

A FOREST SUCCESSION IN THE CATLINS ECOLOGICAL REGION, SOUTH-EAST OTAGO, NEW ZEALAND

Summary: Forest containing rata (*Metrosideros umbellata*) and kamahi (*Weinmannia racemosa*), with scattered trees of silver beech (*Nothofagus menziesii*), was sampled on Cedar Hill, Owaka Valley, Catlins Ecological Region. Diameter frequency distributions, age estimates, and basal area measurements show single cohort establishment of rata and kamahi, whereas three establishment phases of silver beech are evident. Tree population structures, the presence of many large dead and decaying manuka (*Leptospermum scoparium*) stems, and the absence of evidence of windthrow or landslip, suggest that the vegetation originated 250-300 years ago as a result of fire. Initially, manuka and a few silver beech established together. Natural opening of the manuka canopy 50-100 years later allowed invasion by rata, kamahi and a second cohort of beech. A third episode of beech establishment occurred about 70 years ago. Eventually forest structure will be similar to that of adjacent older, more diverse forest.

Keywords: Forest succession, fire, rata-kamahi forest, silver beech forest, manuka, Catlins Ecological Region.

Introduction

Indigenous forest in much of the east of South Island, New Zealand, was destroyed by fire during the past millennium (Molloy *et al.*, 1963). In the relatively moist south-eastern extremity of the island, the Catlins (Fig. 1), fire was used by Polynesian occupants to maintain routes through the main valleys (Hamel, 1977). However, fire probably seldom spread far into the tall forest of valley sides (Halkett and Leitch, 1976; Hamel, 1977).

Over much of New Zealand, manuka (*Leptospermum scoparium*)* is a major small tree species of post-fire successions (eg. Mirams, 1957; Burrell, 1965; Esler, 1967; McKelvey, 1973). Extensive stands of manuka have occupied sites in the Catlins following fire, for example in the upper Tahakopa Valley (Jowett, 1965), Wairepo Creek (Marshall, 1984), and on the MacLennan Range (Allen, 1985). Where manuka stands are situated close to mature silver beech (*Nothofagus menziesii*), they frequently contain a few silver beech trees, usually of similar size to the manuka. Kamahi (*Weinmannia racemosa*) and southern rata (*Metrosideros umbellata*) establish under manuka in the Catlins (McConnell, 1974), as do forest trees elsewhere (eg. Atkinson, 1954; Esler, 1967; Esler and Astridge, 1974).

On the upper slopes of Cedar Hill (Fig. 1), forest of uniform sized rata and kamahi, associated with scattered mixed sized silver beech, contains frequent remains of large manuka stems. It is surrounded by rata-kamahi and beech forest with a greater diversity of tree sizes and lacking manuka.

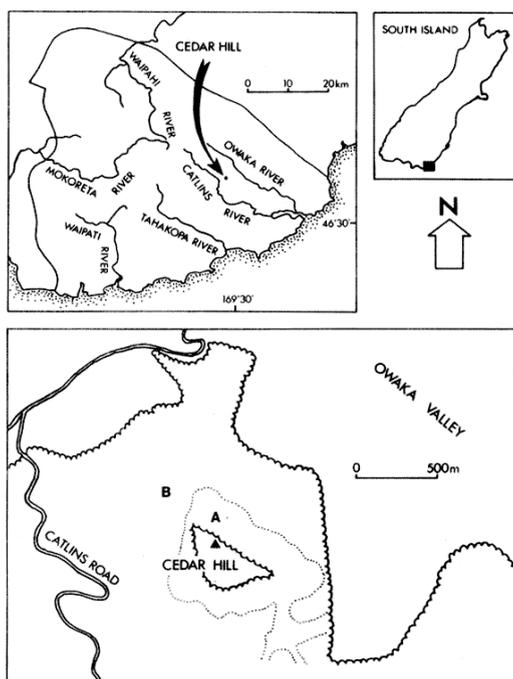


Figure 1: The Catlins Ecological Region (top left), and Cedar Hill (bottom), showing the location of young forest (A) and old forest (B) study sites and the extent of young forest (dotted line). Scrub occupies the summit of Cedar Hill, and farmland the lower slopes in the Owaka Valley.

* nomenclature follows Allan (1961) except where denoted by the addition of authority names.

This study examines the possibility that the uniform sized rata-kamahi forest and associated beech trees established after fire destroyed former forest.

Study area

Below about 450 m on the north aspect of Cedar Hill, rata and kamahi dominate forest in which podocarps (rimu (*Dacrydium cupressinum*), miro (*Prumnopitys ferruginea* (D. Don) de Laubenfels), matai (*P. taxifolia* Sol. ex D. Don), Hall's totara (*Podocarpus hallii*) were prominent before logging during the past century. Silver beech is the dominant tree above this altitude, with kaikawaka (*Libocedrus bidwillii*) becoming increasingly conspicuous towards the summit. The summit (578 m) and several hectares of the slope to its south are occupied by scrub with manuka, inaka (*Dracophyllum longifolium*), tauhinu (*Cassinia vauvilliersii*), *Olearia arborescens*, and mountain flax (*Phormium cookianum*) (Allen, 1978).

Mean annual (1972 - 1980) rainfall at 37 m in the adjacent Owaka Valley is 1036 mm (Allen, 1985), evenly distributed through the year. Temperatures are cool: Owaka, at 5 m and 15 km to the east, experiences a January (summer) daily mean of 13.8°C, and July (winter) daily mean of 5.6°C (New Zealand Meteorological Service, 1980). Frosts can occur in most months, but are seldom severe. Snowfalls are uncommon.

Methods

Samples were taken at 450 m in forest of uniform sized rata and kamahi, containing a small population of mixed size silver beech ('young forest'). This site is situated on the north face of Cedar Hill (NZMS 260 G46 388174; Fig. 1), on a 15-20°, free draining, northerly aspect slope. Soils are lowland yellow-brown earths (Owaka Hill soils), silt loams of medium natural nutrient status (N.Z. Soil Bureau, 1968), and overlie Jurassic sandstone, mudstone and conglomerate (McKellar, 1966). Structurally more diverse rata-kamahi and beech forest ('old forest') was sampled about 250 m to the west on a similar site.

In the young forest, areas of beech and rata-kamahi dominance were distinguished by the boundary of the beech canopy (Fig. 2). Six contiguous 10 x 30 m quadrats were laid out with their long axes vertical to the contour, giving sampled areas of approximately 1100 m² and 700 m² for rata-kamahi and beech dominance, respectively. Within each quadrat, the diameter at breast height (dbh; approximately 1.2 m)

was recorded of every stem ≥ 10 cm dbh of the main tree species.

The positions of all stems ≥ 2 m tall, including tree ferns (*Cyathea smithii* and *Dicksonia squarrosa*), and of all recognisable stumps and fallen logs, were mapped at a scale of 1:200.

The old forest had been sampled in the same season as part of a separate study of silver beech ecology in the Catlins (Allen, 1985). A grid of 21 50 x 50 m plots was arranged in three rows vertical to the contour across a boundary between silver beech and rata-kamahi forest, the latter defined by the absence of silver beech stems ≥ 10 cm dbh. Eight plots contained rata-kamahi forest, and 11 beech forest. In each of these a randomly placed 10 x 10 m quadrat was used to record diameter and density by species of stems ≥ 2 m tall, giving a total sampled area of 1900 m² for use in the present study.

In both young and old forest, increment cores were removed from beech and kamahi trees for determination of age and growth rate. Growth rings were assumed to be annual (Wardle, 1966; 1967). The hard wood of rata presents technical difficulties for this procedure, and manuka stems were too decayed to be useful. Where cores did not reach the tree centre, ages were estimated by extrapolation to the length of the mean radius of the stem. For cores < 90% of the stem radius, mostly from the larger silver beech stems, ages are likely to be underestimated because growth is slower early in the tree's life (Norton *et al.*, 1987).

Results

1. Diameter frequency distributions

(a) Young forest

The majority of rata and kamahi stems occurred in two diameter classes, 10-19.5 and 20-29.5 cm (Fig. 3). In the rata-kamahi area, diameter frequency distributions of rata and kamahi were similar.

The majority of manuka stems were also in these diameter classes, but only one living plant was recorded, in the rata-kamahi area. Most manuka stems were fallen and decaying.

Silver beech diameter distribution was markedly different, with most stems less than 10 cm in diameter, a few in the 10-49.5 cm classes, and three greater than 90 cm. Beech stems in the first category were mostly confined to the vicinity of the two largest beech trees (Fig. 2).

(b) Old forest

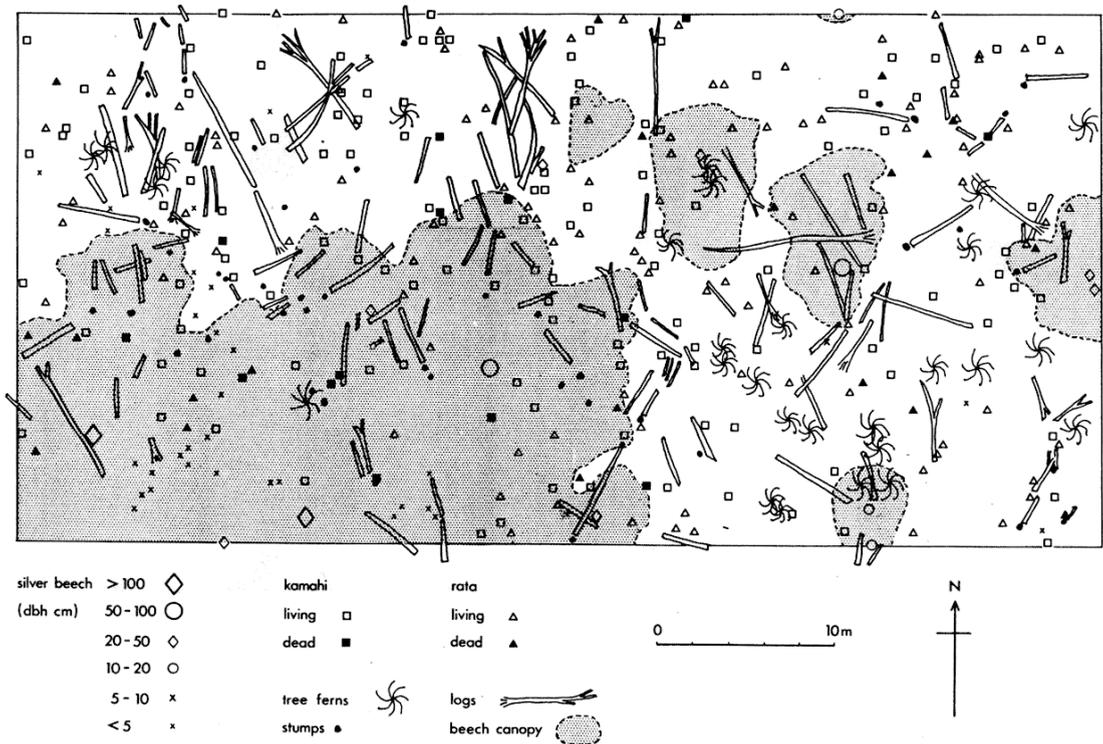


Figure 2: Map of the sample area in young forest showing the distribution of rata and kamahi stems > 10 cm dbh, and of silver beech stems by diameter class, in relation to tree ferns, logs, stumps and the beech canopy.

In rata-kamahi forest, diameter frequency distributions of rata and kamahi (Fig. 4), were markedly different, both from each other and from those of the young forest. Nearly half of the kamahi stems were less than 10 cm dbh, and kamahi size class frequency distribution approximated the reverse exponential curve of continuous recruitment. Rata had a high proportion of dead stems in the two smallest diameter classes, peaked in frequency in the 20-29.5 cm class, and had similar and low frequencies in classes greater than 30 cm dbh. Manuka was absent.

In beech forest, kamahi diameter frequency distribution was concentrated towards the middle range (10-39.5 cm), with no stems less than 10 cm dbh. In contrast, rata stems were mostly less than 30 cm dbh, with a high proportion dead, only a few larger individuals, and none less than 10 cm dbh. Silver beech diameter frequency distributions were

similar to those in the young forest.

2. Age and growth rate

(a) Young forest

Age and mean diameter growth rate (overall and for the outermost 20 growth rings) of kamahi and silver beech stems are shown in Table 1. Silver beech overall mean growth rates were higher than those of kamahi within all but the 20-29.5 cm diameter class and, in all but the largest tree, beech growth rates for the outermost 20 growth rings were also higher than kamahi. Kamahi ages ranged from 148 to 215 years, whereas those of silver beech ranged from 68 to a conservative 279 years, falling in three distinct groups: c. 70 years, 100-160 years, > 210 years.

(b) Old forest

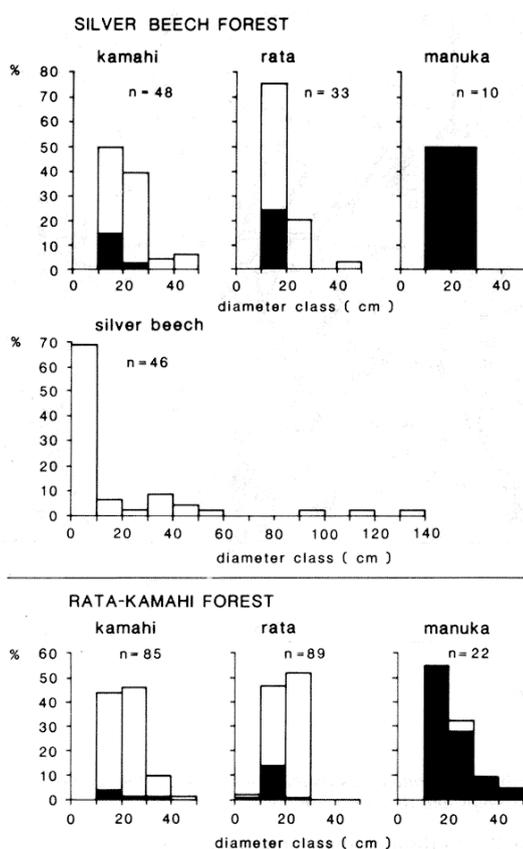


Figure 3: Diameter frequency distributions of kamahi, rata and manuka in silver beech and rata-kamahi areas of young forest, and of silver beech in the former. Black parts of columns represent dead stems.

growth rings, exceeded those of kamahi within each comparable diameter class. Kamahi were > 100 years older than in the young forest. The silver beech age range showed no distinct gaps and had a maximum similar to that of the young forest.

3. Basal area

Substantial differences in basal area were recorded between and within species and forest types (Table 2).

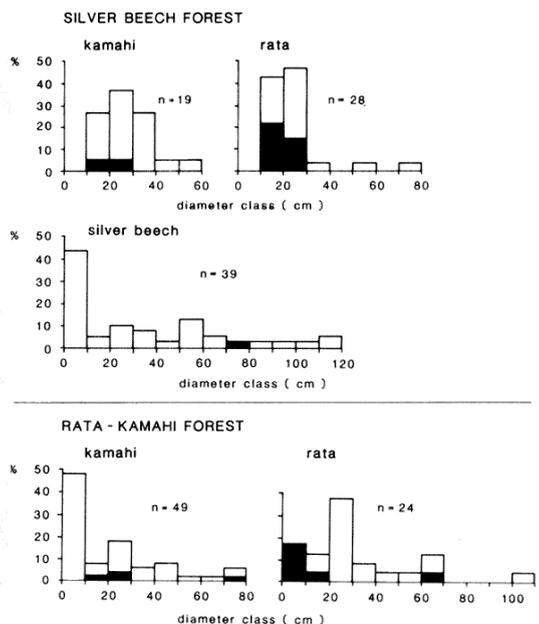


Figure 4: Diameter frequency distributions of kamahi and rata in old silver beech and rata-kamahi forest, and of silver beech in the former. Black parts of columns represent dead stems.

(a) Young forest

Kamahi basal area exceeded that of rata in both beech and rata-kamahi areas. Basal areas of rata and kamahi were markedly lower in the beech than the rata-kamahi area. A high proportion of rata basal area was contributed by dead stems in the beech area.

Manuka had low basal area in both beech and rata-kamahi areas of the young forest, and that of other species was negligible.

(b) Old forest

Beech basal area was greater than in the young forest, and far exceeded that of the sum of all other species in the beech area. Rata basal area was similar to that of kamahi within both beech and rata-kamahi forest. However, basal areas of both species were markedly lower in the former than the latter forest type. Dead stems contributed much of the basal area of rata and kamahi in beech forest.

Table 1: Diameter class (diam, em); mean age (years) and range; mean overall diameter growth rate (mogr, mm/yr) and range; mean diameter growth rate over outermost 20 growth rings (20 gr, mm/yr) and range; of silver beech and kamahi in young and old forest.

	diam	n	age	range	mogr	range	20gr	range
young forest								
beech	10 - 19.5	3	70	68- 72	1.9	1.8-1.9	2.4	1.9-2.7
	20 - 29.5	1	153	-	1.3	-	1.8	-
	30 - 39.5	3	152	72-227	2.5	2.3-2.9	3.9	2.5-6.6
	40 - 49.5	2	126	100-151	3.4	2.9-3.8	3.7	3.0-4.5
	90 - 99.5	1	229	-	4.2	-	3.1	-
	110 - 119.5	1	210	-	5.2	-	3.3	-
kamahi	130 - 139.5	1	279	-	4.7	-	0.6	-
	20 - 29.5	4	164	148-176	1.5	1.2-1.8	0.9	0.4-1.6
	30 - 39.5	3	195	165-215	1.8	1.4-2.2	0.8	0.5-1.3
	40 - 49.5	1	160	-	2.3	-	1.3	-
old forest								
beech	10 - 19.5	2	109	90-128	1.4	1.1-1.8	1.1	1.0-1.2
	20 - 29.5	4	124	111-134	2.1	1.8-2.2	2.8	1.2-4.4
	30 - 39.5	2	141	78-204	3.3	1.6-4.9	5.6	5.3-5.8
	40 - 49.5	1	64	-	6.8	-	8.0	-
	50 - 59.5	5	160	119-197	3.8	2.6-5.3	2.8	0.9-5.2
	60 - 69.5	2	108	58-158	7.6	4.3-11.0	6.9	4.4-9.3
	80 - 89.5	1	166	-	3.0	-	1.0	-
	90 - 99.5	1	251	-	3.9	-	3.3	-
	100 - 109.5	1	216	-	4.9	-	4.0	-
	110-119.5	2	230	203-256	5.0	4.5-5.5	2.9	1.4-4.3
kamahi	10 - 19.5	1	170	-	1.0	-	0.3	-
	30 - 39.5	1	205	-	1.3	-	0.6	-
	40 - 49.5	3	194	137-230	2.2	1.9-2.6	0.6	0.4-0.8

Basal area of the other main tree species - kaikawaka (*Libocedrus bidwillii*), broadleaf (*Griselinia littoralis*), and putaputaweta (*Carpodetus serratus*) - was small.

kamahi forest, and exceeded that in young forest. A substantially higher proportion of the kamahi population was dead in old than in young rata-kamahi forest. .

4. Density

(a) Young forest

In the beech area, density of rata stems ≥ 10 cm dbh was about 50%, and that of kamahi less than 75%, of these values in the rata-kamahi area (Table 3). The proportion of dead stems of rata exceeded that of kamahi in both areas.

(b) Old forest

Rata and kamahi densities were lower in beech forest than in rata-kamahi forest, but the difference in rata was not so marked. Kamahi had a lower proportion of dead stems than rata in beech forest, and than in the beech area of young forest. The proportion of dead rata in beech forest was greater than in rata-

5. Fallen logs

Under the young forest, fallen logs were all less than 50 cm diameter and most were less than 10m long, including remaining crown branches (Fig. 2). There was no discernable pattern of fall direction other than a tendency to alignment downslope. No living tree stems ≥ 10 cm dbh were established on fallen logs.

Table 2: Basal area (m^2/ha), living (a) and dead (b) stems, and percentage dead basal area, of tree species, stems ≥ 10 cm dbh, in young and old beech and rata-kamahahi forest.

		young forest		old forest	
		beech	rata-kamahahi	beech	rata-kamahahi
kamahi	a	29.26	39.93	13.50	43.06
	b	2.59	3.53	2.35	1.74
	% dead	8.13	8.12	14.83	3.88
rata	a	12.76	33.58	16.20	45.50
	b	3.90	1.29	3.32	0.30
	% dead	23.41	3.70	17.01	0.66
beech	a	22.38	-	60.58	-
	b	0	-	4.32	-
	% dead	0	-	6.66	-
manuka	a	-	0.35	-	-
	b	6.07	8.71	0.12	-
	% dead	100.00	96.14	100.00	-
kaikawaka	a	-	-	4.32	-
	b	0.34	0.57	0.90	-
	% dead	100.00	100.00	17.24	-
broadleaf	a	-	0.95	1.29	9.17
	b	-	-	-	0.72
	% dead	-	0	0	7.28
putaputaweta	a	-	0.08	0.49	4.08
	b	-	-	-	-
	% dead	-	0	0	0
Total	a	64.40	74.89	96.38	101.81
	b	12.90	14.10	11.01	2.76
	% dead	20.03	18.83	11.42	2.71

		young forest		old forest	
		beech	rata-kamahahi	beech	rata-kamahahi
rata	a	328	710	155	180
	b	114	82	99	20
	% dead	25.8	10.4	39.0	10.0
kamahi	a	527	729	155	210
	b	128	46	17	40
	% dead	19.5	5.9	9.9	16.0
beech	a	199	-	207	-
	b	0	-	9	-
	% dead	0	-	4.3	-

Table 3: Mean density (stems/ha) of living (a) and dead (b) stems ≥ 10 cm dbh, and percentage of dead stems, of rata, kamahi, and silver beech in young and old beech and rata-kamahahi forest.

Discussion

In the young forest, size class distributions of rata and kamahi demonstrate a single cohort establishment of both species. Kamahi ages suggest establishment 160-200 years ago. A mean diameter growth rate for rata of 1.54 mm/yr. was recorded at Tautuku Bay, on the coast some 20 km south of Cedar Hill (Smith *et al.*, 1985). Applied to rata diameters in the study area, it results in a population age structure similar to that of kamahi. Manuka diameters suggest a population of advanced age. McConnell (1974) recorded 108 growth-rings in a manuka stem 15.8 cm in diameter in the Tahakopa Valley, 22.5 km west of Cedar Hill. A similar growth rate applied to the larger manuka stems on Cedar Hill gives an age at death of about 200 years, the maximum attributed to manuka by Burrows (1973).

The ages of silver beech trees show three establishment phases: more than 210 years ago, 100-160 years ago, and about 70 years ago. Taking into account underestimation due to growth rate increase with diameter, these phases occurred before, contemporaneous with, and after, the establishment of rata and kamahi. In the catchment of Wairepo Creek, 12.5 km west of Cedar Hill, a few silver beech saplings are situated in dense manuka stands which established after destruction of former forest by fire (Marshall, 1984). Beech stature (similar to or slightly larger than the surrounding manuka) is consistent with opportunistic establishment at the same time as the manuka. The first establishment phase of beech in the young forest on Cedar Hill also seems to correspond with the establishment of manuka.

Reproductive maturity of the first beech trees on the site coincided with the natural decline of manuka, between 50 and 100 years later, allowing establishment of the second generation of beech where the manuka canopy was senescing or suppressed by the parent beech canopy. This process is evident elsewhere in the Catlins, for instance at the boundary of beech stands and scrub vegetation on the MacLennan Range (Allen, 1985). Opening of the manuka canopy by collapse of moribund stems during this period also allowed the establishment of rata and kamahi, previously excluded by competition from manuka for light (Wardle, 1971), and a lack of suitable establishment sites (Wardle, 1966), respectively. McConnell (1974) recorded rata and kamahi overtopping manuka on a 110 year old slip face in the upper Tahakopa Valley, and Mark *et al.* (1964) reported a sequence of similar chronology on a slip face in Fiordland, in the south-west of South

Island.

The location of the majority of small beech saplings in the vicinity of the two largest trees in the young forest area suggests a response to beech canopy density decline. The growth rate of the largest of these trees over its outermost 20 growth rings is less than 15% of its overall mean growth rate, indicating a recent decline in vigour that could be reflected in foliage loss.

The paucity of small plants of both rata and kamahi in young forest is due to the seedling light demands of the former (Wardle, 1971) and the establishment sites, particularly tree fern trunks, required by the latter (Wardle, 1966). In the old forest, kamahi regeneration success reflects the availability of tree ferns and other sites such as decaying stumps and large logs, but that of rata is still limited by insufficient light. Vegetative reproduction of rata, as described on Bench and Stewart Islands to the south-west of the Catlins (Veblen and Stewart, 1980), does not occur on Cedar Hill, and has not been recorded elsewhere in the Catlins. Neither does kamahi show vegetative reproduction as described elsewhere (Wardle, 1966).

In old beech forest, diameter frequency distributions of silver beech ≥ 10 cm dbh show recruitment inadequate to maintain the density of stems in most diameter classes. Age frequency distributions show a similar trend, despite the wide range of ages which occurs in several of the diameter classes. The similar density of stems ≥ 10 cm dbh, but much lower basal area, of beech in young forest indicates that existing trees are likely to increase in stature without further recruitment. A comparison of canopy spread of old and young beech trees in the young forest shows that a continuous beech canopy, and with it, beech dominance of the site, could be attained by the existing trees. At that stage, diameter and age frequency distributions of beech may mirror those in the existing old beech forest.

Despite the similarity of kamahi basal area in young and old rata-kamahi forest, its much higher density in the former demonstrates that further mortality will occur as the trees increase in diameter to maturity. The trend to lower kamahi density and basal area under a beech canopy, seen in both old and young forest, indicates confinement of kamahi to the subcanopy under beech, its status in beech forest throughout the Catlins (Allen, 1988). The lower density and basal area of rata than of kamahi under a beech canopy in young forest reflect the earlier sensitivity of rata, as a more light-demanding species,

to competition from beech. The durability of rata wood probably contributes to the comparatively high density of dead rata stems recorded in old beech forest; evidence of dead kamahi stems would disappear relatively rapidly with decomposition. Thus rata and kamahi in the young forest, like beech, are developing population structures similar to those in existing old forest.

The young forest provides strong circumstantial evidence of destruction of a former forest cover by fire. Its location and extent, and the absence of a scarp or debris accumulation, preclude a landslide as the cause of its origin. The alternative explanation of windthrow is also unlikely, as there are no log or stump remains of former large (>50 cm diameter) trees, evidence of which could persist for the lifetime of subsequent trees which establish on them. In the young forest all the trees are clearly terrestrially established. The dense shrub understorey remaining after canopy destruction by wind would have prevented establishment of manuka, a light-demanding pioneer species which was present throughout the study area. Following windthrow, advance growth of both canopy and understorey tree species would have resulted in much faster re-establishment of forest similar in composition to the original, probably much like the existing old beech-dominated forest on Cedar Hill.

Conclusion

It is suggested that between 250 and 300 years ago fire completely destroyed forest on the upper slopes of Cedar Hill. Massive establishment of manuka occurred on the cleared ground from wind-borne seed, possibly originating from the manuka component of scrub vegetation occupying the summit as it does at present. Some opportunistic silver beech establishment also occurred, seed originating from beech forest outside the range of the fire on Cedar Hill or from the more continuous beech forest occupying the Catlins Valley south of the summit.

A few silver beech trees survived in competition with the manuka, but further beech establishment, as well as that of other forest trees, was precluded by the dense manuka canopy. Natural opening of the manuka canopy, about 50-100 years after establishment, allowed establishment of rata" kamahi, and a second wave of beech. Some manuka persisted until the taller trees formed a closed canopy during the past century.

Silver beech, present in the young forest only as an

opportunist as a result of destruction of the former forest cover, is able to maintain its population in the adjacent mature forest only by occasional opportunist establishment (Allen, 1988). Nevertheless, it is able to reach a greater height, and has a faster growth rate, than rata and kamahi, so is suppressing these species where they occur beneath its canopy. Within two or three centuries rata will be present here predominantly as a few large trees, and kamahi, while regenerating adequately, will be confined to the subcanopy.

Beyond the beech canopy, young rata-kamahi forest will develop a structure similar to that of the old forest nearby, with a denser and more diverse understorey of small trees and tree ferns, a continuously regenerating kamahi population with a wide range of diameter classes, and a rata population increasingly dominated by large trees.

Acknowledgements

Mr D.S. Hunt assisted with field work, and Dr W.G. Lee, Dr P.N. Johnson and Mr A.E. Esler provided helpful criticisms of the manuscript.

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