comparison of Tables 1 and 2 indicates that freezing resistance generally exceeds extreme screen minima, measured over a decade, by several degrees. However, in the long term, the limits of freezing resistance of some species native to the three lowland stations have been reached or even exceeded. "Grass minima", measured by unprotected thermometers close to the ground on an open lawn, are 3°C to 5°C lower than screen minima, and are still more likely to exceed the tolerance of local species. This suggests that while winter cold is likely to damage plants in the forest only rarely, it may effectively exclude seedlings of many woody species from open, frosty depressions.

The natural southern limits of some species, including *Agathis australis,* lie well within their present limits of cold tolerance, and possibly were set during the last glacial period. It is also well-known that species limits can be determined by temperature factors other than extreme winter minima. Summer warmth, in particular, determines the altitude of most alpine timberlines. including those of New Zealand (Zotov, 1938).

Natural incidence of damage by winter cold

There are few published accounts of winter damage to woody plants in New Zealand. Cockayne (1928) mentions that a prolonged period of frost in an inland district of the South Island, during which temperatures probably did not fall below -11°C, killed various native species, including *W,einmannia racemosa, Leptospermum scoparium* and *Senecio bennettii*. MacKenzie and Gadgil (1973) describe frosting of *Beilschmiedia tawa*. "Frost desiccation" affects *Nothofagus* at the alpine timberline, and is probably the main factor preventing its seedlings from colonising frosty depressions (Wardle and Campbell, 1976).

Most species naturally confined to northern parts of New Zealand cannot be grown in Christchurch except where sheltered from frost, and even some South Island species, including *Ascarina lucida*. are susceptible to frost in cultivation. On the other hand, North Island conifers such as *Agathis australis* are winter-hardy in Christchurch.

Comparison of New Zealand species with those of other regions

A selection of evergreen trees native to eastern Australia and southern South America cultivated in Christchurch exhibits a range of freezing resistance similar to that of New Zealand species (Table 4). In particular, the results for *Podocarpus lawrencei* and *P. nivalis* reflect the close relationship, if not conspecificity, of these plants. On the other hand, two deciduous species of *Nothofagus* scored as being considerably hardier than the evergreen *N. solandri* of New Zealand and *N. nitida* of Chile (despite anomalously low cortex and xylem resistance measured in *N. antarctica* in 1977). *Podocarpus compactus,* originally collected above 3500 11} in New Guinea, showed the lowest resistance of any conifer tested, reflecting the absence of severe cold in the New Guinea timberline region.

Three papers (Sakai and Okada, 1971; Sakai, 1975; Sakai and Kurahashi, 1975) allow comparison of the freezing resistances of plants in New Zealand

TABLE 4. *Freezing resistance in °C of other southern hemisphere trees, mainly grown in Christchurch, New Zealand.*

	Leaf	Bud	Cortex	Twig	Xylem	Native habitat Region	Zone	Collecting Locality	Year	Family
Araucaria cunninghamii	–5(–5)	–5		–5(–5)		Queensland	Subtropical	Chch	1976	Araucariaceae
Araucaria bidwillii	–7(–5)			–7(–5)		Queensland	Subtropical	Chch	1976	Araucariaceae
Callitris oblonga	–10(–10)			–10(–10)		Tasmania	Lowland	Chch	1976	Cupressaceae
Athrotaxis selaginoides	–17(–15)	–15(–10)		–15(–13)		Tasmania	Subalpine	Chch	1976	Cupressaceae
Podocarpus lawrencei	(–20)			(–20)		S.E. Australia	Subalpine-alpine	New South Wales	1974	Podocarpaceae
Eucalyptus pauciflora	(–17)			(–15)		S.E. Australia	Subalpine	New South Wales	1974	Myrtaceae
Nothofagus gunnii	D	–17		–17		S.E. Australia	Subalpine	Tasmania	1974	Fagaceae
Nothofagus obliqua	D	–10	–10		–15	Chile	Montane	Chch	1977	Fagaceae
Nothofagus nitida	–10	–10	–10		–12	Chile	Montane	Chch	1977	Fagaceae
Nothofagus nitida	–10(–10)	–13(–13)		–13(–13)		Chile	Montane	Chch	1976	Fagaceae
Nothofagus antarctica	D	–23	–13		–15	Chile	Subalpine	Chch	1977	Fagaceae
Nothofagus antarctica	D	–22(–20)		–22(–20)		Chile	Subalpine	Chch	1976	Fagaceae
Podocarpus compactus	–5(–3)	–3		–5(–3)		New Guinea	Subalpine	Chch	1976	Podocarpaceae

Headings as in Table 2.

Freezing resistance assessed from 4 hours exposure to test temperatures, except for bracketed data, which were assessed from 16 hours exposure.

D = deciduous.

with those plants in Japan, and archipelago which, though similar in size, topography and latitude to New Zealand, differs in lying close to a continental land mass. This is reflected in both climate (Table 5) and flora. Most New Zealand conifers compare in freezing resistance only with the least hardy Japanese conifers, such as *Podocarpus macrophyllus,* that are native to warm temperate sea coasts below 34° N and subtropical districts. The four hardiest conifers in Table 2, which are subalpine or low-alpine, show the same order of resistance as species native to temperate parts of Japan, such as *Cryptomeria japonica*.

temperature climates. In the first context, the differences among populations of *Phyllocladus alpinus, Nothofagus solandri* and *Weinmannia racemosa* parallel those measured for northern hemisphere species. In *Pseudotsuga menziesii,* which grows extensively throughout western North America, the winter buds of Pacific Coast collections resisted freezing to only -20°C, but those native to Idaho (altitude 1200m) and Colorado survived freezing to -50°C (Sakai and Weiser, 1973).

In an extensive study of winter hardiness of *Larix leptolepsis,* Scheumann and Schönbach (1968) found large differences in the freezing tolerance of trees from 25 provenances from a relatively small area in Japan (latitude 35°-37° N, longitude 137°-140° E and altitude from 1300-2400 m). Almost all of the trees from northern provenances were more hardy than southern ones, and tolerance of early frosts was closely related to the timing of growth cessation. Very similar results were obtained in a study of *L. leptolepis* from 20 provenances planted in two uniform plots in Hokkaido, Japan (Okada *et al.,* 1971).

These results show that climatic stresses, including low temperatures, are important among the natural selection pressures which have led to the evolution of adapted ecotypes and species. There is evidently a close and direct connection between resistance to mid-winter minimum temperatures and plant distribution, although such resistance is only one of several types of winter hardiness. Simple studies

TABLE 5. *Climatic data from selected latitudes in Japan and New Zealand*.

	Latitude	Altitude (m)	Temperature °C) Mean annual air	Mean daily (winter)*.	Mean daily min. (winter)	Extreme min.	Mean daily max. (summer)†	Annual precipi- tation (mm)	Rain-days
Sapporo	43 ° 03' N	18	7.8	-5.5	-9.5	-23.9	21.7	1141	118
Tokyo	35° 41' N	36	15.0	4.1	-0.4	-9.2	26.7	1503	49
Kagoshima	31° 34' N	5.3	17.0	6.7	2.0	-6.7	27.3	2433	91
Yakushima	30° 20' N	11.6	-	11.6	8.9	0	-	-	283
Auckland	36° 51' S	49	15.3	10.8	7.8	-0.1	22.9	1268	140
Christchurch	43° 32' S	7	11.4	5.5	1.3	-7.1	21.3	658	85
Invercargill	46° 25' S	0	9.5	4.7	0.5	-7.2	18.4	1042	157

* January or July † August or January

The least hardy New Zealand broad-leaved trees (Le. the first nine entries in Table 2), compare with subtropical and warm temperate broad-leaved trees of Japan. The remainder fall into the same range of tolerance as evergreen and deciduous temperate species growing at low altitudes in the warm temperate part of Honshu. Conifers and broad-leaved trees that reach higher altitudes in Honshu, or grow in the far northern island of Hokkaido at 42°-43° N, greatly exceed the freezing resistance of any New Zealand species.

SOME GENERAL PRINCIPALS IN THE DEVELOPMENT OF FREEZING RESISTANCE

Freezing resistance may be discussed in different contexts; for instance, as it concerns ecotypic differences within a species, or, at the other extreme, the relation of hardiness of species to regional of the kind reported here should therefore prove useful in plant introduction programmes and contribute to understanding how plants adapt to natural selection pressures.

The timing of cold hardening in the autumn is also an important aspect of winter hardiness and differs significantly among ecotypes and climatic races of widely ranging species. In general, clones from high latitudes harden earlier than those from warmer or coastal regions, which sustain injury to branch tip's in late fall and early winter. This influence of geographic origin, specifically latitude, on the winter survival of eastern cottonwood *(Populus deltoides)* seedlings was determined by Mohn and Pauley (1969) in a study of 540 seedlings grown in a uniform plot at S1. Paul. After the first winter, nearly all seedlings from southern sources (30°-35° N) were killed to ground level. They sprouted from the roots the following spring. Four years later all seedlings from latitudes 30°-35° N had died, while almost all the seedlings from latitudes 38°-46° N had grown to a height of 3-5 m. In this species, the. time of growth cessation has been observed to be inversely correlated with the latitude of origin (Pauley and Perry, 1954). However, the senior author found that twigs of *Populus deltoides* from Mississippi (latitude 33° N) survived freezing to at least -50°C when they were artificially hardened, which suggests that the winter injury sustained by the southern provenances was probably due to late onset of cold acclimation rather than insufficient inherent ability to harden.

By and large, a high degree of freezing resistance characterises overwintering woody plants of continental land masses, even those from southern latitudes such as the Mississippi provenance of *Populus deltoides* mentioned above. Hokkaido, although an island, is under the climatic influence of the Asian mainland and experiences severe winters, and its trees show a corresponding degree of cold hardiness, with freezing resistances that can exceed-70°C. Even on subtropical Yakushima Island in the south of the Japanese archipelago at latitude 30° 20' N, where lowland species show little cold hardiness, upland species growing above 1000 m exhibit freezing resistances of a high order, generally greater than -25°C, although the mean January temperature at 1000 m is 5.5°C (Sakai, 1974).

In contrast, the mildness of South Temperate winters is reflected in the comparatively low freezing resistances measured in New Zealand and other southern hemisphere material, especially that from low elevations. It will be interesting to find whether or not hardy northern hemisphere conifers that have been successfully grown in New Zealand (e.g., *Pinus contorta, Larix decidua)* retain their original freezing tolerance through later generations.

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