

Propagule dispersion and forest regeneration in *Leptospermum scoparium* (manuka) – *L. ericoides* (kanuka) forests following fire in Golden Bay, New Zealand

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Abstract

Regeneration dynamics were studied in 13 post-fire manuka-kanuka forests age 9 to 56 yr in Golden Bay, New Zealand. Height and age were measured for the tallest trees of each species and distances determined to the closest propagule sources. The number of tree species per stand increased from 4 at 9 yr to 31 at 56 yr with a mean of 23 and a total of 58. Propagule origin in percent was <4.4 seed bank, <5.7 gravity and water, 34 wind, 38 bird-dispersed small fleshy fruits (2-5 mm diameter) and 17 bird-dispersed large fleshy fruits (>5 mm diameter). The mean time for propagule arrival increased significantly from manuka-kanuka, to all wind, to small fleshy to large fleshy species. Propagule size was positively correlated with mean species entry period. Species arrivals were significantly earlier at decreasing distance from propagule source. With increasing propagule distance, the percentage of wind species entry declined with time, small fleshy declined, but then increased and large fleshy declined and then increased strongly. These patterns may reflect early packing by wind and small fleshy species and a later upsurge by large fleshy once the manuka-kanuka canopy can support the larger perching birds. Seedlings from bird-dispersed propagules were significantly closer to tree boles and mostly arrived when manuka-kanuka heights were from 4 to 6 m. Pigeon flock feeding may lead to great distance dispersal of large fleshy fruits. With increasing tree age, there was an increase in maximum height increment, paired height, and top height values. There were no significant differences between the various height indexes at 0-25 m versus >25 m from propagule source, but the ratios between paired height growth values consistently decreased with increasing age. From around 40 yr, taller growing species begin to overtop kanuka so that by 100 yr, all 13 stands should have a kanuka canopy shared with various combinations of podocarps and angiosperms of which *Dacrydium cupressinum* (rimu), *Podocarpus dacrydioides* (kahikatea), *P. totara* (totara), *Nothofagus menziesii* (silver beech) and *Weinmannia racemosa* (kamahi) will be predominant.

Keywords: Propagule type, size and source distance - wind and bird dispersion - perching trees - height growth - regeneration dynamics

Introduction

As part of a study of forest regeneration in the northern South Island, we sampled 13 stands of post-fire *Leptospermum scoparium* (manuka) and *L. ericoides* (kanuka) forest aged 9 to 56 yr. Particular attention was paid to the date of post-fire

entry for each species in relation to propagule type and distance to source and to the chronologic changes following disturbance including height growth relative to age and to distance from propagule source. Our results should contribute to a greater understanding of the mechanisms of forest regeneration (Finegan

1984, Crawley 1986, Bray 1989, and Cook 1994) and may prompt a greater use of such mechanisms in regeneration modeling as suggested by de Velice (1988) and Sheil (1997).

Materials and Methods

The study area is in Golden Bay at the NW tip of the South Island. Thirteen stands were studied in four sites: B1 and B2 at Butler, near the town of Rockville 40° 40.3'S, 172° 30.5'W; BE 1, BE 2, BE 3 and BE 4 at Bainham East near the town of Bainham 40° 40.6'S, 172° 30.5'W; BS 1, BS 2, BS 3, BS 4 and BS 5 at Bainham South 40° 49'S, 172° 30'W; and W 1 and W 2 at Wanganui, near Wanganui Inlet southwest of the town of Puponga 40° 30.4'S, 172° 30.8'W.

The 13 stands are all on old, near level river terraces except Wanganui, which has gently eroded slopes above an estuary. The four sites have fairly similar mean elevation, slope and slope facing with 90 m, 4° and 129° for Bainham South, 50 m, 5° and 255° for Bainham East, 75m, 10° and 213° for Butler and 15m, 11° and 191° for Wanganui. The climate is warm temperate with a yearly mean of 11-13°, a mean summer maximum of 22° and a mean winter maximum of 10°. Precipitation is within a range of 2.5 to 3.0 m. Total solar radiation in cal/cm² ranges from 150-175 in June to 525-550 in December (Coulter 1973).

The mature forests adjacent to the four sites are similar to the Podocarp-hardwood-beech forest (Category I) of Meurk (1995) and reflect a complex disturbance history caused by mining and the effects of clearing, burning and grazing. Each of these adjacent forests were composed mainly of small to large patches in varying stages of post disturbance regeneration and each contained sexually mature trees of the species found in the nearby manuka-kanuka stands. The more important canopy species were various mixtures of podocarps and angiosperms and included rimu, kahikatea, *Podocarpus hallii* (Hall's totara),

kanahi, kanuka and silver beech with totara, *Podocarpus ferrugineus* (miro), *P. spicatus* (matai), *Phyllocladus trichomanoides* (tanekaha), *Metrosideros robusta* (Northern rata) and *Nothofagus fusca* (Red beech) less common.

There were charcoal and burnt stumps or boles in every stand. The dates of the fires, judged by the age of the oldest sampled trees, were Bainham East 1 and 2, 1926, Bainham East 3 and 4, 1928 (these dates probably estimate the same fire), Bainham South 1 to 5, 1938, Wanganui 1, 1929, Wanganui 2, 1930 (probably the same fire) and Butler 1 and 2, 1939.

The chronologic method we used was to construct a history for each stand based on the ages of its oldest trees. In each of the 13 stands, we selected the tallest individuals of each species on the assumption that since all the stands were young and the result of post-fire regeneration, the tallest individuals were likely to be the oldest. Each plant was cut at the base with a sharp axe and then cut again, if necessary, to get a clean and clear cross section for counting the number of annual rings. The entire cross section was used to avoid counting of non-annual incomplete or false rings. Two of us made a separate age count on each cut tree and if the result varied by more than 1 yr, the stem was jointly counted and each ring subjected to scrutiny. Height and basal circumference of each tree were then measured. For rarer species, one or two individuals per stand were cut to avoid depletion of the species. For common species up to 10 or more individuals were sampled.

When early analysis of age results showed that stands adjacent to mature forest had shorter species entry times, we divided the four sites into 13 stands relative to distance from the edge of a mature forest propagule source. In Bainham East, stands 1 and 3 were 0-25 m from a propagule source and were adjacent to stands 2 and 4 which were, respectively >25 m and >75 m distant from the same propagule source. Bainham South was divided into 5 stands, a more developed forest at 0-25 m from a propagule source and a down-

hill series of four regenerating manuka stands which were 0-25, 26-50, >200 and >300 m distant from the same propagule source. Butler was divided into stands 0-25 m and >25 m and Wanganui into stands 0-25 m and >75 m from mature forest propagule sources.

During our field study we noticed that bird-dispersed tree seedlings were more common beneath tree canopies, often being found in clumps, and were less common in the centre of spaces between the trees. To test the distribution of wind-dispersed versus bird-dispersed seedlings we sampled intertree quadrats in four manuka stands in a downhill sequence at Bainham South which were aged 9, 17, 31 and 39 yr. Each intertree quadrat was laid between the bole of a randomly selected tree and the bole of its nearest neighbour. These quadrats varied in length from 83 to 153 cm, and were 40 cm in width. The distance of each seedling to the nearest bole was measured within each quadrat.

On 15 and 16 August, 1987, we measured light intensity with a L.I.-185A Photometer for one hour before and after noon under clear skies in the 9, 17, 31 and 39 yr stands at Bainham South. Twenty readings were made at a height of one metre on each day in each stand and these readings were compared with light intensity in the open which ranged from 13800 to 16500 lux on 15 August and from 12150 to 16050 lux on 16 August.

Plant nomenclature is after Allan (1961) and propagule data and potential tree heights are from Allan (1961) and Poole & Adams (1963).

Results

Post-disturbance species entry dates

In each of the 13 stands it was assumed that the oldest plants present, in every instance either manuka or kanuka, germinated within a year of the fire which killed the above ground parts of the preceding vegetation. The age of the oldest individual was considered the stand age and the

oldest sampled individual of each species was compared with this age to determine its entry year into the stand. Stand ages were 9, 17, 31, 39, 43, >43, 47, 52, 52, 53, 53, 55 and 56 yr.

There were 58 woody tree and shrub species with potential heights greater than 4 metres and ages from 1 to 56 years present in at least one of the 13 stands. Twenty-five of these species, 9 gymnosperms and 16 angiosperms, occurred in at least 2 stands as shown in Table 1. Species in this table are divided into those with wind-dispersed propagules, bird-dispersed propagules from small, fleshy fruits with diameters of 2-5 mm and bird-dispersed propagules from large, fleshy fruits greater than 5 mm. Hereafter they are referred to as wind, small fleshy and large fleshy.

Species entry relative to propagule distance

The mean period between disturbance and the arrival of each of the 25 species is shown in Table 1 for all of the 13 stands at distances of 0-25, 26-75 and >75 m from propagule source and for a subset of four stands which occurred at Bainham South in a downhill sequence at 0-25, 26-75, >200 and >300 m from propagule source. If total number of arrival dates per stand is tabulated, then for the 67 dates at 0-25 m, there is a range of 1 to 53 years with a mean for all dates of 15.6 yr; at 26-75 m there are 31 values from 1 to 38 yr with a mean of 18.2 yr and at 75 m from propagule source there are 52 values with a range of 1 to 52 years and a mean of 28.0 yr. Mean entry dates per propagule type are summarized in the last four lines of Table 1. In seven of the eight possible comparisons, not including the category of all species, there was an increase in propagule arrival time with increasing distance from propagule source ($\chi^2=4.5$, $P<0.04$). For the downhill subset, the range in arrival dates is 1 to 8 yr (mean=6.3 yr) at 0-25 m, 1 to 17 yr (mean=13.0 yr) at 26-75 m, 1 to <31 yr at >200 m (mean=24.2 yr) and 1 to 38 yr (mean=30.2 yr) at >300 m from propagule source. For these four stands there were 11 in-

Table 1 Mean period in years for species entry following fire destruction of previous vegetation in relation to distance to propagule source. Two data sets are shown: all of the 13 stands sampled and a subset of 4 stands in a downhill sequence.

Species	No. stands	Propagule distance (m)						
		All stands			Downhill sequence			
		0-25	26-75	>75	0-25	26-75	>200	>300
Wind-dispersed								
<i>Leptospermum ericoides</i>	13	1.7	8.0	10.7	2	16	21	20
<i>L. scoparium</i>	13	8.0	1.0	12.7	1	1	1	1
<i>Librocedrus bidwillii</i>	2	38.0	26.0					
<i>L. plumosa</i>	2	49.0		38.0				
<i>Metrosideros robusta</i>	4	26.0	31.0					36
<i>Nothofagus menziesii</i>	5	9.7	19.0	4.0				
<i>Olearia rani</i>	4	25.0	35.0	35.0				
<i>Weinmannia racemosa</i>	7	14.0	20.0	36.0				30
Bird-dispersed 2-5mm								
<i>Ascarina lucida</i>	3	19.0		38.0	8			38
<i>Carpodetus serratus</i>	3	24.0		<29.0				
<i>Coprosma areolata</i>	11	25.2	16.3	38.0	7	<17	29	30
<i>C. rhamnoides</i>	3		<17.0	42.0		<17		31
<i>Cyathodes fasciculata</i>	11	19.0	19.3	27.0	7	7	16	22
<i>Dacrydium cupressinum</i>	11	10.6	15.0	21.5			30	31
<i>Phyllocladus trichomanoides</i>	3	11.0		19.0				32
<i>Podocarpus dacrydioides</i>	9	4.2	9.5	22.0	8			
<i>P. hallii</i>	10	20.3	26.0	37.0	8			
<i>P. totara</i>	6	15.3	24.0	29.5			28	
<i>Pseudopanax crassifolium</i>	2	19.5						
Bird-dispersed >5mm								
<i>Coprosma robusta</i>	5	8.0	<17.0	<40.3	8	17	<31	37
<i>Griselinia littoralis</i>	2		22.0	36.0				38
<i>Myrsine salicina</i>	4	8.0	16.0	32.0	8	16	29	35
<i>Neopanax arboreum</i>	2	41.0		33.5			<31	36
<i>Podocarpus ferrugineus</i>	8	31.0	38.0	27.3			26	36
<i>P. spicatus</i>	3	8.5	38.0					
Mean entry date per stand								
All species		15.6	18.2	28.0	6.3	13.0	24.3	30.3
Leptospermum spp.		4.8	4.5	11.7	1.5	8.5	11.0	10.5
Wind dispersed		13.3	14.8	21.0	3.7	8.5	11.0	22.0
Bird dispersed 2-5mm		15.3	17.8	30.0	7.5	13.7	26.0	32.2
Bird dispersed >5mm		22.0	26.2	33.6	8.0	16.5	29.2	36.0

creases and 1 decrease in arrival relative to increasing distance from propagule source ($\chi^2=8.3$, $P<0.004$).

In the above comparisons, both manuka and kanuka are considered in two different propagule dispersion categories because they both have two modes of arrival, one by gravity from existing trees whose capsules open when the stand is burned and the other by wind. For statistical consistency, if the manuka-kanuka data are included only in the wind dispersed propagule type then, for the 13 stands as a whole, there are six increases and no decreases in arrival time at increasing distance from propagule source ($\chi^2=6.0$, $P<0.02$) and for the downhill sequence there were nine increases and no decreases ($\chi^2=9.0$, $P<0.003$).

The mean entry dates at the bottom of Table 1 are for the sum of the species in each stand of occurrence for each propagule type and are not a mean of the mean species entry dates shown in the body of the table. The high variability of mean species entry dates for the first and third

propagule types in Table 1 is largely the result of the inclusion in the table of species which occurred in only a few stands. Eliminating species which occurred in less than four stands from Table 1 substantially reduces this variability and increases the chi-square values on arrival time in relation to distance from propagule source.

Species entry per decade relative to propagule distance

The percentage of entry dates per stand is shown in Table 2 for wind, small fleshy and large fleshy propagules for the first five post-disturbance decades in relation to three propagule distance classes. In Part A of Table 2 the number of species entrants per decade for each propagule type in each propagule distance class is shown as a percentage of the total number of entrants in each class. At 0-25 m from propagule source, there is a steep and consistent decline in the sum of percent entrants from 44 in the first decade to 4 in the fifth decade. For 26-200 m from source, the sum of entrants shows little trend for

Table 2 The mean percentage (A) and mean cumulative percentage (B) per stand of species entrants in each decade for wind-dispersed (w), small fleshy 2.5 mm bird-dispersed (sf) and large fleshy >5mm bird-dispersed (lf) propagules in relation to distances of 0-25m, 26-200m and >200m from propagule source.

Species entry year	A											
	0 - 25 m				26 - 200 m				>200 m			
	w	sf	lf	Σ	w	sf	lf	Σ	w	sf	lf	Σ
1-10	20.2	18.3	5.1	43.6	13.8	10.5	0.0	24.3	7.9	0.0	0.0	7.9
11-20	5.6	14.9	4.4	24.9	6.2	10.5	7.1	23.8	2.9	5.0	0.0	7.9
21-30	3.9	11.2	2.7	17.8	4.3	9.5	2.9	16.7	7.9	23.8	10.0	41.7
31-40	3.7	1.7	3.7	9.1	7.6	10.9	6.7	25.2	2.9	14.7	24.7	42.3
41-53	2.2	1.2	1.0	4.4	1.4	7.1	1.4	9.9	0.0	0.0	0.0	0.0
B												
1-10	20.2	18.3	5.1	43.6	13.8	10.5	0.0	24.3	7.9	0.0	0.0	7.9
11-20	25.8	33.2	9.5	68.5	20.0	21.0	7.1	48.1	10.8	5.0	0.0	15.8
21-30	29.7	44.4	12.2	86.3	24.3	30.5	10.0	64.8	18.7	28.8	10.0	57.5
31-40	33.4	46.1	15.9	95.4	31.9	41.4	16.7	90.0	21.6	43.5	34.7	99.8
41-53	35.6	47.3	16.9	99.8	33.3	48.5	18.1	99.9	21.6	43.6	34.7	99.8

the first four decades, but declines in the fifth, while at >200 m to propagule source there is an increase in the sum of percent entrants to the fourth decade.

The sum of cumulative species arrival (Table 2, Part B) shows that with increasing propagule distance, both wind and small fleshy species decline in all five decades, but large fleshy species decline in the first three decades and then strongly increase. At 0-25 m from source, total cumulative entry is 44% by the first decade, 68% by the second and 86% by the third. This rate is much faster than at 26-200 m from source where cumulative entry increases from 24% to 65% by the third decade. Arrival at >200 m is even slower, increasing from 8% to 57% by the third decade.

Species entry relative to propagule type

Manuka-kanuka in Table 1 arrived sooner than other wind-dispersed species, wind species as a whole arrived sooner than small fleshy fruits, which in turn, arrived sooner than large fleshy fruits. This resulted in a total of 9 earlier arrivals and no later arrivals for the rank order of propagule type in Table 1 ($\chi^2=9.0$, $P<0.003$). For

the same comparisons in the downhill sequence, there were 10 increases and 2 ties ($\chi^2=8.3$, $P<0.004$). If manuka-kanuka are included in the wind-dispersed category, then there were six increases and no decreases ($\chi^2=6.0$, $P<0.02$) and for the downhill sequence, there were eight increases and no decreases ($\chi^2=8.0$, $P<0.005$).

Seedling density and proximity to tree boles

Seedling density at 0-20, 21-40 and 41-60 cm from tree boles is shown in Table 3. The species with wind-dispersed seedlings were either manuka or kanuka except for five kamahi seedlings. The youngest of the manuka and kanuka seedlings could not be distinguished so that the two species cannot be shown separately in the table. The unknown angiosperm is assumed to be bird-dispersed because its seedlings did not resemble any of the wind-dispersed species in Table 1.

The seedling density of species with bird-dispersed seeds in the first 20 cm from the tree bole (Table 3) was more than double their density at 41-60 cm from the bole ($\chi^2=35.4$, $P<0.001$). Wind species show no significant trend ($\chi^2=1.3$,

Table 3 Seedling density of bird-dispersed and wind-dispersed species at 0-20, 21-40 and 41-60 cm from perching tree boles in stands of 9, 17, 31 and 39 years.

Species	Distance from bole			χ^2	P
	0-20 cm	21-40 cm	41-60 cm		
	No. individuals per m ²				
Bird-dispersed	16.2	11.0	7.1	35.4 ¹	<0.001
Wind-dispersed	88.3	93.4	91.2	1.3	>0.5
<i>Coprosma areolata</i> plus <i>Cyathodes fasciculata</i> ²	7.7	6.0	1.5	19.8	<0.001
<i>C. areolata</i> plus <i>C. fasciculata</i> ³	15.4	1.2	8.5	9.8	<0.007
Unknown Angiosperm	1.6	0.3	0.0	21.0	<0.001
<i>Coprosma foetidissima</i> x <i>robusta</i>	0.9	0.0	0.0	14.2	<0.001
<i>C. rhamnoides</i>	0.5	1.0	1.3	5.0	<0.03
Other Angiosperm bird-dispersed	0.8	0.7	0.2	4.2	>0.1
<i>Podocarpus totara</i> plus <i>P. dacrydioides</i>	0.8	0.3	0.5	2.4	>0.3

¹ Chi square calculated on total number of individuals per samples of equal area for 0-20 cm versus 41-60 cm from bole

²Data for 9 and 17 year stands only.

³Data for 31 and 41 year stands only.

$P>0.5$) with increasing distance from bole. Of the seven bird-dispersed species, or species groups, six had patterns of consistent decrease from 0-20 to 41-60 cm from bole, of which four were significant. There was a significant increase away from bole for *Coprosma rhamnoides*. With increasing stand age, there was a shift in the percentage of *Coprosma areolata* and *Cyathodes fasciculata* (mingimingi) in the three distance classes. At 9 and 17 years, these percentages steeply declined from 51 to 40 to 9 with increasing distance from bole, but by 31 and 39 years the steepness of the decline decreased to 44, 32 and 24 percent. This may be the result of the seed-carrying birds perching further from the bole as the branches widen and strengthen.

A study of the bird-distributed seedlings in the 39 year stand showed spaces with no seedlings in the mid-area between tree boles in all but one quadrat. The diameter of these spaces increased from 19.3 cm at quadrat lengths of 83-98 cm to 53 cm at maximum quadrat lengths of 115-153 cm. Mean diameter as a percentage of quadrat length increased from 28 to 41. We assume these spaces are the result of birds not perching on the flimsier outer branches where

the canopies of the two perching trees intersect. Measurements of seedling clump size were made with a clump defined as two or more individuals 10 cm or less distant from their nearest neighbours. There were 39 seedling clumps with the number of individuals varying from 2 to 13 (mean=4.5). Clump diameters varied from 1 to 38 cm (mean=12.7). Measurements on what appeared to be discrete clumps of seedlings resulting from bird defecations were made at Bainham East. Two clump shapes were seen: an elongated oval shape, which we assumed was a splatter from a flying bird and a circular shape containing a decreasing area density of seedlings towards its perimeter which resulted from a defecation by a sitting bird. There were seven clumps which contained 6 to 13 kahikatea seedlings (mean=9.1) and which had diameters from 5.5 to 17.6 cm (mean=10.2).

Seedlings of bird-dispersed species relative to tree height and size

The distribution of the 32 bird-dispersed tree species which occurred beneath the canopy of either a manuka or kanuka tree is shown in Table 4. Column 1 of the table lists the shortest

Table 4 The distribution of 32 species of bird-dispersed tree seedlings in relation to the height of the canopy trees under which they occurred. Data are shown for the shortest, the mean and the tallest canopy heights under which each species occurred as a seedling in the four sampled sites. The mean of the median values for bole diameter for manuka and kanuka is listed for each canopy tree height class.

Canopy tree height class (cm)	No. of species			Tree bole diameter (cm)	
	Shortest canopy height	Mean canopy height	Tallest canopy height	Manuka	Kanuka
0-100	0	0	0		0.8
101-200	3	0	0	1.3	1.9
201-300	2	1	1	2.5	2.4
301-400	3	1	0	4.2	3.7
401-500	5	2	0	5.0	5.3
501-600	12	6	5	5.5	6.0
601-700	2	13	2	6.0	6.8
701-800	1	4	9	8.6	9.0
801-1000	4	5	15		11.1

canopy height at which a species appeared as a seedling, column 2 shows the mean canopy height under which the seedlings of each species were found and column 3 shows the tallest tree height at which each species occurred as a seedling. There is a substantial peak of 17 species under canopy tree heights of 401-600 cm for the shortest height of occurrence with 16 of these arrivals between heights of 450 to 562 cm. Mean number of arrival heights peak at 17 species in the 501-700 cm canopy height classes of which 15 species occurred from 612-725 cm. The tallest canopy tree heights at which the bird-dispersed species occurred as seedlings peaked in the 801-1000 cm canopy height class, but the upper limits of this range would expand if there had been samples of canopy manuka or kanuka trees greater than 10 m in height. Bole diameters under which the mean number of species peaked were 6.0 cm for manuka and 6.8 cm for kanuka and the trend for the larger median bole diameters shifted from manuka at heights of up to 400 cm to kanuka thereafter.

Tree height and increment relative to propagule source and type

Maximum height data in order of increasing potential species heights are shown in Table 5 for the seventeen species which had maximum height estimates for at least three stands. The results show a fairly consistent increase in height with increasing age of stand. The downhill sequence of stands from BS 1 to 4 has an increasing age and distance to propagule source and there is a clear height increase with age which is significant, with the median test for small samples (Walker and Lev 1953), from BS 3 to BS 4 ($\chi^2=8.0$, $P<0.005$) and from BS 4 to BS 5 ($\chi^2=12.0$, $P<0.001$).

Top height values in Table 5, which show the mean height of the ten tallest individuals in each stand (Garcia 1983), increased from 164 cm at 9 yr to 904 cm at 55 yr to 964 cm at 56 years. To reduce the influence of varying stand environments on height growth, only the maximum

heights of species which occurred in both stands of each of the seven pairs of directly adjacent stands listed in Table 5 were used to calculate a maximum stand height. These mean paired height values reflect the top height trends, but are around 100 to 200 cm lower. The increase in individual maximum heights and in the two height indices with increasing age is accompanied by a rapid entry and subsequent vigorous height growth by the longer-lived and taller-growing podocarps and angiosperms which reach and often exceed the height of the fast-growing earlier arrivals like manuka, kanuka, *Myrsine salicina* (toro), mingimingi and *Coprosma areolata*. At 39 years kamahi is the third-tallest species and at >43 yr silver beech is the tallest. Other species to exceed manuka and kanuka in height are rimu at >43 yr, totara and silver beech at 53 yr and silver beech at 56 yr. This increase in height by the taller and longer-lived species is reflected in changes in their percent densities relative to manuka and kanuka. As shown in Table 5, manuka density declined from 66.2 to 20.4% between 9-43 yr and 47-56 yr and kanuka increased slightly from 23.8 to 26.8%. For the same periods, rimu increased from 2.6 to 8.6%, kahikatea from 0.5 to 20%, matai from 0 to 1.6% and tanekaha from 0 to 1.8% with Hall's totara and miro slightly declining. The taller angiosperms showed a similar increase, from 0 to 5.9% for silver beech and 1.9 to 4.2 for kamahi, although Northern rata declined to 0%.

Since species entry periods following disturbance are closely related to distance to source, it might be expected that the height increments of later arrivals would be lower than those of earlier arrivals. To test this possibility height age curves were calculated for 47 sets of species that had sufficient height measurements to allow calculation of increments at 0-25 m and >25 m from propagule source. These curves were supplemented by separate calculations of the mean height increment of the tallest individual of each species in each propagule distance class and by the determination of the greatest height incre-

Table 5 Maximum height (cm) per stand for all species with data from at least three stands, together with top height¹ per stand, mean paired height² per stand and percent species density from 9-43 yr and 47-56 yr. Identity of species: Ca, *Coprosma areolata*; Cf, *Cyathodes fasciculata*; Al, *Ascarina lucida*; Ls, *Leptospermum scoparium*; Or, *Olearia rani*; Ms, *Myrsine salicina*; Le, *Leptospermum ericoides*; Ph, *Podocarpus hallii*; Ptr, *Phyllocladus trichomanoides*; Pf, *Podocarpus ferrugineus*; Ps, *Podocarpus spicatus*; Wr, *Weinmannia racemosa*; Mr, *Metrosideros robusta*; Nm, *Nothofagus menziesii*; Pt, *Podocarpus totara*; Dc, *Dacrydium cupressinum*; Pd, *Podocarpus dacrydioides*.

Stand No.	Age (yr)	Propagule distance (m)	Ca	Cf	Al	Ls	Or	Ms	Le	Ph	Ptr	Pf	Ps	Wr	Mr	Nm	Pt	Dc	Pd	Top height ¹ (cm)	Mean paired height ² (cm)
BS 1	9	0-25	<4	<4	<4	194		<4	139	<4					<4					164	83
BS 2	17	26-50		56		301		6	5											270	92
BS 3	31	>200	4	201		404		6	196			11						5	6	381	104
BS 4	39	>300	220	353	3	671		12	472	<4	57	85		449	19		109	14	12	605	202
BS 5	>43	0-25	479	389	12	635		>600	778	518		202		617	51	1067	556	789	762	805	529
B 2	43	>25	531	409		559	173	146	735	318				730	146			650	43	689	445
B 1	47	0-25		549		677	549	>500	775	438		207		721				667	621	736	623
W 2	52	>75	78	348		550	388		987	268	543			290				556		759	511
W 1	52	0-25			668	580	505		1000	600	890	191		535				725		884	691
BE 3	53	>25	548	445		630			752	377		117	180	173		577	350	650	610	647	524
BE 1	53	0-25	409	303		605			940	323			516			1060	976	490	750	904	661
BE 4	56	>75	361	290		490			1095	222		501				1097	466	650	715	964	623
BE 2	55	0-25	567	521		675			963	567		512	782			763	910	590	860	904	712
Mean percent density																					
9-43 yr			1.4	1.6		66.2	0.5		23.8	0.9		0.3		1.9	0.3			2.6	0.5		
47-53 yr			1.1	1.1	0.9	20.4	0.5	2.4	26.8	0.3	1.8	0.1	1.6	4.2	0.0	5.9	4.0	8.6	20.0		

¹Top height is the mean height of the ten tallest individuals in each stand.
²Mean paired height is the mean of all species which occur in each pair of stands (BS 1 and 2, BS 3 and 4, BS 4 and 5, B 2 and B 1, W 2 and W 1, BE 3 and BE 1 and BE 4 and BE 2).

ment regardless of individual height for each species in each propagule distance class. For the 47 sets of height age curves there was a negligible decline in mean height increment from 16.0 to 15.9 cm/yr from 0-25 to >25 m from propagule source. This decline included 23 increases and 24 decreases in value, a non-significant change ($\chi^2=0.02$, $P>0.9$). The mean height increment of the tallest individual of each species decreased, with increasing distance from propagule source, from 18.5 to 17.5 cm/yr, a non-significant change with 24 increases and 23 decreases. For maximum height increment regardless of individual height there was a decrease, with increasing source distance, from 20.6 to 19.3 cm/yr with 27 increases and 20 decreases, again, non-significant ($\chi^2=1.0$, $P>0.3$).

For mean height increment calculated on species height age curves of angiosperms, there were 16 increases and 11 decreases from 0-25 to >25 cm to propagule source ($\chi^2=0.93$, $P>0.3$) while for gymnosperms, there were 7 increases and 13 decreases ($\chi^2=1.5$, $P>0.15$). Similar non-significant patterns for angiosperms and gymnosperms with increasing distance to propagule source occurred for the height increments of the tallest individual and for the maximum individual height increment.

Light intensity in four manuka stands

Measurements on the floor of the 9, 17, 31 and 39 yr stands at Bainham South showed that for the 9 yr stand, light intensity was 16.7% of light in the open. At 17 yr, intensity declined to 2.3% and then increased to 4.2% at 31 yr and 9.2% at 39 yr.

Discussion

Species arrival and survival

Fifty-eight tree species with potential heights of 4 m or more arrived in the 13 stands of which 25 occurred in two or more stands. At 0-25 m from source, mean per stand arrival time varied

from 6.3 to 23.7 yr with a mean of 13 yr. Seven of 13 overstorey species and six of the seven overstorey species which occurred in over half the stands, arrived within five years after fire. This pattern resembles that of Amazonia tropical forest where Uhl & Jordan (1984) found that over half of the eventual overstorey canopy established within 5 years after disturbance.

Arrival of seedlings following destructive disturbance does not ensure a species will survive. When there is a dense initial manuka or kanuka invasion, many of the other arriving species may have a low survival. In the downhill sequence at Bainham South, *Ascarina lucida* was 1 yr old in the 9 yr stand and 1 yr old in the 39 yr stand. Mingimingi was 2 yr old in the 9 yr stand, 10 in the 17 yr stand, 15 in the 31 yr stand and 17 in the 41 yr stand. Toro was 1, 1, 2 and 4 yr old in the 9 to 39 yr stands. If these early-arriving species in the 9 yr stand had made the same early entry in the 17, 31 and 39 yr stands then their ages in these stands should be higher. The poor survival of these juveniles could be influenced by changing light intensity. Measurements on the floor of the four downhill stands showed that in the 9 yr stand, which had been killed by fire leaving an open canopy of dead blackened and leafless stems, visible light as a percentage of light in the open was 16.7%. At 17 yr, the mean canopy height was 230 cm, but this canopy was living and dense and light intensity was only 2.3% of light in the open. At 31 yr, there was still a dense canopy with a height of 321 cm and light at 4.2% of open and by 39 yr mean canopy height was 511 cm and light had increased to 9.2% of open. Measurements that we made in regenerating manuka elsewhere showed a similar pattern of an initial decrease in light on the floor with increasing canopy height and density followed by an increase in light as canopy height continued to increase and there were more canopy openings from a greater difference in the heights of individuals and from a more uneven canopy surface. Low light intensity in dense young manuka regeneration is probably a major

factor in the poor survival rate of early species entrants, many of which will continue to re-enter until they perhaps succeed.

Species arrival and propagule source and type

After fire, all our stands had an initial cover of manuka or kanuka or of both species from seeds that were released in place from capsules opened by fire or from wind transport. From this event onwards distance to propagule source and type of propagule were major variables. The summary data at the bottom of Table 1 show a consistent and statistically significant increase in arrival date with an increasing distance from propagule source. This result is supported by the conclusions of McClanahan (1986) and by Clarke *et al.* (1998) who also found that fecundity of propagule production was positively correlated with dispersal distance. Summary data in Table 1 also show a significant and consistent increase in arrival time relative to propagule type with a mean arrival of manuka and kanuka earlier than all wind species which had an earlier mean arrival than small fleshy species which arrived sooner than large fleshy bird-dispersed species.

Even though mean arrival dates, as noted above, had the same rank order of species arrival for each propagule type, there was a clear shift amongst the three propagule types in decadal percentage arrivals in relation to propagule source distance. Wind species, shown in Part A of Table 2, consistently decreased in the first and fifth decades, increased in the third and increased and then decreased in the other two decades. Small fleshy and large fleshy species both decreased in the first two decades and then increased in the next two with a decrease in the fifth decade. If cumulative arrival percentages are considered, as shown in Part B of Table 2, a more consistent pattern emerges. Wind species at increasing distance to propagule source consistently decline in all decades. Small fleshy species decline in the first two decades and increase in the next two with large fleshy species following a similar pattern. When the three propagule dispersion types

are considered in relation to each other, a consistent pattern emerges. With increasing distance to propagule source, wind, and to a lesser extent small fleshy species, dominate the first decade with both small fleshy and large fleshy species declining to nil. Small fleshy species are predominant in the second decade, gradually declining with increasing propagule distance. Small fleshy species also dominate the third decade, increasing to a substantial maximum at >200 m to source. Large fleshy species, which declined to nil in the first and second decades, increased in the third decade and then strongly increased in the fourth decade to reach the highest arrival percentage of any of the propagule dispersion types.

The consistent decline in wind-transported species with increasing distance to propagule source shows a lesser effectiveness of wind at greater distances. Preest (1963) estimated that for Podocarpaceae, wind dispersal "never extends much beyond a distance equal to the height of the tree" and that wind dispersion of silver beech was not much beyond 200 m with 500 to 3000 m the absolute limit. Other species of *Nothofagus* have been found, however, from 3 km to over 20 km from a seed source (Haase 1990, Burrows & Lord 1992).

Seeds of fleshy species are mainly carried by birds, but their high percent arrival values in the first two decades at 0-25 m and to a lesser extent at 26-200 m may be partly due to gravity and wind transport. The decline in the rate of decrease of small fleshy arrivals in the second decade and the subsequent increase in the third and fourth decades with increasing propagule distance probably reflects an increase in small bird visits and their dispersion of seeds from small fruits as these birds begin to perch in the low, but rapidly growing manuka and kanuka saplings.

Most large fleshy species arrivals in the first decade are probably by wind, gravity, or, less likely, from the seed bank since, as noted below, the longevity of their seeds in the seed bank is

usually less than two to four years. Later arrivals are nearly always the result of transport by larger birds which depend on there being trees of sufficient height and strength to support their heavier weight. Since these larger birds, mainly *Hemiphaga novaeseelandiae* (pigeon) and *Prosthemadera novaeseelandiae* (tui), require this support many species originating from large fleshy propagules would not be expected in the first or second decades of forest growth. Subsequent large fleshy species entrants in the third and fourth decade would have to compete with an already established population of seedlings and saplings of wind and small fleshy species whose cumulative percentage arrival is 74% by year 30 at 0-25 m from propagule source. At a greater distance from propagule source, in the >200 m class the number of wind and small fleshy species is less than 50% by the end of the third decade. This is a much lower level of species packing than at 0-25 m from source which means there were probably more microhabitats available for the large fleshy species as they arrived. By the end of the third decade, the maximum height of manuka and kanuka in BS 4 was 671 cm and 472 cm, respectively, heights which were probably sufficient to support larger birds such as tui and pigeon. Evidence to support this possibility can be seen in Table 4 which shows there were 16 species whose shortest canopy height for seedling occurrence was under trees 450 to 562 cm tall. Ten of these 16 species were carried by larger birds as shown by their propagule diameters which were greater than 5 mm with a mean of 7.6 mm. This mean was significantly higher ($\chi^2=8.7$, $P<0.004$), using the median test, than the mean propagule diameter of 4.4 mm for the seven species in Table 4 whose shortest canopy height for seedling occurrence was from 160 to 420 cm and which included only one species with a diameter greater than 5 mm.

For both wind and bird-dispersed propagules, species with smaller fruits arrived sooner than those with larger fruits. Smaller wind dispersed

seeds arrived sooner because they were more easily blown by the wind. Smaller fruited bird-dispersed propagules were likely carried by a larger number of bird species, a possibility supported by data in Whelan *et al.* (1998), which show a larger number of frugivore birds carry small fruited propagules as compared with larger fruited. Their data show plant species with fruit diameters of 9.0-11.9 mm are carried by one frugivore bird species, diameters of 7.0-8.9 mm are carried by a mean of 8.0 species and diameters of 4.0-6.9 mm by 9.8 species. Another reason for the earlier arrival of plants with small fleshy propagules is that the smaller birds can perch in younger and shorter manuka or kanuka plants compared with the larger birds which require larger, firmer perching trees. When the diameters of the wind- and bird-dispersed propagules were compared with their mean species entry periods, there was a strong positive correlation in each propagule distance class in Table 1, which was significant ($r=+0.65$, $P<0.05$) for the 25-75 m propagule class.

Birds as dispersal agents

Our observations on early stages of post-fire regeneration showed that the seedlings of many tree species with fleshy propagules were often found close to the boles of living or recently fire killed trees. These observations prompted the study in Table 3 which showed bird-dispersed seeds, but not wind-dispersed seeds, were non-random by being distributed closer to the boles of perching trees. Such non-randomness has also been noted by Guevara *et al.* (1986) who found bird-dispersed seeds under isolated remnant trees and by Loiselle *et al.* (1996) who noted both bird foraging activity and habitat preference resulted in non-random seed rain. Experiments by McClanahan & Wolfe (1993) found 340 bird-deposited seeds/m² under an artificial tree erected over soil with no seed bank compared with 2 seeds/m² in the control. Our present work on regeneration in a 28 year old kanuka forest is showing a strong tendency for bird-carried seed-

lings to occur closer to the boles of perching trees than in the intertree spaces. The above results support the conclusion of Preest (1963) and Beveridge (1964) that birds usually defecate while perching or, as we have observed, immediately on take-off, especially when startled.

For bird-dispersed species those with small fleshy fruits have an advantage since their seeds can be carried by birds of all sizes. The large fleshy species have a more limited number of larger bird species available for their dispersal and, in general, the larger the bird, the lower its population. For example, the large populations of silver eye that regularly visit young *Leptospermum* stands can disperse only small fleshy fruits as compared with the rarer pigeon which carry much larger fruits, but visit young *Leptospermum* less often. The importance of larger birds for transporting large propagules is underlined by the conclusion of Clout & Hay (1989) that there has been a decline through extinction in the number of frugivorous birds that disperse large fruited tree species, except for pigeon, which varies from rare to common, and the very rare *Callaeas cinerea* (kokako).

There is evidence that large fruits may be carried by birds to great distances. The two furthest stands from propagule source that we sampled were at >200 m and >300 m and both contained all or all but one of those species in Table 1 with propagule diameters greater than 5 cm. This dispersal may reflect the tendency for pigeons to flock feed over great distances. We have observed two instances of flock feeding, one near Abel Tasman National Park, the other at Duncan Bay, Tennyson Inlet, where groups of pigeons, one greater than 100 and the other 16, gathered for flock feeding. On dispersing, in both instances, these pigeons traveled for up to 4 km. Pigeon movements up to 18 km, including three return trips per year, were found by Clout *et al.* (1991) at Pelorus Bridge, near Rai. We have no comparable data on medium-sized birds like tui, bell-bird, blackbird or song thrush except to note that during nesting they rarely flock feed and are

strongly territorial, some tui defending their nesting territory throughout the year. Smaller frugivores are also territorial while nesting and apparently only travel great distances, if, like *Zosterops lateralis* (silver eye), they flock in the autumn (Clout, M.N., pers.comm. 1999). From these observations it appears that pigeons, New Zealand's largest frugivore, may travel greater distances than most other frugivores, and in so doing, deposit propagules of a larger mean diameter. This conclusion is at variance with Hoppes (1987) for central Illinois, U.S.A., that frugivores disperse small seeds further than large seeds.

Propagule dispersion from seed banks

There is little indication from species arrival dates that a substantial number of propagules had survived in a seed bank. If there had been such a component, it could be expected there would be a peak number of arrivals in the first few years following disturbance, but this was not the case. In the first five two yearly periods there were 4, 4, 5, 8 and 0 arrivals for the fleshy fruited species and 15, 5, 2, 3 and 0 arrivals for the wind-dispersed species. The fleshy species show no peak except in years 7 and 8, an unlikely time for seed bank propagules to suddenly germinate. The strong peak of fifteen arrivals for wind species in the first two years was composed of six manuka, eight kanuka and one silver beech. While it may be possible for a small light seed like those of kanuka to survive in soil storage for up to a few months (Burrows 1997b), it doesn't seem there would be a large contribution from such an unlikely source. Our observations on slips and tip-up mounds where subsoil that is unlikely to contain any manuka or kanuka seeds was exposed to the light, are that they contain up to 1000 or more seedlings/m², which probably originated from wind-dispersed seeds.

Another reason a seed bank origin may be rare is that many of the species we sampled have a short post-dispersal germination period. For gymnosperms, as shown by data in Beveridge

(1964), Clout & Tilley (1992) and Burrows (1997a), kahikatea all germinated in the summer following their shedding, most totara and rimu germinated within 18 months and only some of the larger fruited matai and miro could remain dormant for up to four years or more. In our study, there was one stand in which matai entered at 5 years and this seed could have come from a seed bank, but the earliest entry of miro was at 17 years, and a seed bank origin is unlikely. Kahikatea had three entries in the first two years and these could have come from the seed bank, but neither rimu nor totara entered until the fourth year or later. Reported angiosperm germination periods for the species in Table 1 were shorter than for gymnosperms, varying from one to nine months (Burrows 1997a, 1997b). Other than manuka and kanuka, the only angiosperm to enter in the first four years was silver beech which, like the *Leptospermums*, is mainly wind transported and which had one entry in year 1 and two in year 4. We conclude seed rain is the overwhelming source of propagules. Our highest possible estimate of seed bank contribution is 4.4%. This value is similar to the 2% seed bank contribution found by Alvarez-Buylla & Garcia-Barrios (1991) for revegetation in pioneer tropical forest.

Gravity and water propagule dispersion

Entrance of propagules by gravity fall from trees in the absence of wind was stated by Preest (1963) as limited to the tree perimeter, but we have seen heavy matai seeds bounce and roll up to 3 m outside the perimeter. Water dispersal along streams (Preest 1963) is important in long distance dispersion of beech seeds. Sheet water flow down slope during high intensity rain storms may be of great importance since it can carry off propagules in the lighter organic matter on the surface as well as portions of upper soil layers that may contain seed bank propagules. The downhill sequence at Bainham South may have included sheet water transport since there was a high species list in the oldest stand at >300 m

downslope. Our maximum estimate for gravity and water dispersal would be 5.7% of total entrants.

Combining this value with the maximum estimate of 4.4% for seed banks then, by subtraction, entrance of species by wind dispersal would be 34%, small fleshy species 38% and large fleshy 17%.

Height growth and distance from propagule source

Given the differences in distance from propagule source and in various site aspects such as soils, it could not be expected that the maximum heights per species or the top height values shown in Table 5 should show a strict linear height increase with time. Nevertheless, the trends in Table 5 show a general increase in height with age and for most species this increase is consistently higher if the data are smoothed with a running average. Top height values showed fairly consistent increases with age, but the pattern was clearly influenced by distance to propagule source which shows a mean of 877 cm for stands 0-25 m from source compared with 790 cm for stands >25 m from source, for all stands 52-56 yr. Mean paired heights for closely adjacent stands from 53-56 yr show that each stand pair at 0-25 m has a higher mean paired height (688 cm) than at >25 m from propagule source (586 cm). Paired height ratios between the 0-25 m and >25 m propagule distance class consistently decreased with increasing age, from 2.6 times at 39-43 yr to 1.40 at 52 yr, 1.35 at 53 yr and 1.14 at 55-56 yr.

Contrary to what might be expected, there were no significant differences in height increment, height increment of the tallest species or maximum height increment between 0-25 m and >25 m from propagule source, although angiosperm height increments were slightly higher and gymnosperm slightly lower. This difference may be related to their differing height-age curves. A survey we are making shows a tendency for angiosperm species to reach their maximum height increments from late in their first decade to early in their third decade, while gym-

nosperms peak around a decade later. For the 13 stands we sampled, the ages of all species were lower in the > 25 m to propagule class than in the 0–25 m class which means gymnosperms in the 0–25 m class would more often be sampled before they reached their age of maximum height increment than would angiosperms. For this reason we predict that the difference between angiosperm and gymnosperm increments should decrease in the future.

Podocarp regeneration and cattle browsing

All of our stands had abundant gymnosperm regeneration and in 15 years of field work we often noted the influence of cattle browsing on this abundance. Unlike sheep, which nibble most podocarps, even the prickly rimu and totara, cattle less often browse on podocarps, but strongly browse many angiosperm species, even *Melicetyus ramiflorous* which may be toxic to them. Our observations show light cattle browsing favours gymnosperm saplings and seedlings in competition with angiosperms. We found that a reserve which was lightly browsed by cattle had podocarp regeneration repressed in places by angiosperms after the reserve was fenced against cattle.

Species arrival and species longevity

Species longevity is now recognised as a major factor in regeneration dynamics (Hibbs 1983, deVelice 1988, Bray *et al.* 1994, Chapin *et al.* 1994). We found maximum ages of 20 yr for *Coprosma robusta*, 25 yr for *C. australis*, 24 yr for *Schefflera digitata* and 31 yr for *Aristotelia serrata* (Bray *et al.* 1994) and, in the present study, 31 yr for mingimingi, 35 yr for *Olearia rani* and 35 yr for *Coprosma areolata*. These seven species have potential maximum heights of from 6 to 10 m and it is likely that their short life spans are influenced by the lower light intensities they experience as their maximum heights are exceeded by upsurging neighbouring trees of greater potential height. Whether endogenous or environmental, their short life spans will prohibit an

accurate estimate for their arrival time in stands which are greater in age than their life expectancy. It is possible that there were earlier entrants of these species that died before our sampling began and that the arrival dates of mingimingi, *Olearia rani*, *Coprosma areolata* and *C. robusta* were earlier than we determined.

Conclusions

In the time since fire disturbance, the 13 stands amassed from 4 to 31 shrub and tree species for a total of 58 species which had a potential height of 4 or more metres. The number of species per stand increased from 4 at 9yr to between 17 and 31 from 39 to 56 yr with a mean of 23 species.

There were significant tendencies for the time of species arrival following disturbance to increase with increasing distance from a propagule source both for the 13 stands as a whole and for the four stands in the downhill sequence. There were also significant tendencies for mean manuka-kanuka arrival to occur before wind fruits as a whole which arrived earlier than small, fleshy, bird-dispersed fruits 2–5 mm diameter, which in turn were earlier, on average, than large, fleshy, bird-dispersed fruits >5 mm diameter.

The entrance of wind-dispersed species predominated in the first decade, small fleshy species in the second and third decades and large fleshy species in the fourth decade, while small fleshy species predominated in all three propagule distance classes. Cumulative species entrance percentages for wind species declined with increasing distance to propagules in all decades while small and large fleshy species declined in the first two decades, declined and then increased in the third and consistently increased in the fourth decade.

After the first decade, wind-dispersed species quickly declined with time and with distance from propagule source. This rapid decline with time clearly reflects the decreasing effectiveness of wind in blowing propagules past the barriers created by upsurging tree growth while the de-

cline with increasing distance from propagule source is a function of the decreasing wafting effectiveness of wind at increasingly greater distances. Small fleshy species consistently decreased with time in the lowest propagule distance class and decreased with increasing distance to source in the first and second decades. These trends were reversed in the third and fourth decades in which small fleshy species increased with increasing distance from propagule source. The failure of small fleshy species to appear in the first decade at greater than 200 m from source shows an initial decreasing effectiveness of birds as dispersal agents at greater distances and suggests that if this same initial failure occurs at lesser propagule source distances than other dispersal mechanisms like gravity, water or wind may also have operated to disperse the small fleshy fruits. Large fleshy species also decline with time in the 0-25 m propagule class, but increase in the greater than 200 m class and strongly increase with increasing propagule distance in the third and fourth decades. This increase of both small and large fleshy species in the third and fourth decades at the greater propagule distances is likely the result of a rapid increase in the strength of bird perching sites which apparently occurs when trees reach heights of around 450 to 560 cm. The low incidence of large fleshy species at the lowest propagule distance was probably due to an early packing of available niches by plants which came from wind or small fleshy propagules.

Barring catastrophe, mean heights, top heights and paired heights will continue to increase and, at 0-25 m compared with >25 m from propagule source, the ratio between paired height values will continue to decline and the slight difference between the higher angiosperm and the lower gymnosperm height increments is predicted to decline.

Taller growing angiosperms and gymnosperms will increasingly dominate the canopy along with the surviving kanuka whose maximum potential height we have observed as reaching to >20 m in the Moutere district of Nelson, substantially

higher than the 16 m reported in Poole & Adams (1963). Judging by their present growth forms, these canopy trees will be thrifty with straight boles and few lower limbs. Within a century, the forests we studied will have an overstorey of kanuka, various podocarps, silver beech, kamahi, Northern rata (if it survives possum browsing) and other angiosperms and will be declared 'virgin' and vigourously protected.

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