

Structure and canopy tree species regeneration requirements in indigenous forests, Westland, New Zealand

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Glenn H. Stewart

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Structure and canopy tree species regeneration requirements in indigenous forests, Westland, New Zealand

Glenn H. Stewart

Ecology & Entomology Group, P.O. Box 84, Lincoln University, Canterbury, New Zealand

ABSTRACT

This report reviews the literature on regeneration requirements of main canopy tree species in Westland. Forests managed for production purposes have to be harvested in an ecologically sustainable way; to maintain their natural character, harvesting should facilitate regeneration of target species and ensure that their recruitment is in proportion to the extent of extraction. The reasons for species establishing at any point in time are unclear; however, they are probably related to the availability of suitable microsites for establishment, the size of the canopy openings formed by disturbance, and whether or not seeds are available at or around the time of the disturbance. Age structures from throughout Westland show that extensive, similar-aged, post-earthquake cohorts of trees are a feature of the region. This suggests that infrequent, massive earthquakes are the dominant coarse-scale disturbance agent, triggering episodes of major erosion and sedimentation and leaving a strong imprint in the forest structure. In other forests, flooding and catastrophic windthrow are major forms of disturbance. The findings suggest that, in general, large disturbances are required for conifer regeneration. This has implications for any sustained yield management of these forests if conifers are to remain an important component. Any harvesting should recognise the importance for tree establishment of: forest floor microsites, such as fallen logs and tree tip-up mounds; and the variable way in which canopy gaps are formed. Harvesting should maintain the 'patchy' nature of the natural forest—large patches of dense conifers interspersed with more heterogeneous patches of mixed species.

Keywords: indigenous forests, regeneration requirements, species differences, canopy gaps, microsites, Westland, New Zealand.

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1. Introduction

The Forest Amendment Act (FAA) 1993 requires that the natural character of forests managed for production purposes be maintained, i.e. that harvesting is ecologically sustainable. One aspect of the maintenance of the natural character is that harvesting facilitates regeneration of the target species, and that recruitment of the species is in proportion to the extent of extraction. Species harvested under the FAA legislation, such as rimu, miro, kahikatea, matai, and beech, all have different ecological requirements for regeneration and recruitment. These should be reflected in available substrates for establishment and in the size of openings created by harvesting (i.e. coupe size or the area harvested). Single-tree extraction may be appropriate for some species, whereas others may require a greater level of canopy opening. This will also depend on the 'age' or stage of development of the forest to be harvested, i.e. the harvesting regime in a pole stand may be different to that of a mature, mixed species forest.

There is a considerable body of information on forest structure for indigenous forests in Westland. Much of this has been gathered in the course of survey and scientific research, both in virgin forests and in forests managed for timber production in the past (e.g. Saltwater and Okarito forests) by universities, Crown Research Institutes, the New Zealand Forest Service, the Department of Conservation (DOC), and more recently Timberlands West Coast Limited. The bulk of this structural information is based on tree diameter and, in considerably fewer instances, tree age. Although it is possible to infer patterns of forest development from tree diameter data (if a significant relationship between tree diameter and age exists), information on tree age and spatial location of individual trees enables a more robust interpretation of regeneration patterns. There is also a good deal of information on substrate requirements for regeneration of the dominant canopy tree species in natural forests. What is lacking is information on natural canopy opening ('gap') sizes for most of the forests, although inferences can be made on likely gap sizes from tree age and spatial data that have been collected in a few studies. In some instances, the sizes of patches of even-aged trees that establish after natural disturbances can give an indication of the size of natural openings.

The amount of information available varies widely for different forest types, depending on the research effort in different parts of Westland, and the particular aspect of research investigated. The best information available on regeneration requirements and natural gap sizes is from relatively few sites that have been the subject of intensive research, such as the north Westland red-silver beech forests where a concentrated research effort has been conducted since 1986/87, and the coniferous forests on outwash surfaces in south Westland.

This report reviews the literature in three key areas of indigenous forest ecology for Westland that are relevant to sustainable forest management:

1. Regeneration requirements of main canopy tree species – primarily substrate establishment requirements but, in some instances, establishment patterns in gaps.
2. Natural gap sizes that occur in old-growth forests (where available).
3. The area affected by natural disturbances as reflected by patch sizes of relatively even-aged groups of trees.

2. Review of relevant ecological literature

2.1 NORTH WESTLAND

2.1.1 Inland valleys

Valley floor red beech–silver beech forests

The most striking feature of red beech–silver beech forests is the canopy dominance of red beech (*Nothofagus fusca*). Silver beech (*N. menziesii*) is less conspicuous in the canopy but numerically dominates the lower tiers, often forming a dense sapling layer in the understory. The numerical dominance of silver beech, especially of small stems, led many ecologists in the past to conclude that silver beech was replacing ancient red beech. However, the

presence of red beech of a range of diameters indicates frequent and sporadic regeneration, a pattern verified by age data with tree ages up to around 400 years (Fig. 1.) (Stewart & Rose 1990; Stewart 1992). The high number of small silver beech and declining numbers in larger size classes suggests a more continuous regeneration pattern, but the lack of trees > 200 years indicates that, of the many silver beech that establish and survive, few reach the main canopy (Stewart & Rose 1990).

Tree species differ in their requirements for germination and establishment, leading to species seedling preferences for different microsites. In the Maruia Valley red beech–silver beech forests, elevated substrates (logs, stumps and mounds) constitute only c. 31–37% of the available microsites for seedling establishment (Table 1). However, from 50% to over

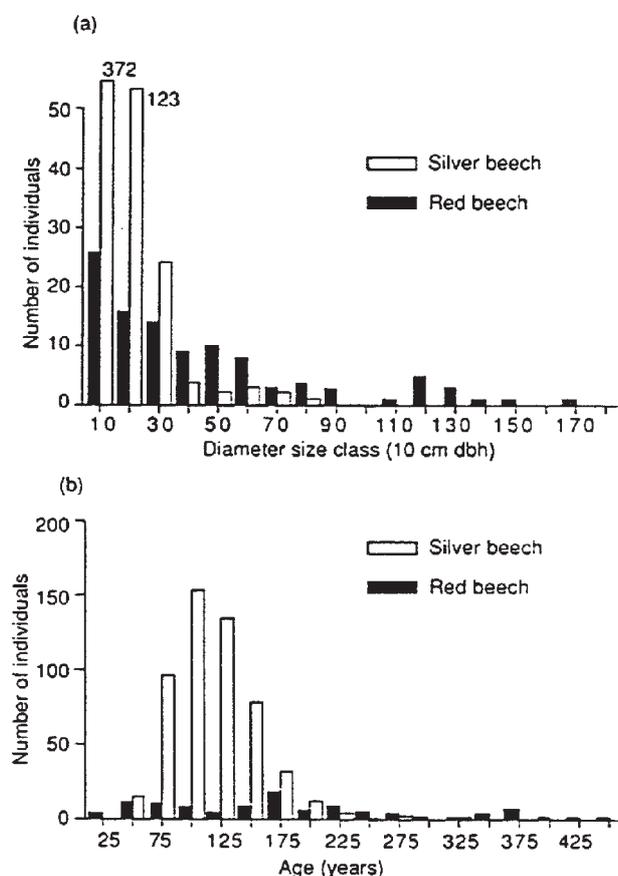


Figure 1. (a) Diameter and (b) age class distributions for red beech (*Nothofagus fusca*) and silver beech (*N. menziesii*) in an old-growth red beech–silver beech forest, Maruia Valley, north Westland. Red beech of all diameters and ages are present but the numerous small silver beech are quite old. After Stewart & Rose (1990).

TABLE 1. FREQUENCY OF DIFFERENT MICROSITES IN TWO PLOTS, MARUIA VALLEY, NORTH WESTLAND. MODIFIED FROM STEWART & ROSE 1990.

PLOT NO.	PLOT SIZE (m ²)	NO. OF SAMPLE POINTS	FREQUENCY (%)				
			FOREST FLOOR	LOG	STUMP	MOUND	PIT
1	4800	662	56	17	7	13	6
2	3000	332	63	13	8	10	6

75% of both silver and red beech seedlings < 45 cm tall occur on these microsites (Stewart & Rose 1990). Furthermore, beech seedling survival is greatest on elevated microsites, particularly in wet forests, where they provide 'safe sites' above a dense competing fern understorey.

Variation in the life history attributes of species means that they can exploit gaps in different ways. In the Maruia forests for example, Runkle et al. (1997) compared the growth responses of pairs of red and silver beech that had established in the same gaps. Red beech height growth was rapid, often outperforming silver beech, whether it established at the same time or after silver beech (Fig. 2). Silver beech, because of its more shade-tolerant nature, can vary its growth rate depending on the resources available for growth. If an opening in the canopy becomes available silver beech will respond with increased height growth but if the opening closes silver beech has the capacity to remain in the sub-canopy until another opening occurs whereupon it could increase in height growth again. The more light-demanding red beech would be more likely to die if suppressed for long periods of time. Furthermore, within gaps, Runkle et al. (1995) found that the two beech species partitioned the gap

environment, with *N. fusca* having maximal radial growth in the gap centre while *N. menziesii* grew faster to the south of gap centre.

Dead standing trees and gaps formed by bole snap dominate the type of gap formation for these forests. *N. menziesii* saplings and small trees dominate gaps formed by dead standing trees, as they can increase in height growth in partial shade while *N. fusca* seedlings and saplings are more abundant in more well-light gaps formed by uprooting or bole snap (Table 2). The number of gapmaker trees per gap ranged from 1 to 14 at the 3 Maruia study sites but on average, between 3 and 5 gapmaker trees contributed to gap formation in a single gap. Few gaps were formed by only one gapmaker tree.

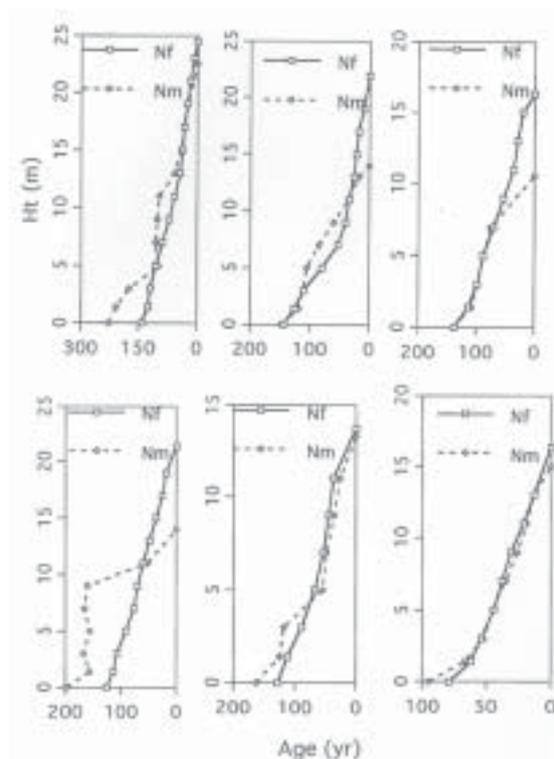


Figure 2. Height growth curves for pairs of *Notbofagus fusca* and *N. menziesii* canopy trees that established in the same gap. Nf = *N. fusca*, Nm = *N. menziesii*. X-axis indicates years before 1988 AD. After Runkle et al. (1997).

TABLE 2. *Notbofagus* SAPLING AND SMALL TREE (< 5 cm dbh) DENSITY (no./ha) IN GAPS FORMED BY DIFFERENT GAPMAKERS, MARUIA VALLEY, NORTH WESTLAND (AFTER STEWART ET AL. 1991)

GAPMAKER TYPE	<i>N. fusca</i>	<i>N. menziesii</i>
Dead standing	43 ⁺	193*
Bole-snapped	235 ⁺	244
Uprooted	342 ⁺	189
All gaps combined	199	218*

⁺ Significant difference ($P < 0.05$) for *N. fusca* between gapmaker types.

* Significant difference ($P < 0.05$) between *N. fusca* and *N. menziesii* within the same gapmaker types.

In the Maruia forests, natural ‘expanded’ gaps (*sensu* Runkle 1982) range in size from c. 200 to 1000 m² but most are around 200 to 400 m² (Fig. 3) (Stewart et al. 1991). *N. menziesii* saplings and small stems dominate in gaps < 400 m² whilst *N. fusca* becomes more common in gaps larger than 400 m² (Fig. 4) (Stewart 1992).

At the three sites studied at Maruia, the percentages of the forest in ‘canopy’ gaps (*sensu* Runkle 1982) varied from c. 4% to 15% and for expanded gaps from c.11% to 30%. The lack of identifiable gaps > 60 years old (only one gap at Rough Creek of 68 years (Stewart et al. 1991)) and data on height/age relationships for even-aged *N. fusca* stands in north Westland (Moorhouse 1939; Smale et al. 1987; Stewart & Rose 1990) suggest that 60 years is an approximate estimate for the time taken for most gaps to fill. However, canopy lateral crown expansion can be rapid, even in small gaps, resulting in gap closure in as little as 5–10 years for expanded gaps < 400 m² (Stewart unpubl. data).

The disturbance regime for the three Maruia study localities combined was characterised by small gaps. Canopy gaps covered c. 8.5%, and expanded gaps 22% of the land area, remarkably similar estimates to those found in other temperate forests such as the eastern hardwood forests of North America (9.5%

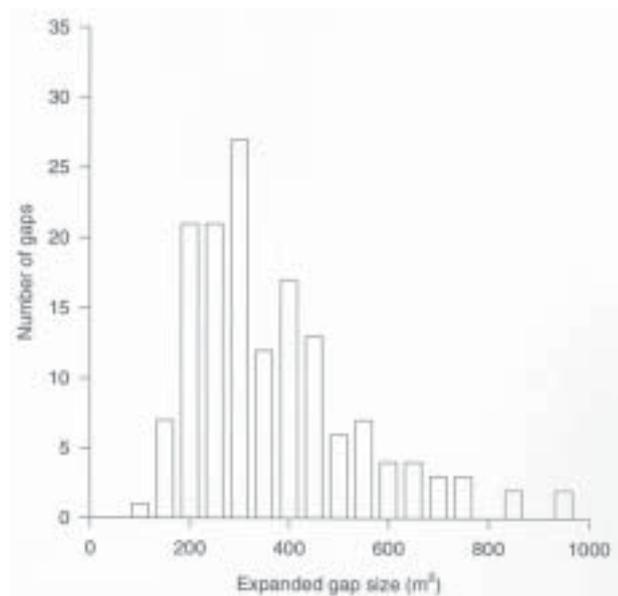


Figure 3. Pooled size class frequency distribution for 150 expanded gaps (*sensu* Runkle 1982) for three localities in the Maruia Valley, north Westland. Graphed from data presented in Stewart et al. (1991).

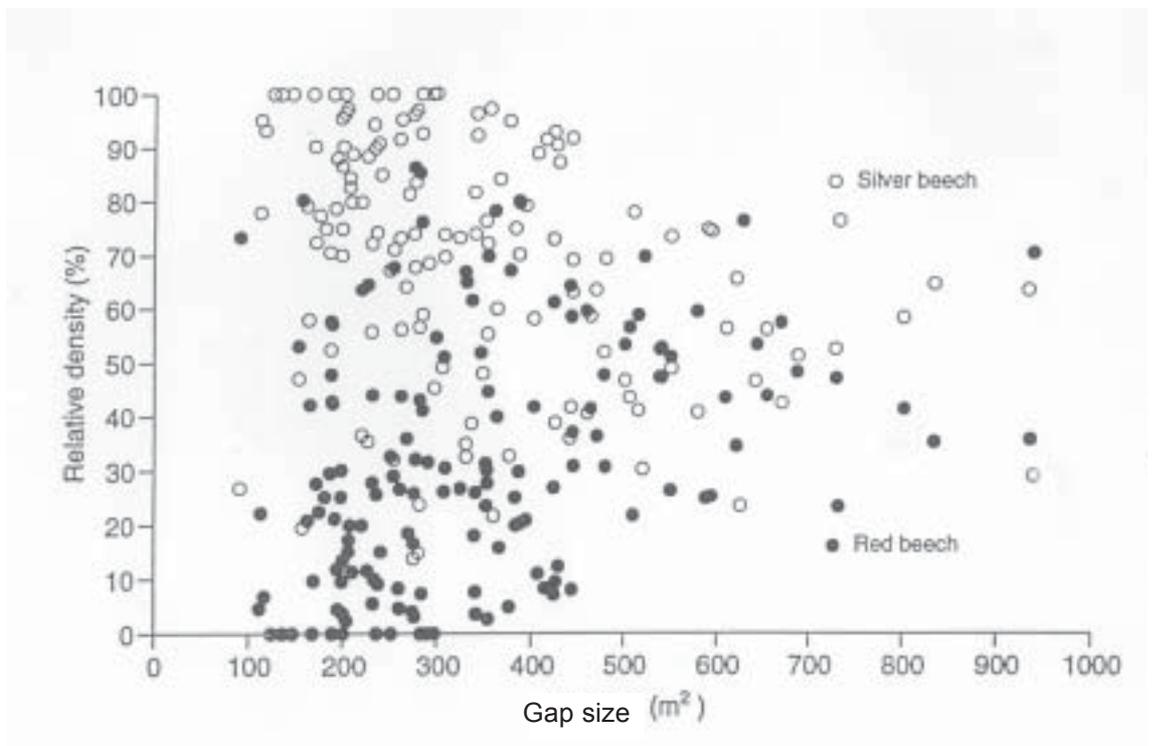


Figure 4. Relative density of red and silver beech saplings and small stems in 150 expanded gaps of various sizes for 3 localities in the Maruia Valley, north Westland. Silver beech outnumbers red beech in most gaps, especially those less than 400 m². After Stewart (1995).

and 21%, respectively (Runkle 1982)) and within the range found for many other temperate forests such as the *Fagus* forests of Japan (see Nakashizuka 1984). This is noteworthy, since direct comparisons are often difficult, as estimates of the percentage of land area in gaps are dependent on a number of factors including: minimum gap size sampled (e.g. 10 m² (Nakashizuka 1984), 20 m² (Stewart et al. 1991)); total area sampled; number of areas sampled; number of gapmakers per gap; crown size of gapmakers and on the definition of 'gap'.

Although large-scale disturbances such as earthquakes and windstorms periodically influence the regeneration dynamics of beech (*Nothofagus*) forests, in north Westland smaller-scale tree-falls are a primary determinant of local (stand-scale) regeneration processes. In forests dominated by *N. fusca* and *N. menziesii*, small tree-fall gaps (< 400 m²) are rapidly captured by the more shade-tolerant silver beech. In larger gaps (up to 1000 m²) red beech attains dominance due to a faster height growth rate. These differences in the regeneration dynamics of the two species mean that silvicultural practices will have to be adopted to mimic as close as possible the natural variation in gap sizes, to maintain the compositional and structural variation typical of a natural forest.

If sustainable management practices can mimic the natural distribution of gap sizes, it is likely that a range of heterogeneous gap environments will be maintained which will maximise biodiversity. This is important because gap size influences the number of species present, larger gaps tending to have a greater number of species than small gaps (Table 3). This is partly because large gaps have greater substrate heterogeneity than small gaps and therefore tend to have greater species richness as indicated by a correlation between gap size and substrate heterogeneity (Duncan et al. 1998).

TABLE 3. CORRELATION COEFFICIENTS OF GAP SPECIES RICHNESS WITH GAP CHARACTERISTICS, MARUIA VALLEY, NORTH WESTLAND.
($n = 32$, after Duncan et al. 1998)

GAP CHARACTERISTICS	CORR. COEFF. (r)
Substrate heterogeneity	0.39 *
Gap area	0.65 ***
Gap age	0.14
Gap shape	0.27
Gap orientation	0.07

* $P < 0.05$, *** $P < 0.001$

Hillslope red-silver beech and hardwoods/podocarps

The forest structures for *N. fusca* and *N. menziesii* on hillslopes (Stewart 1997) are remarkably similar to those of the valley floor forests (Stewart & Rose 1990). Numerous stems in all size-classes from 5 to > 100 cm dbh for *N. fusca* indicates an all-aged structure resulting from sporadic regeneration. An inverse-J shaped size class distribution for *N. menziesii* indicates a more continuous regeneration pattern for this species. Conifers such as *Podocarpus hallii* and hardwoods such as *Weinmannia racemosa* also occur in forests on the hillslopes. *Weinmannia* is often the second most abundant tree in the subcanopy (after *N. menziesii*), constituting up to c. 25% of the basal area in some cases. The way in which *P. hallii* and *W. racemosa* regenerate in these forests is unknown. A detailed investigation of the establishment requirements of these species, especially in relation to variation in understorey cover, is warranted. In contrast to the relatively species-poor valley floor red beech-silver beech forests, the hillslope forest understoreys contain over 22 different sub-canopy tree and shrub species.

As for the valley floor forests, elevated substrates such as logs and tip-up mounds are likely to be important sites for the establishment of *Nothofagus* seedlings, especially because of dense competing fern understoreys and the abundance of competing woody species (see above). A detailed understanding of substrate regeneration requirements for canopy and sub-canopy tree species is lacking for these forests.

Gaps are predominantly formed by bole snapping or tree uprooting, and dead standing tree gaps appear to be less common than in the valley floor forests (Stewart 1997; Stewart et al. 1991). Because of *N. fusca* saplings being less common in gaps formed by dead standing trees than those of *N. menziesii*, and of the greater abundance of gaps formed by bole snap and uprooting on hillslopes, *N. fusca* saplings and small trees are more common than in valley floor forests. In contrast to the valley floor forests, there were generally fewer gapmakers per gap, the number ranging from one to 10 with an average of 2–3 gapmakers per gap.

The proportions of land area in canopy gaps (5.9%) and expanded gaps (16.8%) were similar to those at the nearby terrace site at Station Creek (3.7 and 12.9% respectively, Stewart et al. 1991). Gap size distributions were also similar apart from 1 large gap on the hillslopes of c. 1100 m² (Fig. 5). Many gaps were

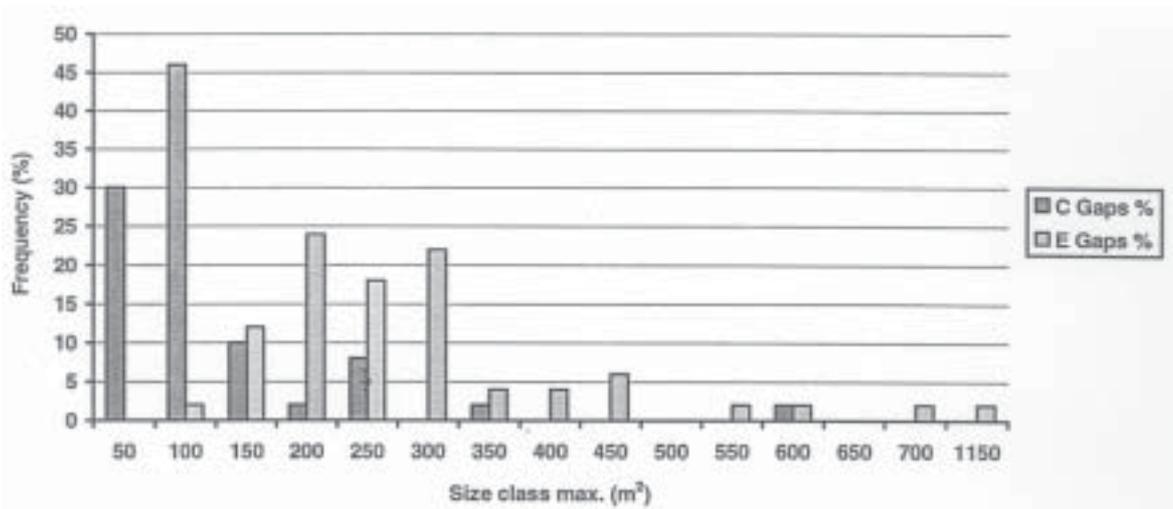


Figure 5. Canopy and expanded gap size class frequency distributions for 50 gaps on a lower hillslope site in the Maruia Valley, north Westland. After Stewart (1997). E = expanded gaps, C = canopy gaps (*sensu* Runkle 1982).

< 10 years old, or in the 40 to 60 years range, although several gaps in excess of 90 years were encountered on the hillslopes as well.

2.1.2 Western valleys

Valley floor forests

1. Old post-glacial terraces, beech-conifer-hardwood forests

Forest structures are complex and reflect the varying responses of the three groups of trees (beeches, conifers, and hardwoods) to natural disturbances. Recent research (Urlich 2000) shows that conifers (e.g. *Dacrydium cupressinum*) regenerate in large canopy openings in response to infrequent large disturbances such as earthquakes and storms, whereas the beeches and other hardwoods regenerate in even-aged groups in smaller openings after lesser disturbances. For example, in a very poorly drained stand at Mt Harata in the Grey Valley, north Westland (Urlich 2000) found large patch sizes for several age groups of *Dacrydium cupressinum* and relatively small patches of *Nothofagus menziesii* (Fig. 6). Apparently, the *D. cupressinum* had regenerated after a large storm event c. 300 years ago, while relatively even-aged groups of *N. menziesii* had established in response to a variety of lesser disturbances on at least four occasions over the last four centuries. Whilst large patch sizes appear to be the norm for conifers in these forests (especially *D. cupressinum*), there are occasions where conifers can regenerate in smaller openings, particularly on poorly drained sites. For example, in a poorly drained plot at Mt Harata, small patches (c. 50-100 m²) of *Dacrycarpus dacrydioides* were evident, and had regenerated in small canopy openings caused by a storm c. 125 years ago (Urlich 2000).

Species responses, and hence forest structure may vary markedly. At Mt. Harata, different species can regenerate in response to the same disturbance depending on local site conditions, especially soil drainage (Urlich 2000). For example, a disturbance approximately 200 years ago resulted in the regeneration of kahikatea (*Dacrycarpus dacrydioides*) on very poorly drained sites and the hardwood kamahi (*Weinmannia recemosa*) on well-drained soils (Table 4).

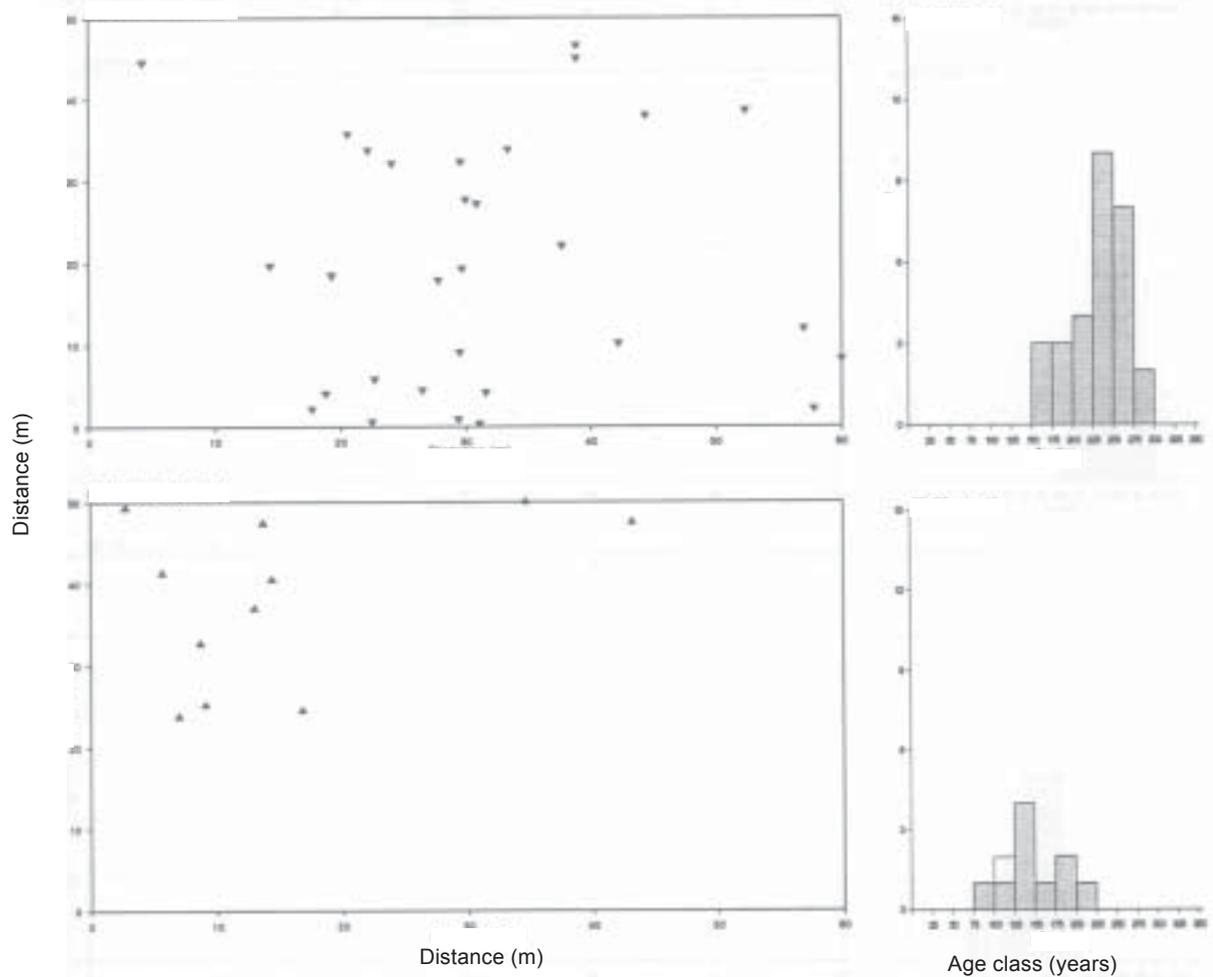


Figure 6. Stem distribution maps and age-class frequency distributions for different age cohorts of *Dacrydium cupressinum* in conifer/beech/hardwood forest on a very poorly drained terrace site, Mt Harata, north Westland. After Urlich (2000). (Upper graphs) Group 2, age 151-275 years ($n = 32$). (Lower graphs) Group 3, age 95-213 years ($n = 11$). Unfilled bars are for un-aged stems whose ages were predicted from age/dbh regression equations.

Alternatively, on the same site, different suites of species may establish at different times as a result of different disturbances. For example, on a poorly drained site in the Grey Valley following what was most probably an earthquake c. 375 to 425 years ago, a pulse of conifer (*D. cupressinum*, *D. dacrydioides*) and beech (*N. menziesii*) establishment occurred, while 200 years on the same site after what was probably a storm event, predominantly *N. menziesii*, *W. racemosa* and *Q. acutifolia* established (Table 4).

Disturbances also appear to be critical in providing the environmental heterogeneity that enables species to coexist in these forests by making available a range of microsite types for different species to establish. There were two broad groups of species that partitioned microsites according to drainage characteristics: *Nothofagus* and hardwoods on well drained microsites, and conifers and *Elaeocarpus bookerianus* on poorly drained microsites. On poorly drained microsites, *Dacrydium*, *Dacrycarpus* and *E. bookerianus* were associated with forest floor sites or around pit edges. The availability of better-drained sites such as logs and mounds also enables species to establish in areas where they would not normally be found, such as *N. fusca* on these sites in poorly drained areas. The type of disturbance and the way in

TABLE 4. DISTURBANCES, DISTURBANCE DATES, AND TREE SPECIES ESTABLISHMENT, LOWLAND TERRACE PODOCARP-BEECH-HARDWOOD FOREST, GREY VALLEY, NORTH WESTLAND (AFTER URLICH 2000).

DISTURBANCE	DATE (years BP)	REGENERATION RESPONSE		
		Well drained	Poorly drained	Very poorly drained
Storm	100-125	<i>Nothofagus fusca</i> <i>N. menziesii</i> <i>Weinmannia racemosa</i> <i>Quintinia acutifolia</i>	<i>N. fusca</i> <i>N. menziesii</i> <i>Dacrycarpus dacrydioides</i> <i>Elaeocarpus bookerianus</i>	
Storm?	200	<i>W. racemosa</i>	<i>N. menziesii</i> <i>W. racemosa</i> <i>Q. acutifolia</i>	<i>Dacrydium cupressinum</i> <i>D. dacrydioides</i> <i>N. menziesii</i>
	275-300	<i>N. fusca</i> <i>N. menziesii</i> <i>W. racemosa</i> <i>Q. acutifolia</i>	<i>N. menziesii</i> <i>W. racemosa</i>	<i>D. cupressinum</i> <i>D. dacrydioides</i> <i>Libocedrus bidwillii</i> <i>Podocarpus ballii</i>
Earthquake	375-425	<i>N. menziesii</i>	<i>D. cupressinum</i> <i>D. dacrydioides</i> <i>N. menziesii</i> <i>N. fusca</i>	<i>D. dacrydioides</i> <i>N. menziesii</i>
?	650		<i>D. cupressinum</i>	
?	850		<i>D. cupressinum</i>	

which it influences tree mortality also has an influence on available microsites. For example, blowdown provides mound and log microsites that are preferred establishment sites for *Nothofagus* seedlings, but if trees die standing (as a result of insect attack for example) no such microsites will be available for a number of years for these species.

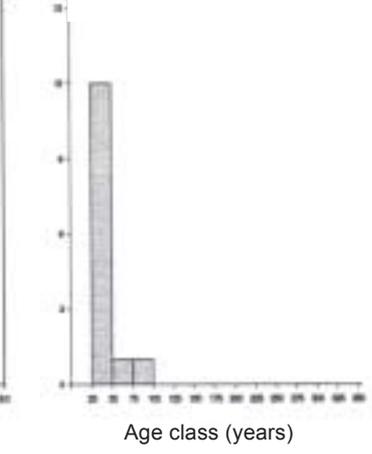
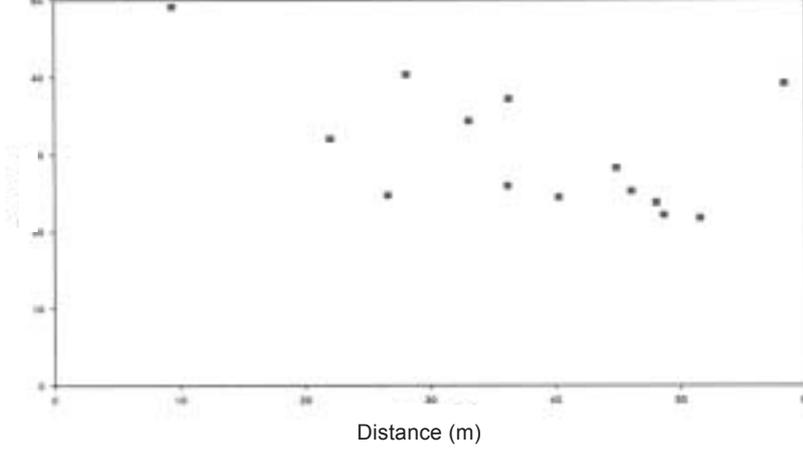
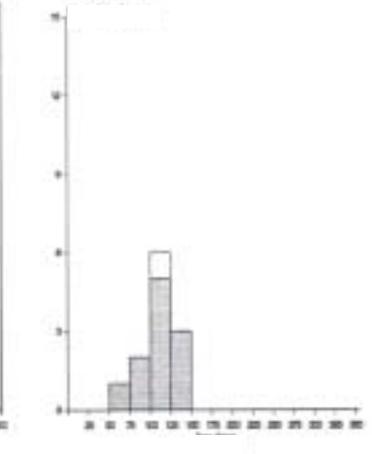
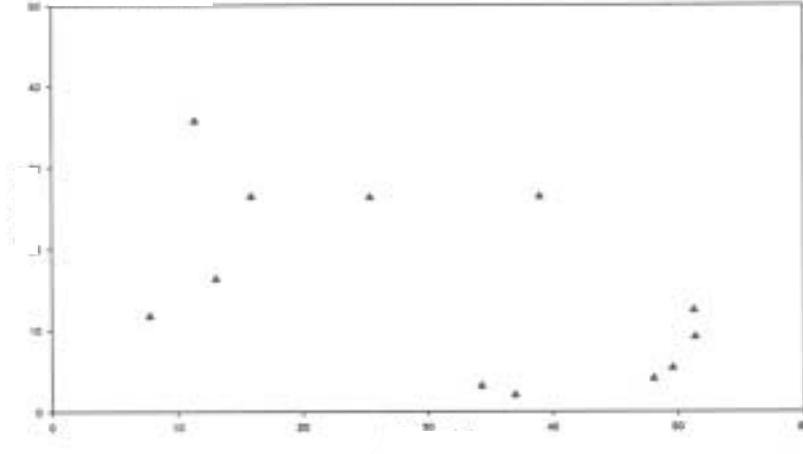
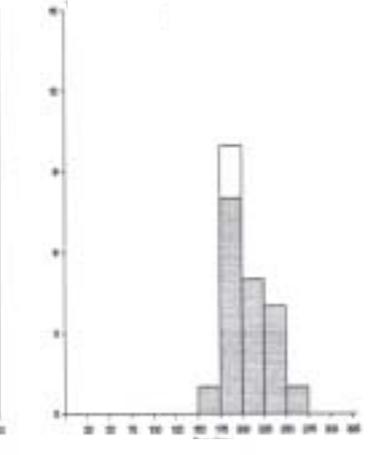
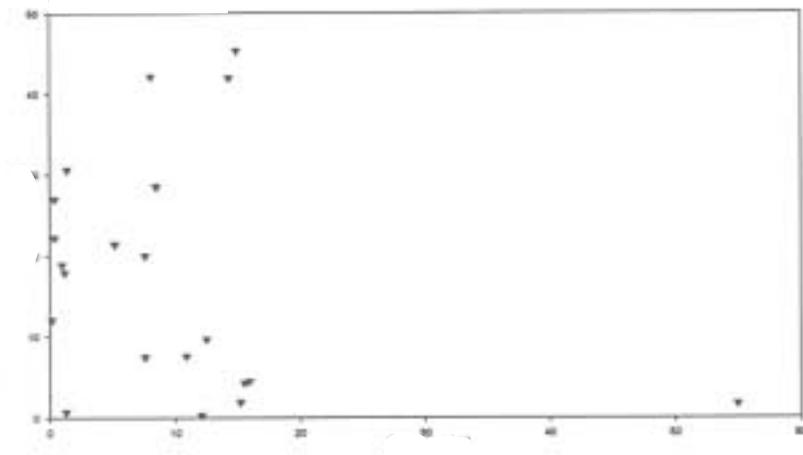
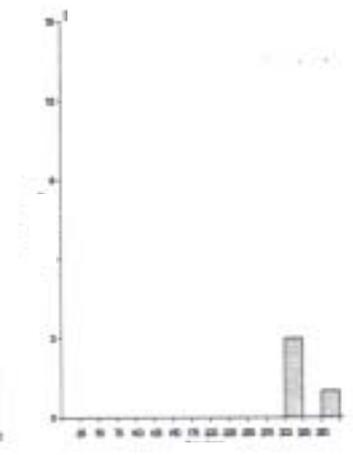
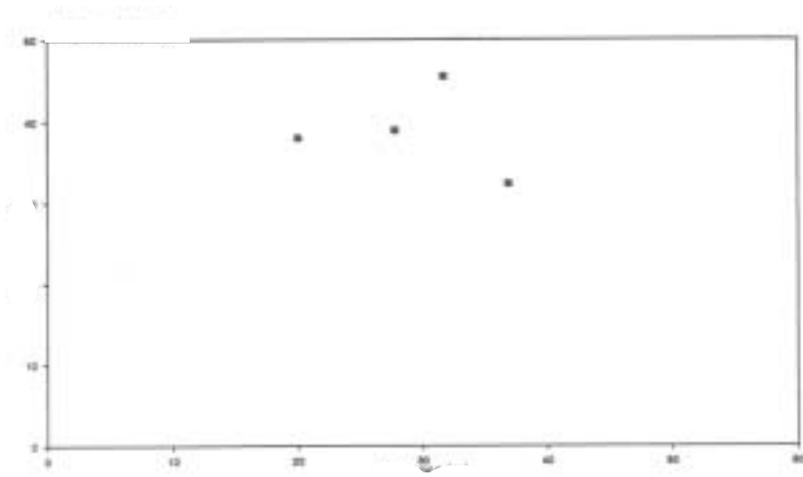
The reasons for species establishing at any point in time are unclear but are likely to be related to the availability of suitable microsites for establishment, the size of the canopy openings formed by disturbance, and whether or not seeds are available at or around the time of the disturbance. The beeches seed heavily during 'mast seeding' events that occur every 5-7 years, but produce few viable seed in between (Wardle 1984; Ogden et al. 1996). Further research on the requirements for seedling establishment is required.

Similar forest structures were noted by Burrows et al. (1975) further south, near Haupiri. Large, old *D. cupressinum* were emergent over a canopy of three beech species and hardwoods, and few small *D. cupressinum*. The ages of several of the canopy *D. cupressinum* indicate establishment around 1600 AD, a similar time to those that established in the Mt Harata area after an earthquake (Urlich 2000). Furthermore, the beeches present (*N. fusca*, *N. truncata*, *N. solandri*) exhibited small-group even-aged structures, similar to those found at Mt Harata (Urlich 2000).

Figure 7. (opposite) Stem distribution maps and age-class frequency distributions for different age cohorts of *Nothofagus menziesii* in conifer/beech/hardwood forest on a very poorly drained terrace site, Mt Harata, north Westland. After Urlich (2000).

Graphs, from top to bottom: Group 1, age 305-384 years ($n = 4$); Group 3, age 174-282 years ($n = 21$); Group 4, age 86-147 years ($n = 12$); Group 5, age 25-80 years ($n = 14$). Unfilled bars are for un-aged stems whose ages were predicted from age/dbh regression equations.

Distance (m)



Distance (m)

Age class (years)

Compared to the relatively simple *Maruia* beech forests, the conifer-beech-hardwood forests in north Westland are extremely complex. Any sustainable management of these forests would need to account for this complexity. The apparent but variable nature, timing and severity of disturbances in these forests, and the complex species responses to these disturbances, may mean that any form of sustainable management will have to be precautionary and developed along with or after further research (Stewart et al. 2001).

2. Young terraces

Various admixtures of conifers, beeches and hardwoods occur on recent alluvial terraces in north Westland, but few studies have addressed the structure and dynamics of these forests. June (1982) noted the dominance of large, old stems of *D. cupressinum* with few young trees and saplings in these forests and those on adjoining lower hillslopes, but he interpreted age-class peaks between 300 and 600 years ago as representing continuous regeneration that was interrupted by a major disturbance c. 300 years ago, rather than these peaks representing past responses to large disturbances. Furthermore, he suggested that vigorous regeneration of hardwoods after this disturbance led to the suppression of *D. cupressinum* regeneration. Based on our current knowledge, it now seems likely that the age-class distributions that June described reflect past disturbances such as earthquakes.

In the Grey Valley south of Reefton, Stewart et al. (in prep.) sampled a forest remnant on recent soils derived from glacial outwash and alluvium at Stony Creek ('Rakanui'). The forest was dominated by emergent *D. cupressinum* and occasional *Prumnopitys taxifolia* over a main canopy of *Nothofagus fusca* and *N. menziesii*, and a few *P. ferruginea*. Forest size- and age-structure analysis revealed that the conifers and beech were even-aged and had established after flooding. Some of the *Dacrydium* had survived several floods and were several centuries older than the oldest *N. fusca*. Many of the emergent *Dacrydium* and large canopy *N. fusca* were dying of old age, and *N. fusca* was replacing them in the resultant canopy openings. Logs were crucial establishment sites for beech regeneration, above the dense *Blechnum discolor* understorey. In the absence of large disturbances such as flooding events it appears that beech species will replace the conifers in these alluvial forests. Recent terraces immediately adjacent to Stony Creek that were dominated by dense regeneration of *N. fusca* < 100 years old contained some young *Dacrydium*, indicating once again that flooding promotes *Dacrydium* regeneration.

Hillslope beech/conifer/hardwood forests

The beeches, *N. fusca* and *N. truncata* exhibit predominantly 'gap-phase' regeneration in these forests (June 1982); thus, forests in which they predominate are likely to consist of small even-aged patches of various ages. Smale et al. (1987) sampled stands in north Westland dominated by these species, ranging in age from 20 to 100 years. They provide invaluable information on a range of stand parameters including growth rate but no data on gap or 'patch' size.

Occasional catastrophic blow-downs are also a feature of these hillslope forests (Smale et al. 1987, Stewart et al. 1993). The resultant pole stands may be dominated by *N. fusca* and/or *N. truncata* with occasional conifers and in some

instances older conifers that survive the blowdown events. After blowdown, the majority of beech seedlings and saplings establish on the down logs and associated root plates (Urlich 2000). Patches of trees that establish after these blowdowns may vary in size from a few hundred square metres to several hectares (Stewart et al. 1993, Stewart unpubl. data).

It is unclear how the conifers regenerate in these forests. Occasional *Dacrydium cupressinum* occur at low elevations and *Podocarpus hallii* at mid to high elevations (Stewart et al. 1993). When conifers are found in these stands they frequently occur in canopy openings but there are no data on gap sizes required for regeneration. The hardwoods, *Weinmannia racemosa* and *Quintinia acutifolia*, which are of intermediate to low shade tolerance, numerically dominate canopy openings but are generally suppressed by the faster growing beeches.

2.1.3 Coastal forests

The structure and regeneration dynamics of the coastal forests of north Westland have received almost no scientific investigation. Dobson et al. (1977) gathered some basic structural and compositional data for a small kamahi stand near Westport. They document adequate regeneration for most species such as *Weinmannia racemosa*, *Myrsine salicina*, *Melicytus ramiflorus*, and *Hedycarya arborea*, resulting in apparently balanced all-aged populations. No tree age data, however, were collected. Conifers occurred sporadically within the stand and the authors considered that their regeneration was adequate, although no explanations were given as to how they were regenerating.

2.2 CENTRAL WESTLAND

2.2.1 Inland valleys

Numerous vegetation surveys have been conducted in these forests by the Forest Service and subsequently by the Forest Research Institute over the last 50 years. The extensive nature of the data collection and the basic stand data gathered at each plot site provides a broad picture of forest compositional and structural variation for many, if not most inland forests catchments. However, detailed structural information at any one site is limited due to the small plot size (20 × 20 m). No data are generally gathered on disturbance history, regeneration requirements or on gap size.

Valley floor forests

These forests have been included in surveys (as above) but once again detailed information on forest structure, regeneration requirements or on gap size are lacking.

In a regional study of the regeneration ecology of *Libocedrus bidwillii*, Veblen & Stewart (1982) sampled several stands at Cedar Flat in the Toaroha catchment, a tributary of the Hokitika River. They found that *Libocedrus* regenerated in even-aged patches in response to flooding on the alluvial terraces. The hardwoods *Metrosideros umbellata* and *Weinmannia racemosa*

regenerated in a gap-phase manner and, especially on wet sites, required well-lit elevated sites such as logs for successful regeneration.

Hillslope forests

Few studies have been conducted that contain data on forest structure and regeneration requirements of inland hillslope forests. Stewart & Veblen (1982) investigated the structure and regeneration ecology of mid-slope *Metrosideros umbellata*/*Weinmannia racemosa* (southern rata/kamahi) forests in the Taramakau catchment. In old-growth forests, *M. umbellata* size-class distributions containing a range of tree diameters indicated intermittent regeneration in canopy gaps. Seedlings occurred on elevated microsites such as logs and as epiphytic seedlings in the crowns of conifers such as *P. ballii*. *W. racemosa* seedlings also occurred in canopy openings, but *Weinmannia* also reproduced vegetatively by epicormic sprouting. The conifers (primarily *P. ballii* and *Libocedrus bidwillii*) exhibited even-sized diameter frequency distributions indicative of even-aged populations that had established in large canopy openings, probably formed by blowdown. The dependence on catastrophic disturbances such as landsliding and blowdown for the regeneration of *L. bidwillii* has been subsequently documented in other studies (Veblen & Stewart 1982; Norton 1983; Stewart & Rose 1989).

2.2.2 Coastal forests

Norton (1991) described regeneration patterns in a coastal podocarp/hardwood forest fragment just south of Hokitika. In the absence of major disturbance, *D. cupressinum* seedling and saplings established via bird dispersal of seed underneath *W. racemosa* and eventually replaced them as the canopy *Weinmannia* grew old and died. A similar pattern has been noted in many North Island forests and in some South Island forests such as the *Dacrycarpus* forests on the Ohinemaka floodplain in south Westland (Duncan 1991).

I am unaware of any studies that have investigated age structure and regeneration patterns of forests on pakihi.

2.3 SOUTH WESTLAND

2.3.1 Inland valleys

The most comprehensive study of disturbance and the dynamics of these forests is that of Wells et al. (2001). They reconstructed the history of forest disturbance in two study areas (Copland and Karangarua catchments), totalling 1412 ha, to quantify the role of disturbances in structuring the conifer/hardwood forests. The study area was divided into different landsurface types, trees were aged on each landsurface and cohorts of trees that had established in response to past disturbance identified. The type of disturbance (tree fall or erosion/sedimentation event) that initiated cohort establishment was determined from the type of landsurface and other physical evidence. Abrupt growth releases or suppressions in tree rings were also identified to aid disturbance history reconstruction.

Erosion and sedimentation events dominated the disturbance regime, affecting 86% of the study area in the last 650 years. Catchment-wide episodes of forest cohort-initiating disturbances were centred around 1820–30, 1710–20, 1610–20 and 1460 AD (Wells et al. 2001). Of the 51 tree cohorts identified in the study area, 47 were initiated during one of these episodes, when disturbance by erosion or sedimentation affected 10–50% of the study area. Consequently, over 80% of the forested area currently comprises simple, first-generation cohorts of trees established after catastrophic disturbance. Only 14 % of the study area was more complex, all-aged forest.

Three disturbance episodes coincide with the three most recent Alpine Fault earthquakes (c. 1717, 1630, and 1460 AD), while one coincides with earthquakes recorded to the south of the study catchments in 1826 AD. Age structures from throughout Westland show that extensive, similar-aged, post-earthquake cohorts of trees are a feature of the region, suggesting that infrequent, massive earthquakes are the dominant coarse-scale disturbance agent, triggering episodes of major erosion and sedimentation and leaving a strong imprint in the forest structure.

Few studies have been carried out in the coastal hillslope forests of south Westland. Lusk & Smith (1998) sampled a mixed stand dominated by *D. cupressinum*, *N. menziesii*, *P. ferruginea* and *W. racemosa* in the Jackson River Valley. They concluded that all four species were represented by all-aged populations and that each regenerated in a continuous manner in response to patchy small-scale disturbance over the last 400 years. This finding differs from all other studies that have investigated the dynamics of stands containing conifers such a rimu, where large-scale disturbances drive the rimu regeneration pattern. However, on closer examination of the data presented in Lusk & Smith (1998), it is apparent that the authors did not recognise the influence of major disturbances in their stand. Two lines of evidence suggest that major disturbances have had an influence on the population structures of main tree species: (1) many of the present canopy trees had established on stumps or logs; (2) the age class distributions for *D. cupressinum* and *P. ferruginea* clearly show two groups of trees—those aged from c. 200 to 300 years (both species) and an older group from 400 to 600 years (*P. ferruginea*) and 500 to 800 years (*D. cupressinum*). Furthermore, all *N. menziesii* were less than about 300 years. The 200- to 300-year age group for all species above could well have established after the last major Alpine Fault earthquake, and the older age groups for *D. cupressinum* and *P. ferruginea* fall within the time frames for earlier earthquakes.

2.3.2 Coastal outwash surfaces

Flooding, catastrophic windthrow and synchronous canopy collapse create conditions suitable for the establishment of *Dacrydium cupressinum* and/or *D. dacrydioides* (Poole 1937; Wardle 1974; Six Dijkstra et al. 1985; Duncan 1993). These disturbances create openings of from 0.2 to at least 20 ha and occur with a high enough frequency to maintain the dominance of these species on outwash surfaces in south Westland (Hutchinson 1928, 1932; James 1987; Cornere 1992).

Floodplain forests

On the extensive lowland flood-plains of south Westland, tracts of kahikatea forest occur on recent alluvial surfaces, suggesting that flooding is a major form of disturbance initiating stand regeneration. Duncan (1991, 1993) described the regeneration patterns in stands of kahikatea with varying mixtures of rimu, miro, and kamahi. Duncan (1993) recognised three distinct cohorts related to past flooding, the oldest being 475–500 years old. In some instances several cohorts were identified in individual stands that reflected these different flood events (Fig. 8).

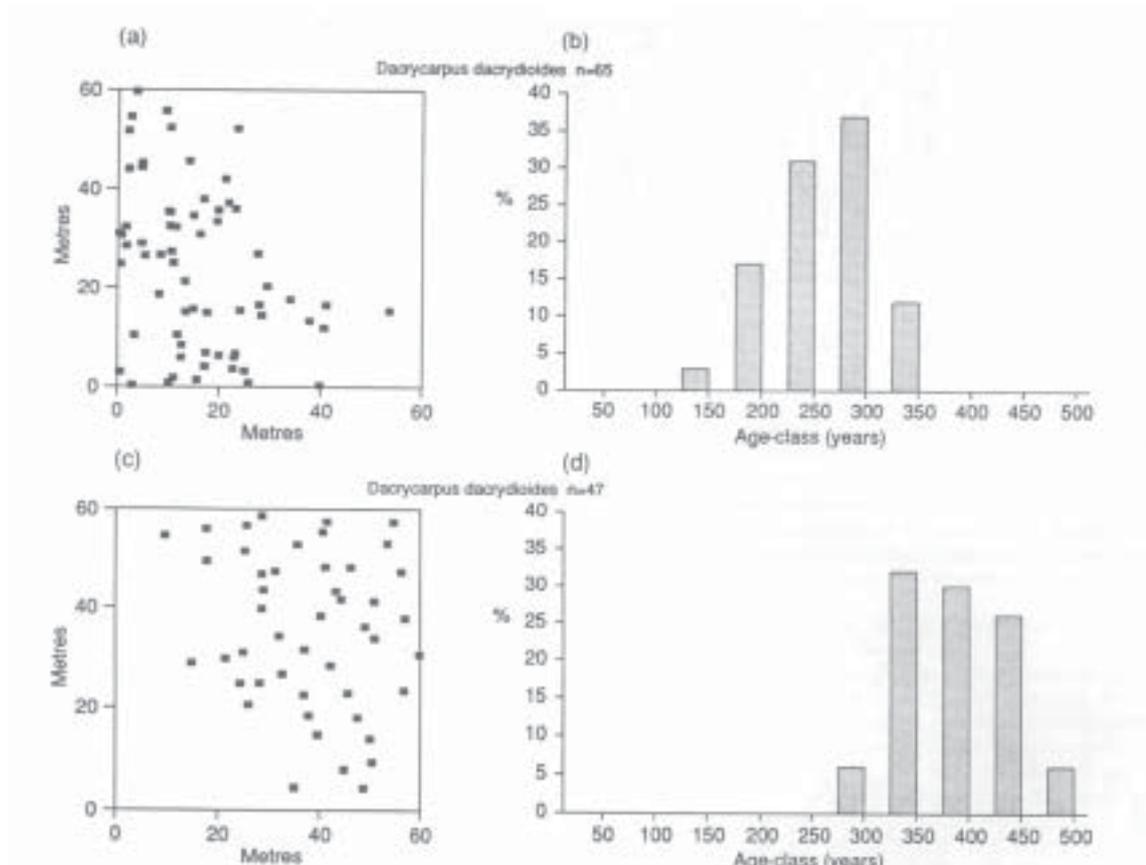
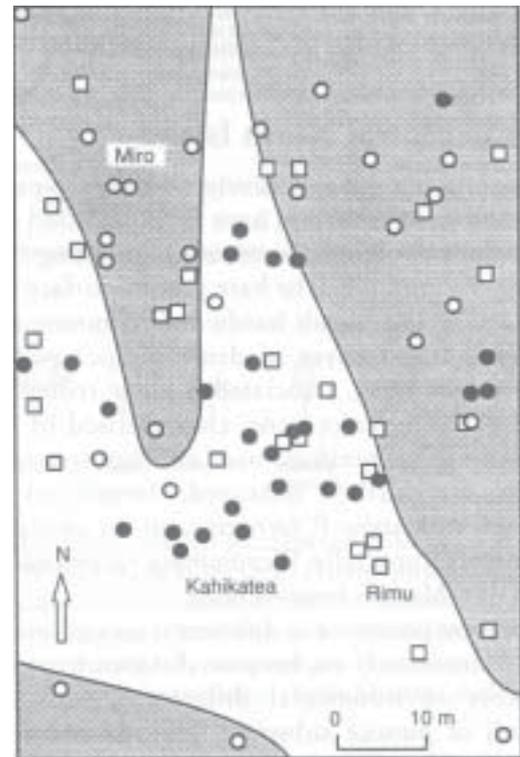


Figure 8. Stem location maps (a and c) and age class frequency distributions (b and d) for two separate cohorts of *Dacrydium dacrydioides* in a stand at Ohinemaka forest, south Westland, identified by spatial analysis. The two cohorts regenerated after two different flooding events. After Duncan & Stewart (1991).

Kahikatea established abundantly from seed on open silty soil surfaces following catastrophic floods. However, dispersal of seeds on to the fluvial surface depends on the development of a shrub cover to attract birds (which disperse the podocarp seeds), prolonging the interval of colonisation by this first cohort for over a century or more. Rimu seeds are similarly dispersed, but the seedlings of this species are strongly dependent on raised substrates for establishment. These two species become spatially segregated: kahikatea forms dense stands in areas of major flooding where silt has been deposited and the overstorey removed, while rimu preferentially colonises more limited microsites which are created by fallen logs and piles of debris in the marginal flood zone (where some canopy trees may also survive, Fig. 9). Clumps of the

Figure 9. Distribution of rimu (*Dacrydium cupressinum*), kahikatea (*Dacrycarpus dacrydioides*), and miro (*Prumnopitys ferruginea*) stems < 250 years in a 90 × 60m plot in a south Westland forest subject to flooding sampled by Duncan (1993). The shaded area includes the distribution of all trees > 250 years and is taken to indicate the area of pre-flood disturbance forest. Note the segregated distribution of the three conifers with respect to the area of disturbance. After Ogden & Stewart (1995).



former species thin out as a result of intraspecific competition, leading to a random or regular distribution of mature canopy trees. Miro establishes later in the sequence, usually on elevated microsites beneath the mature canopy, while kamahi tends to occupy similar sites in tree-fall gaps. In the absence of catastrophic disturbance the latter two species would presumably increase in abundance but this is prevented by the frequency of large-scale disturbance events.

These four species coexist in the flooded forests by partitioning establishment sites with respect to the amount of overhead canopy cover and the type of forest floor microsite (Duncan 1993). Rimu and kahikatea colonise periodically after large-scale forest destruction, but their seedlings favour different microsites. Kahikatea tends to occupy the best-lit sites, rimu can establish with some shade, while miro favours shady locations. This sequence of shade tolerance has been confirmed in several other studies (e.g. June 1982).

There have been few other studies that have examined the structure and regeneration patterns of forests on floodplains in south Westland. McSweeney (1982) collected limited tree age data from several matai/totara stands on the Whataroa and Waiho floodplains, and ages of cohorts in these stands corresponded to establishment after Alpine Fault earthquakes (Wells et al. 1998).

Moraine forest

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 supports the notion that lesser storms or other disturbances initiate local canopy collapse and subsequent recruitment. If the oldest trees in a stand 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).

In Saltwater Forest, for example, at an individual plot or perhaps, even stand level, the *Dacrydium* forests on the moraines do not appear to be all-aged (Stewart et al. 1998). Rather, the presence of distinct even-aged cohorts of trees indicates at least two major establishment periods (c. 500 and 200–350 years ago) over the last 700 years. In the ablation zone and moraine edge areas, a cohort of *D. cupressinum* also established c. 500 years ago, but a younger cohort (c. 300–350 years) was only clearly evident for *P. ferruginea*. In some instances, the presence of *D. cupressinum* and *P. ferruginea* in small clumps of individuals of similar age suggest intermittent regeneration in small patches (up to c. 1000 m², Fig. 10) whilst in other situations similarly aged individuals spread throughout the stand indicate establishment after partial canopy breakdown (plots 1 and 3, Stewart et al. 1998).

The predominance of the 500 year age class for *D. cupressinum* and the 300–350 year age class for *P. ferruginea* on the moraines at Saltwater Forest 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

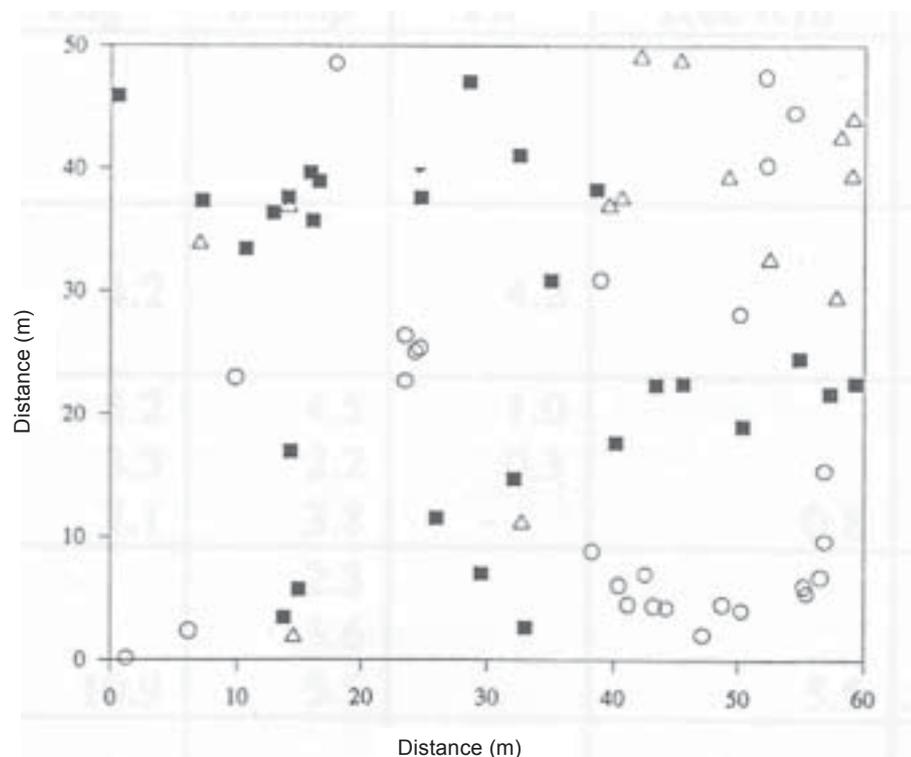


Figure 10. Spatial distribution of *Dacrydium cupressinum* and *Prumnopitys ferruginea* of three different age groups (circles < 200 years; triangles 200–350 years; squares > 350 years) on moraines in Saltwater Forest, south Westland. After Stewart et al. (1998).

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.

Patterns of species replacement in already established stands are determined by drainage and the degree of mortality caused by natural disturbances. If canopy mortality is low and scattered on reasonably well-drained sites, *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 (Almond, P.C.; Duncan, R.P. pers. comm.).

The differences in structure and disturbance history between the forests of the terraces and moraines in Saltwater Forest 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 result in complex and intermingled age cohorts (e.g. Cornere 1992, see next section). This complex pattern of interspersed, 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). However, in contrast to the removal of small groups of trees at regular intervals by harvesting, even-aged cohorts appear to establish naturally only once every one to two centuries.

Terrace forest

Six Dijkstra et al. (1985) described forest structure in five stands in Saltwater Forest selected to illustrate the regeneration cycle of terrace rimu forests. Windthrow was thought to initiate the cycle, imposing the mosaic pattern, but catastrophic destruction was not necessary. Rather, opening of the mature rimu canopy was envisaged as a rather gradual and progressive process, death of a few trees leading to destruction of the subcanopy angiosperm layer, rendering the remaining canopy trees more vulnerable to further windthrow. It now appears that this interpretation is a little simplistic and does not take account of the recurring influence of catastrophic disturbances.

Cornere (1992) identified five periods of *D. cupressinum* cohort establishment in the terrace forests at Saltwater within the last 700 years (250, 300–350, 400, 500, and 650–700 years ago). The dominant period of cohort establishment on the terraces was 250 years ago, resulting in variation in the peak periods of establishment between the terraces and moraines by several centuries (peak establishment on the moraines was 500 years ago, Stewart et al. 1998). The

disturbance(s) that initiated the 250-year *D. cupressinum* cohorts on the terraces either did not affect the forest 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 that time in small disturbance openings beneath a surviving *D. cupressinum* canopy.

The cohorts identified by Cornere (1992) all had restricted age-ranges and were spatially discrete, coinciding with abrupt changes in soils and landforms (Fig. 10). The youngest cohorts of trees were generally found in areas of more poorly-drained soils, adjacent to older cohorts of trees on better-drained mineral soils (Almond, P.C.; Duncan, R.P. pers. comm.). Furthermore, trees on more poorly-drained soils are more susceptible to disturbance and are turning over more often than trees on better drained soils. In these situations trees may never reach a large diameter. This has important implications for sustainable management of these forests since it would appear that patterns of tree mortality and subsequent cohort recruitment are predictable from the soil pattern.

The cohorts defined by Cornere (1992) also provide some indications as to the size of disturbance openings in terrace rimu forests. The width of cohorts identified along transects 1 and 2 varied from c. 100 to 250 m (Fig. 11), suggesting canopy-opening sizes ranging from around 1000 to 6000 m². In contrast, on the moraines Stewart *et al.* (1998) noted patches of *D. cupressinum* and *P. ferruginea* of only 20 to 40 m wide (gap sizes possibly 400–1600 m²).

Rogers (1995, 1999) sampled three stands on terraces of varying post-glacial age at Saltwater forest (oldest terrace > 22 600 years BP, others younger but certainly older than 10 000 years BP) and identified a peak in the establishment of *D. cupressinum*, *Lagarotrobus colensoi* and *P. ferruginea* at c.150 to 250 years ago. This peak was most pronounced on the most poorly drained terrace and broadly corresponds to an establishment peak 250 years ago noted by Cornere (1992) and Stewart *et al.* (1998) in Saltwater Forest and by Van Uden (1997) in Okarito Forest. Although Rogers (1999) documented even-aged establishment patterns, especially for *D. cupressinum* and *Lagarotrobus colensoi*, he also noted that intermittent regeneration of *D. cupressinum*, *Phyllocladus alpinus* and *Prumnopitys ferruginea* occurred in response to lesser disturbances on the younger and better drained terraces. He identified small groups of even-aged trees that overlapped spatially and temporally. As concluded by Cornere (1992) and Almond, P.C. & Duncan, R.P. (pers. comm.). Rogers (1999) suggested that *D. cupressinum* on the most poorly drained terrace characterised by fluid peat soils would be more susceptible to disturbance (windthrow) than those on better drained sites.

As noted by others (e.g. Urlich 2000; Duncan 1991) elevated microsites such as logs are important for the successful establishment and survival of many species in *D. cupressinum* forests. On the oldest and poorest terrace, 100% of *D. cupressinum* and 81% of *L. colensoi* occurred on logs (Rogers 1999).

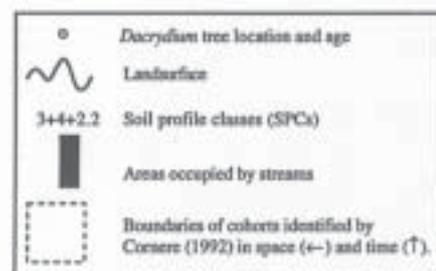
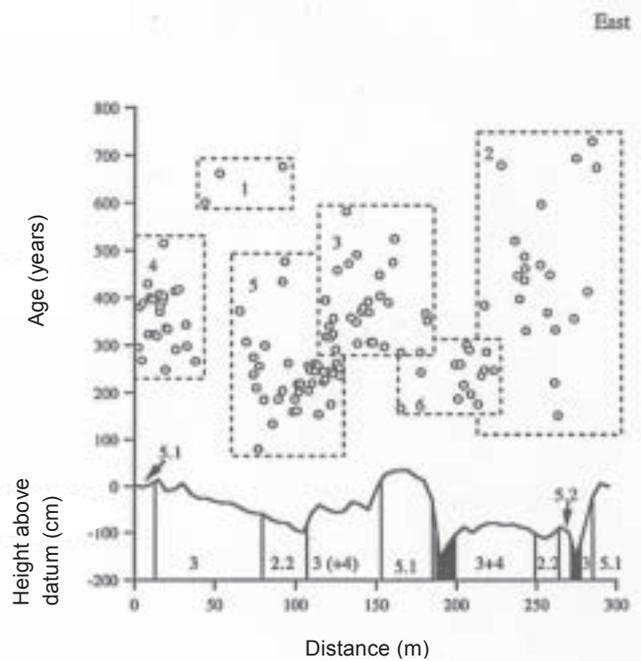
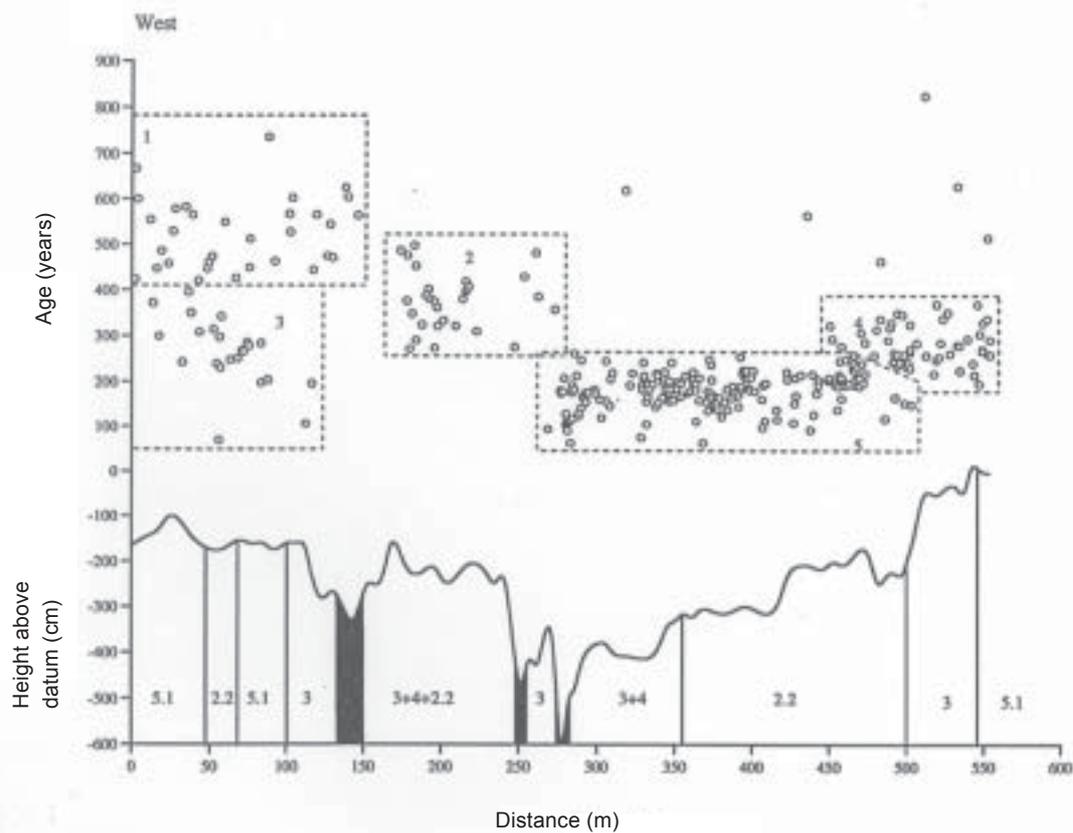


Figure 11. *Dacrydium cupressinum* tree age, cohort boundaries and topography along transects 1 and 2 sampled by Cornere (1992) on a terrace in Saltwater Forest, south Westland. Soil profile classes are on a scale from 1 to 10, with 1 being extremely poorly drained and 10 well drained. Note the distinct boundaries between differently-aged cohorts and that the youngest cohorts occur on the most infertile and poorly-drained soils. After Almond, P.C.; Duncan, R.P. (pers. comm.).

3. Regional forest structure and disturbance history

It is now evident that the regional forest pattern in Westland has been strongly influenced by region-wide disturbance events over the last few centuries. Three major, historical earthquakes, resulting from ruptures of the Alpine Fault (South Island), have been identified using a combination of fault trenching, ^{14}C dating of landslides and terraces, forest age structure, and tree-ring growth anomalies (see Wells et al. 1999, and also Fig. 12). These earthquakes have been dated to 1460 AD ± 25 years, 1630 AD ± 25 years and 1717 AD (Wells et al., 1999). These dates coincide with three major periods of conifer forest regeneration in Westland starting 1460 AD, 1610-1620 AD and 1710-1720 AD (Wells et al., 1998, 2001). Based on this coincidence in timing, Wells et al. (2001) conclude that infrequent, massive earthquakes, through triggering erosion, sedimentation and flooding events, are the dominant forest disturbance agents in Westland and that earthquakes have a profound effect on forests over much of the region. The most recent earthquake in 1717 AD caused a rupture that extended from Milford to the Haupiri River, a distance of 375 km (Fig. 12, Wells et al. 1999).

Regeneration of the conifer component of Westland's forests, although occurring intermittently after small storm induced landslides, blowdowns and floods is primarily after these large earthquakes. In some instances tree toppling may occur over relatively small areas (e.g. old glacial terraces at Mt Harata, moraines and terraces at Saltwater Forest) providing openings large enough for conifer regeneration. - in small patches (Mt Harata terraces) or interspersed among surviving trees (Saltwater Forest moraines). Generally though large openings will be created (e.g. Welcome Flat terraces and fans in the Copland Valley, Ohinemaka floodplains) resulting in large patches of even-aged conifer cohorts.

The regional extent and impact of these earthquakes has been variable. In a recent study, Cullen, L. et al. (pers. comm.) examined forest structure on several floodplains in south Westland and found that even-aged conifer cohorts dating from the 1717 AD earthquake were found near the Alpine Fault and in the frontal ranges of the Southern Alps but rarely on the floodplains. In contrast, even-aged conifer stands that established after the earthquake in 1630 AD could be found on the floodplains and right out to the coast. This temporal and spatial pattern reflects earthquake magnitude and the length of time between earthquakes that affects the amount of sediment build-up in the headwaters and the resulting surface inundation (Peter Almond pers. comm.). Because of the relatively long time between the 1460 AD and the 1630 AD earthquakes (170 years) the amount of sediment build-up would have been high. During and after the 1630 AD earthquake this sediment would have been released, resulting in widespread inundation affecting forests across the floodplain. In addition, the 1630 AD earthquake may have been larger than the 1717 AD event, leading to more landsliding and shaking damage, and it may have occurred during a wetter period, which would have increased flooding and river flow-levels, increasing

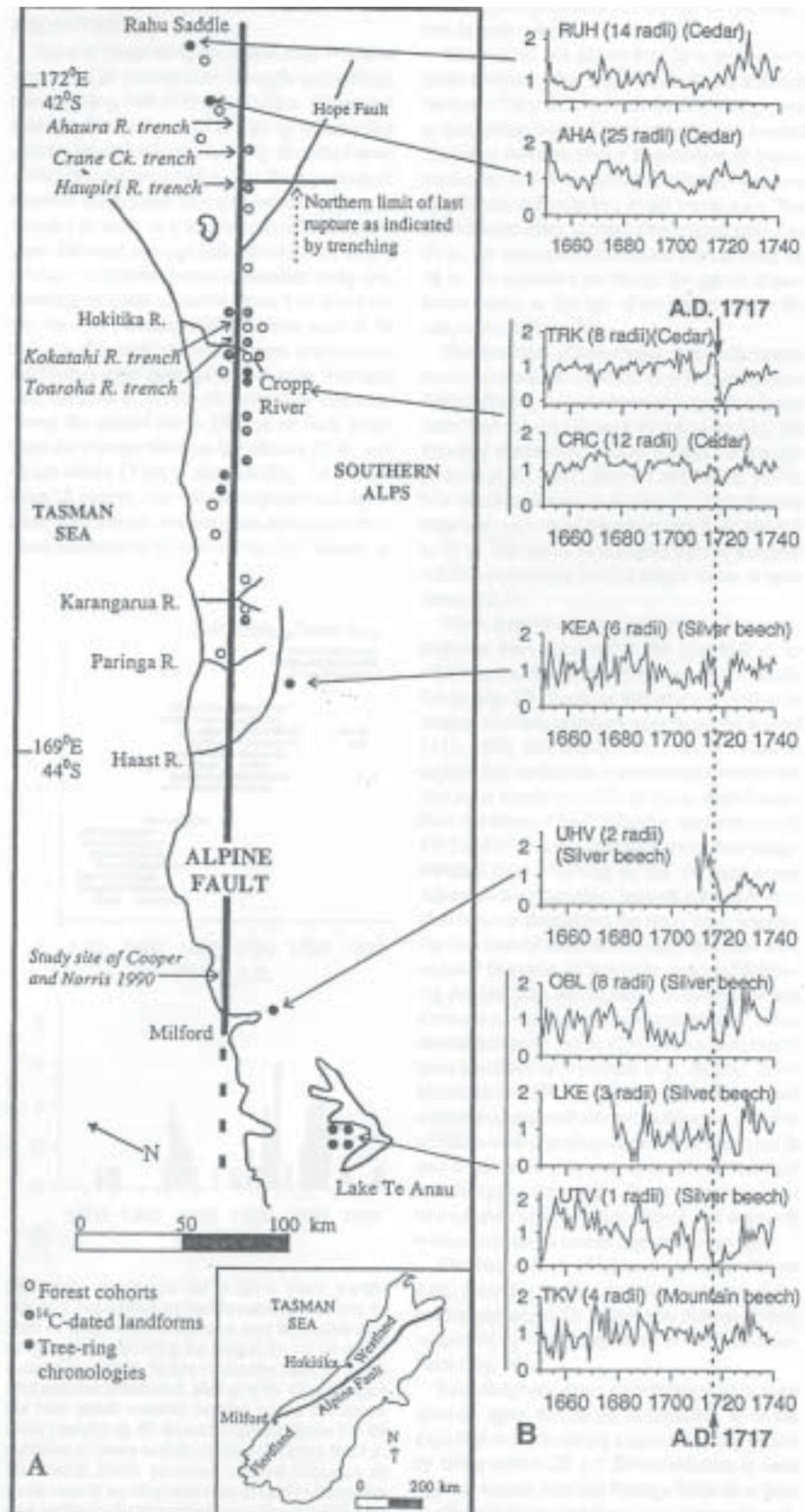


Figure 12. A. Map of Westland, showing the Alpine Fault and locations of fault trenches, ¹⁴C-dated landslides and terraces, forest cohorts, and tree ring chronologies. B. Tree-ring chronologies from sites along the strike of the Alpine Fault between Rahu Saddle in the north and Lake Te Anau. The y-axis on all graphs is ring-width index, and the x-axis is year AD. Note the abrupt growth decline in 1717-19 at sites within the rupture zone of the most recent Alpine Fault earthquake (sites TRK to TKV) but not above (sites RUH and AHA). After Wells et al. (1999).

the spread of debris across the floodplain (Yetton et al., 1998). With less time passing (87 years) until the next earthquake in 1717 AD and a smaller magnitude, sediment loads and the subsequent spread of sediment across the floodplain would have been less, only affecting the floodplain some way out from the Fault. In some cases, such as the Ohinemaka floodplain, the extent of sediment spread following the 1717 AD earthquake appears to have been even more limited to just along river channels, as older stands near the Alpine Fault but away from the Ohinemaka River are evident and do not seem to have been affected by the 1717 AD event.

These findings suggest that, in general, large disturbances are required for conifer regeneration and this has implications for any sustained yield management of these forests if conifers are to remain an important component.

4. Future research needs

Areas in need of further research include:

1. Microsite regeneration requirements in a range of forest types including: hillslope red-silver beech forests, north Westland; coastal forests, north Westland; alluvial outwash surfaces, north Westland.
2. Structure and regeneration dynamics of several forests types including: hillslope beech/conifer/hardwood forests, north Westland; alluvial valley floor forests, north Westland; coastal forests, north and central Westland; mixed conifer/broadleaved hardwood forests, central and south Westland.
3. Size of openings created by disturbances in many forests types including: hillslope beech/conifer/hardwood forests, north Westland; alluvial valley floor forests, north Westland; coastal forests, north and central Westland; mixed conifer/broadleaved hardwood forests, central and south Westland; terrace and moraine forests, south Westland. The sizes of openings created by earthquakes could possibly be determined from an examination of current conifer cohort patch sizes (e.g. as in Wells et al. 2001).
4. Disturbance patterns and conifer regeneration in the interval between large earthquake events. More research is required on the influences of lesser disturbances such as landsliding, flooding and tree blowdown on replacement patterns within stands.

5. Relevance to forest management

No single management scheme could be applied universally to the diverse array of forests in Westland that differ in structure, disturbance history and regeneration pattern. However, there are several aspects of the structure and regeneration ecology of Westland's forests that are relevant to proposed forest management.

Because the disturbance regime varies regionally, a landscape level approach to sustainable forest management would seem appropriate. In some instances, like the red beech/silver beech forests of north Westland where small-scale disturbances, such as windfalls, resulting in the formation of small treefall gaps predominate, different habitats and environmental heterogeneity could be maintained by careful extraction of small groups of trees. For example, this might mean the extraction of small groups of trees over areas ranging from 400 to 1000 m² in these forests. In other instances where catastrophic disturbances such as earthquakes drive the regeneration pattern, any management system would need to recognise the spatial and temporal variability in cohort establishment to ensure that different habitats and levels of environmental heterogeneity to which species with different life history traits respond are maintained in the landscape. For example, in Saltwater Forest, south Westland, the extraction of large groups of trees might be appropriate on older terraces where large groups of trees establish naturally, but on younger terrace surfaces small group extraction may be appropriate. This would maintain the 'patchy' nature of the natural forest—large patches of dense conifers interspersed with more heterogeneous, mixed species patches. This mosaic of stands of different structure and composition is vital as it contributes to the maintenance of regional biodiversity.

Any harvesting should take cognisance of the important role of forest floor microsites in tree establishment and the variable way in which canopy gaps are formed. For example, the removal of canopy trees may result in the loss of seedling establishment sites such as logs and tree tip-up mounds. These may be crucial to the maintenance of certain species, for example *N. fusca* seedling establishment is often restricted to these microsites where drainage is very poor. This might mean that a proportion of harvested trees have to be left to rot on the forest floor, or perhaps new methods of harvesting may have to be adopted to mimic natural establishment microsites, e.g. winching over of canopy trees would create tree tip-up mounds. The way in which gaps are formed can also influence species response. For example, in red/silver beech forests, *N. menziesii* predominates in gaps formed by dead standing trees whereas *N. fusca* seedlings and saplings are more common in gaps formed by uprooting or bolesnap. It would therefore be important in any management system to leave a proportion of canopy trees to die naturally (as dead standing trees, in this example). Both the above considerations have implications for the maintenance of within stand biodiversity, not only for the constituent tree

species but also for the biota that are associated with these microhabitats and gap situations.

Management systems would need to be flexible to allow for variation in the natural forest regeneration pattern. For example, it may be appropriate in some instances to selectively extract individual trees to create a situation that would mimic the natural regeneration pattern. It appears that, on the moraines in Saltwater Forest, partial canopy breakdown by disturbance does not create openings large enough to allow the regeneration of *D. cupressinum* but results in the sporadic regeneration of *P. ferruginea*. The extraction of single *D. cupressinum* canopy trees scattered throughout a stand may mimic this pattern and allow the persistence of *P. ferruginea*.

Any management system must take into account variation in growth rate on different sites. In many instances, tree diameter may not accurately reflect tree age. This might mean that trees on some sites may be the same age as those on others but are considerably smaller in diameter. For example, the measured radial growth rate of *Dacrydium cupressinum* (0.7 mm/year) on moraines at Saltwater Forest (Stewart et al. 1998) 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 considerably faster than on the terraces (0.4 mm/year, Cornere 1992; Rogers 1995). It follows that *P. ferruginea* would take longer to reach a harvestable diameter on the terraces, and should therefore be extracted at a lower rate than on the moraines. This highlights the importance of information on tree age and growth rate in making decisions on harvesting within any management system.

An intriguing issue now arises with the shift in sustained yield management from Crown to private lands. In many instances, the scale issues that I have raised will be difficult to address on many areas of private land simply because of their small size. For example, the continued maintenance of a mosaic structure (both in terms of forest age structure, species composition, and hence biodiversity) in small areas of conifer forest would be difficult. In all likelihood, any given small area of a few tens or hundreds of hectares would not contain the variation typical at a large catchment or regional scale. It may well be that any proposed sustained yield management in a particular area has to be considered in the context of *all* proposed management schemes for a region as a whole, both in terms of the regional maintenance of structural variation more typical of natural stands, and in terms of habitat heterogeneity generally with a view to maximising indigenous biodiversity.

6. References

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