

SEASONAL CYCLE OF TOLERANCE TO LOW TEMPERATURES IN THREE NATIVE WOODY PLANTS, IN RELATION TO THEIR ECOLOGY AND POST-GLACIAL HISTORY

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SUMMARY: The post-glacial pollen sequence for inland regions of the eastern South Island is from grass and *Coprosma* → *Dacrydium* (probably *D. bidwillii*) → *Phyllocladus* (probably *P. alpinus*) → *Podocarpus* and *Dacrycarpus* → *Nothofagus* (*solandri* and/or *fusca*). If this is interpreted simply as a response to climatic warming, the position of *Dacrydium* is anomalous, as at present it does not often reach altitudes as high as *Phyllocladus* and *Nothofagus solandri* var. *cliffortioides*. Nor can its position be explained in terms of pedogenesis, for it is characteristic of overmature soils that are leached and often boggy.

Dacrydium bidwillii stands are mostly situated on valley terraces subject to severe frost. This suggests (1) that this species is more tolerant of winter cold than either *Phyllocladus alpinus* or *Nothofagus s. cliffortioides* even though the latter reach the alpine tree limit, and (2) that early post-glacial times, as well as being generally cooler than now, may also have been characterised by severe temperature inversions. To test these hypotheses, twigs of the three species were collected from mature plants throughout one year, and subjected to artificial freezing. Temperatures were dropped gradually, and samples removed at intervals of 1-4°C. Species were consistently in the following order of increasing resistance to freezing damage: *Nothofagus* collected at 800 m, *Nothofagus* at 1200 m, *Phyllocladus* at 1200 m, *Dacrydium* at 700 m, although the hardiness of each species varies according to season.

These results are in good agreement with patterns of damage in the field although, in *Nothofagus* at least, natural damage during winter is manifested as "frost desiccation". Experimental results are also consistent with present ecology and relative abundance in the pollen record.

INTRODUCTION

Pollen diagrams for the post-glacial period of inland regions east of the Divide in the South Island have the earliest phase dominated by pollen of grasses and *Coprosma*. This is followed by a relatively short phase with *Dacrydium* dominant, and modern distribution indicates that the species is *D. bidwillii*. The third phase is characterised by *Phyllocladus* pollen, and on the basis of macrofossils and present distribution, this is certainly the shrub or small tree *P. alpinus*. The return of forest around 10 000 years ago is indicated by the partial replacement of *Phyllocladus* at lower altitudes by tree podocarps, including *Podocarpus spicatus* and *Dacrycarpus dacrydioides*. Finally, *Nothofagus* rises from low pollen frequencies, and at most sites becomes overwhelmingly dominant in the latter part of the post-glacial period. The pollen is of the *fusca* type, and on the basis of present distribution and recovery

of plant fragments, is likely to be mainly *N. solandri* var. *cliffortioides*, although *N. fusca* is probably also represented (Moar, 1971; Lintott and Burrows, 1973).

The simplest interpretation of this sequence would be that it reflects progressive warming, in which case it should be paralleled in the altitudinal sequence of vegetation on mountainsides today. In fact, the downwards altitudinal sequence is generally from grassland with an increasing proportion of shrubs including *Coprosma*, through a more-or-less well defined shrub belt which includes *Phyllocladus alpinus*, to *Nothofagus* forest (which, however, is absent from wide areas) and, finally, mixed podocarp-hardwood forest. The positions of *Nothofagus* and tree podocarps are therefore reversed in the two sequences. Cranwell and Von Post (1936) postulated that the replacement of podocarps by *Nothofagus* in some pollen sequences from Southland was caused by a climatic decline from a post-glacial optimum,

and it is also certain that the slow return of *Nothofagus* species to areas deforested during the Otiran glaciation has also to be taken into consideration.

Dacrydium bidwillii is not a regular component of the sequence of vegetation on mountainsides. East of the Main Divide in the South Island, it mainly grows as thickets and scattered bushes on the podzolised yellow-brown earths of high terraces and moraines in the inland basins, usually in otherwise grassy vegetation. It does not often reach the climatic timberline, evidently because subalpine slopes are usually too steep for soils to develop to the degree of overmaturity at which *D. bidwillii* is competitive with more vigorous species. The phase of *Dacrydium* pollen dominance between the grass-*Coprosma* and the *Phyllocladus* phases of the early post-glacial cannot therefore be explained simply as a succession analogous to the modern altitudinal sequence.

An alternative is that the sequence of vegetation during the post-glacial was influenced by soil development. At the beginning of post-glacial time, there would have been extensive areas of unweathered soils formed by glacial and periglacial processes. Study of modern successions on similar unweathered material (moraine, outwash, river gravel and landslide debris) at a range of altitudes on both sides of the Southern Alps show that grasses, *Coprosma* and *Nothofagus* species can begin to colonise within a decade (e.g. Wardle, 1972). *Podocarpus spicatus* and *Dacrycarpus* can also establish freely on surfaces less than 100 years old.

On the other hand, the small *Dacrydium* species are characteristic of old soils which are considerably leached and weathered, but can also occupy acidic bogs and rock outcrops that have resisted weathering. Near Mt Cook, for example, *Phyllocladus alpinus* is abundant on moraines of the Mueller Glacier that have formed within the last 200 years (Burrows, 1973), whereas *Dacrydium bidwillii* dominates on very old moraines further down the valley. The early appearance of *D. bidwillii* in the post-glacial sequence therefore does not reflect its position in modern successions.

A third possibility is that *Dacrydium bidwillii* can grow on the floors of intermontane basins because it is more tolerant of severe frosts than species such as *Nothofagus s. cliffortioides* and *Phyllocladus alpinus* that predominate at higher altitudes. If this could be demonstrated, it would follow that the early post-glacial *Dacrydium* phase was also characterised, not only by low mean temperatures, but also by very low minimum temperatures. Accordingly, we compared the resistance of shoots of three key species, *Dacrydium bidwillii*, *Phyllocladus alpinus* and

Nothofagus solandri var. *cliffortioides*, to artificial freezing throughout a year.

METHODS

The three species were collected in the catchment of Broken River, Canterbury. The *Dacrydium* was from an isolated stand at 700 m in an intermontane basin, on a wind-deflated Cass soil developed on an outwash terrace of the penultimate (Blackwater) advance of the last glaciation (Vucetich, 1964; Gregg, 1964). *Nothofagus* was collected from two sites, one at 1200 m where the alpine timberline dips towards a cirque-form valley head, and the other the 800 m, at the lower edge of the forest where it abuts on the grassy terraces of the intermontane basin. *Phyllocladus* was also collected from the 1200 m site, though from open shrubland beyond the forest margin. At each sampling, one branch was taken from each of 5 trees or shrubs of each species at each site. To avoid over-harvesting, more than 5 trees or shrubs were used over the year.

The foliage was dampened, placed in polythene bags and packed in a polystyrene bin with snow or frozen glycol pads to keep it just above 0°C, and brought to the laboratory. On the same day or next morning, twigs were cut from the branches and apportioned among small sealed polythene bags, so that each individual plant was represented in every treatment. All the material was then placed in a refrigerator set at -1°C and the temperature lowered at the rate of 1.5 to 2°C/hour until the first trial temperature (i.e. the lowest temperature at which damage would be unlikely to occur) was reached. Temperatures were measured with glass-alcohol minimum thermometers set beside the bags. Samples were then removed at 1-4° (usually about 2°) intervals until the refrigerator reached either its lowest possible temperature, or a temperature at which no survival would be expected. Intervals between each removal were at least 1 hr 20 min., but were up to 16 hours as samples were not removed overnight. A run of thermistor readings showed that temperatures fell to within 0.3°C of the required level during the first 40 minutes of each interval, and then remained stable until a sample was removed and the next level set. It was not feasible to strictly standardise the rate of rewarming of samples, but it was made as gradual as possible; first, a polystyrene box was cooled nearly to the treatment temperature, and the sample placed in it and transferred to a refrigerator at 0°C for 1 hour; they were next taken out of the box, but left in the refrigerator for at least 4 hours; and finally they were kept overnight in a cool room at around 15°C.

In the next stage of the experiment, the bases of the twigs were re-cut and supported in trays of water at room temperature (which varied between 10° and 24°C) and ambient humidities. Damage, which showed as darkening of the foliage followed by desiccation, was assessed for each twig on a scale of 0-3. The incidence of damage was usually evident within three days, and in the conifers often within minutes of thawing. Undamaged shoots, on the other hand, remained green for at least two weeks. In most recordings, it was useful to distinguish between damage to unfolding buds or the current season's foliage, and damage to older foliage. Detailed results are given in the appendix.

RESULTS

Fig. 1a was drawn by joining points interpolated between the lowest temperature at which no damage was detected, and the highest temperature at which there was damage definitely attributable to freezing. Likewise, Fig. 1b joins points interpolated between the highest temperature that resulted in death of all twigs within a few days, and the nearest temperature above this at which evidence of life persisted for some time after thawing. Some features of Fig. 1 are analysed in Table 1. Broadly speaking *Dacrydium* withstands temperatures about 3°C lower than *Phyllocladus*, and 5-10°C lower than *Nothofagus*; although the hardiness of each species varies according to season, as does the magnitude of the hardiness difference between species. Departures from a smooth sinusoidal curve can be reasonably attributed to sampling and experimental errors. An exception is the sharp increase in sensitivity shown by *Phyllocladus* in Fig. 1b in July and August. At these samplings, the bushes were buried in snow, which possibly may have de-hardened them.

A marked irregularity in the detailed results is that a particular treatment sometimes showed less damage than the treatment next above (e.g. 26 November 1974). We could not detect any consistent relationship between the incidence of these reversals and the date of collection or the rate of cooling or warming of the sample concerned, and are unable to offer a convincing explanation.

The foliage tested in *Dacrydium* was in the adult, cupressoid phase which has no distinct resting buds. During spring and summer, the distal, growing portions of the twigs were the first to show freezing damage, but they were the most resistant portions during winter (see Appendix). Similarly, the young, expanding cladodes of *Phyllocladus* were damaged around -6°C, but during winter the youngest whorl

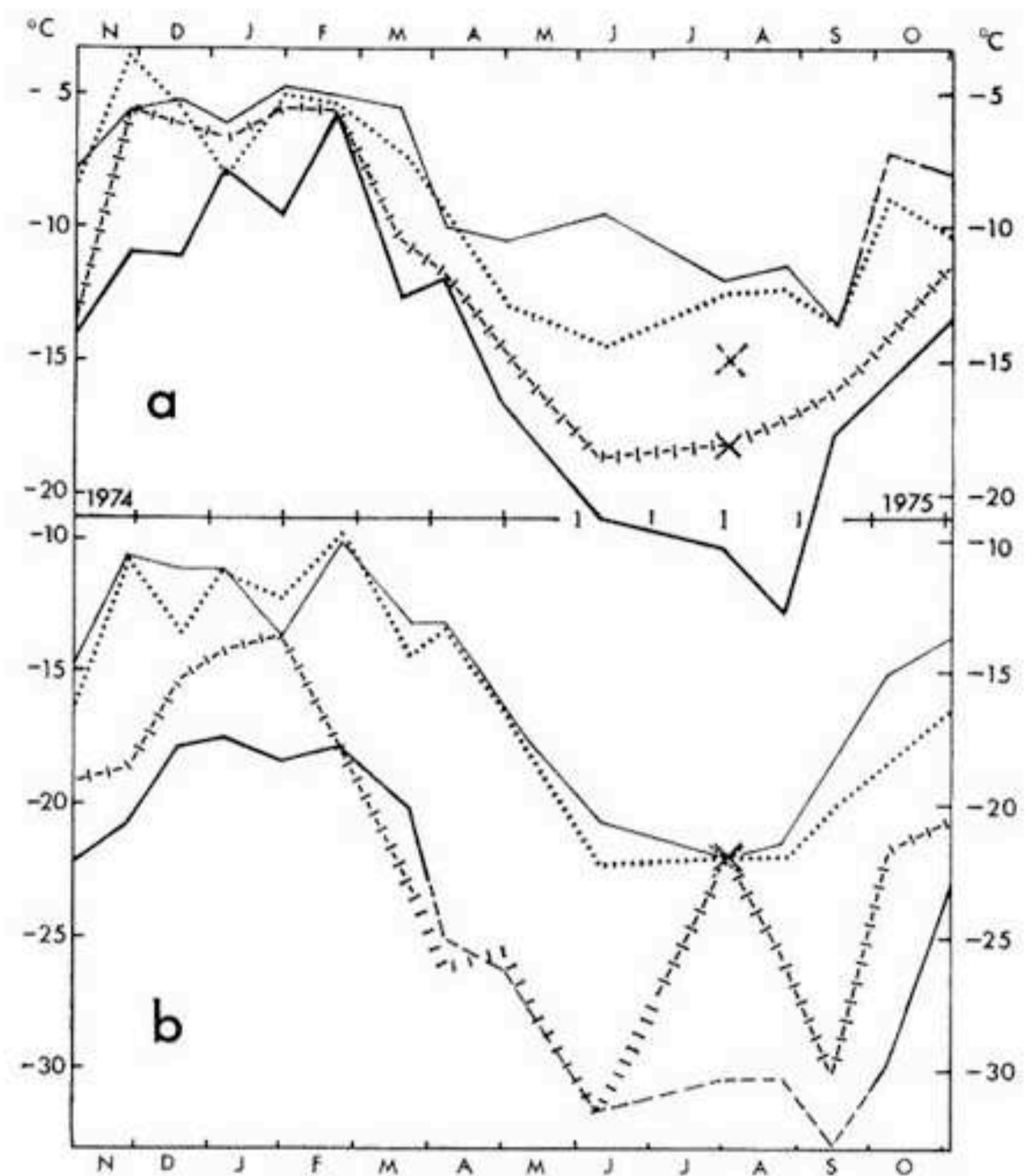


FIGURE 1. Graphs for minimal (a) and maximal (b) freezing damage (see text)

--- Nothofagus s. cliffortioides 1200 m
 — Nothofagus s. cliffortioides 800 m
 -|-|-|-|- Phyllocladus alpinus
 ——— Dacrydium bidwillii

In 1b, *Dacrydium* and *Phyllocladus* are represented by broken lines between points that were extrapolated because the lowest temperatures used did not result in complete killing.

× N. s. cliffortioides 1200 m
 × N. s. cliffortioides 800 m

Points for minimal and maximal damage to buds on 29 July 1975.

was the hardest. The buds also became sensitive to damage in spring. Severe freezing blackened them, whereas milder damage resulted in inability to open.

Buds of *Nothofagus* in the July collection were dissected to reveal any freezing damage. The points for maximal damage (Fig. 1b) coincided with those for leaves. Minimal damage (Fig. 1a) was noted 3-6° lower than for leaves, but very slight damage would have been less easily detected in buds. In spring, buds progressively decreased in hardiness, to reach maximum sensitivity as they expanded into new leaves.

In another paper (Wardle and Campbell, 1976) we point out that winter buds of older *Nothofagus* seedlings are truly winter dormant, and mention that results from the present experiment suggest that this applies also to adult trees. Some undamaged shoots opened their buds under room temperatures in September, but not during earlier months (see Appendix).

Nevertheless, freezing and drought are physiologically related, and many plants that are cold-resistant are also resistant to drought (Levitt, 1972).

In field experiments, *N. s. cliffortioides* seedlings grown on a frosty terrace in the Broken River intermontane basin dried out during winter unless protected by screens; minimum temperatures at ground level commonly fell within the range that gave the

TABLE 1. Numerical comparisons from Fig. 1, in °C. Note that in the comparisons with *Nothofagus* from 800 m, all the data represent tolerance of lower temperatures.

	<i>Nothofagus</i> 800 m	<i>Nothofagus</i> 1200 m	<i>Phyllocladus</i>	<i>Dacrydium</i>
Maximum difference between summer and winter sensitivity:—				
From Fig. 1a	9	11	13	18
From Fig. 1b	12	13	>18	>15
Mean difference between <i>Nothofagus</i> from 800 m and other material:—				
1. Over all sampling dates				
From Fig. 1a	—	1	3	6
From Fig. 1b	—	1	> 7	>10
2. Summer only (26 Nov. 74/ 18 Mar. 75)				
From Fig. 1a	—	0	1	4
From Fig. 1b	—	1	5	7
3. Winter only (10 June 75/ 14 Sept. 75)				
From Fig. 1a	—	2	6	9
From Fig. 1b	—	1	> 7	>12

COMPARISON BETWEEN EXPERIMENTAL AND NATURAL COLD DAMAGE

In the field, expanding young leaves and shoots of *Nothofagus s. cliffortioides* are consistently frosted if air temperatures fall below -3°C (Wardle, 1971). Cold snaps during late October and November often damage seedlings and saplings in subalpine forest, but adult trees flush later and are rarely damaged in this way. In our experiment using adult trees, the only shoots tested at the most critical stage were from the 1200 m site on 26 November 1974; they were undamaged at -3°C and blackened at -4°C .

Leaves of *Nothofagus* suffering natural winter damage turn reddish-brown and dry out, instead of developing the dark mottling indicative of damage by artificial freezing. Presumably, this is because of excessive transpiration caused by high evaporative demand during times when low temperatures restrict the supply of water from soil and roots. There is a considerable overseas literature on this phenomenon of "frost desiccation" (e.g. Larcher, 1972, Sakai, 1970).

beginnings of freezing damage in the refrigerator (i.e. -10° to -15°C cf. Wardle, 1971). Effects of frost were seen also on naturally growing young plants of *N. s. cliffortioides* in the upper reaches of the Ahuriri River in Otago. Forest of this species clothes the mountainsides, but the broad, coalescing fans that form the valley floor support native grassland. At one point, a gully about 1 m deep has been cut down the slope of the fan, and young beeches have become established on the bared soil. These show three conditions. The smallest seedlings are still protected within the gully, and have undamaged foliage. Saplings which project above the rim of the gully to a height of less than 1 m show severe frost desiccation, much of it attributable to the winter of 1974. Finally, saplings that have managed to grow above 1 m have undamaged foliage in their upper portions. Similar frosting of lower foliage of *N. menziesii* along inverted timberlines has been seen in western Otago (A. F. Mark, pers. comm.).

At the upper timberline winter minima do not fall

as low as on treeless valley floors, but the growing season is so short that seedlings are inadequately hardened against a degree of winter drying that can be tolerated by plants grown at lower altitudes. Foliage of *Nothofagus* trees is usually unaffected by winter desiccation, both at inverted timberlines and at the upper forest limit. However, persistent frost desiccation giving rise to "crippled" trees of beech is prevalent where downslope winds build snow drifts along the forest margin (Wardle, 1971). Frost desiccation is also associated with depressed *Nothofagus* timberlines in valley heads and cirques. For instance, it was very pronounced at the 1200 m collection site during the winter of 1975. Whether it is the chief or only cause of these depressions, however, is still not clear. Finally, an instance of winter killing following strong, cold winds on forest edge trees and saplings of *Nothofagus menziesii* on Maungatua, Otago at altitudes of only 550-730 m (Baylis, 1959) shows that occasionally the phenomenon can occur well below timberline.

The opening buds of *Phyllocladus alpinus* are occasionally frosted in the field, but in the freezing experiments, this species proved considerably hardier than *Nothofagus*, at least when shoots exposed above the snow in winter were tested. This probably explains why it is one of the species which contributes to the narrow and generally discontinuous belt of tall scrub above beech timberlines. East of the Main Divide it is also frequently dominant in the scrub which occupies valley heads to the exclusion of *Nothofagus* forest. This adds weight to the suggestion that the depression of timberline in these valley heads is related to winter cold; but it disproves, at least for *P. alpinus*, an earlier suggestion that the pattern is somehow related to a lower amplitude of seasonal variation in cold tolerance among the shrub species (Wardle, 1965).

The freezing resistance developed by *Dacrydium bidwillii* is markedly greater than in the other two species studied, and more than sufficient to withstand the lowest temperatures recorded in intermontane basins. This resistance is relaxed only during the warmest summer months. The scarcity of *D. bidwillii* at the alpine timberline reflects the scarcity at high altitudes of the overmature soils on which it is competitive.

PALAEOECOLOGY

The results of the experiment firmly support the proposition that the sequence of pollen dominants in the earlier part of the post-glacial is a response to decreasing intensity of frosts as well as increasing

mean temperatures. For some time after the recession of the glaciers, cold air would still have gathered over persisting ice- and snowfields during calm weather and flowed downwards to form deep inversion layers in intermontane basins. Twelve thousand years ago, through its tolerance of these severe frosts, *Dacrydium bidwillii* may have formed extensive communities on overmature soils, in areas beyond the limits of recent glaciation. Even by the time of *Phyllocladus* pollen dominance, forest in inland areas may still have been restricted to narrow, mid-slope "thermal belts" and opportunities for its spread limited accordingly. When forest became general, it was podocarp-dominated, and recent interpretations indicate that this was a mild period experiencing less frost than at present (McGlone and Moar, 1975). The final spread of *Nothofagus* may well have been assisted by reversion towards more extreme conditions.

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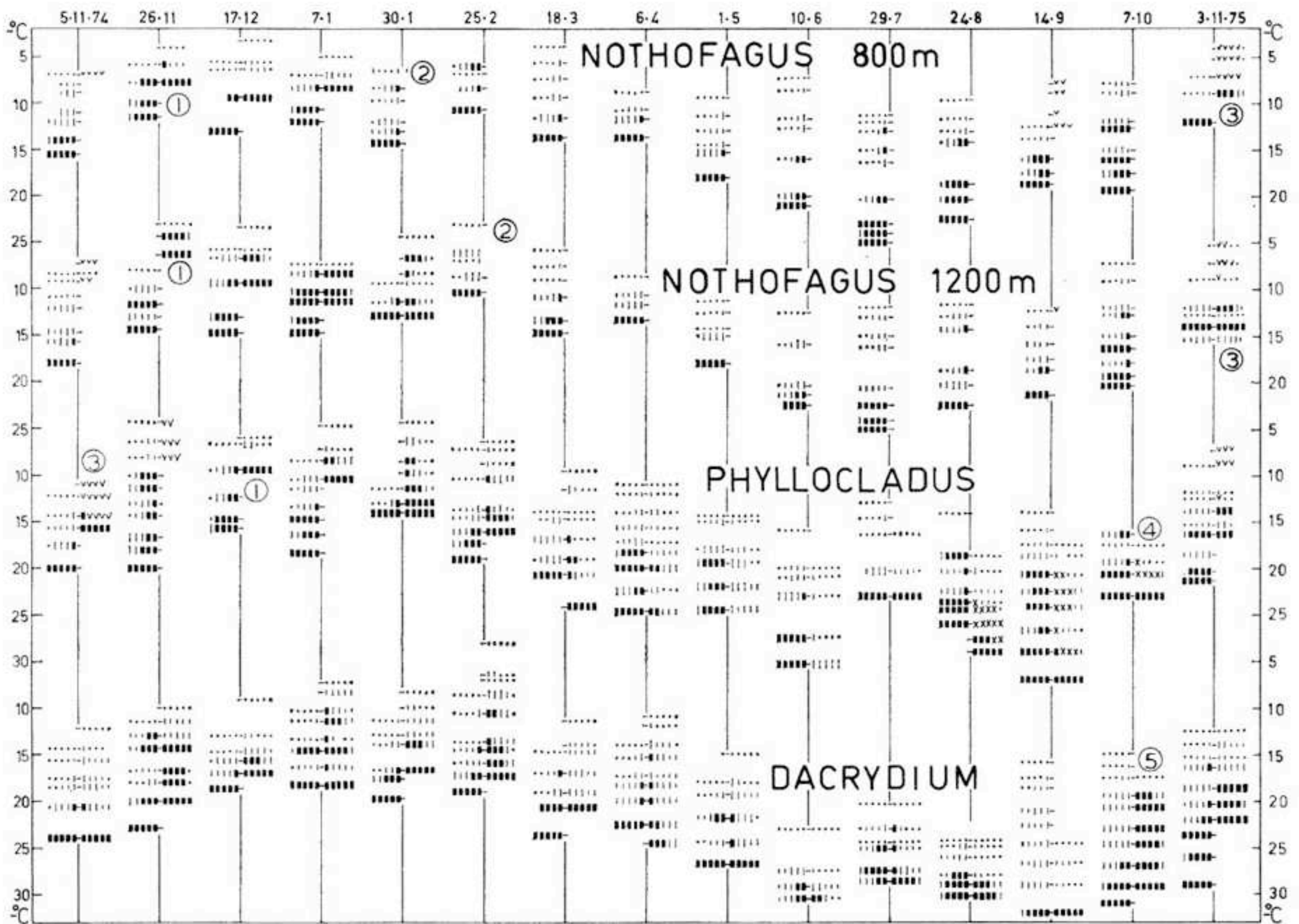
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APPENDIX: Degree of freezing damage to individual shoots. For each sampling date, data to right of vertical axes represent opening buds, or leaves, cladodes or shoots formed during the current or most recent summer; those to the left represent older foliage.

- No visible damage.
- 1 Slight, but definite damage.
- l Moderate damage, i.e. twig still alive after 7-10 days.
- Severe damage; whole twig dead within 3-4 days of thawing.
- X For *Phyllocladus* only; top cladodes not severely discoloured immediately after thawing, but soon drying with the rest of the twig.
- V Buds opening in water trays.

The circled numerals refer to observations on the right of the vertical axes:
 1 New leaves or cladodes expanding at collection date.
 2 New leaves fully developed; not recorded separately from here on.
 3 Observations apply to axillary buds (*Nothofagus*) or terminal buds (*Phyllocladus*).
 4 Up to here, observations apply to cladodes formed during 1974/75 summer.
 5 From this date, observations apply to actively growing short tips.



CORRIGENDUM

WARDLE, P.; CAMPBELL, A. D. 1976. Seasonal cycle of tolerance to low temperatures in three native woody plants, in relation to their ecology and post-glacial history. *Proceedings of the New Zealand Ecological Society* 23: 85-90.

On p. 87 of this paper the legend was incorrect for *Nothofagus s. cliffortioides* 1200 m. The correct notation for Fig. 1 (a) is:

.....	Nothofagus s. cliffortioides	1200 m
————	Nothofagus s. cliffortioides	800 m
— — — — —	Phylocladus alpinus	
————	Dacrydium bidwillii	
