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Distribution and population structure of the loranthaceous mistletoes *Alepis flavida*, *Peraxilla colensoi*, and *Peraxilla tetrapetala* within two New Zealand *Nothofagus* forests

DAVID A. NORTON
JENNY J. LADLEY
HAMISH J. OWEN*
Conservation Research Group
School of Forestry
University of Canterbury
Private Bag 4800
Christchurch, New Zealand
*Present address: Carter Holt Harvey, Private Bag 242, Whangamata, New Zealand

Abstract Our results confirm the findings of an earlier study that suggested niche partitioning in the way *Alepis flavida* and *Peraxilla tetrapetala* utilise the available resources within the *Nothofagus solandri* canopy; *Alepis flavida* is almost exclusively an outer branch parasite while *Peraxilla tetrapetala* occurs most often on inner branches and the host trunk. *Peraxilla colensoi* has a similar distribution within host trees to *Peraxilla tetrapetala*, except that it parasitises *Nothofagus menziesii*. All three mistletoes showed non-random distribution patterns in terms of the host trees they parasitise, being found more often on larger trees. Larger host trees also carry a greater volume of mistletoe than do smaller host trees. For *Alepis flavida* and *Peraxilla tetrapetala* we found no evidence of host exclusion, whereby the presence of one mistletoe excludes the other mistletoe species establishing, observing the converse where host trees were more likely to have both mistletoe species present than expected. *Peraxilla colensoi* was found to be more common in *Nothofagus*-podocarp forest than in *Nothofagus* or *Nothofagus-Weinmannia-Metrosideros* forest. *Alepis flavida* and *Peraxilla tetrapetala* population structures suggest that recruitment of young mistletoe plants has been relatively continuous over the past few years in the *Nothofagus solandri* forest we studied while the *Peraxilla colensoi* population structure showed an apparent absence of small plants suggesting a lack of recruitment in the *Nothofagus menziesii* forest we studied.

Keywords *Alepis flavida*; *Peraxilla colensoi*; *Peraxilla tetrapetala*; Loranthaceae; mistletoes; population structure; parasitism; ecology; conservation; *Nothofagus menziesii*; *Nothofagus solandri*

INTRODUCTION

There has been considerable recent interest in the status and conservation of New Zealand mistletoes, especially those in the family Loranthaceae (e.g., de Lange & Norton 1997). Seven loranthaceous mistletoes have been recorded from New Zealand (de Lange et al. 1997a), although *Trilepidea adamsii* is extinct and *Muellerina celastroides* is extinct in New Zealand but still present in Australia. Several studies have documented declines in mistletoe distribution and abundance (e.g., Ogle & Wilson 1985; de Lange et al. 1997a) and these have been linked to a variety of factors including browsing by introduced brushtail possums (*Trichosurus vulpecula*; Ogle & Wilson 1985; Ogle 1997), loss of pollinating and dispersing birds (Norton 1991; Ladley & Kelly 1995a, 1995b, 1996) and overcollecting (Norton 1991; de Lange 1997).

Conservation management of mistletoes requires an understanding of the biotic and abiotic factors regulating mistletoe abundance and distribution (Norton & Reid 1997). Broad geographical distributions are known for New Zealand mistletoes as is the overall importance of host species availability in regulating mistletoe distribution (Barlow 1966; de Lange et al. 1997b; Norton 1997). Aspects of their reproductive biology have also been documented (Ladley & Kelly 1995a, 1995b, 1996; Ladley et al. 1997). However, less is known about other aspects of their ecology, especially their distribution patterns

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within forests and population structures. The need for such information is urgent given the current concerns about the conservation status of New Zealand mistletoes and because many populations are small and relictual (de Lange & Norton 1997; Norton & Reid 1997).

Loranthaceous mistletoes are predominantly arboreal xylem parasites dependent on their host for water and nutrients (Ehleringer et al. 1985; Ullmann et al. 1985) but producing their own sugars. These mistletoes show a strong dependence on birds for pollination and dispersal (Kuijt 1969; Reid et al. 1995; Ladley & Kelly 1995a, 1995b, 1996; Norton & Reid 1997; Ladley et al. 1997), although some species are insect pollinated (Kuijt 1969). The dependence on birds for dispersal (Reid 1989; Overton 1994; Ladley & Kelly 1995a, 1996) places a strong limit on where mistletoes can grow; birds are necessary to remove the fleshy pericarp from around the seed and place the seed on an appropriately sized branch of the correct host species. However, mistletoes are also dependent on abiotic factors such as light, host water, and host nutrient for germination, establishment, and growth (Norton & Reid 1997).

In this paper we describe the distribution patterns and population structure of *Alepis flavida* and *Peraxilla tetrapetala* within a *Nothofagus solandri* forest in the Craigieburn Ecological District, and of *Peraxilla colensoi* in a *Nothofagus menziesii* forest in the Mataketake Ecological District, New Zealand. Specifically we address the questions: (1) How are mistletoe individuals distributed within and among host trees? (2) For *Alepis flavida* and *Peraxilla tetrapetala*, does the presence of one mistletoe species on a host tree affect the probability that the other species will be present? (3) How are *Peraxilla colensoi* individuals distributed among forest types? (4) Is recruitment of new individuals occurring within these mistletoe populations?

STUDY AREAS

Although possums appear to be less common in *Nothofagus* forests than in other forest types (Owen & Norton 1995), browsing by possums can damage or destroy mistletoe foliage to the extent that plants are killed (Ogle & Wilson 1985; Ogle 1997) making it difficult to assess mistletoe distribution patterns and population structures. The two sites studied here have low possum numbers and show no or limited evidence of mistletoe dieback, making these ideal locations for this research.

Craigieburn forest

Alepis flavida and *Peraxilla tetrapetala* were studied at an c. 100 ha study site on the gently undulating lower slopes of the Craigieburn Range, eastern South Island (900–1000 m a.s.l.; 43° 09′ S, 171° 43′ E; Craigieburn Ecological District). Underlying rocks are Mesozoic indurated sandstones and mudstones. The following 1964–1979 means have been recorded at a 914 m a.s.l. climate station within the study area (McCracken 1980): mean annual air temperature 8.0 °C; mean January maximum temperature 19.2 °C; mean July minimum temperature –2.5 °C; annual rainfall 1447 mm, with a spring–early summer maximum; mean daily windspeed 1.3 m/s.

The vegetation is characterised by a monodominant canopy (at 15–20 m) of *Nothofagus solandri*, varying in height and density depending on previous disturbance history (Burrows 1977). *Alepis flavida* and *Peraxilla tetrapetala* are common, and almost exclusively parasitise *Nothofagus solandri* trees. The Craigieburn *Nothofagus solandri* forests have formed the focus of a number of recent studies on mistletoe biology (Powell & Norton 1994; Ladley & Kelly 1995b, 1996; Norton et al. 1997; Ladley et al. 1997).

Thomas River

Peraxilla colensoi was studied in an c. 2000 ha area in the 25 km long north-east–south-west orientated valley of the Thomas River, western South Island (43°54′S, 169°12′E; Mataketake Ecological District). The study area is located in the middle reaches of the valley, extending up both sides from valley floor (c. 180 m a.s.l.) to the upper limits of *Peraxilla colensoi* (c. 700 m a.s.l.). Underlying Upper Paleozoic to Mid Mesozoic rocks belong to the Haast Schist group. There are no climate data for the study area, but rainfall is likely to be higher than at Haast (3500 mm) 15 km to the west. Mean annual temperature at mid slope (400 m a.s.l.) is 9.6 °C, with a January mean maximum of 20.0 °C and a July mean minimum of 0.8 °C (based on equations in Norton 1985).

Nothofagus menziesii dominates the canopy (Mark 1977), with scattered emergent *Dacrydium cupressinum* and *Prumnopitys ferruginea* below 400 m. *Weinmannia racemosa* is usually the dominant subcanopy tree and there is a diverse understorey of small trees and shrubs. With increasing altitude, the forest structure becomes simpler, with *Nothofagus menziesii* often the only canopy species and *Weinmannia racemosa* forming a relatively sparse subcanopy. On ridges, *Metrosideros*

umbellata can be codominant with *Nothofagus menziesii* and *Weinmannia racemosa*, forming a lower stature forest. Three mistletoe species are present, although only *Peraxilla colensoi* is common and almost exclusively parasitises *Nothofagus menziesii* trees. *Alepis flavida* and *Peraxilla tetrapetala* are occasionally present, usually above 600 m (Mark 1977).

METHODS

Data collection

Craigieburn forest

Two square 1 ha sample plots (plots 1 and 2) were subjectively located in areas containing mistletoes in order to collect information on mistletoe distribution and population structure within a *Nothofagus solandri* forest. A third 1 ha area was sampled based on a 5 m wide transect 2000 m long for a broader representation of mistletoe distribution and population structure within the forest (plot 3). The mid point of the transect was randomly chosen along a walking track and two 1000 m transects were run in opposite directions along compass bearings that aimed to minimise altitudinal variation.

The same information was recorded in each sample plot. For each *Nothofagus solandri* tree ≥ 5 cm diameter at breast height (dbh; 1.4 m), we recorded its diameter and carefully searched it for mistletoes using binoculars. The species and number of mistletoes present in each tree and the height and size of each mistletoe were then recorded. Position within the host tree was recorded as outer branches (outer 50% of branches relative to the trunk), inner branches (inner 50% of branches relative to the trunk), or main trunk, and as upper, middle, or lower third of the tree. Mistletoe size was measured or estimated to the nearest 10 cm for the longest axis, and then the two axes perpendicular to this. These measurements were used to derive an estimate of plant volume based on the formula for an ovoid.

Mistletoes can be difficult to see from ground level because of obscuring foliage and small size, and a systematic search method and a similar search time was used for each tree to ensure that results were comparable. Because mistletoes are more conspicuous during flowering, the majority of the sampling was undertaken prior to flowering to avoid bias. While it was easy to estimate mistletoe dimensions for plants low in the canopy, it was more difficult for plants higher in the canopy. However, with regular reference to plants of known size, errors associated with estimated dimensions were reduced.

Thomas River

Sample points were systematically located at 200 m intervals along six transects 1–2 km apart, three on each side of the valley. The transects were located up valley slopes that were of relatively even slope and free of major streams or bluffs. At each sample point a 20 m × 50 m plot (0.1 ha) was laid out with its long axis perpendicular to the transect. Sampling continued along each transect until the altitudinal limit of *Peraxilla colensoi* was reached based on reconnaissance of forest at higher elevations. Thirty seven plots were established, ranging from 180 to 730 m altitude.

For each plot, altitude, aspect, and landform class (face, ridge, terrace) were recorded, and the dbh of all trees ≥ 15 cm dbh measured. The species and number of mistletoes present in each tree and the height in the canopy and size of each mistletoe were then assessed. Height in the canopy was subjectively estimated in four classes corresponding to the lower trunk (below the crown), lower crown, mid crown, and upper crown of the dominant *Nothofagus menziesii* trees. Mistletoe size was subjectively estimated in four classes; juvenile (one or two small shoots or twigs), small (several twigs present but no branches > 1 cm diameter), medium (at least one prominent branch present with smaller side branches), and large (several large axial branches with numerous side branches).

Analysis

Data were analysed using the Chi-square goodness of fit test based on equal probability in all groups to assess if mistletoes were non-randomly distributed between different positions within host trees (*Alepis flavida*, *Peraxilla tetrapetala*), between different host tree size classes (*Alepis flavida*, *Peraxilla colensoi*, *Peraxilla tetrapetala*), and in different altitudinal bands (*Peraxilla colensoi*). Simple linear regressions were used to assess if there were relationships between the volume of *Alepis flavida* and *Peraxilla tetrapetala* in a host tree and host tree size. Chi-square goodness of fit tests were also used to test if the distributions of *Alepis flavida* and *Peraxilla tetrapetala* were independent of each other with respect to the host trees occupied.

For the Thomas River plots, the number of individuals of each tree species was tallied in four diameter size classes (15–39 cm, 40–64 cm, 65–89 cm, 90+ cm) for each plot. These size

structure data were subjected to indicator species analysis as implemented in TWINSPAN (Hill 1979) using default options to quantitatively identify the main forest types present based on stand structure. Analysis of variance and Duncan's multiple range test as implemented in PROC GLM of SAS (SAS 1990) was used to assess differences in *Peraxilla colensoi* density among the forest types identified in the indicator species analysis.

RESULTS

Craigieburn forest

Alepis flavida and *Peraxilla tetrapetala* occupy different positions within host trees, with differences between the two species being significant for both branch position ($P < 0.001$) and height within the host tree ($P < 0.01$) in all three plots (Table 1). *Alepis flavida* typically occurs in the outer branches and is uncommon or absent from the inner branches (Table 1a), while *Peraxilla tetrapetala* is most abundant on the host trunk, although it does occur on inner and outer branches. The greater than expected number of *Peraxilla tetrapetala* plants on host trunks is, however, only apparent for larger plants, with smaller plants of both mistletoes occurring more often than expected on outer branches (Table 2). Both species are most common in the lower part of the host tree (Table 1b), but *Peraxilla tetrapetala* has a more even distribution with respect to height then *Alepis flavida*. However, these results may be biased by the difficulty of detecting small plants in the upper third of host trees.

The distribution of *Alepis flavida* and *Peraxilla tetrapetala* among host trees is significantly different ($P < 0.001$) from what would be expected if they were randomly distributed amongst all available host trees (Fig. 1). Both *Alepis flavida* and *Peraxilla tetrapetala* are significantly more abundant on larger host trees (based on basal diameter) than expected and significantly less abundant than expected on smaller host trees. This is most apparent in plots 2 and 3 where there are large numbers of small (< 20 cm dbh) trees and relatively few of these have mistletoes.

Table 1 Distribution of mistletoes in the three study plots with respect to (a) branch position and (b) height within host trees. Af, *Alepis flavida*. Pt, *Peraxilla tetrapetala*.

	Plot 1		Plot 2		Plot 3	
	Af	Pt	Af	Pt	Af	Pt
(a) Branch position						
outer	1574	32	467	37	585	22
inner	107	23	32	41	27	21
trunk	6	94	0	101	2	80
df	2		2		2	
c^2	1100.7		408.5		485.1	
P	< 0.001		< 0.001		< 0.001	
(b) Height						
upper	203	12	36	21	55	21
middle	432	53	110	82	158	41
lower	1054	85	353	76	400	61
df	2		2		2	
c^2	7.55		79.1		12.6	
P	< 0.01		< 0.001		< 0.005	

Table 2 Summary of plots where the observed number of mistletoes is more than (+) or less than (-) expected for five mistletoe volume-classes in outer branches, inner branches and on the hosts trunk. Plots where the difference between observed and expected is significant ($P < 0.05$) are highlighted by double symbols (++ or —). No *Alepis flavida* were present on the host trunk in plot 3.

	mistletoe volume class (m^3)				
Mistletoe species	0–0.1	0.11–1.0	1.1–5.0	5.1–10.0	>10.0
Peraxilla tetrapetala					
	++	+	—	—	—
outer branches	++	+	+	—	—
	+	+	+	—	—
	+	+	+	—	—
inner branches	+	—	+	—	—
	—	+	+	—	—
	—	—	—	+	++
trunk	—	—	—	+	++
	—	—	—	+	+
Alepis flavida					
	+	+	—	—	—
outer branches	+	+	+	—	—
	—	—	—	—	—
	—	—	+	+	++
inner branches	—	—	—	+	++
	—	+	+	+	++
	—	—	+	—	++
trunk	—	—	—	+	—
	.	.	.	.	.

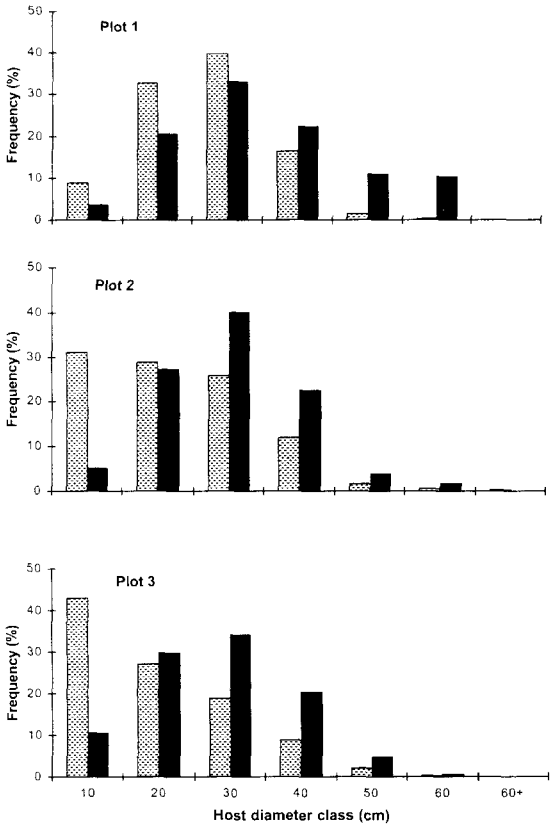

Fig. 1 Diameter class percent frequency distributions for *Nothofagus solandri* trees infected with mistletoes (either *Alepis flavida* or *Peraxilla tetrapetala*; solid) and for all *Nothofagus solandri* trees (dotted) in each study plot. Host diameter classes are 10 cm.

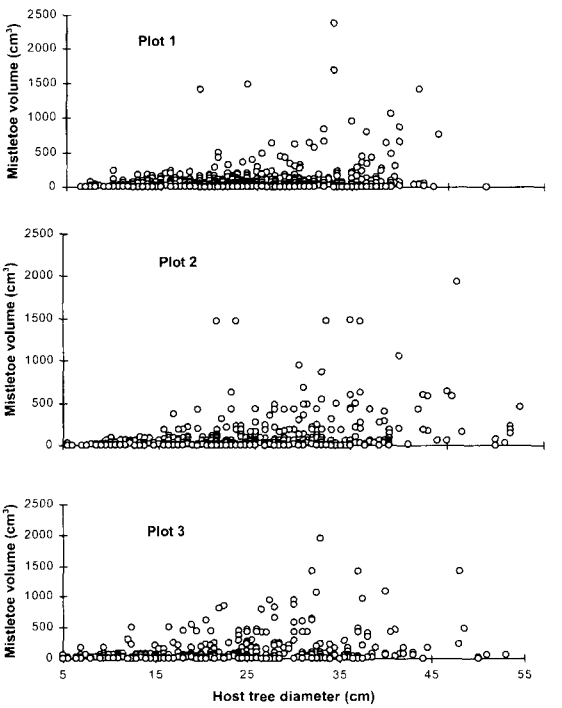

Fig. 2 Scatter plots of total mistletoe volume (both *Alepis flavida* and *Peraxilla tetrapetala*) versus host tree diameter for the three study plots.

Table 3 Distribution of mistletoes in host trees with respect to the presence of the other mistletoe species. Expected values (as used in the χ^2 goodness of fit test) are given in brackets.

	Plot 1	Plot 2	Plot 3
Trees with only *Alepis*	470	235	243
	(494)	(262)	(269)
Trees with only *Peraxilla*	25	82	59
	(49)	(109)	(81)
Trees with both mistletoes	85	59	43
	(61)	(32)	(17)
Trees with no mistletoes	418	929	1338
	(394)	(902)	(1312)
Total number of trees	998	1305	1683
df	1	1	1
c^2	23.5	33.8	46.5
P	< 0.001	< 0.001	< 0.001

Combined *Alepis flavida* and *Peraxilla tetrapetala* volume appears to be only weakly associated with tree size (Fig. 2). While small trees (< 20 cm dbh) usually support small mistletoe volumes, large trees support a range of mistletoe volumes. However, large mistletoe volumes (> 1000 cm^3) are only found on larger trees (> 20 cm dbh). This pattern appeared consistent in all three study plots.

The distribution of *Alepis flavida* and *Peraxilla tetrapetala* in host trees with respect to the presence of the other species was significantly different ($P < 0.001$) than expected (Table 3). The two species occurred significantly more often together than expected, while they occurred significantly less often by themselves than expected. The distribution of trees infected by only one mistletoe species with respect to tree size does not appear to be different to the distribution of trees infected by both species (Fig. 3).

The volume class distributions for *Alepis flavida* and *Peraxilla tetrapetala* were very similar among the three plots (Fig. 4). Both species were charac-

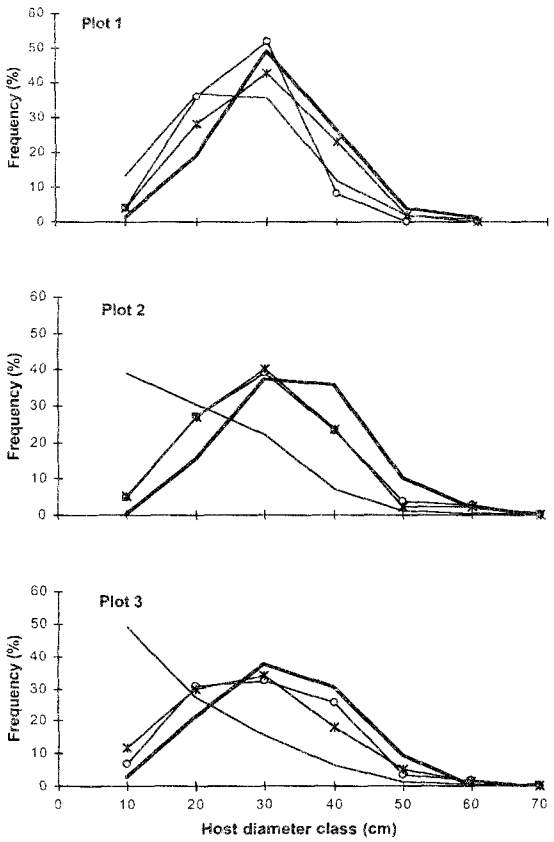

Fig. 3 Percent frequency of host trees without mistletoes (thin line), with infections of only one mistletoe species (*, *Alepis flavida*; o, *Peraxilla tetrapetala*), or with infections of both mistletoe species (thick line), with respect to host tree diameter class for the three study plots. Host diameter classes are 10 cm.

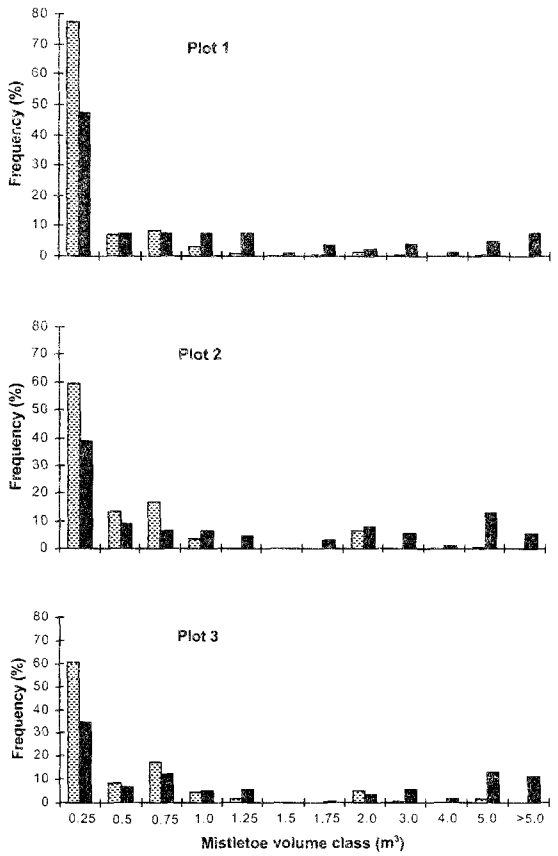

Fig. 4 Volume class percent frequency distributions for *Alepis flavida* (dotted) and *Peraxilla tetrapetala* (solid) in the three study plots. Volume classes are 0.25 m^3 from 0–0.2 m^3, then 1.0 m^3.

terised by an abundance of small plants, especially for *Alepis flavida*, but *Peraxilla tetrapetala* had more large plants, both proportionally and in absolute numbers, than *Alepis flavida* in virtually all volume classes >0.76–1.0 m^3. However, it is likely that the number of small plants was underestimated for both species because of difficulties in detecting small plants high in host tree canopies. In all three plots, both species showed a slightly bimodal size distribution, with an apparent scarcity of plants in the 1.26–1.75 m^3 class.

Thomas River

Peraxilla colensoi was non-randomly distributed among potential host tree sizes (Fig. 5). Large diameter *Nothofagus menziesii* trees are parasitised significantly more often than expected compared with the numerically more abundant smaller diameter trees (Fig. 5a, $\chi^2 = 146.6$, $P < 0.001$). However, the distribution of *Peraxilla colensoi* was not significantly different from that expected based on the basal area distribution of *Nothofagus menziesii* trees (Fig. 5b, $\chi^2 = 3.4$, $P = 0.1$). *Peraxilla colensoi* was also unevenly distributed through the forest profile, with most individuals present in the upper canopy (Fig 6). The upper two height classes contained 78% of plants recorded and only 4% of plants were recorded from the lowest height class.

Peraxilla colensoi was significantly more common in mid elevation plots than in lower or higher elevation plots ($\chi^2 = 22.8$, $P < 0.001$), and was not found above 680 m (Fig. 7). There was no signifi-

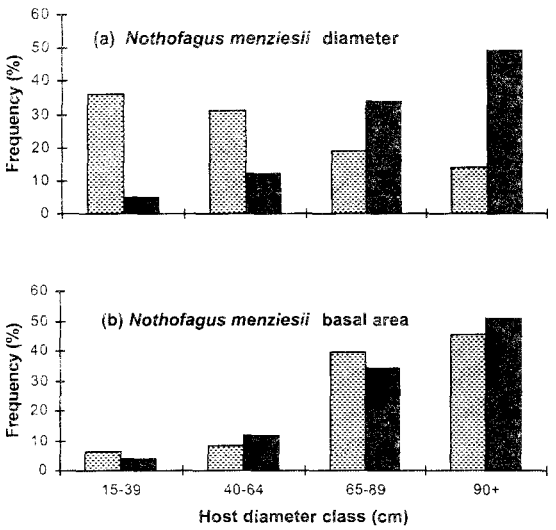

Fig. 5 (a) Diameter class frequency distributions for *Nothofagus menziesii* trees infected with *Peraxilla colensoi* (solid) and for all *Nothofagus menziesii* trees (dotted). (b) Proportion of basal area by tree diameter class for *Nothofagus menziesii* trees infected with *Peraxilla colensoi* (solid) and for all *Nothofagus menziesii* trees (dotted).

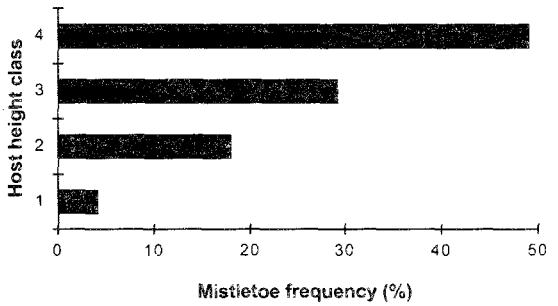

Fig. 6 Distribution frequencies of *Peraxilla colensoi* within *Nothofagus menziesii* crowns by strata (n = 72). Height classes correspond to the lower trunk (below the crown; 1), lower crown (2), mid crown (3), and upper crown (4).

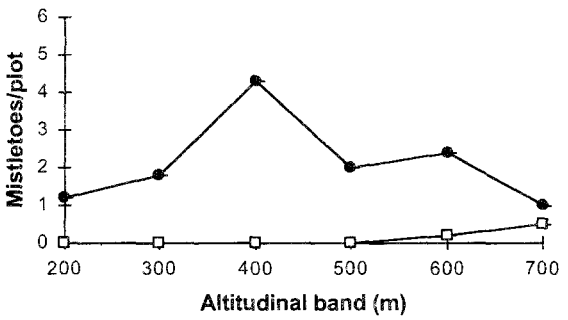

Fig. 7 Altitudinal distribution of *Peraxilla colensoi* (l) and *Peraxilla tetrapetala* (M) in 100 m altitudinal bands in the Thomas Valley (error bars ± one standard deviation).

cant difference in *Peraxilla colensoi* abundance with aspect, with 2.1 ± 0.8 mistletoes per plot on north-west aspects (n = 18) and 1.9 ± 0.6 on south-east aspects (n = 19). The number of plots on ridges (n = 5) and terraces (n = 7) was too small to allow for confident statistical comparison with *Peraxilla colensoi* abundance on faces (n = 25), although *Peraxilla colensoi* appeared to be more abundant on faces (2.6 ± 3.3 mistletoes per plot) than on ridges (0.8 ± 1.2) or terraces (0.7 ± 1.2).

Four forest types were identified in the indicator species analysis (Table 4), although one group comprised only one plot and lacked mistletoes, and is not discussed further here.

***Nothofagus*-podocarp forest** (19 plots) occurs on slope faces at low to mid altitudes. Large scattered tall (often > 30 m) *Nothofagus menziesii* (often >100 cm dbh) are emergent or form a multi-tiered canopy with large scattered podocarp trees (mainly *Dacrydium cupressinum*) over a *Weinmannia racemosa* understorey.

***Nothofagus* forest** (12 plots) comprising dense stands of *Nothofagus menziesii* forming a tall closed canopy at 20–30 m is dominant on river terraces and at higher altitudes. *Weinmannia racemosa*, *Pseudopanax crassifolius*, and *Griselinia littoralis* form a sparse subcanopy.

***Nothofagus-Weinmannia-Metrosideros* forest** (5 plots) typically occurs on broad ridges with impeded drainage. *Nothofagus menziesii* and *Weinmannia racemosa* codominate in a low canopied (12–16 m) forest. *Metrosideros umbellata* is moderately important, and *Elaeocarpus hookerianus* and *Phyllocladus alpinus* occur in wetter sites.

Mean *Peraxilla colensoi* densities were significantly higher in the *Nothofagus*-podocarp forest than in the other forest types (Table 4). *Nothofagus*-podocarp forest made up 51.8 % of the forest area surveyed, contained only 31.8 % of the *Nothofagus menziesii* trees, but included 86 % of the *Peraxilla colensoi* (Table 4). In contrast, *Nothofagus* forest, although only accounting for 32.4 % of the forest area, contained 50 % of *Nothofagus menziesii* stems but contained only 8.2 % of *Peraxilla colensoi*.

Peraxilla colensoi was also most common on

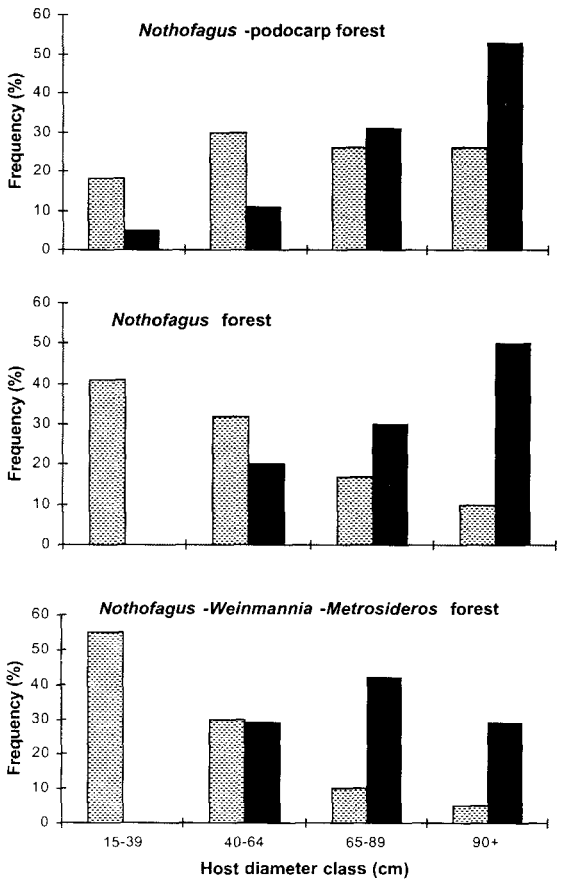

Fig. 8 Diameter class frequency distributions for *Nothofagus menziesii* trees infected with *Peraxilla colensoi* (solid) and for all *Nothofagus menziesii* trees (dotted) in the three forest types containing *Peraxilla colensoi*.

Fig. 9 Size class frequency distribution for *Peraxilla colensoi* ($n = 72$). See text for explanation of size classes.

larger diameter *Nothofagus menziesii* trees in the individual forest types (Fig. 8 cf. Fig. 5). The relative abundance of large diameter *Nothofagus menziesii* trees in the *Nothofagus*-podocarp forest (Table 4) helps explain the abundance of *Peraxilla colensoi* in this forest. Although more *Nothofagus menziesii* trees are present in *Nothofagus* forest (Table 4), they are mainly small diameter trees.

The size distribution of *Peraxilla colensoi* was heavily weighted towards larger size classes (Fig. 9), with only 3% of the *Peraxilla colensoi* being classified as juveniles while 85% were classified as medium or large plants. Smaller *Peraxilla colensoi* are less conspicuous, especially in the canopy of 30 m tall *Nothofagus menziesii* trees, so these data are likely to underestimate the abundance of juvenile and small plants.

Table 4 Summary data and tree densities (stems/ha) in different diameter size classes for the three dominant tree species in the four forest types. Different letters after values for number of mistletoes/ha indicate that they are significantly different ($P < 0.001$) between forest types. Tree size classes: 1, 15–39 cm; 2, 40–64 cm; 3, 65–89 cm; 4, ≥90 cm diameter. A, % *Nothfagus* stems; B, % mistletoe plants; C, number mistletoes/ha.

					Nothofagus menziesii				*Weinmannia racemosa*				*Metrosideros umbellata*			
Diameter class:	%plots	A	B	C	1	2	3	4	1	2	3	4	1	2	3	4
Forest type																
Nothofagus-podocarp	51.4	31.8	86.0	36.0[a]	17	22	22	22	163	40	7	0	2	2	0	0
Nothofagus	32.4	50.9	8.2	6.0[b]	87	68	38	22	12	3	0	0	0	0	0	0
Nothofagus-Weinmannia -Metrosideros	13.5	15.4	5.5	8.0[b]	108	60	18	3	147	13	2	0	23	12	7	3
Weinmannia-Metrosideros	2.7	2.0	0.0	0.0	0	58	40	0	138	50	0	0	100	90	0	0

DISCUSSION

Mistletoe distribution within and among host trees

Powell & Norton (1994) showed that *Alepis flavida* and *Peraxilla tetrapetala* have strikingly different modes of development, which allows them to exploit similar resources in the *Nothofagus solandri* canopy in different ways (i.e., niche partitioning). Our data (Tables 1a and 2) support this view, with the majority of *Alepis flavida* plants confined to the outer branches (93–95% of records) while *Peraxilla tetrapetala* plants are far more common on the inner branches and trunk of host trees (79–82% of records). The suggestion of Powell & Norton (1994) that *Alepis flavida* plants remain at their initial place in the crown, producing medium sized clumps, while *Peraxilla tetrapetala* spreads down the branch to other adjacent locations, often on to the trunk, is strongly supported by our data (Table 2). Although we did not collect any data for *Peraxilla colensoi*, it appears that this species has a similar distribution within the host tree to *Peraxilla tetrapetala*. We are not aware of any other examples of mistletoes partitioning the available niche in the same way as *Alepis flavida* and *Peraxilla tetrapetala*.

The three mistletoe species are non-randomly distributed with respect to height in the host plant, with *Alepis flavida* and *Peraxilla tetrapetala* most common in the lower and middle part of the host tree (Table 1b), while *Peraxilla colensoi* is most common in the middle and upper part of the host tree (Fig. 6). Constant differences in height distribution occurred between *Alepis flavida* and *Peraxilla tetrapetala* (Table 1b), with 62–71% of *Alepis flavida* plants present in the lower part of the host tree compared with 42–57% for *Peraxilla tetrapetala*, while only 22–26% of *Alepis flavida* plants were present in the middle part of the host tree compared with 33–46% for *Peraxilla tetrapetala* plants. Thus the two *Peraxilla* species appear to have a more similar height distribution than they do in comparison with *Alepis flavida*.

Hollinger (1989) observed that most mistletoe foliage (*Alepis flavida* and *Peraxilla tetrapetala*) occurred in the middle portion of a *Nothofagus solandri* canopy at Craigieburn, although he obtained data from only one 42 m^2 sample area (approximately the area occupied by one *Nothofagus solandri* canopy tree). Both Lamont & Southall (1982) and Dawson et al. (1990) observed maximum mistletoe densities at mid height in the host.

The difference in the vertical distribution of mistletoes between the two areas studied here may in part reflect differences in forest structure. At Craigieburn the *Nothofagus solandri* forest canopy is relatively dense and even, while at Thomas River the canopy comprises large scattered *Nothofagus menziesii* emergent above the canopy or forming a multi-tiered canopy. Mistletoe position within the forest is likely to be dependent on the opportunities available for seed dispersing birds to defecate or regurgitate seed (Dawson et al. 1990). It may be that the different forest structures at the two sites present different opportunities for birds and hence for mistletoe establishment, with mistletoes most common in those parts of the forest canopy most frequented by birds. Furthermore, at Craigieburn the often dense *Nothofagus solandri* canopy may offer fewer opportunities for mistletoe growth because of lower light levels and higher wind speeds than occur in the large canopies of *Nothofagus menziesii* trees at Thomas River.

In common with several other studies (e.g., Smith & Wass 1976; Lamont & Southall 1982; Thomson & Mahall 1983; Reid & Lange 1988; Overton 1994) we observed that for all three mistletoe species, larger host trees were more likely to be infected by mistletoes than smaller host trees (Fig. 1, 3, 5). Furthermore, larger trees tend to support greater total mistletoe volume than smaller trees (Fig. 2). However, Nowak & McBride (1992) observed the opposite pattern, with more *Arceuthobium campylopodum* (Viscaceae) on smaller host trees (*Pinus radiata*) in California than on larger trees and suggested that this was due to seed dispersal downwards onto smaller host plants, although this mistletoe has explosively dispersed seeds (Hawksworth & Weins 1996) rather than the bird dispersed seeds in the species we studied.

The usual explanation for the positive relationship between tree size and mistletoe infestation is that larger trees receive more mistletoe seeds as they are better perches for birds (Overton 1994). However, Overton (1994) suggests that the better occupancy of larger host trees may simply be explained by limited between-tree dispersal of mistletoes and that trees become larger with age, hence providing more establishment sites. He suggests that age-specific differences in host suitability for dispersing birds may reinforce this relationship, but are not essential. Dawson et al. (1990) also suggest that there may be considerable within-tree dispersal in larger trees, providing more regeneration opportunities. Murphy et al. (1993) have shown that the gut passage time of fruit from an Australian mistletoe through the

common disperser *Dicaeum hirundinaceum* is very short (13.6 ± 0.48 min) which would also favour increased within-tree dispersal if birds continue to feed in the same tree. It may also be that larger trees provide a more reliable water supply for mistletoes than smaller trees, especially during periods of moisture limitation (cf. Reid & Lange 1988). Given the higher water demands of mistletoes than their hosts (Ullmann et al. 1985), this could make larger trees with reliable water supplies more suitable for mistletoe growth.

Interactions between mistletoe species

It has been argued that the presence of one mistletoe species can exclude the establishment of a second (competitive host exclusion; Hawksworth 1969). Hawksworth & Weins (1996) summarise data that show that if the dominant mistletoe on a particular host tree is present, other mistletoe species do not infect the host, suggesting that the presence of one mistletoe can exclude the establishment of other species, presumably because of chemical cues. In a similar manner, Hoffmann et al. (1986) have shown that if one large plant of the mistletoe *Tristerix tetrandrus* is present on the host, even seedlings of the same species will not establish. However, for the *Nothofagus solandri* forest mistletoe system studied here, we found no evidence for either one mistletoe species excluding the second (Table 3) or for the presence of one mistletoe excluding more plants of the same species. Furthermore, our data show that the distribution of trees infected by either mistletoe species individually, or with both mistletoes together, in terms of tree size is not different (Fig. 3). Our data suggest that there is no evidence for chemical exclusion and instead factors that make a host tree suitable for one mistletoe species (e.g., increased water or light availability, or more attractive to dispersing birds) also makes the tree attractive to the other host species. Overlap in fruiting times between the two mistletoes (D. Kelly pers. comm. 1996) must also increase the probability that fruit of one species will be dispersed to an host tree containing the other species. The differential use of the *Nothofagus solandri* canopy between the two species (Tables 1a, 2; Powell & Norton 1994) also means that these two species can coexist without the need for exclusion mechanisms.

Peraxilla colensoi distribution among forest types

At Thomas River mistletoes were common in only one of the four forest types present, *Nothofagus*-podocarp forest (Table 4). This may be due to both forest structure and the dynamics of the host tree populations. *Peraxilla colensoi* is most common on large *Nothofagus menziesii* trees and its distribution within the forest is largely related to the distribution and density of large *Nothofagus menziesii* trees. However, the distribution and abundance of large host trees does not fully explain the observed patterns of *Peraxilla colensoi* distribution and abundance. For example, large *Nothofagus menziesii* trees are at least as common in *Nothofagus* forest as they are in *Nothofagus*-podocarp forest, yet the latter forest type contains significantly more mistletoes (Table 4). It appears that *Peraxilla colensoi* occurs more often on large *Nothofagus menziesii* trees in a particular forest type (*Nothofagus*-podocarp). It would therefore seem likely that the principal factors determining mistletoe distribution and abundance in these forests relate to temporal and spatial variations in forest structure which affects bird habitat quality and perhaps host tree physiology. Given that variations in the structure of these forests are a function of forest disturbance and regeneration (Stewart 1986), the distribution of *Peraxilla colensoi* is likely to be intimately linked to these dynamic forest processes.

The abundance of *Peraxilla colensoi* within the Thomas Valley appears to follow a structural gradient in the forest. At one end of this gradient where *Peraxilla colensoi* densities are highest, are diverse, open canopied, all-aged forests (*Nothofagus*-podocarp forest). At the other end are dense-canopied, even-aged forests which contain little or no *Peraxilla colensoi* (*Nothofagus* forest). These differences reflect, at least in part, differences in disturbance history. However, as these latter stands age their composition and structure changes towards that more typical of all-aged forests with their more frequent gap-phase regeneration (Stewart 1986) and as time passes could be expected to contain higher densities of *Peraxilla colensoi*.

So why is forest structure so important to *Peraxilla colensoi*? Unfortunately, there is no published information on the conditions required for *Peraxilla colensoi* establishment and growth to evaluate this fully. Two broad groups of factors appear important for the successful establishment and growth of mistletoes within forests (Reid et al. 1995; Norton & Reid 1997): biotic factors associated with the dispersal and establishment of mistletoes, and physical factors associated with the suitability of host trees and establishment sites within host trees. Forest structure affects both of these.

Biotic factors influencing mistletoe establishment and growth include attractiveness of the host to seed dispersing birds and differences in host susceptibility. Mistletoe establishment requires the successful dispersal of the seed to a suitable host branch (usually of small diameter; Reid 1989; D. A. Norton & J. J. Ladley unpubl. data). *Nothofagus*-podocarp forest is preferred feeding habitat for many south Westland forest birds including key dispersers of *Peraxilla colensoi* fruit (O'Donnell & Dilks 1994) while the upper forest canopy of *Nothofagus menziesii* trees contains most of the small twigs (Beets 1980) suitable for mistletoe establishment. Individual hosts may also differ in their susceptibility to infestation (Clay et al. 1985; Sargent 1995; Reid, Norton, & Stafford Smith unpubl. data), with susceptible individuals accruing a disproportionate number of mistletoes.

Light and host water and nutrient relations are also important determinants of mistletoe germination, establishment, and growth. Germination in most mistletoes is substantially higher in light than dark, and some species only germinate in light (Lamont 1983). The importance of canopy light regimes for mistletoe growth is less certain. However, correlations have frequently been established between high mistletoe abundance and particular topographic situations, aspects, and slopes, which may be related to light intensity (Hawksworth 1961). Mistletoes are entirely dependent on the host for water and nutrients (Ehleringer et al. 1985). Although water may not be limiting in south Westland *Nothofagus menziesii* forests, hosts with greater concentrations of xylem nutrients may provide a more favourable habitat for mistletoe establishment (Norton & Reid 1997).

Patchy distributions of mistletoe populations are frequently observed (Reid & Lange 1988; Norton et al. 1995; Norton & Reid 1997) and the patchy distribution observed here appears to be no exception, reflecting variations in habitat quality in terms of both dispersing birds and light environments. Habitat quality will vary temporally as well as spatially as forest types change in response to changing disturbance regimes (cf. Stewart 1986).

Mistletoe population structures

We did not measure mistletoe age directly in this study, although Norton et al. (1997) found for *Alepis flavida* that mistletoe age is significantly correlated with mistletoe volume suggesting that size class distributions can be used as surrogates for mistletoe age distributions. For *Alepis flavida* and *Peraxilla tetrapetala*, our data (Fig. 4) suggest that recruitment of young mistletoe plants has been relatively continuous over the past few years in all three study plots. This is in contrast with *Peraxilla colensoi*, where there appears to be an absence of small mistletoe plants (Fig. 9), with the majority classified as medium or large. A survey of *Peraxilla colensoi* on roadside *Nothofagus menziesii* trees in the Cascade Ecological District (40 km to the south-west of Thomas Valley) also recorded limited numbers of small mistletoes (D. A. Norton unpubl. data), with only 10% of mistletoes in the two smallest size categories ($n = 130$) compared with 15% found at Thomas River. Similar population structures have been interpreted elsewhere as evidence of episodic recruitment (Dawson et al. 1990; Reid et al. 1995), with either climatic or biotic factors suggested as causative. There is little evidence to assess any potential effects of climate on recruitment.

Ladley & Kelly (1995a, 1996) have suggested that an absence of dispersers may be a key factor in the decline of mistletoes elsewhere in New Zealand and it may be that similar biotic factors are responsible for the apparent absence of small mistletoe plants at Thomas River. In a study of *Peraxilla colensoi* fruit dispersal in the Cascade Ecological District (D. A. Norton unpubl. data), only eight (2%) of the 406 bird visits to fruiting *Peraxilla colensoi* plants resulted in a bird actively feeding on *Peraxilla colensoi* fruit and hence potentially dispersing the fruit away from the parent plant. Seven of the visits involved *Zosterops lateralis lateralis* and one *Anthornis melanura melanura*. Ladley & Kelly (1996) observed similar low levels of fruit dispersal at Craigieburn and suggest that this is evidence for dispersal limitation as a result of loss of key dispersers. While it is tempting to ascribe the paucity of juvenile and young mistletoes observed at Thomas River to a loss of dispersers, more data are required on bird dispersal and seedling distributions, and on temporal patterns in mistletoe abundance, before this can be confidently done.

The abundance of young mistletoe plants at Craigieburn is a striking contrast to the Thomas River situation and suggests that neither physical nor biotic factors are currently limiting mistletoe dispersal, establishment, or growth at this site. If anything, our data probably underestimate the number of small mistletoe plants as it is likely that some small mistletoes high in host tree canopies were not detected. The abundance of young mistletoes observed at Craigieburn is somewhat surprising given that a substantial proportion of non-aborted *Alepis flavida*

and *Peraxilla tetrapetala* fruits was not dispersed at Craigieburn during 1993 (Ladley & Kelly 1996). This may have been because of a shortage of dispersers (especially *Anthornis melanura melanura*) because their numbers had declined due to predation or competition for honeydew food resources from introduced wasps and honeybees (Ladley & Kelly 1996). Our data suggest that recruitment at Craigieburn appears to have been adequate in recent years. This may be because the 1993 observations of Ladley & Kelly (1996) were for an atypical year, because any decline in dispersers and dispersal has been recent and is not yet evident in the population structure data, or because limited dispersal is still sufficient to ensure adequate recruitment of new mistletoes into the population. Ladley & Kelly (1996) do note that in 1993 *Peraxilla tetrapetala* fruit did not appear to ripen normally, suggesting that this may have been an atypical year.

CONCLUSIONS

The data presented here provide a useful comparison for other studies of New Zealand mistletoes. Our results are particularly important because of the healthy nature of the mistletoe populations we studied compared with others elsewhere in New Zealand (see papers in de Lange & Norton 1997). An understanding of the population structures and especially within- and among-host mistletoe distribution patterns will also be of considerable value for mistletoe conservation. It is hoped that future studies will allow us to compare mistletoe population structures and distributions among mistletoe species and sites as a basis for a better understanding of the ecology of these fascinating plants.

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