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The structure and dynamics of rimu-dominated forests on glacial moraines, South Westland

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Abstract

Size and age structure analysis, spatial pattern analysis, and disturbance history were used to reconstruct the population dynamics of three stands dominated by Dacrydium cupressinum on glacial moraines in South Westland, New Zealand. D. cupressinum and Prumnopitys ferruginea age structures in the three plots were not all-aged populations that would have arisen by small-scale individual tree replacement. Rather, the presence of distinct even-aged cohorts of trees indicated at least two major establishment periods in the stands (c. 500 and 200-350 years ago) over the last 700 years. In some instances, the presence of D. cupressinum and P. ferruginea in small clumps of individuals of similar age suggested intermittent regeneration in small patches (up to c. 1000m²), whilst in other situations similarly-aged individuals were spread throughout the stand, suggesting establishment after partial canopy breakdown. Conifer stands containing similar age cohorts have been documented in several areas of Westland, both in the uplands on landslide debris deposits and on fluvio-glacial terraces of the lowlands.

Introduction

Lowland rainforests dominated by the podocarp rimu (*D. cupressinum*) occur extensively on fluvioglacial terraces and moraines throughout South Westland. The fluvioglacial terraces are characterised by poorly-drained soils and support dense stands of rimu. In contrast, moraine hills and terrace edges are better drained and support lower density stands. In terrace forests, previous workers have suggested that tree replacement patterns differ from those on the undulating hills of the moraines and terrace edges (e.g., Hutchinson 1932, James 1987). On terraces, flooding and catastrophic windthrow resulting in synchronous canopy collapse create conditions suitable for the establishment of relatively even-aged stands of *Dacrycarpus dacrydioides* (kahikatea) and/or *Dacrydium cupressinum* (Wardle 1974, Six Dijkstra *et al.* 1985, Duncan 1993). These disturbances can create large openings up to 20 ha and occur with a frequency high enough to maintain the dominance of these species (Hutchinson 1932, James 1987, Cornere 1992, Rogers 1995). In contrast, tree replacement patterns on moraines have been less studied, although it has been suggested that small group blowdowns may initiate small patch regeneration (c. 0.2 ha) resulting in a mixed-age structure over large areas (Six Dijkstra *et al.* 1985).

The 1993 amendments to the Forests Act (1949) require management of New Zealand's remaining indigenous forests for timber production to be on the basis of ecologically sustainable silviculture. In north Okarito and Saltwater forests, 9000 ha of rimu-dominated forests have been gazetted for sustained timber production. In fact, from 1994 these forests have provided the only indigenous timber from South Westland. Although these forests are exempt from the Act, to attain sustainability ecological research is required on many aspects of 'natural' forest structure and regeneration (Benecke 1996). The type of information required includes detailed and accurate information about tree size and age structure, replacement patterns, and species growth rates. Forest age structures on the lower terraces of Saltwater forest have been studied and regeneration patterns are reasonably well understood (Six Dijkstra *et al.* 1985, Cornere 1992, Rogers 1995). Our objectives were to determine the age structure and natural replacement patterns of *D. cupressinum* and *P. ferruginea* (miro) on the adjacent moraines and to compare them to those reported for the terraces.

Methods

Tree size and age structure

Data were gathered on tree size and age structure, tree spatial locations, patterns of tree establishment and evidence of past disturbance. From these data patterns of natural disturbance (including the size and frequency at which blowdown patches are formed), and information on the patterns of tree replacement in response to treefall openings can be inferred. In addition, tree size and age can be used to estimate stand basal area and growth rate.

A fixed area plot (40 x 80m, 50 x 60m, and 50 x 60m) was located randomly at each of three topographic positions across a moraine sequence (moraine crest, ablation zone, and moraine edge) identified by Almond (1996). Each plot was divided into 5 x 5m contiguous quadrats. The species and diameter at breast height (dbh) were recorded for all trees > 5 cm dbh. The podocarps rimu, miro (*Prumnopitys ferruginea*), kahikatea (*Dacrycarpus dacrydioides*), and Hall's totara (*Podocarpus hallii*) were also tagged with a numbered metal tag for ease of relocation for tree ageing. In each contiguous quadrat the numbers of saplings (> 1.4m tall but < 5 cm dbh) of all tree and shrub species were also recorded. Size-class distributions for all tree species were constructed from these data to provide information on forest structure.

All podocarp trees were bored with an increment corer at a height of c. 1m. Many trees were cored several times and some trees had to be cored up to six to eight times to obtain cores that were close to the chronological centre and/or missed portions of rot. The increment cores were mounted on blocks and sanded using progressively finer sandpaper (to 400 grit) until annual growth rings could be easily counted under a binocular microscope. All cores were counted and measured on a tree-ring measuring system comprising binocular microscope, Henson Bench, and associated TRIMS (Tree Ring Incremental Measuring System) computer software.

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Individual tree ages were pooled into 50-year age classes to obtain information on forest age structure. For cores missing the chronological centre of the tree, two methods were employed to estimate the missing core length:

1) Where arcs of the inner growth rings were visible (i.e. the core passed close to the chronological centre), Duncan's (1989) method for calculating the missing length of radius based on the height and length of the innermost ring arc was used.

2) Where there were no inner arcs present, the core length was subtracted from the radius of the tree (based on diameter at breast height) as a means of estimating missing core length. This method is likely to be less accurate than the first, as the absence of arcs of inner growth rings indicates that the core was further from the chronological centre than those that had arcs present. It is widely recognised that rimu typically exhibits wedging and lobate growth (Franklin 1969, Norton 1986, Duncan 1989, Cornere 1992, Rogers 1995). Generally, rimu age estimates are fairly accurate if the increment core is extracted from the longest radius of the trunk (Stewart & White 1995).

For both method 1) and 2) above, the missing number of rings was estimated by dividing the estimated missing core length by the mean width of the inner 20 growth rings (c.f. Duncan 1989).

Spatial distribution of tree ages

The x and y coordinates of all trees >5 cm dbh were recorded in each plot and used in the analysis of spatial pattern. We statistically tested for groups of even-aged trees that would indicate synchronous establishment of individuals in a disturbance open-

Figure 1. Panoramic view of Saltwater forest showing emergent, scattered *Dacrydium cupressinum* on moraines in the foreground, and dense, even-canopied stands of *Dacrydium* on terraces in the background (Photo: Peter Almond)

ing (Stewart & Rose 1990, Duncan & Stewart 1991). The spatial distribution of groups of trees of different age often indicates
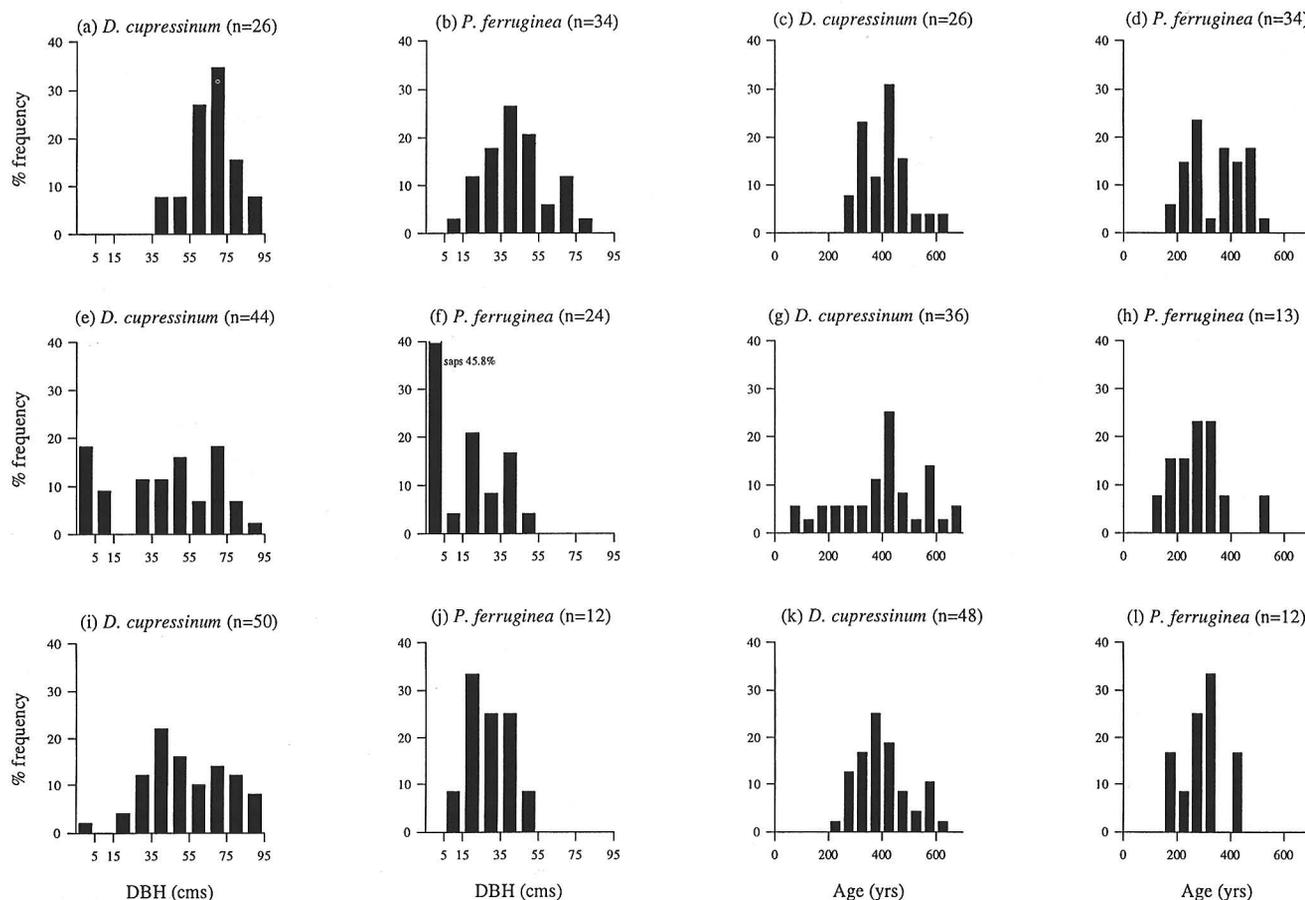
Figure 2. Diameter- and age-class distributions (percent frequency) of *D. cupressinum* and *P. ferruginea* in plot 1 (a-d), plot 2 (e-h), and plot 3 (i-I).

a specific type of tree replacement; e.g., small groups of even-aged trees may indicate regeneration in small canopy gaps formed after treefalls.

Further information on patterns of tree establishment was obtained by recording where possible the substrate on which each sapling or tree had established (i.e. log, stump, windthrow pit, mound, forest floor).

Results

Plot characteristics

D. cupressinum dominated all plots in terms of basal area, and in two of the three plots in stem density (Table 1). *P. ferruginea* was an important component of the moraine crest plot only. Although *P. ferruginea* stems were reasonably common in the other plots they were of small to medium diameter and contributed little to overall basal area.

Table 1: Basal area and stem density for *D. cupressinum* and *P. ferruginea* in the study plots.

plot	basal area (m² per ha) D. cupressinum P. ferruginea	stem density (# > 5 cm dbh per ha) D. cupressinum P. ferruginea
1	94.5 54.4	81 106
2	86.3 9.8	123 43
3	132.7 8.4	167 40

Tree size and age structure

D.cupressinum

The unimodal size-class frequency distribution of *D. cupressinum* in the moraine crest plot (plot 1) suggested a relatively even-aged population with no recent recruitment (Fig. 2 a). In contrast, in the ablation zone and moraine edge plots, the presence of trees in a number of size-classes suggested a more intermittent pattern with several possible periods of establishment and/or mortality (Figs 2 e, i). The *D. cupressinum* age-class frequency distribution for the moraine crest plot (Fig. 2c) indicated that most trees were 300-500 years. The onset of *D. cupressinum* establishment also occurred at c. 500 years ago in the other two plots (Figs 2 g, k). The only recent recruitment had occurred in plots 2 and 3 and most saplings in plot 2 (although not aged) were probably <100 years (based on an annual radial increment of 0.7 mm/yr and the time taken to reach coring height) and restricted to an area of broken canopy in one portion of the plot (Fig. 4).

P. ferruginea

Diameter-class frequency distributions of *P. ferruginea* in the plots mirrored the *D. cupressinum* pattern except that stems were generally smaller (Fig 2 b, f, j). In plot 1 the c. 500-year-old age class was present but a younger age-class of c.200-350 years was also evident in all three plots (Fig 2 d, h, l). As for *D. cupressinum*, stems < 150 years were evident only in plot 2 (Fig. 2 e - h).

Hardwoods

Size-class distributions for hardwoods such as *Weinmannia racemosa* and *Quintinia acutifolia* in all plots indicated continuously-regenerating populations, with generally 70 to 90 % of stems < 15 cm dbh, and declining numbers in progressively larger size-classes. The only exception was in plot 1 where approximately 40% of all stems of *W. racemosa* occurred in each of the first two diameter classes (5 to 14 and 15 to 24 cm dbh).

Age/diameter relationships

For *D. cupressinum* and *P. ferruginea* diameter at breast height and age were usually significantly related (Table 2). However, relationships were weak on an individual plot basis, especially for *D. cupressinum*. Substantial variation in growth rate is indicated, e.g., *D. cupressinum* of c. 400 years ranged in diameter from c. 40 to 90 cm dbh. For all plots combined, the size-age rela-

Table 2: Best fit diameter-age regression equations for *D. cupressinum* and *P. ferruginea* in the study plots.

Species	Plot	n	dbh range	Regression equation	r²	P<
D.cupressinum	1	26	40.7 - 92.7	$\log_e Y = \log_e 102.88 + 0.32 \log_e X$	0.11	NS
	2	36	6.1 - 88.7	$\log_e Y = \log_e 31.17 + 0.65 \log_e X$	0.64	0.001
	3	48	20.0 - 88.1	$\log_e Y = \log_e 94.26 + 0.36 \log_e X$	0.28	0.001
	all	110	6.1 - 92.7	$\log_e Y = \log_e 47.29 + 0.53 \log_e X$	0.50	0.001
P.ferruginea	1	34	12.8 - 76.0	$\log_e Y = \log_e 38.50 + 0.58 \log_e X$	0.61	0.001
	2	13	14.2 - 51.7	$\log_e Y = \log_e 34.18 + 0.62 \log_e X$	0.50	0.01
	3	12	12.2 - 49.2	$\log_e Y = \log_e 41.24 + 0.59 \log_e X$	0.71	0.001
	all	59	12.2 - 76.0	$\log_e Y = \log_e 41.06 + 0.57 \log_e X$	0.62	0.001
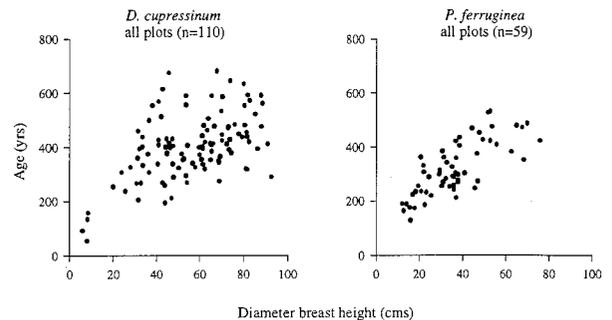
Figure 3. Scatter plots of diameter and age for *D. cupressinum* and *P. ferruginea* in the study plots.

tionships for *P. ferruginea* were stronger than for *D. cupressinum* (Table 2, Fig. 3b).

Mean radial increment, calculated by dividing radius at breast height by age for all trees combined was 0.72 ± 0.24 mm/year ± S.D. for *D. cupressinum* and 0.57 ± 0.16 mm/year ± S.D. for *P. ferruginea*.

Spatial distribution of tree ages

For *D. cupressinum* and *P. ferruginea* in plots 1 and 3 tree ages were randomly distributed. In plot 2, however, trees of similar age were clumped (Fig. 4). Trees of both species < 200 years were aggregated in three major clumps, trees 200-350 years occurred primarily in only the top right hand corner of the plot, and trees in the oldest cohort (> 350 years) were dispersed across the plot in two loosely aggregrated patches.
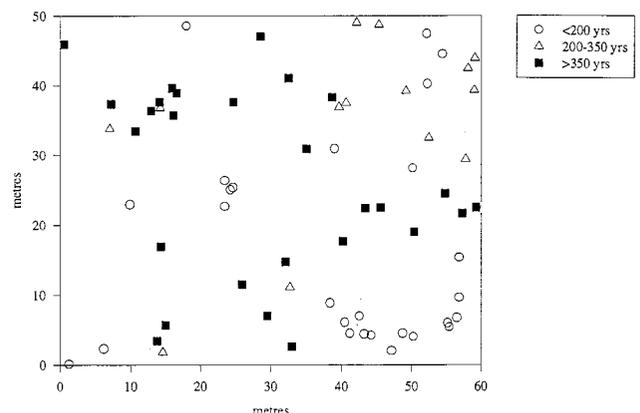
Figure 4. Spatial distribution of *D. cupressinum* and *P. ferruginea* stems according to age-class in plot 2.

Patterns of microsite establishment

D. cupressinum established solely on the forest floor whilst the hardwoods *W. racemosa* and *Q. acutifolia* commonly occurred

on elevated microsites, especially mounds (Table 3). These were also favoured sites for *Myrsine australis*, especially around the elevated trunk bases of *D. cupressinum*. The treefern *Dicksonia squarrosa* also occurred frequently on mounds, logs and stumps. Elevated sites, especially mounds, were more important establishment sites in the poorly-drained plot 2, even for species that occurred predominantly on the forest floor in the other plots, such as *P. ferruginea*.

Discussion

Forest dynamics on the moraines

The forest structures of all three plots did not indicate all-aged populations that had arisen from small-scale individual tree replacement. Rather, *D. cupressinum* and *P. ferruginea* age structures in all plots showed distinct periods of cohort establishment. The cohort initiation dates will not be the actual dates of disturbance events because no correction was made for the time taken to reach coring height, and because colonisation will not necessarily occur immediately following disturbance. The magnitude of this difference between disturbance and cohort initiation dates, however, is likely to be small. Data on seedling height growth rate indicate that rimu growing in closed forest take 30-40 years to reach 1 m but under open conditions growth is considerably faster (Norton *et al.* 1988). Furthermore, where trees establish in dense cohorts, as in the stands analysed, establishment is likely to have occurred relatively quickly (Ogden & Stewart 1995). Therefore, contemporaneous establishment of both species occurred on the moraine crest in two episodes, c. 500 and 200-350 years ago. In the ablation zone and moraine edge areas, a cohort of *D. cupressinum* also established c. 500 years but a younger cohort (c. 200 - 350 years) is only clearly evident for *P. ferruginea*.

Although rimu-dominated forests tend to have a group, even-aged structure, producing a mosaic of differently-aged stands (Hutchinson 1932, Franklin 1973, James 1987, Cornere 1992, Rogers 1995), small patches can be superimposed on larger areas representing an earlier cohort (Cornere 1992). The presence of younger age cohorts amongst older groups of trees would support the notion that lesser storms or other disturbances initiated

local canopy collapse and subsequent recruitment. If the oldest trees all established at a similar time after catastrophic disturbance, subsequent small-scale canopy disturbance and regeneration would lead to a spreading out of ages as proposed in the so-called "lozenge model" of cohort structure (Ogden & Stewart 1995). Small, even-aged patch structure in plot 2 (Fig. 4) supports the notion of intermittent regeneration in small patches (up to c. 1000m²) within an older cohort of trees. In plots 1 and 3, trees of both age cohorts were interspersed, suggesting that regeneration of the younger cohort occurred amongst surviving older trees.

The predominance of the 500-year-old age class for *D. cupressinum* and the 200-350-year age class for *P. ferruginea* is interesting. Other workers have noted that *P. ferruginea* tends to become established 100-200 years after *D. cupressinum* (Six Dijkstra *et al.* 1985, Lusk & Ogden 1992). It is possible that partial breakdown of the canopy after disturbance may, in many instances, create openings that are too small for the light-demanding *D. cupressinum* to regenerate but allow for recruitment of the apparently more shade-tolerant *P. ferruginea*.

The continuous regeneration pattern of the hardwoods *Weinmannia racemosa* and *Quintinia acutifolia* contrasts with the intermittent regeneration pattern evident in the conifers. This pattern of regeneration is consistent with other published studies for *Weinmannia* and *Quintinia* in Westland in a range of forest types (e.g. Stewart & Veblen 1982, Duncan 1993). Furthermore, both species regenerate vegetatively in the absence of disturbance.

Comparison with forest dynamics on the terraces

Cornere (1992) identified five periods of *D. cupressinum* cohort establishment in the terrace forest he studied within the last 700 years (250, 300-350, 400, 500, and 650-700 years ago). A cohort that established c. 500 years ago dominates the age-class distributions of *D. cupressinum* on the moraines (Fig 5a). The dominant period of cohort establishment on the terraces, however, was 250 years ago, resulting in variation in the peak periods of establishment between the terraces and moraines by several centuries (Fig. 5a). The disturbance(s) that initiated the 250-year *D. cupressinum* cohorts on the terraces either did not affect the for-

Table 3: Percentage of total no. of stems of each species occurring on different substrates.

Species	Plot	Floor	Mound	Log	Stump	Pit	Tree fern	n
D. cupressinum	1	100.0						26
	2	100.0						44
	3	100.0						50
P. ferruginea	1	88.2	11.8					34
	2	70.8	20.8	4.2		4.2		24
	3	91.7	8.3					12
Weinmannia racemosa	1	69.3	22.0	3.2	4.5	1.0		309
	2	71.3	22.8	3.3	2.2	0.3		359
	3	77.9	10.4	7.1	3.8		0.8	240
Quintinia acutifolia	1	81.8	15.9		2.3			44
	2	66.3	30.1		3.6			83
	3	72.7	5.5	10.9	5.5		5.5	55
Elaeocarpus hookerianus	2	89.5	10.5					38
	3	100.0						16
Myrsine australis	1	64.5	22.6		12.9			31
	2	43.8	50.0		6.3			16
	3	25.0	50.0		25.0			4
Dicksonia squarrosa	1	73.7	21.1	5.3				19
	2	82.6	15.3	1.4	0.7			144
	3	86.5	7.7	4.5	0.6		0.6	156

est on the moraines, or at least not catastrophically, as there was no resulting pulse of *D. cupressinum* establishment. It is possible, however, that the forests were partially damaged, as many of the shade-tolerant *P. ferruginea* on the moraines established at the time perhaps in small disturbance openings beneath a surviving *D. cupressinum* canopy (Fig. 5b).

The young *D. cupressinum* that were present on the moraines were mostly in areas of canopy collapse on the most poorly-drained deep organic soils of plot 2. Cornere (1992) also found the youngest cohorts of *D. cupressinum* on the deep and poorly-drained soils on the terrace he studied. Cornere (1992) suggested that forests on poorly-drained surfaces are predisposed to windfalls, causing canopy openings large enough to allow *D. cupressinum* establishment. If the same disturbance event caused less canopy damage and resulted in the formation of smaller openings on the better-drained moraine crests, the establishment of shade-tolerant *P. ferruginea* would be more likely, a pattern that we observed in plot 1.

Regional disturbance perspectives

Stands with similar age cohorts have been documented in several areas of Westland, both in the uplands on debris deposits (e.g., *Libocedrus bidwillii*, Stewart & Rose 1989, Wells *et al.* in press), and on fluvio-glacial terraces of the lowlands (e.g., *Dacrycarpus dacrydioides*, Duncan 1991, 1993; and *Dacrydium cupressinum*, Cornere 1992, Rogers 1995). Stands containing these age classes established on terraces on the lowlands after windthrow (Cornere 1992, Rogers 1995) or flooding (Duncan 1991, 1993). On the moraines, the most likely disturbances to initiate regeneration would be treefalls caused by windstorms. Another possibility is that cohorts established after major earthquakes along the Alpine Fault. Stands established on extremely poorly-drained and essentially liquid soils on terraces are likely to topple over large areas with severe lateral ground shaking from earthquakes because of the rooting patterns and low strength root/soil attachment. On the more well-developed and better-drained soils of the moraines tree toppling is also likely, as was observed on well-drained hillslopes in the *Nothofagus* forests of inland Canterbury after the Arthur's Pass earthquake in 1994 (Rob Allen, pers. comm.). Although it is speculative to suggest that the stands sampled in this study could have established after a major earthquake, the presence of similar age classes to those in other areas of Westland is intriguing and worthy of further investigation.

Relevance to forest management practices

There are a number of aspects of the regeneration ecology of these forests that are relevant to forest management. They include:

1. At an individual plot or perhaps, even stand level, the *Dacrydium* forests on the moraines do not appear to be all-aged. Rather, they contain age cohorts of trees that reflect regeneration after intermittent natural disturbances. Further age structure studies would need to be conducted to determine the extent to which this pattern is characteristic of the moraines over a much wider area of Saltwater forest.

2. Any management system must take into account variation in growth rate on different sites. The measured radial growth rate of *Dacrydium cupressinum* (0.7 mm/year) varied little from recorded growth rates on the adjacent terraces where Cornere (1992) and Rogers (1995) recorded values of 0.6 - 0.8 mm/year. However, *Prumnopitys ferruginea* (0.6 mm/year) on the moraines grew faster than on the terraces (0.4 mm/year, Cornere 1992, Rogers 1995).

3. Patterns of species replacement in already established stands are determined by drainage and the degree of mortality caused
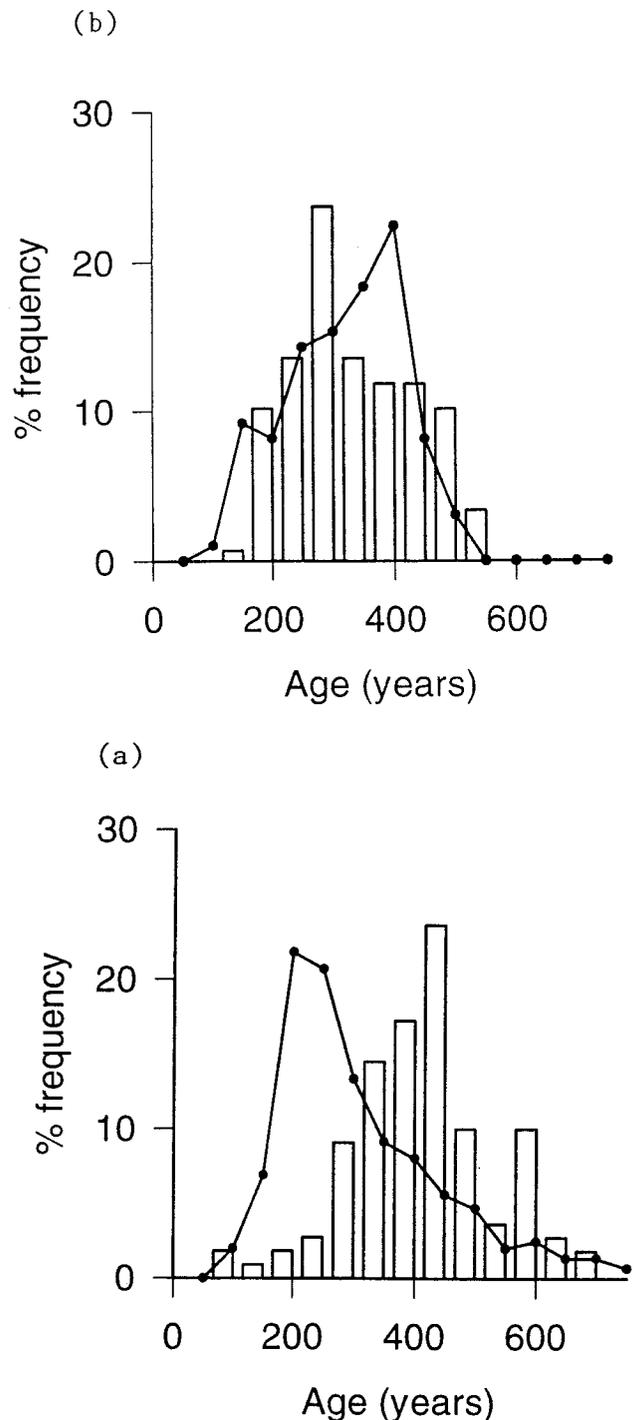
Figure 5. Age-class distributions (percent frequency) for (a) *D. cupressinum* on the moraines (bars) and on the terraces (solid line, after Cornere 1992) and *P. ferruginea* on the moraines (bars) and on the terraces (solid line, after Cornere 1992).

by natural disturbances. If canopy mortality is low and scattered, *Prumnopitys ferruginea* may become a more important component of the forest at the expense of *Dacrydium cupressinum*. If canopy mortality is concentrated in patches of several trees (e.g., > 0.1 ha), even-aged groups of *Dacrydium* and/or *Prumnopitys* are more likely to establish. The degree to which the forest canopy is destroyed by natural disturbances appears to be related to the drainage and soil characteristics of the landform on which the forest is located.

4. The differences in structure and disturbance history between the forests of the terraces and moraines are not as clear-cut as

has been suggested. Although more frequent stand devastating disturbances on the terraces occasionally produce even-aged *D. cupressinum* cohorts in large patches (up to 20 ha), less frequent stand-devastating disturbances and partial canopy destruction also results in complex and intermingled age cohorts (e.g., Cornere 1992). This complex pattern of small even-aged cohorts suggests that current management practices on the terraces and moraines that concentrate on the removal of small groups of trees may be appropriate if it is desirable to mimic the natural regeneration pattern (as suggested by Richards 1994). Naturally, however, even-aged cohorts appear to establish only once every one to two centuries.

Acknowledgements

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ANNUAL CONFERENCE PROMISES TO BE INTERESTING

The 1998 NZIF Conference and AGM is being held in Wanganui from April 20 to 22 with the theme of "Investment in NZ Forestry". Organising Committee Chairman Ian Moore says that the Conference promises to hold a lot of appeal not only due to its location in part of the country rarely visited by the forestry fraternity but more importantly as a forum in which the current Asian economic crisis can be discussed in depth.

An interesting array of speakers will cover investment options from its importance in the NZ economy through to Maori investment in forestry and the importance of investing in indigenous vegetation. The Minister of Forests, Lockwood Smith, will make the concluding speech on the Government's role in forestry investment.

Mr Moore says that the speeches will be complemented by an interesting trip through the Wanganui hinterland looking at the forestry development that has occurred over the last 25 years.

A special event coincidental with the AGM will be linked to the century old riverboat industry.