Mistletoe (*Tupeia antarctica*) recovery and decline following possum control in a New Zealand forest

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Abstract: The condition of 79 plants of the loranthaceous mistletoe *Tupeia antarctica* in a podocarp-hardwood forest in the central North Island, New Zealand, was monitored over 4 years during a period of increasing possum density, following previous possum control. Mistletoe comprised 1.2% of total possum diet during the three years following possum control. Incidence of possum browse on mistletoe plants increased from 2.6% of plants when the trap-catch index of possum density was < 3%, to 75.9% of plants when trap-catch rates reached 4.6%. Mistletoe foliage cover declined from 49.8% to 15.6% and mean plant size declined by about 55% over the same period. The mistletoe population was dominated by plants with large haustoria, located in heavily shaded locations in the lower crown of their *Carpodetus serratus* hosts. Most plants established more than 20 years ago, and the current potential for recruitment of new individuals into the population is severely limited by possum browsing and the senescent nature of the mistletoe population. Intensive management of host crowns and possum populations will be necessary to ensure the long-term viability of mistletoe at the study site.

Keywords: impacts; mistletoe; population status; possums; *Trichosurus vulpecula*; *Tupeia antarctica*.

Introduction

Five indigenous extant species of loranthaceous mistletoes have a wide distribution in New Zealand, but their distribution and density have declined markedly since European settlement, particularly in the North Island, Nelson, northern Westland, and Southland (Ogle and Wilson, 1985; Ogle, 1997; Overmars, 1997). Possums (*Trichosurus vulpecula*) have been widely blamed as a major cause of this decline (Ogle and Wilson, 1985; Barlow, 1987; James, 1990; Webb *et al.*, 1990; Clark, 1993). However, the evidence linking possums to mistletoe decline is largely circumstantial (Ogle, 1997), and the few quantitative studies undertaken have been equivocal. Wilson (1984) concluded that possums were having a detrimental impact on *Peraxilla* species at his Nelson Lakes study site, whereas two other studies drew the opposite conclusion. Possums exerted minimal browsing pressure on *Peraxilla* and *Alepis* mistletoes at four sites in the eastern South Island (Sessions, 1999) and on *Peraxilla colensoi* near the Haast River, South Westland, (Owen, 1993; Owen and Norton, 1995) where mistletoes were common.

Besides possums, other factors potentially contributing to the decline of mistletoes include habitat loss or modification, insect browsing, over-collecting (de Lange, 1997; Norton, 1991; Norton and Reid, 1997), and the decline in pollinating and seed-dispersing bird species (Ladley and Kelly, 1996; Ladley *et al.*, 1997a; Robertson *et al.*, 1999). However, while the causes of mistletoe decline and the relative importance of the role of possums remain unclear (de Lange, 1997; Norton, 1997), there are now a number of reports of improvements in mistletoe vigour following reductions in possum densities, or protection from possum browse (e.g. Courtney, 1997; King and de Lange, 1997; Ogle, 1997; Sessions *et al.*, 2001). In this paper we document such recovery and, in addition, show that the recovery persisted only while possums remained at low densities.

Between 1990 and 2000 we undertook a study of possum diet and impacts, before and after an aerial-1080 possum control operation in August 1994, in podocarp-angiosperm forest in the central North Island. The presence of mistletoe species in this area was not detected prior to possum control, but within one year of the control operation regrowth of the mistletoe *Tupeia antarctica* was noted on large haustoria (gall-like growths) on the trunks of some putaputaweta (*Carpodetus serratus*) trees within the study area. Subsequent searches revealed that *T. antarctica* was locally common in parts of the study area and, from

December 1996 onward, plants were permanently marked and their status monitored annually. While the main aim of this paper is to describe trends in condition of this mistletoe population as possum densities increased, it also describes some of the physical characteristics of this population, and interprets these in terms of past possum impacts and the future status of this population.

Methods

Study area

The aims, study area, and initial results for the overarching study on possum and deer diets and impacts, of which this work is part, are described in detail by Nugent *et al.* (1997). That study was undertaken in 25 km^2 of forest in the headwaters of the Waihaha and Waitaia catchments, between 700 and 800 m a.s.l. on the south-eastern flank of the Hauhungaroa Range in Pureora Forest Park, in the central North Island (Fig. 1). These forests contain high densities of emergent rimu (*Dacrydium cupressinum*), Hall's totara (*Podocarpus hallii*), miro (*Prumnopitys ferruginea*) and matai (*Prumnopitys taxifolia*), over a canopy dominated by kamahi (*Weinmannia racemosa*) and tawheowheo (*Quintinia serrata*) (Nugent *et al.*, 1997). Numerous small patches of low-stature vegetation, dominated by ferns, pepper tree (*Pseudowintera colorata*) and small-leaved *Coprosma* species, are scattered throughout the whole study area. Scattered tree fuchsia (*Fuchsia excorticata*) logs on the ground in many of these patches indicate the former presence of this species. Numerous mature putaputaweta trees occur on the fringes of tall forest surrounding these low-stature patches, on which *T. antarctica* plants or haustoria were sometimes present.

This study was undertaken in part (4 x 1 km) of the larger study area established in 1990 to study possum diet and impacts before and after possums were controlled in August 1994. Possums have been present in the study area for at least 40 years, as possum numbers are reported to have peaked before 1978 (Jane, 1979) and possum populations take about 20 years to peak following initial invasion of an area (Pekelharing and Reynolds, 1983; Leutert, 1988).

Assessment of possum densities

Relative possum densities in the year prior to possum control, and each year since possum control, were determined from capture rates using leg-hold traps. Possums captured during trapping after control were marked and released. Six transects of 23 traps spaced at 20 m intervals were used to monitor densities prior to possum control, and 4-12 transects of 20 or 23 traps were trapped each year from 1997 to 2000, following standard monitoring methods (Warburton, 1996). No possum trapping was undertaken in 1996 and 1997. All transects were systematically located along the north-south access transects (Fig. 1), with pre-control and 1995 transects running north-south, and transects in other years running east-west across the 400 ha possum study area. Transect origins were shifted from year to year to avoid inducing trap-shyness. Total trap-nights were adjusted down by 0.5 trap-nights for each sprung and empty trap or non-target capture.

Assessment of possum impacts

The first mistletoe plants were detected in September 1995. Systematic searches for mistletoe plants on putaputaweta trees were subsequently conducted during the summers of 1996-1997 and 1997-1998 along four 500 m long transects and along one 3 km transect that had been marked previously as vegetation survey lines or access tracks (Fig. 1). Thirteen mistletoe monitoring plots, 60-1000 m apart, were established at locations where mistletoes were found. Host trees were permanently marked, and one to two mistletoe plants were tagged and measured on each host tree, with the lowest and highest plants above ground level selected when more than two plants were present on a single host tree. Thirty-three mistletoe were tagged on one plot and between two and six plants (mean = 3.5) were tagged on the remaining 12 plots.

Forty mistletoe on four plots were located, tagged and measured during the third growing season after possum control (summer 1996-1997). These plants and an additional 39 mistletoe on nine new plots were measured in March 1998. All 79 plants were searched for and, if found, remeasured in March 1999 and March 2000. We were able to closely examine and measure 67 of the marked mistletoes with the aid of a ladder, or by climbing host trees. However, 12 plants were out of reach, precluding the measurement of their dimensions. Percent foliage cover, using a 10-point scale, and quantity of possum browse damage, using a 5-point scale, were recorded for each mistletoe following Payton *et al.* (1999). The number of fruits present on each plant was also recorded.

For accessible plants, we recorded the longest horizontal dimension, the maximum horizontal width at right angles to this, and the vertical height of live stems and foliage, in mm, and calculated plant volume using the following formula:

$$\text{Volume (l)} = \frac{4\pi(0.5(\text{longest})\text{x}0.5(\text{width})\text{x}0.5(\text{vertical}))}{3000}$$

The length of the longest live stem was also measured, and the maximum number of annual shoot

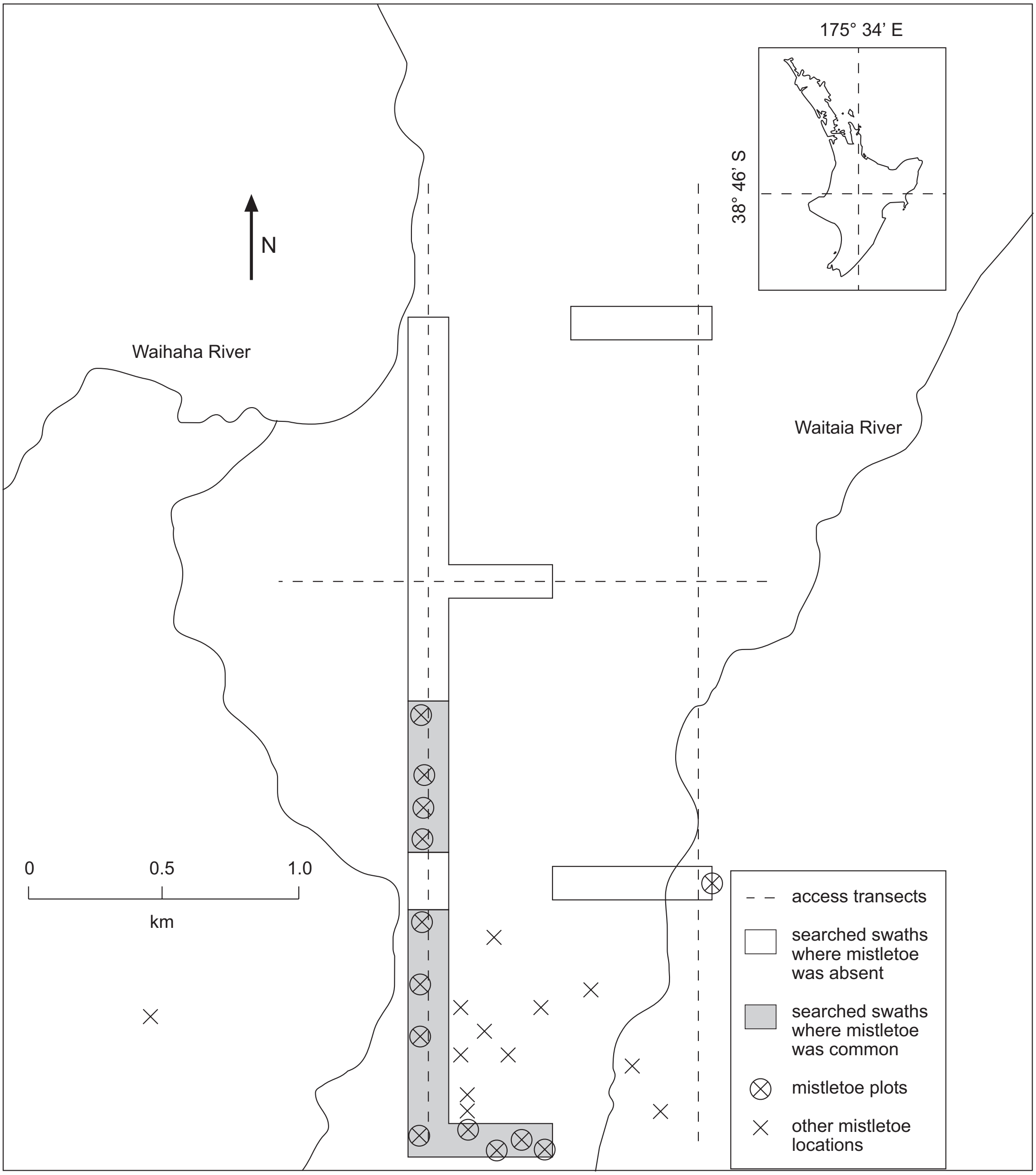

Figure 1. The study site showing the location of mistletoe plots, search swaths, and other recorded mistletoe locations.

extensions on any one stem counted, as evidenced by annual resting bud scars (i.e. the number of growing seasons that the oldest stem had been present). The length of each annual extension on the longest stem was also measured during the initial measurement of each plant.

Assessment of mistletoe in possum diet

Ninety-eight possum stomachs were collected from throughout the study area during the first three years following possum control, and their contents sorted by the layer separation method (Sweetapple and Nugent, 1998). The mean percent dry weight of *Tupeia antarctica* in this sample was calculated. Relative *T. antarctica* foliage biomass present in the study area, expressed as a percentage of total foliage biomass, was estimated from cover score data from 128 forest reconnaissance plots (RECCEs) (Allen, 1992) randomly located within the study area, and measured in September 2000, following the methods described in Owen and Norton (1995). From these data a possum preference index (*PI*) for *T. antarctica* was calculated as:

$$PI = \frac{D - A}{D + A}$$

where D = % in diet and A = % available. Potential values range from -1 (not present in diet) to 1 (present in diet but not recorded as present in the study area) (Nugent, 1990). Although mistletoe plants may have been smaller in 2000 than they were when possum stomachs were collected, this would not have resulted in an over estimation of the *PI* as even large healthy plants would be given the lowest cover score on the RECCE plots.

Population status

To characterise the current status of this mistletoe population, the diameter of the haustorium, host stem diameter immediately below the haustorium, and overhead shading (using the foliage-cover scoring system, see above) were recorded during initial measurements of accessible plants. Ten haustoria were found in recently windfallen or standing dead trees or branches. These were sectioned to determine the age of the host stem, its age when the mistletoe established, and, by subtraction, the age of the mistletoe. Haustoria were sectioned repeatedly at about 10-mm intervals to ensure that the earliest point of haustorial connection was determined.

Data analysis

Data for foliar cover, volume and length of longest stem were analysed by fitting linear mixed effects models using maximum likelihood in S-Plus (2000). Year was treated as a fixed effect, and plots and plants as random effects (i.e. we assume random samples of plots and plants within plots). The autocorrelation between repeated measurements on the same plants was modeled as an autoregressive process of order 1. All variables were square-root transformed prior to analysis and likelihood ratio tests were used to test for changes with time.

Alternating logistic regression (Smith, 1997) was used to determine whether the probability that a plant was browsed changes with year. We assumed a constant odds ratio between responses on the same plant. Differences between years in possum trap-catch rate were tested using ANOVA on square-root transformed data. For all variables, pairwise comparisons of years were made using the Bonferroni adjustment to compute P-values. Two sample t-tests were used to compare mean annual shoot-extension length and mean haustorium size between selected groups of plants. One-tailed Spearman's rank correlation was used to investigate the relationship between mistletoe age and haustorium size and host stem diameter.

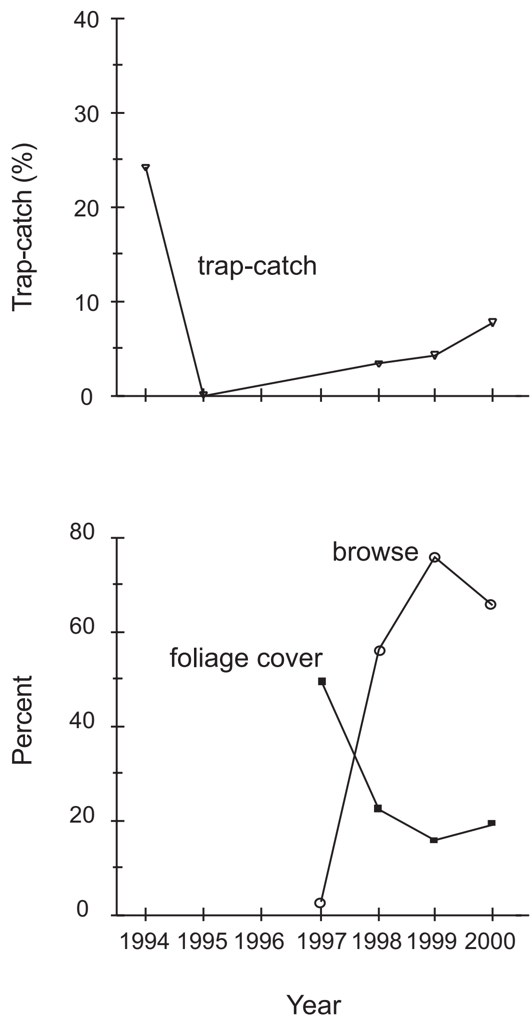

Figure 2. Means for possum trap-catch rate, mistletoe foliage cover, and percent of mistletoe plants browsed by possums, from 1994 to 2000.

Table 1: Test statistics and *P*-values of tests of changes in mistletoe parameters and possum trap-catch rate with time. Between-year pairwise comparisons are given; years with the same letter are not significantly different at the 5% level of significance.

			Pairwise comparisons (years)						
Parameter	Test statistic	*P*-value	94	95	96	97	98	99	00
foliage cover	$\chi^2_3 = 48.8$	< 0.001				a	b	b	b
volume	$\chi^2_3 = 15.9$	0.001				a	b	b	b
longest stem	$\chi^2_3 = 25.1$	< 0.001				a	bd	c	cd
% browsed	approx. $Z = 4.47$	< 0.001				a	b	b	b
trap-catch	$F_{4,34} = 25.4$	< 0.001	a	b			b	c	c

Results

Recovery after possum control

Possum trap-catch rates dropped from 24.2% for the year before the 1994 poison operation to 0% immediately following the control operation, then increased to 7.7% over the next 4 years ($F_{4,34} = 25.4$, $P < 0.001$) (Fig. 2, Table 1).

In 1997, during the third growing season after possums were controlled, 82% of measured mistletoe had stems with a maximum age of 3 years. The remainder were evenly divided between plants with stems up to 2 years old and those with stems up to 4 or 5 years old (Fig. 3). One and 2 years later, the oldest stem on the majority of unbrowsed plants was 4 and 5 years old, respectively (Fig. 3). These data demonstrate that, in the absence of possum browsing, annual resting bud scars are a reliable means of aging *T. antarctica* stems, up to at least 5 years of age, and that the majority of stems seen on mistletoe during monitoring commenced growth after possums were controlled in 1994.

From the few plants that had stems surviving from before the control operation, it was apparent that possums had restricted the stem growth (prior to possum control). Mean shoot extension for the 1993-1994 growing season on the longest stems was 40 mm, which was significantly smaller than the 84 mm for the first year's shoot extension on longest stems of plants that commenced growing after possum control ($t_{71} = 8.22$, $P < 0.001$).

Unbrowsed plants in well-sun-lit locations were capable of rapid growth. One plant attained a volume of 109 l and a longest stem length of 0.69 m by the end of the fifth growing season following possum control. There was no evidence that this plant had retained any shoots from before possum control.

Possum impacts following possum density increase

Possum trap-catch rate was not measured during the first year that mistletoe plants were measured (1997), but was just 3.1% one year later. In 1997 just 2.6% of mistletoes showed evidence of possums browse, and mean foliage cover was 49.8% (Fig. 2). One year later, 56.4% of mistletoe plants had been browsed by possums, and mean foliage cover had dropped significantly to 22.3% (Fig. 2, Table 1). Rates of possum browse remained high (66-76%) and foliage cover remained low (16-19%) over the following 2 years (Fig. 2, Table 1).

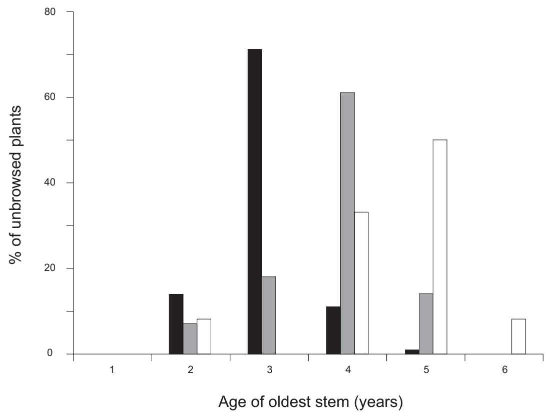

Figure 3. Frequency distributions of the age of the oldest stem on unbrowsed mistletoe plants in 1997 (dark bars, n = 35), 1998 (light bars, n = 28), and 1999 (open bars, n = 12).

The damage we recorded as possum browse always took the form of coarsely truncated stems and bark stripping (Fig. 4a). Broken stems were often seen in conjunction with possum browse. This damage could only have been caused by a relatively large arboreal herbivore, with possums being the only possible animal. Possum browse on mistletoe at the time of measurement was always several months old. A few observations of browsed plants were made in late winter 1997, 1998, and 1999, when the browse damage often looked fresh. Close inspection of this browse and of discarded leaves on the ground confirmed that damage was primarily petiole, stem and bark chewing by possums.

The mean size of mistletoe plants also declined markedly during the time that they were monitored.

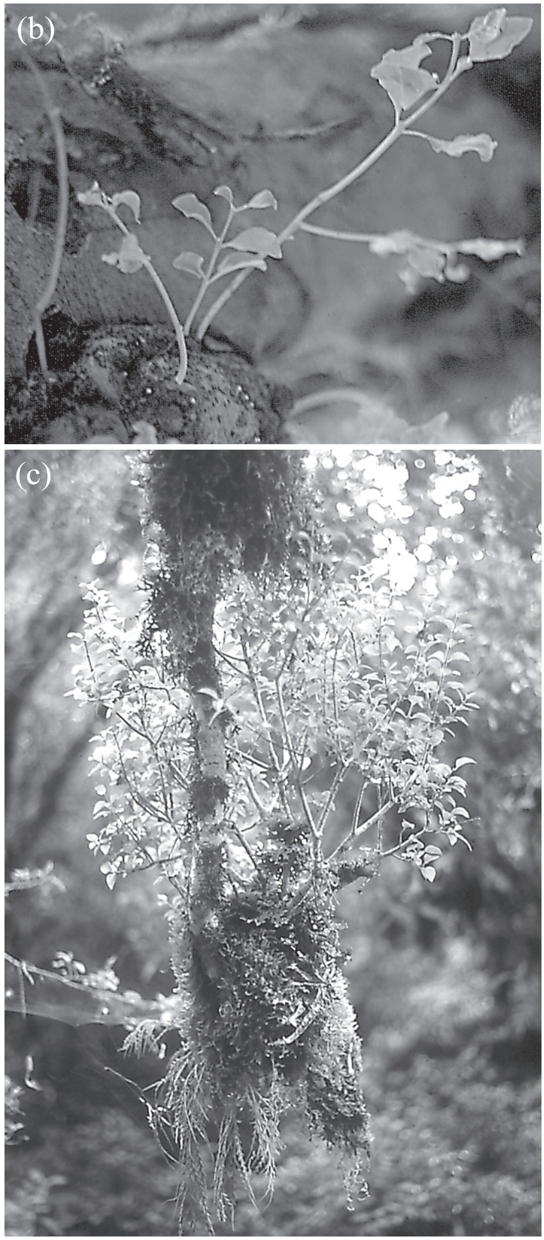

Figure 4. *Tupeia antarctica* plants showing (a) typical possum browse damage; heavily truncated stems and stripped bark, (b) sparse foliage and thin stems typical of heavily-shaded specimens, and (c) the robust branching habit and dense foliage of a well-sun-lit specimen without significant browse.

Both plant volume and longest stem length dropped dramatically between 1997 and 1999 (Fig. 5, Table 1).

Mistletoe in possum diet

Mistletoe comprised 1.2% of total possum diet within the study area during the three years following possum control. This material was dominated by stems and bark but did include some foliage. It was mainly recorded in winter (August) but was also present in some December-collected stomachs. Mistletoe was recorded on eight of the 128 RECCE plots and accounted for just 0.003% of the estimated total foliage biomass within the study area. The resulting preference index for *Tupeia antarctica* was 0.995, indicating that possums had a strong dietary preference for this species.

Population status

The majority of monitored mistletoes had large haustoria and were located on large branches or on the main stem in heavily-shaded locations in the lower and mid-crowns of putaputaweta trees. The mean haustorium diameter was 180 mm and their host stems had a mean diameter of 106 mm immediately below the haustoria

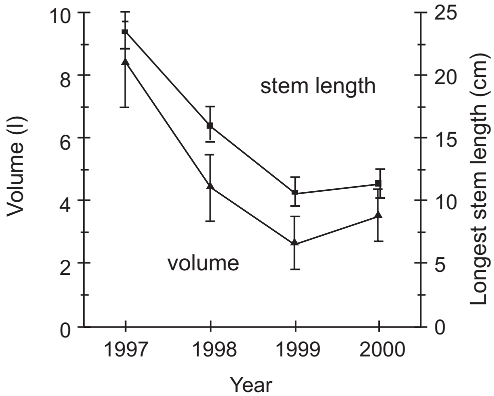

Figure 5. Means (± 95% confidence intervals) for mistletoe volume (triangles) and maximum stem length (squares) from 1997 to 2000.

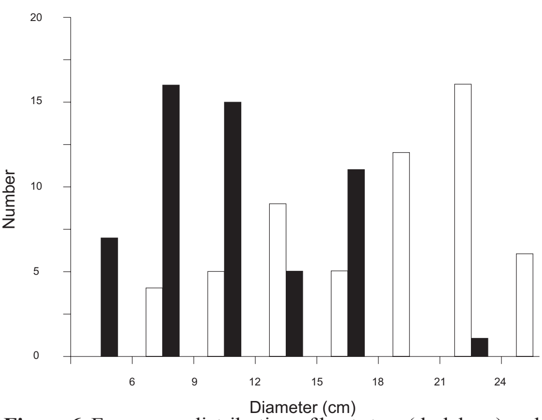

Figure 6. Frequency distribution of host stem (dark bars) and mistletoe haustorium (open bars) diameter when plants were first measured.

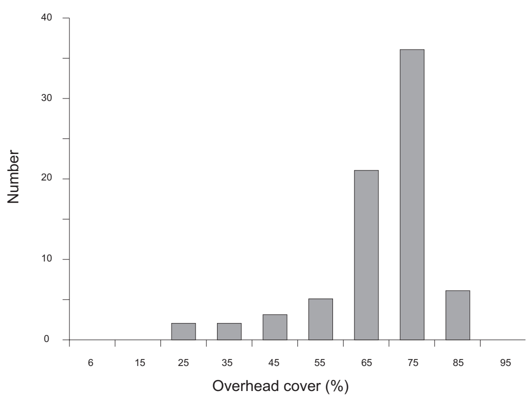

Figure 7. Frequency distribution of the degree of overhead foliage cover for each monitored mistletoe plant.

(Fig. 6). No small, recently established haustoria on young (small diameter) branches were found (Fig. 6). Overhead foliage cover exceeded 55% for 67 of the 79 monitored mistletoes (Fig. 7). The four plants with less than 45% overhead foliage cover were located immediately adjacent to canopy gaps, or on host trees that had suffered crown damage.

Heavily shaded plants typically had just a few small-diameter (*c*. 2 mm) stems and sparse foliage (Fig. 4b) in all 3 years they were monitored. Their generally feeble appearance contrasted markedly with the relatively large diameter (*c*. 10 mm) stems, heavy branching habit, and dense foliage of plants in brightly-lit locations (Fig. 4c).

Few fruit were produced by monitored mistletoes throughout the study, with just 3.3% of plants producing some fruit each year. Most of this was recorded during the final 2 years when a few lightly or unbrowsed plants had attained large sizes. All but one of these fruiting plants produced fewer than 13 drupes, but one well-irradiated plant produced 120 drupes. All fruit was immature at the time of monitoring and, although one unmonitored plant produced ripe fruit in 1997, it is unknown whether any of the green fruit recorded reached maturity.

The mean age of 10 mistletoe haustoria on dead or windfallen branches was 34 years (range: 22-55, Table 2), and haustorium age was correlated to haustorium diameter ($r = 0.67, Z = 1.99, P = 0.02$), but not host stem diameter ($r = 0.34, Z = 1.01, P = 0.19$). These aged haustoria had a mean diameter of 118 mm, and were significantly smaller than the mean diameter of the monitored sample ($t_{65} = 3.54, P < 0.001$). Some larger haustoria on dead or windfallen branches were found but these could not be aged because they were rotten in their centres.

Most of the aged mistletoe haustoria established when the host stems were young, 70% establishing when the host branch was ≤ 4 years old and ≤ 1.0 cm diameter. However, the remaining three established on much older (11-27 years) and larger branches (40-64 mm). Four monitored host branches and/or mistletoe haustoria died during the study period, and another two branches were lost to windfalls, giving a mean annual survival rate of 97.5%.

Discussion

Recovery following possum control

Through examining bud scars on unbrowsed plants, we were able to determine the maximum number of growing seasons that the extant stems of any one plant had survived. Our first quantitative assessment of this, undertaken three growing seasons after possum control, showed that 91% of plants had stems that were less than

4 years old, while the few with older stems had at most only 5 years growth. The shift in the maximum stem age of unbrowsed plants in the subsequent remeasurements (Fig. 3) indicates clearly that stems produce one resting bud scar per year, and that they routinely survive for more than 3 years in the absence of possum browse. It is also clear that almost all of the monitored haustoria on live hosts had produced leafy growth in the first season after possum control, so it is likely that these haustoria had also produced such stems in previous years. However, no mistletoe was recorded in the diet of possums prior to 1994 (Nugent *et al.,* 1997), either because it was absent from the samples analysed or was present in such small amounts that it was overlooked. Either way, it is clear that the amount being eaten each year was very small. The strong implication is that any leaf material produced was eaten before any substantial biomass could be accumulated to underpin increased production.

Possums colonised the study area in the 1960s or 1970s and are likely to have increased to peak numbers some time in the 1970s (Jane, 1979). The area had not been officially controlled before 1994, and commercial possum-skin hunters are unlikely to have significantly reduced possum numbers in such a remote area. In other words, it is likely that possum numbers have been at pre-control (1993-94) densities since the 1970s. It is possible that most plants in this population had persisted in an almost leafless state for over two decades. This survival may have been facilitated by the presence of chlorophyll within the haustoria of *Tupeia antarctica* (B. Fineran, University of Canterbury, Christchurch, N. Z., *pers. comm*.). Similar resprouting from leafless haustoria following possum control has also been noted for *Peraxilla tetrapetala* in the Canterbury foothills and in North Westland (D. Norton, University of Canterbury, *pers. comm.*).

The one-hit reduction in possum density in 1994 therefore benefited existing plants by allowing them to escape temporarily from this cycle of near-total annual depletion, and to begin to recover a substantial leaf-and-stem structure over the ensuing 3 years.

Possum impacts

Browse damage recorded on *T. antarctica* during this study can only have been caused by possums. The severity of the damage unequivocally indicates browsing or other activity by a relatively large animal, rather than by any small indigenous herbivore (invertebrates or birds). The heavily truncated stems and stripped bark seen on many plants is unlikely to have been caused by kereru (*Hemiphaga novaeseelandiae*), the only large bird species present capable of browsing foliage. This inference is supported by evidence that possums within the study area have a strong dietary preference for mistletoe (this study).

The current study provides just the second [after Owen and Norton (1995)] published account of mistletoe in the diet of New Zealand possums. This paucity of diet records is likely to reflect the absence or low biomass of mistletoes at sites of most previous possum diet studies rather than a low preference for mistletoe by possums in New Zealand. Mistletoe has been recorded in possum diet from at least two other South Island beech forests, and comprised up to 60% of seasonal possum diet (P. J. Sweetapple, *unpubl.*).

Possum browsing on mistletoes appeared to be seasonal, with all browse recorded during monitoring being several months old, and most records of presence in possum diet being from winter. Fresh browse sign was noted on plants in winter during 1997, 1998 and 1999. Our observations suggest that putaputaweta fruit usually ripens during winter in the study area, and possums eat large quantities of it when it is available (Nugent *et al.,* 1997). The browsing of mistletoe mainly in winter may, therefore, reflect increased possum activity in putaputaweta trees as they search for fruit. Consumption of another mistletoe (*Peraxilla colensoi*) by possums at a site in South Westland was also strongly seasonal, but with peak use in spring (Owen and Norton, 1995).

Within this study area the present position of most mistletoe plants on large branches and trunks of their host trees may increase their vulnerability to possum browse. Plants would be easily encountered by possums climbing host trees. Smaller, younger plants on the outer crown of host trees may be less vulnerable to possum browse, as suggested for *Alepis flavida* by Powell and Norton (1994).

After 3 years, once possum densities reached 3% trap-catch, mistletoe condition began to decline and the incidence of possum browse on mistletoe plants increased (Figs. 3, 5). Foliage cover, volume, and maximum length indices all declined dramatically. Although both plant volume and maximum stem length exhibited identical trends over time, the greater variance around estimates of mean volume (Fig. 5) indicates that, of the two parameters, maximum stem length may be the more useful index of plant size. Six years after possum control, possum densities were approximately 32% of that before control, and the biomass of mistletoe leaf and stem had declined to an estimated 20% of the peak following control. For this site it appears, therefore, that any possum density above about 3% trap-catch there is likely to be sufficient possum browse pressure to prevent an increase in mistletoe biomass. Elsewhere, we assume that in any forest in which possums can reach moderate or high densities, *T. antarctica* will be heavily impacted at all but low densities.

Wilson (1984) also demonstrated that intensive possum control was necessary to protect mistletoes. Possums continued to browse annually approximately a third of all *Peraxilla* mistletoes on Mt Misery, Nelson Lakes National Park, even after trap-catch rates were reduced to 4.3% . Clearly trap-catch rates below 4.3% were required to fully protect mistletoe at this site.

Although our "experiment" was not replicated and had no non-treatment control, the strong link between the timing of recovery and possum control, the nature of the observed browse, the link between possum increase and the decline in condition of mistletoe from 1997, and the presence of mistletoe in possum stomachs leaves no doubt that possums are the primary causal agent of mistletoe decline at Waihaha. Other factors, such as heavy shading of old plants, may now be exacerbating that decline.

Population status

As *Tupeia antarctica* is strongly light demanding (Smart, 1952), plants will usually establish on small, well-sun-lit stems near the extremity of the host crown. This is demonstrated by the haustorial connection occurring on host stems of ≤ 1 cm diameter in seven out of the ten aged haustoria. This pattern of establishment primarily on small diameter stems parallels that described for *Alepis flavida* (Norton and Ladley, 1998). The large host stem and haustorium diameters recorded here suggest, therefore, that most mistletoe plants in this study established many years ago. This is supported by the age range (22-55 years) of the aged mistletoe haustoria. The significant relationship between haustorium diameter and age, and the small haustorium size of the aged sample compared with the monitored population, suggest that this aged sample underestimates the mean age of the study population. Clearly this is a senescent population with few mistletoe plants having been recruited into the population since possum populations peaked during the 1970s.

The lack of correlation between mistletoe age and host stem diameter contrasts with the findings of Norton *et al.* (1997), who found that stem diameter at the base of the haustorium provided an accurate predictor of *T. antarctica* age. The diameter-age relationship may only be valid for young mistletoe as the entire Norton *et al.* (1997) sample was ≤ 10 years old.

Mistletoe at this study site are clearly in a "predator pit", with the "predators" (possums) able to consume all of the annual crop of "prey" (mistletoe) at all but the lowest possum densities. Temporary reduction in possum density to low levels permitted a short-term reprieve. That recovery could not be sustained, however, because other food resources enable possums to reach densities at which they are routinely able to encounter and eat all mistletoe foliage produced.

What is not clear is whether mistletoe would ever be able to escape the predator pit by reaching biomass levels, during periods of possum control, at which the possum demand for mistletoe foliage was less than the annual production. We believe that to be unlikely in this forest because possum-preferred foods are abundant enough to ensure that possum carrying capacity is moderately high. Long-term maintenance of this mistletoe species at Waihaha will require ongoing stringent possum control aimed at keeping densities below 3% trap-catch, rather than the current regime of periodic aerial control every 5-6 years.

The heavily-shaded and senescent nature of this population means that protection from possum browse alone may not be enough to ensure its survival and recovery. Only a few fruit were produced by some plants that were protected from possum browse for 4-5 years. The only plant which produced abundant fruit was exposed to bright sunlight as a result of wind damage to an adjacent tree. Therefore, active management of host and adjacent tree crowns to increase light levels to mistletoe plants and possibly hand planting of mistletoe seeds (Ladley *et al.*, 1997b) may also be necessary to ensure the long-term viability of this population. Such intensive management would only be practical on a small scale but could be used to help initiate fruit-production and seedling-recruitment foci at sites, such as in the current study, where protection from possum browse alone is unlikely to boost mistletoe recruitment.

The substantial possum impacts on *T. antarctica* recorded in this study demonstrate that possums are the primary threat to mistletoe health at Waihaha. This study also demonstrates that rapid and dramatic recovery of extant plants is possible, but only when possum populations are reduced to very low densities.

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