Mountain beech forest dynamics in the Kaweka Range and the influence of browsing animals

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Abstract

Manaaki Whenua – Landcare Research was contracted by the Hawkes Bay Conservancy, Department of Conservation, to: 1) determine changes in the structure of Kaweka Range mountain beech forests over the last 15 years, and consider potential future changes; 2) evaluate the degree to which mountain beech seedlings and saplings are adequate for canopy replacement; and 3) assess the impact of browsing by deer on regeneration of mountain beech. This was achieved by analysing data from 30 plots (20 x 20 m) established in 1979–81 and remeasured in 1995. Only a small decline in mean basal area of the dominant mountain beech was recorded. However, this did not imply little canopy mortality, because rapidly growing stands compensated for stands with high mortality of tree stems. There was no evidence for higher mountain beech seedling or sapling densities in plots of low basal area. Mountain beech showed little change in seedling or sapling density over the 15 years, irrespective of basal area. A decline in broadleaf basal area appeared to be a consequence of deer browse inhibiting recruitment, while other species unpalatable to deer (e.g., Hall's totara) appeared to increase as a component in these forest. Ground cover changes appeared to be minimal over the period of study. These results, combined with evidence from other studies, suggest browsing by deer is having a widespread influence on biodiversity patterns in Kaweka Range mountain beech forests. On a few sites regeneration of mountain beech appears to be at levels such that maintenance of a complete forest canopy is unlikely. If mountain beech forest is to be retained, the Department of Conservation needs a prompt management response to ensure that a regeneration pulse takes place on as wide a range of sites as possible.

1. Introduction

Canopy dieback has been a prominent feature of the high-elevation mountain beech forests of the Kaweka Range for at least 30 years (Elder 1959; Hosking and Hutcheson 1988). The impact of deer browsing on the expected regeneration by canopy species, particularly mountain beech, has been of concern for at least 20 years (e.g., Wardle 1979). This is because even partial canopy damage usually results in prolific regeneration by mountain beech (e.g., Wardle and Allen 1983; Wardle 1984). Concern has been expressed also about the impact of browsing animals on a wide range of subcanopy species, and the creation of a browse-tolerant turf on the forest floor (e.g., Elder 1959, Wardle 1979).

These concerns were highlighted at a workshop held by the Hawkes Bay Conservancy, Department of Conservation, in October 1993. As a result of a strategy developed at that meeting, Manaaki Whenua – Landcare Research, Lincoln, was contracted to analyse data and report on trends in the structure and composition of these important conservation forests. This report is based on remeasurement of 30 permanent forest plots established over the summers of 1979/80 and 1980/81, and re-measured over the summer of 1994/95.

2. Objectives

- To determine changes in the structure of mountain beech forests in the Kaweka Range over the last 15 years, and consider potential future changes.
- To evaluate the degree to which mountain beech seedlings and saplings are adequate for canopy replacement.
- To assess the impact of browsing by deer on regeneration of mountain beech.

3. Methods

3.1 DATA COLLECTION

A network of permanent forest plots was established in the Kaweka Range in successive vegetation surveys by the former New Zealand Forest Service. Thirty of these plots located within the high-elevation mountain beech forest form the basis of this report (see Fig. 1). They were selected from plots established in two earlier surveys:

- eleven were from a series of subjectively located plots established over the summer of 1979/80 in the Makahu area (with high recreational hunting pressure) and more remote areas, and included stands with a range of basal areas;
- nineteen were from a series of plots located systematically along random transect lines established over the summer of 1980/81, and sampled the core mountain beech area of the Kaweka Range, including stands with a range of basal areas and seedling densities at the time plots were established. In addition, several of these plots sampled the Makahu area.

All thirty plots were remeasured by Department of Conservation staff over the summer of 1994/95.

Each plot is a permanently marked 20 x 20 m quadrat, upon which all tree stems with a diameter >2.5 cm at breast height (dbh; 1.35 m) were tagged and their diameters recorded by species (Allen 1993). Saplings — woody plants >1.35 m tall but dbh <2.5 cm — were counted on each plot by species. Twenty four seedling (plants <1.35 m tall) subplots were also measured on each plot. These circular subplots with an area of 0.75 m^2 were located systematically over the plot area. All vascular plant species with individuals <15 cm tall were recorded by presence in each subplot. Within each understorey subplot woody

FIGURE 1. MAP OF KAWEKA RANGE SHOWING LOCATION OF 19 PLOTS ALONG 13 TRANSECTS AND 11 PLOTS THAT WERE SUBJECTIVELY LOCATED. PLOTS ARE INDICATED AS HAVING A 1995 BASAL AREA OF <25 m^2/ha (F) OR >25 m^2/ha (M).

seedlings were counted by species, and other plant species were recorded by presence, in four height classes: 16–45 cm, 46–75 cm, 76–105 cm, 106–135 cm. A visual estimate was made of the % vascular plant cover below 1.35 m.

Site variables recorded for each plot included elevation, aspect and slope. Aspect and slope were used in combination with latitude to calculate a potential solar radiation index for each plot (see Frank & Lee 1966). A mean angle to the horizon was calculated from angles measured from the plot centre along a compass bearing every 45° (8 values), and was used as an index of exposure (McNab 1993).

3.2 DATA ANALYSIS

Changes in forest canopy structure (tree stems) were analysed using the package PC-DIAM (Hall 1994a), and changes in the forest understorey (saplings and seedlings) using PC-USTOREY (Hall 1994b). Changes in canopy structure were often summarised in terms of basal area because this parameter serves as an indicator of site occupancy with a clear link to regeneration (Wardle 1984). Understorey changes are commonly presented in terms of density (numbers of individuals per unit area), because the adequacy of a regenerative response to replace canopy gaps is fundamentally a population process. In presentation of results, 1979 refers to first measurement of plots and 1995 to second measurement of plots.

4. Results

4.1 CHANGES IN FOREST CANOPY STRUCTURE

Mean basal area of all tree and shrub stems for the thirty plots declined by 2.5% from 42 m^2/ha in 1979 to 41 m^2/ha in 1995, and was associated with a decline in mean tree diameter and an increase in stem density (Appendix 1). Mean basal area of mountain beech — the only species present on all plots, contributing approx. 90% of total mean basal area (range 48 to 100% in 1979) — also declined by a small amount (4%). There was considerable variability in individual plot basal area ranging from 13 to 67 m^2/ha in 1979, and 2 to 68 m^2/ha in 1995.

The species with the most marked decline in basal area (53%) and stem density (39%) was *Pseudopanax simplex.* Such declines in basal area were balanced by increases in basal area of several species, particularly *Podocarpus hallii* and *Phyllocladus alpinus*. Both markedly increased in density but decreased in mean diameter between 1979 and 1995, which suggests that the basal area increase was due to recruitment. In contrast, the density of broadleaf stems declined and the mean diameter increased, with basal area relatively constant, suggesting little contribution from recruitment in maintaining basal area. Although insignificant in terms of basal area, many of the small subcanopy shrubs such as *Coprosma pseudocuneata* increased in density.

Although only a small decline in overall mean basal area of mountain beech was evident this does not necessarily indicate little canopy mortality because some rapidly growing stands may compensate for stands with high mortality of tree stems. Averaged for all plots, basal area mortality between 1979 and 1995 was high at 8.1 m^2/ha, or 21%, while basal area growth was also high at 6.7 m^2/ha, or 18%.

Figure 2 shows that this was largely a consequence of several plots accumulating a small amount of basal area, and a few plots losing large amounts of basal area. Overall, the mean diameter growth rate was 1.6 mm per annum

FIGURE 2. FREQUENCY OF MOUNTAIN BEECH BASAL AREA CHANGE, WITHIN CLASSES, FOR ALL 30 PLOTS BETWEEN 1979 AND 1995. AXES TICK MARKS SHOW LOWER LIMIT OF EACH CLASS.

and mortality rate was 2.0% per annum. As large-diameter trees may more often be senescent, it was rather surprising that the mortality rate for large diameter-trees (>0.5 m dbh) was only 1.6% per annum and their diameter growth was equal to the overall average. Highest mortality rates and slowest growth rates occurred in small-diameter trees (<0.12 m dbh), while diameter growth was fastest in trees of intermediate diameter.

Mountain beech basal area growth was strongly related to initial stand structural characteristics, although it was not related to site characteristics (Table 1). High growth rates occurred in dense stands with low average stem diameter and high initial basal area. Basal area mortality was greatest in stands with high initial basal area (Table 1). The balance between growth and mortality — basal area change — was unrelated to stand structural and site characteristics (Table 1).

TABLE 1. SPEARMAN'S RANK CORRELATIONS OF MOUNTAIN BEECH BASAL AREA GROWTH, MORTALITY, AND NET BASAL AREA CHANGE BETWEEN 1979 AND 1995, WITH SELECTED 1979 MOUNTAIN BEECH STAND STRUCTURAL AND SITE CHARACTERISTICS (N=30). *SIGNIFICANT (P< 0.001)

	BASAL AREA (m^2/ha)		
	GROWTH	MORTALITY	CHANGE
Stand structural characteristics			
Basal area (m^2/ha)	0.50*	-0.48*	-0.19
Stem density (no./ha)	0.75*	-0.46	0.07
Average diameter (mm)	-0.61*	0.13	-0.31
Diam. coefficient of variation (%)	-0.32	0.21	0.27
Vascular plant ground cover (%)	-0.30	0.20	-0.11
Site characteristics			
Elevation (m)	0.26	-0.08	0.12
Solar radiation (Langleys)	0.15	-0.23	-0.13
Slope (degrees)	0.20	-0.24	-0.05
Angle to horizon (degrees)	0.24	-0.02	0.16

4.2 CHANGES IN FOREST UNDERSTOREY

Mountain beech had the highest seedling density of any tree or shrub species in 1979 and 1995 (Appendix 2). A small increase in the density of intermediate-sized mountain beech seedlings occurred between 1979 and 1995 (Appendix 2). The dominance of mountain beech in the forest understorey was less marked in terms of sapling density. On average, the number of mountain beech saplings increased.

There was no evidence for higher mountain beech seedling (15–135 cm tall) or sapling densities in plots with low total basal area (Fig. 3a and b). Indeed, seedling densities appeared comparatively low in the three plots with very low basal area (<25 m^2/ha), and the lowest basal area (2 m^2/ha in 1995) was recorded in a plot having no seedlings (Fig. 3a). These plots were scattered around the study area — Mangatatunui Stream, Mangaturutu Stream, and Ngaawapurua (see Fig. 1). The highest, and most variable, seedling densities were found on plots with intermediate basal areas (Fig. 3a). Mountain beech seedling and sapling densities (in either year) were not correlated with any other stand structural characteristics, or site characteristics, except that sapling densities were higher on plots with a high diameter coefficient of variation – Spearman's rank correlation of 0.64 (P< 0.001) in 1979.

In analysing changes in mountain beech seedling (15–135 cm tall) or sapling density it may be expected that the most marked increases in density between 1979 and 1995 would occur in the low basal area plots. This relationship is depicted graphically for seedlings in Fig. 4a, and for saplings in Fig. 4b. Of the

FIGURE 3a, b. MOUNTAIN BEECH SEEDLING AND SAPLING DENSITY IN 1995 ON EACH PLOT, VERSUS FINAL TOTAL PLOT BASAL AREA. THE TREND CURVE HAS BEEN FITTED USING A DISTANCE-WEIGHTED LEAST SQUARES PROCEDURE.

a) SEEDLING

b) SAPLING

FIGURE 4a, b. CHANGE IN TOTAL MOUNTAIN BEECH SEEDLING AND SAPLING DENSITY BETWEEN 1979 AND 1995 ON EACH PLOT, VERSUS PLOT TOTAL BASAL AREA IN 1979. THE TREND CURVE HAS BEEN FITTED USING A DISTANCE-WEIGHTED LEAST SQUARES PROCEDURE.

a) SEEDLING

b) SAPLING

three plots noted earlier as having low basal area in 1995, two exhibited a decline in seedling density (Fig. 4a) and one a decline in sapling density (Fig. 4b). The greatest increases in seedling density tended to occur on some of the plots with intermediate basal area (Fig. 4b). Many plots showed little change in seedling or sapling density irrespective of basal area.

Phyllocladus alpinus was the next most abundant tree seedling, and *Coprosma ciliata* and *C. pseudocuneata* were the shrub species with most abundant seedlings (Appendix 2). Tree species showed little change in seedling density, although small *Pseudopanax simplex* seedlings increased over the period 1979–95 and the density of *Podocarpus hallii* seedlings declined. There was little change in the sapling densities of tree species. Shrub seedlings also showed little change, although small *Pseudowintera colorata* seedlings increased (Appendix 2). A virtual absence of *Pseudopanax simplex* and *Griselinia littoralis* saplings was a conspicuous feature in 1979 and 1995.

Two sets of evidence suggest that ground cover changes were minimal between 1979 and 1995. Firstly, the mean vascular plant ground cover estimate for all plots was 32% in 1979 (S.D. 13.7) and 38% in 1995 (S.D. 23.5). Secondly, there was little change in the frequency of dominant herbaceous species in the understorey subplots (Appendix 3).

5. Discussion

5.1 ON-GOING CHANGES IN FOREST CANOPY STRUCTURE

Mean basal area for Kaweka Range mountain beech forest (about 40 m^2/ha) is within the range 17–57 m^2/ha reported for this forest type in other localities (Wardle 1984; Ogden *et al.* 1993; Harcombe *et al.* 1995). The lowest mean value reported (17 m^2/ha) is for plots along random transects in the Moa River, Wilberforce catchment, where most of the mountain beech forest exhibits canopy dieback (Harcombe *et al.* 1995). 50 m^2/ha can be used as a basal area typical of fully occupied stands. If the 19 plots located along random transects are viewed as being representative of Kaweka Range mountain beech forest, then 42% of the forest (8 plots) was less than three-quarters occupied (<37.5 m^2/ha) in 1995, while 11% was less than half occupied. All plots had some stems, suggesting that complete canopy collapse was uncommon at a scale of 20 x 20 m. Harcombe *et al.* (1995) found a similar result for biomass loss on 250 plots in Harper-Avoca mountain beech forests.

Between 1979 and 1995, a few stands showed dramatic declines in basal area, and this loss when averaged across all plots was nearly equalled by a small amount of basal area growth on many other plots. Since basal area change on plots was not correlated with stand structural or site characteristics, it is difficult to predict which stands will be subject to further canopy collapse. Harcombe *et al.* (1995) suggested that such lack of correlations was a feature of the early stage of mountain beech forest canopy collapse in Harper-Avoca mountain beech forest. This was then followed by a more pervasive low-intensity opening up of the canopy which was predictable from forest structure. Observations elsewhere suggest canopy collapse in mountain beech forest to be a process that can take several decades, and it may be anticipated that continued canopy collapse will occur in some mountain beech stands.

Although the thirty plots were dominated by mountain beech, there was some evidence of changes in the importance of other tree and shrub species (Appendix 1). For broadleaf, the decline in stem density, and associated increase in mean diameter and basal area, suggests an aging population of this species. Broadleaf seedlings are highly palatable to deer and usually show a growth response with the removal of deer browsing pressure (Wardle 1984). In Kaweka mountain beech forest, broadleaf was widely distributed as seedlings too small to browse (<15 cm; Appendix 2), and the aging trend in the population appears to be a consequence of deer browse inhibiting recruitment from this pool of small seedlings. Species that are unpalatable to deer (e.g., Hall's totara) appear to be an increasing component in these forest.

5.2 ADEQUACY OF MOUNTAIN BEECH REGENERATION

After canopy disturbance, the typical response sequence of mountain beech is prolific regeneration followed by self-thinning (Wardle 1984; Osawa and Allen 1993). For example, in the Harper-Avoca forest Wardle and Allen (1983) showed a forty-fold increase in mountain beech seedlings 75–135 cm tall over an 11-year period when basal area declined from 52 to 47 m^2/ha. Although Kaweka Range mountain beech forest has a basal area of only approx. 40 m^2/ha, seedling and sapling densities (Appendix 2) certainly do not indicate such prolific regeneration, even in the lowest basal area plots where most expected. In fact, there is evidence that some factor operates to reduce seedling densities on the lowest basal area sites (see Fig. 3a).

The ultimate success of seedlings and saplings in replacing the canopy depends on the interaction of their height growth and mortality rates. This is being tested in a Masters thesis currently being undertaken in the Kaweka Range by co-author Cathy Allan, now of Lincoln University. Using the present data for the lowest basal area sites, a prediction can be made as to the adequacy of seedling and saplings for recruitment. On one plot with a basal area of 2 m^2/ha in 1995, no seedlings were found on the 24 understorey subplots, and a careful search of the whole plot area located only one heavily browsed seedling. The sapling density on this plot was 470/ha, which is well short of the average tree stem density (1100 stems/ha) reported in this study for mountain beech, and less than that generally found in intact, mature mountain beech stands. As a consequence, on a few sites there now appears to be insufficient seedlings and saplings to maintain a complete forest canopy.

FIGURE 5. MOUNTAIN BEECH SEEDLING DENSITY VERSUS BASAL AREA ON 34 CRAIGIEBURN RANGE PLOTS IN 1987. THE TREND CURVE HAS BEEN FITTED USING A DISTANCE-WEIGHTED LEAST SQUARES PROCEDURE.

5.3 IMPACTS OF BROWSING BY DEER

Mountain beech forests on the eastern slopes of the Craigieburn Range, Canterbury, are structurally and compositionally similar to those in the Kaweka Range. A comparison of the relationship between seedling density and basal area for the Kaweka Range (Fig. 3) with the Craigieburn Range (Fig. 5) is useful to assess whether the potential for regeneration is different between the two localities. Although seedling densities are variable for any given basal area at

both localities, it can be seen that densities are considerably higher at Craigieburn (Fig. 5; note scale difference from Fig. 3). A similar pattern emerged from comparing sapling densities. In contrast to the Kaweka Range data, there is also a marked tendency for seedling density to be higher at low basal areas. The question is, then, whether the inadequacy of mountain beech seedlings on a few sites, and the fewer seedlings in general, is a consequence of browsing by deer.

Red deer numbers in the mountain beech forest of the eastern slopes of the Craigieburn Range have been very low for the last 20 years. By contrast, deer numbers in the Kaweka Range, in particular sika deer, are relatively high for mountain beech forest (Davidson and Fraser 1991). Some authors have expressed the view that sika deer browse more intensively than red deer, and as a consequence have a greater impact on forest regeneration (see Wardle 1984). On the basis of faecel pellet counts in 1979 and 1995 deer numbers have remained relatively stable in the Kaweka Range for the last 15 years (W. Fleury, pers. comm.).

Green mountain beech foliage recovered from the stomachs of deer shot in Kaweka Range mountain beech forest supports the view there is a browsing impact on the seedlings (W. Fraser, pers. comm.). Recent deer browse on mountain beech seedlings was observed on 65% of plots during the 1995 remeasurement, and 10% of plots had most seedlings heavily browsed. Mountain beech seedlings – and seedlings of other species (e.g., broadleaf) – protected by fallen logs and shrubs were often taller and less hedged than those exposed to browse. Browsing preferences of red deer and sika deer are probably similar (Wardle 1984), and W. Fraser (pers. comm.) has found a similar proportion (% dry weight) of mountain beech in their stomachs.

The most compelling evidence for deer seriously limiting mountain beech regeneration in the Kaweka Range comes from an exclosure study proposed by Wardle (1979). This exclosure, containing a 20 x 20 m plot, was erected in 1981 to exclude deer at a site on Te Puke O Hikarua (see Fig. 1); an adjacent control plot outside the fence was also established. Fleury (1993) reported that by 1992 basal area on both plots had declined from about 50–60 m^2/ha to about 15 m^2/ha. This was associated with rapid growth of mountain beech seedlings within the fenced area, so that by 1992 a sapling density of 1.1 per m^2 was contained within the exclosure. This is greater than any sapling density recorded from the thirty plots exposed to deer browsing that were measured in this study (see Fig. 3b). Yet three of the thirty plots had lower basal areas in 1995 than the plot within the exclosure in 1992. Although mountain beech seedlings were present within the control plot, they were achieving little height growth. Fleury (1993) also showed that some shrub species — e.g., small-leaved *Coprosma* species — were increasing their stature more markedly within the exclosure. Major differences also occurred in the short-statured ground cover vegetation with *Coprosma microcarpa* and *Acaena* species within the exclosure and a mat-like sward of *Hydrocotyle*, *Acaena*, and *Blechnum pennamarina* outside (Fleury 1993).

6. Conclusion

This report concludes that browsing by deer is having a widespread detrimental influence on regeneration and species composition of Kaweka Range mountain beech forest. On a few sites, regeneration of mountain beech appears to be at levels such that maintenance of a complete forest canopy is unlikely. This is consistent with Wardle's (1984) view that the activities of deer inhibit the survival of beech forest on a set of “critical sites”. These sites are often preferred habitat for deer where a species approaches its environmental limits (e.g., timberline; Wardle 1984). In contrast, modification of overall species composition by deer is widespread.

If mountain beech forest cover is to be retained, the Department of Conservation needs a prompt management response to ensure that a pulse of regeneration, and recovery of forest biomass, will take place on as wide a range of sites as possible. This would require a period of time long enough to allow seedlings and saplings to grow above browse height. Just removing or reducing browsing pressure may not be enough, as there now appear to be insufficient seedling numbers on a few sites. On these sites the Department may need to evaluate such options as planting or seeding. Under current conditions the problem will eventually become more extensive as additional mountain beech stands break down.

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8. Appendix 1

TABLE A1. FREQUENCY, DENSITY, MEAN DIAMETER, AND BASAL AREA FOR SPECIES FOUND ON MORE THAN 10% OF PLOTS IN 1979 OR 1995 (STANDARD DEVIATION IN PARENTHESES). STEMS LESS THAN 25 MM DIAMETER HAVE BEEN EXCLUDED.

SPECIES	FREQUENCY		DENSITY (no./ha)		DIAMETER (cm)		BASAL AREA (m^2/ha)	
	1979	1995	1979	1995	1979	1995	1979	1995
Nothofagus solandri var. *cliffortioides*	30	30	1170 (1321)	1110 (989)	16.2 (12.3)	15.7 (12.3)	38.04 (15.3)	36.61 (16.7)
Griselinia littoralis	18	18	122 (286)	99 (244)	12.4 (5.1)	14.1 (5.4)	1.72 (3.7)	1.77 (4.0)
Podocarpus hallii	9	8	82 (166)	116 (255)	8.9 (8.0)	8.6 (7.5)	0.93 (2.6)	1.19 (3.2)
Nothofagus fusca	3	2	10 (45)	6 (32)	23.4 (15.6)	32.0 (16.4)	0.62 (2.4)	0.68 (2.9)
Phyllocladus aspleniifolius	14	20	98 (213)	200 (328)	6.0 (4.3)	4.9 (3.1)	0.42 (0.8)	0.53 (0.9)
Pseudopanax simplex	8	20	23 (66)	14 (31)	9.4 (4.0)	8.2 (3.2)	0.19 (0.4)	0.09 (0.2)
Coprosma linariifolia	3	5	11 (40)	24 (62)	5.3 (2.5)	4.4 (2.2)	0.03 (0.01)	0.05 (0.2)
Carpodetus serratus	2	3	3 (12)	12 (16)	6.7 (3.1)	6.0 (3.5)	0.01 (<0.1)	0.05 (0.2)
Coprosma pseudocuneata	4	8	5 (13)	40 (105)	4.7 (1.5)	3.3 (0.8)	<0.01 (<0.1)	0.04 (0.1)
Pseudowintera colorata	3	4	8 (26)	14 (46)	3.2 (0.7)	3.9 (1.2)	<0.01 (<0.1)	0.02 (<0.1)
Myrsine divaricata	4	8	5 (15)	22 (51)	3.3 (0.5)	3.2 (0.6)	<0.01 (<0.1)	0.02 (<0.1)
Leucopogon fasciculatus	3	3	7 (26)	16 (60)	2.8 (0.5)	3.5 (0.8)	<0.01 (<0.1)	0.02 (<0.1)
Coprosma ciliata	3	17	5 (19)	69 (97)	3.1 (0.4)	4.0 (1.1)	<0.01 (<0.1)	0.07 (0.1)
Leptospermum scoparium	1	4	1 (9)	11 (46)	4.1 (0.5)	4.0 (1.1)	<0.01 (<0.1)	0.02 (<0.1)
Other species	11	10	27 (62)	41 (118)	3.9 (1.4)	4.0 (2.2)	0.04 (<0.1)	0.07 (0.2)
TOTAL	30	30	1583 (1294)	1800 (950)	14.2 (11.6)	12.3 (11.8)	42.04 (14.2)	41.19 (16.2)

TABLE A2. FREQUENCY (0–15 cm) AND DENSITY IN FOUR HEIGHT CLASSES OF SEEDLINGS, AS WELL AS SAPLING DENSITY FOR SELECTED WOODY SPECIES FOUND ON MORE THAN 5% OF UNDERSTOREY SUBPLOTS IN 1979 OR 1995.

SPECIES	YEAR	PERCENT FREQUENCY 0–15 cm	SEEDLING DENSITY (No./m^2)					SAPLING DENSITY (No./m^2)
			16–45 cm	46–75 cm	76–105 cm	106–135 cm	Total	
Trees								
Nothofagus solandri var. *cliffortioides*	1979	56	1.11	0.16	0.04	0.05	1.36	0.07
	1995	52	1.19	0.31	0.10	0.04	1.64	0.11
Griselinia littoralis	1979	51	<0.01	0	0	0	<0.01	<0.01
	1995	48	0.03	<0.01	0	0	0.03	0
Phyllocladus aspleniifolius	1979	7	0.13	0.05	0.03	0.02	0.23	0.04
	1995	6	0.08	0.06	0.03	0.01	0.19	0.06
Pseudopanax simplex	1979	24	0.02	0.01	0	0	0.02	<0.01
	1995	23	0.09	0.01	0	<0.01	0.10	<0.01
Podocarpus hallii	1979	4	0.11	0.02	0.01	<0.01	0.14	<0.01
	1995	5	0.04	0.01	<0.01	0	0.06	0.02
Shrubs								
Coprosma linariifolia	1979	8	0.05	0.02	0.01	<0.01	0.08	0.01
	1995	2	0.01	0.01	0	<0.01	0.03	<0.01
Coprosma pseudocuneata	1979	21	0.33	0.15	0.07	0.13	0.67	0.04
	1995	16	0.31	0.15	0.11	0.06	0.63	0.08
Myrsine divaricata	1979	15	0.10	0.02	0.01	0.03	0.16	0.03
	1995	26	0.18	0.07	0.02	0.02	0.29	0.06
Coprosma ciliata	1979	51	0.87	0.27	0.09	0.09	1.31	0.06
	1995	35	0.63	0.25	0.12	0.06	1.07	0.15
Coprosma microcarpa	1979	8	0.13	0.04	0.02	0.02	0.20	0.01
	1995	9	0.20	0.10	0.04	0.02	0.36	0.04
Coprosma foetidissima	1979	13	0.05	0.02	0.01	<0.01	0.08	<0.01
	1995	11	0.11	0.03	0.01	<0.01	0.15	0.01
Leucopogon fasciculatus	1979	8	0.07	0.03	0.01	0.01	0.13	0.02
	1995	7	0.07	0.03	0.01	0.02	0.13	0.03
Pseudowintera colorata	1979	4	0.03	0.02	0	0	0.04	<0.01
	1995	5	0.09	0.03	0.01	<0.01	0.13	0.02

TABLE A3. PERCENT FREQUENCY OF OCCURRENCE FOR SELECTED HERBACEOUS SPECIES FOUND ON MORE THAN 5% OF UNDERSTOREY SUBPLOTS IN ANY YEAR. FREQUENCY IS GIVEN FOR ALL HEIGHT CLASSES (0–135 cm), FOR TWO MEASUREMENT YEARS.

	PERCENT FREQUENCY	
	1979	1995
Lagenifera strangulata	52	40
Blechnum penna-marina	10	15
Acaena anserinifolia	16	10
Oxalis sp.	11	10
Histiopteris incisa	3	7
Nertera dichondrifolia	8	8
Viola filicaulis	5	6
Polystichum vestitum	3	5