Forest Research Institute, P.O. Box 31-011, Christchurch.

THE EFFECT OF CONTROL OF BRUSHTAIL POSSUMS *(TRICHOSURUS VULPECULA)* ON CONDITION OF A SOUTHERN RATA/KAMAHI *(METROSIDEROS UMBELLATA/WEINMANNIA RACEMOSA)* FOREST CANOPY IN WESTLAND, NEW ZEALAND

Summary: Brushtail possums began colonising a rata/kamahi forest in the Taramakau catchment, Westland, about 1950 and by 1973 had caused widespread conspicuous canopy defoliation. They were poisoned in one block of this forest in 1970, at about the time they reached peak density, and again in 1974. In an adjacent block they were poisoned in 1974 only. A survey of forest canopy condition in 1985 showed that, in the block poisoned at peak density, 21% of the basal area of palatable trees had died compared with 47% in the block where poisoning was deferred for 4 years. This suggested that control at or before populations attain peak density is critically important for limiting canopy mortality. After the 1974 poisoning, possum numbers in both blocks recovered to within 20% of their pre-control level in 10 years, indicating that control should be carried out at about decade intervals. Defoliation indices and species condition patterns showed that canopy dieback was least evident on relatively unpalatable trees. Of the palatable trees, kamahi was in best overall condition with least canopy dieback, followed by cedar, southern rata, then Hall's totara.

Keywords: Brushtail possums; rata/kamahi forests; canopy; defoliation; dieback; browsing damage; control; population dynamics.

Introduction

Browsing by brushtail possums *(Trichosurus vulpecula)* is a major cause of widespread canopy mortality (dieback) in conifer *(Podocarpus, Libocedrus)* - broadleaved hardwood forests (Holloway, 1959; Pekelharing and Reynolds, 1983; Coleman, Green and Polson, 1985; Payton, 1985; Leutert, 1988). In the South Island, these forests reach their northern limit on the north bank of the Taramakau catchment, Westland. Possums spread into these forests about 1950 (Best and Crosier, 1969, Forest Research Institute, unpublished report), and extensive browsing of the major canopy species was first recorded in 1969 (I.L. James, unpubl. data). By 1973, this browsing had caused conspicuous widespread defoliation (Pekelharing, 1979). These conifer-broadleaved forests are possibly predisposed to possum-triggered dieback by their composition and structure, which are largely determined by site stability (Payton, 1987; Stewart and Rose, 1988).

Two major attempts had been made to control possums in these forests, using aerially sown carrot baits poisoned with compound 1080 (sodium monofluoroacetate). In July 1970, the western part of the study area (Block 1, see Fig. 1) was poisoned (Bamford, 1972) and in June 1974, the whole study area was poisoned (Pekelharing, 1979). This gave us two contiguous blocks with similar forest types, similar histories of possum occupation, but different control histories. In Block 1 the possums were poisoned at peak density and again 4 years later. In Block 2 they reached peak density, declined (Pekelharing, 1979), and were then poisoned. This enabled us to examine whether the timing of possum control had had any effect on mortality and condition of the forest canopy.

Methods

The presence of possum faecal pellets was recorded on 8<km radius plots spaced at 20-m intervals along 10 transects (five in each block). The transects were measured in April 1970, 1971 (Bamford, 1972), and in April 1974, 1975, 1977, 1981, and 1985 (representative sample sizes 1006, 764, 740, 755, 866, 684, and 726). Pellet transects started on the riverbed and followed compass bearings uphill to 900 m a.s.l. (Fig. 1). Pellet frequency data were transformed into estimates of relative density using the equation - $\log_e$ (1-f/n), in which pellets are recorded on f of n plots (Greig-Smith, 1983). For all surveys except the one in 1971, relative density estimates for each transect were regarded as replicates for calculating mean relative densities and standard errors.

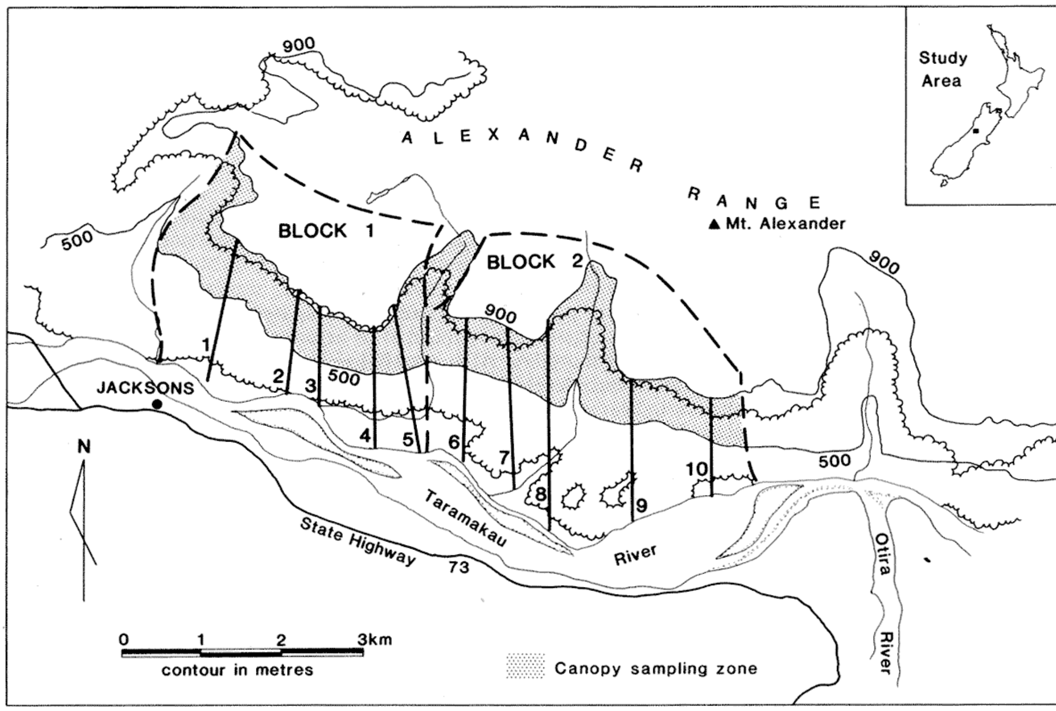

Figure 1: *Map of the study area. Faecal pellets were sampled over the transects shown. The forest canopy was sampled along the same transects in the shaded 500-900 m altitude band. Block 1 poisoned in 1970 and 1974. Block 2 poisoned in* 1974 *only.*

Data on the composition and condition of the canopy (i.e., degree of defoliation and mortality), were obtained from 90 variable area plots (Batcheler and Craib, 1985), 45 in each block. The plots were located along the upper part of the pellet transects, above 500 m a.s.l. (Fig. 1), where more than 40% of the canopy had been defoliated since 1960 (Pekelharing, 1979). The plots were spaced at 50-m altitudinal intervals up to the 900 m contour. The radius of each plot was varied to encompass a minimum of 15 canopy trees - defined as >20 cm diameter at breast height (dbh) over bark - up to a maximum radius of 10 m. Plots without any canopy trees within this maximum radius were included in the sample. The height of the forest surrounding each plot was estimated to the nearest metre.

Basal area estimates for canopy trees were used as an index of their above-ground tree biomass (Wardle, 1984). These estimates formed the basis for determining the impact of possums on the canopy. Diameter at breast height was recorded for all living and indentifiable dead trees. For multi-stemmed trees, all stems were measured and the dbh equivalent of their combined cross sections was used (Batcheler, 1985). The structure of the canopy was determined by grouping species into three dbh size classes. For the larger-boled species, southern rata *(Metrosideros umbellata)*[1], Hall's totara *(Podocarpus hallii),* and cedar *(Libocedrus bidwillii),* 20 and 40-cm size classes were used (small 20-<40 cm, medium 40-<80 cm and large 80 cm dbh). For the smaller-boled species, *Quintinia acuti/olia*. kamahi *(Weinmannia racemosa)* and broadleaf *(Griselinia lit/ora/is),* 100cm classes were used (small 20-<30 cm, medium 30-<40 cm, and large 40 cm dbh).

The degree of defoliation of the crowns of living canopy trees was visually assessed in three classes by comparison with healthy specimens located in the

[1]. Nomenclature follows Allan (1961) and Edgar (1973) and more recent updates Connor and Edgar (1987).

survey area: 'good', <30% defoliated; 'moderate', 31-60% defoliated; or 'poor', >60% defoliated. Dead trees (the fourth class) were recorded as either standing or collapsed. The composition and structure of the pre-dieback forest canopy was determined by pooling all live and dead stems measured. The canopy data of six of the major species were partitioned into relatively unpalatable or palatable trees, following the results of a study of the diet of brushtail possums in similar forest at Mt Bryan O'Lynn, 40 km north of our study area (Coleman, Green, and Polson, 1985), and into two altitudinal zones: mid montane forest, 500-650 m, and upper montane forest, 651-900 m (Pekelharing and Reynolds, 1983).

Mean estimates of canopy basal area (i.e., above ground tree biomass) and tree density were calculated for each block by using the five transects in each block as replicates. Mean basal areas, size classes, and condition (i.e., defoliation and mortality) were compared in the two altitudinal zones and in the two blocks. Differences in crown condition between species, altitudinal zones, and blocks were then determined by Mann-Whitney U tests (Sokal and Rohlf, 1981) by assigning the four crown condition classes (good, moderate, poor, and dead) equivalent indices of 1-4.

Confidence intervals at the 95% level are presented where appropriate. Analysis of variance (ANOVA) was used to identify differences between density and mortality (percent by size classes) of the six most common species in the two blocks. Percentages of dead trees were transformed to arcsin % to normalise the data.

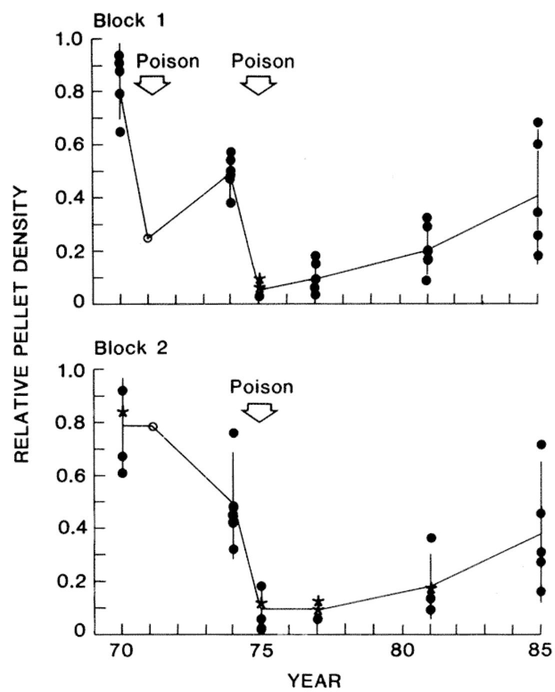

Figure 2: *Relative densities of possum populations in Blocks 1 and 2 as shown by tranformed frequencies of pellets recorded on 80-cm radius plots. Error bars represent one standard error either side of the mean. The* 1971 *estimates, without error bars. were taken from Bamford* (1972). *Dots = pellet density estimates for each transect, those with* indicate overlapping estimates.*

Results

Possum faecal pellet densities

Possum densities in April 1970 were similar in Blocks 1 and 2 (Fig. 2). In July 1970, about 70% of the possums in Block 1 were poisoned (we could not calculate variance of the 1971 estimates because some original data collected by Bamford (1972) have been lost). Block 2 was not poisoned, and densities did not alter, at least through 1971. Densities appeared to have doubled in Block 1 between the poisoning and 1974, but decreased by about 40% in Block 2 between 1971 and 1974. The two population mean densities were again similar in 1974, 38% lower than in 1970.

The 1974 poisoning killed similar proportions of the possums in both blocks, 84.7±8.4% in Block 1 and 81.5±19% in Block 2. Possum densities recovered over the next decade at similar annual rates in both blocks ($p>0.05$, 22% and 18% in Blocks 1 and 2 respectively). This represents an exponential rate of increase for both blocks combined of 0.182 ±0.048 per year.

In 1985, densities in Block 1 and 2 were about 84% and 78% respectively of those in 1974 before the poison operation, but were only 49% and 48% of the peak densities recorded in 1970. Overall, faecal pellet density trends in both blocks were very similar except during the 3-year period (1971-1974) after the 1970 poison operation in Block 1.

Composition and structure of the pre-dieback forest canopy

Basal areas

The forest canopies in the study area were dominated by six species, two relatively unpalatable (*Quintinia* and broadleaf), and four palatable (Hall's

Table 1: *Basal areas and densities/ha of canopy trees (20 cm dbh) measured in the 45 plots in each block. The corresponding 95% confidence intervals are given in brackets. T tests were used to compare Block parameters.*

Species	BLOCK 1 Sample Size	BLOCK 1 Basal area m²/ha	BLOCK 1 Density/ha	BLOCK 2 Sample Size	BLOCK 2 Basal area m²/ha	BLOCK 2 Density/ha
Major species						
Metrosideros umbellata	80	22.2 (18.6)	71.4 (32.3)	85	23.4 (18.0)	94.6 (82.4)
Podocarpus hallii	90	16.7 (15.6)	83.0 (46.9)	66	14.3 (18.5)	65.4 (67.9)
Weinmannia racemosa	114	9.4 (4.6)	106.6 (65.6)	85	10.5 (5.9)	78.6 (50.1)
Griselinia littoralis	79	9.9 (6.7)	74.8 (46.0)	88	8.5 (4.9)	82.6 (44.2)
Libocedrus bidwillii	29	3.9 (3.5)	28.0 (33.4)	20	3.9 (4.5)	19.8 (14.1)
Quintinia acutifolia	66	4.2 (3.7)	71.0 (61.8)	28	2.0 (2.1)	32.2 (32.0)
Minor species						
Fuchsia excorticata	0			15	1.6 (3.4)	12.4 (21.5)
Halocarpus biformis	6	0.8 (1.8)	6.6 (14.0)	8	0.6 (1.1)	7.0 (13.5)
Prumnopitys ferruginea	2	0.7 (1.2)	1.8 (3.1)	1	0.1 (0.3)	0.8 (2.2)
Nothofagus fusca	1	0.3	1.2	0		
Carpodetus serratus	5	0.2 (0.5)	3.6 (10.0)	7	0.4 (0.5)	6.8 (7.5)
Pseudopanax simplex	4	0.3 (0.5)	4.6 (6.3)	2	0.1 (0.2)	2.4 (4.2)
Olearia lacunosa	4	0.3 (0.8)	4.0 (11.1)	2	0.2 (0.6)	2.0 (5.6)
Dracophyllum traversii	0			5	0.4 (0.8)	4.4 (7.9)
Olearia ilicifolia	0			4	0.3 (0.6)	3.6 (6.2)
Pseudowintera colorata	1	0.03	0.8	0		
Aristotelia serrata	3	0.1 (0.3)	2.4 (6.7)	0		
Myrsine divaricata	1	0.1		0		
Archeria traversii	1	0.03	0.8	0		

BLOCK SUMMARY	BLOCK 1 Mean	BLOCK 1 S.E.	BLOCK 2 Mean	BLOCK 2 S.E.	P (0.05)
Stand height (m)	10.2	0.7	10.1	1.1	NS
Stems/plot	14.4	1.2	12.7	1.2	NS
Trees/plot	10.8	0.9	9.1	0.9	NS
Basal area (m²/ha)	68.7	7.6	65.8	8.8	NS
Species/plot	3.5	0.2	3.1	0.3	NS

totara, southern rata, kamahi, and cedar). Living and dead stems 20 cm dbh of these six species made up 93% and 95% of the total basal area of the canopy in Blocks 1 and 2 respectively. Except for *Quintinia,* which had a significantly lower mean basal area in Block 2 ($F^{1,64} = 4.22$, $p<0.05$), the basal areas of the other five dominant species were similar in both blocks (Table 1). Of the 13 minor species recorded in the blocks, only 72 trees were measured. These were included only in the overall summary for the two blocks (Table 1). Overall mean basal areas, mean canopy heights, mean tree and stem densities, and the number of canopy species per plot were similar in the two blocks.

The composition of the canopy differed markedly in the two altitudinal zones (Table 2). The mid montane forest canopies of both blocks were dominated by southern rata and kamahi, with subdominant elements of *Quintinia,* broadleaf, and Hall's totara. The upper montane forest canopies were dominated by southern-rata, Hall's totara, and broadleaf. Cedar was a widespread minor component in this zone.

Table 2: *Mean basal areas (m^2 /ha) of the six dominant species in each block (Bk) in the two altitudinal zones.*

Species	Mid montane Bk 1	Mid montane Bk 2	Upper montane Bk 1	Upper montane Bk 2	F-ratios Altitude F	F-ratios Altitude P
Southern rata	5.66	5.04	5.53	6.50	0.137	NS
Hall's totara	1.71	2.74	6.12	4.22	4.508	<0.05
Kamahi	4.12	4.90	1.11	0.70	27.821	<0.001
Cedar	0.00	0.00	1.69	1.54		
Broadleaf	1.42	1.33	3.29	2.76	6.086	<0.05
Quintinia	1.87	1.12	0.46	0.00	18.569	<0.001

Size classes

Diameters were measured for 458 canopy trees of the six dominant species in Block 1 and for 372 trees

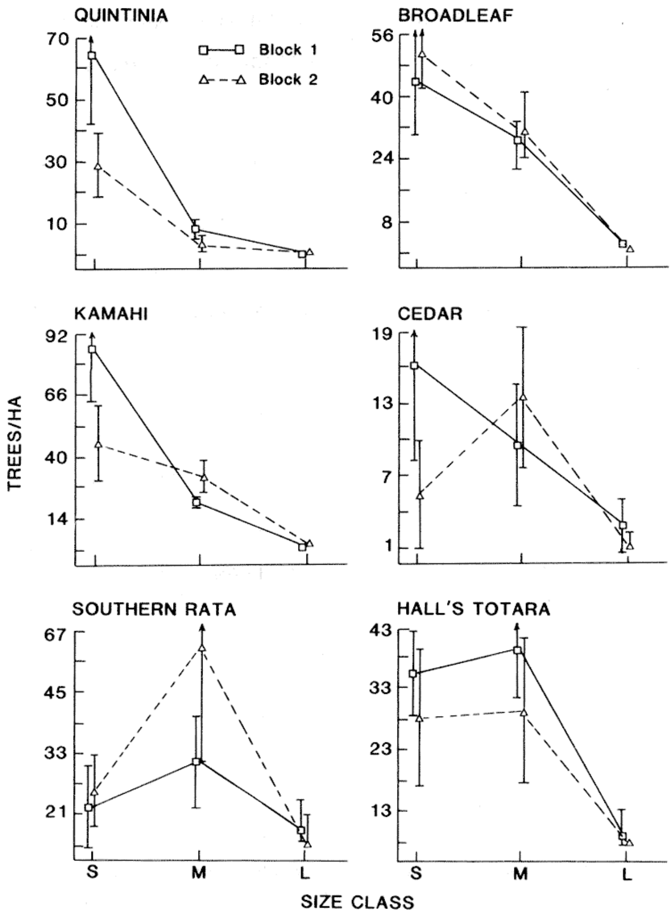

Figure 3: *Densities (trees/ha) and one standard error either side of the mean of small* (8), *medium (M) and large (L) diameter classes (see text) of the six dominant canopy species (live and dead) in the two blocks.*

in Block 2. Mean diameters of these six species in the two blocks were similar (p >0.05). Distributions of the dbh size classes were also similar (Fig. 3). Although the densities of small kamahi and *Quintinia* appeared to be higher in Block 1 than in Block 2 neither difference was significant. The sample size of cedar (29 trees in Block 1 and 20 trees in Block 2) was too low for valid comparisons of the differences in size class distributions.

Canopy condition in 1985

Because forest composition (Table 1) and structure (Fig. 3) appeared similar in the two blocks, we considered it valid to compare condition (i.e., defoliation and mortality) of the six major canopy species between blocks.

In Block 1, 8% of the basal area of the relatively unpalatable species was dead compared with 21% of the basal area of the palatable species. In Block 2, comparable figures were 0.8% and 47% respectively. Generally, individual species "condition" patterns ranged from those in very good condition, with highest mean basal areas in the 'good' condition class and lowest in the 'poor' and 'dead' classes (e.g., broadleaf in the upper montane forest of Block 2) to

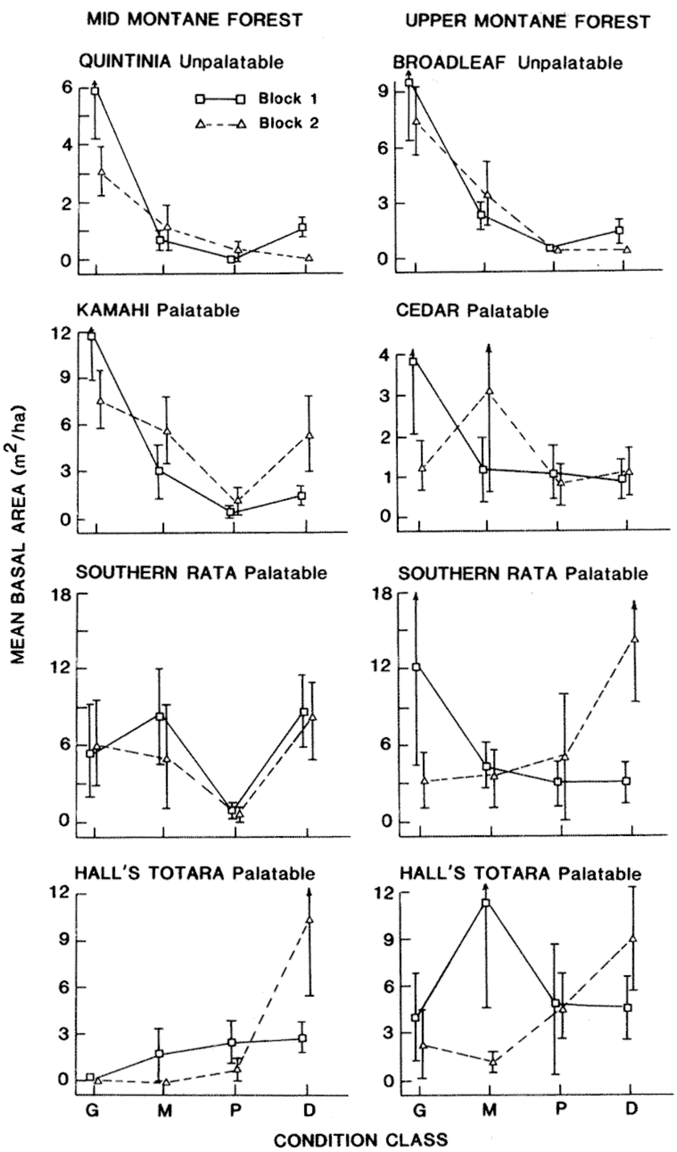

Figure 4: *The pattern of abundance of good (G), moderate (M), poor (P), and dead (D) canopy trees as represented by mean basal area (m^2/ha) and one standard error either side of the mean in the two blocks.*

those in very poor condition, with the reverse pattern (e.g. Hall's totara in the mid montane forest of Block 2) (see Fig. 4). In general, palatable species in the mid montane zone of Block 2 had higher basal areas in the dead class than in Block I. Proportions of dead basal area in Blocks 1 and 2 respectively were: Hall's totara 39% and 93% ($p<0.01$), southern rata 36% and 41 % (NS), and kamahi 8% and 27% (NS).

In the upper montane zone, basal areas of dead palatable trees followed the same general patterns as those in the mid montane forest zone. In Blocks I and 2 respectively, dead basal area for Hall's totara was 19% and 53% ($p<0.05$), for southern rata 13% and 55% ($p<0.0l$), and for cedar 12% and 17% (NS).

Overall condition of the six dominant canopy species in the study area (as indicated by their defoliation indices in both blocks and altitudinal zones combined, Table 3), showed that there was no significant difference in condition between the unpalatable species *(Quintinia* and broadleaf). These species were therefore pooled and their mean defoliation index (assumed to reflect that of trees not browsed by possums) was compared with that of the palatable species. Overall, the unpalatable species were in significantly better condition (lowest defoliation index), than any of the palatable species. Of the palatable species kamahi was in best condition followed by cedar, southern rata, and Hall's totara (differences in defoliation indices between these species were all significant).

Defoliation indices for the mid montane forest zone showed that the condition of *Quintinia* did not differ significantly between blocks (Table 4). Kamahi was in significantly poorer condition in Block 2 than in Block 1. Southern rata was in equally poor condition in both blocks. Hall's totara had the highest defoliation indices, and was in significantly poorer condition in Block 2 than in Block 1.

For the upper montane forest zone indices showed that condition of broadleaf and cedar did not differ significantly between blocks. Southern rata and Hall's totara had the highest defoliation indices and were both in significantly poorer condition in Block 2 than in Block 1.

Table 3: *Mean defoliation indices of the unpalatable and palatable canopy species in both blocks and altitudinal zones combined. Differences between means were determined by Mann- Whitney U-tests. Probability levels are presented.*

Species	Mean	N	Q	K	C	R
Unpalatable:						
Quintinia	1.31	94				
Broadleaf	1.38	167	NS			
Quintinia + Broadleaf	1.36	261				
Palatable:			Q + B			
Kamahi	1.68	199	<0.01			
Cedar	2.04	49	<0.001	<0.05		
Southern rata	2.47	165	<0.001	<0.001	<0.05	
Hall's Totara	2.97	156	<0.001	<0.001	<0.001	<0.001

Note: N = Sample size; Q = *Quintinia*; B = broadleaf; K = kamahi; C = cedar; R = southern rata.

Effect of size on mortality of palatable trees

In Block 1 percentages of dead trees were similar in all size classes (Fig. 5) for all species ($p >0.05$). In Block 2 the average percentage of dead trees was higher than in Block 1 ($p<0.001$) and there was a significant difference in mortality rates between species ($p<0.01$). There tended to be a higher percentage of dead trees in the larger size classes ($p<0.05$). The percentages dead in Blocks 1 and 2 respectively were: Hall's totara 29% and 75%; southern rata 24% and 65%; cedar 13% and 35%; and kamahi 13% and 18%.

In both blocks a higher proportion of dead kamahi stems had collapsed than those of the other species ($p<0.001$). This indicates that the proportion of kamahi would be underestimated if dead standing stems only were recorded. Dead kamahi stems will be less conspicuous in the post-dieback forest canopy than more durable species such as cedar, southern rata, and Hall's totara.

Table 4: *Defoliation indices of the canopy species in Block 1 and Block 2, in the mid montane and upper montane forests.(P values assigned by Mann-Whitney U-tests).*

	Forest zone						
	Mid montane				Upper montane		
Species	Bk 1	Bk 2	P	Species	Bk 1	Bk 2	P
Quintinia	1.40	1.29	NS	Broadleaf	1.46	1.31	NS
Kamahi	1.49	2.15	<0.001	Cedar	1.79	2.22	NS
Southern rata	2.42	2.45	NS	Southern rata	1.84	2.98	<0.001
Hall's totara	3.42	3.87	<0.05	Hall's totara	2.51	3.21	<0.001

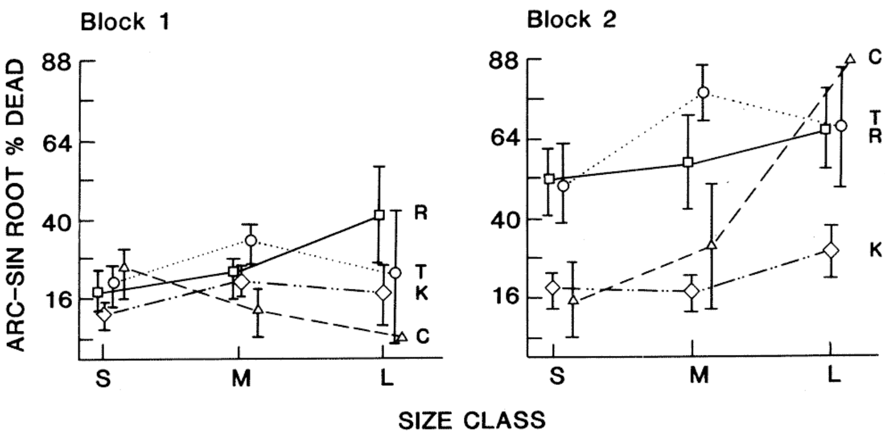

Figure *5: The effect of tree size on mortality, as shown by the arcsin % of palatable dead trees (density/ha) and one standard error either side of the mean in the two blocks. Diameter classes are defined as small (S), medium (M) and large (L) (see text). R = Southern Rata; T = Hall's Totara; K = Kamahi;* C *= Cedar.*

Discussion

Although the survey technique used was technically simple and produced typically large sampling errors (e.g., Lang, Knight and Anderson, 1971), it provided sufficient information for the purpose of this study, which was to assess whether differences in forest canopy condition could be attributed to different histories of possum management.

Progressive deterioration of the canopy in the study area has been noted in a succession of studies. The canopy was intact in 1960 (Pekelharing, 1979); >40% of the trees were browsed in 1969 (I.L. James, unpubl. data); and by 1973, 41 % were severely defoliated in Block 2 (53% in the upper montane forest zone) (Pekelharing, 1979). Our 1985 survey showed that 21 % and 47% of the basal area of palatable canopy trees in Blocks 1 and 2 respectively had died since 1960. This mortality occurred synchronously in both blocks and coincided with the eruption of possum populations in the study area. Canopy condition (i.e., degree of defoliation and mortality) was thus correlated with the intensity and duration of possum browsing, as was also found by Leutert (1988) in the Copland catchment, and A.B. Rose, C.J. Pekelharing and G. Hall (1988, Forest Research Institute, unpublished report) in the headwaters of the Taramakau catchment.

In addition to the canopy dieback recorded here, the shrub and ground cover tiers of the Taramakau forests have been extensively modified by red deer *(Cervus elaphus)* and chamois *(Rupicapra rupicapra)* (Wardle and Hayward, 1970). Conspicuous regeneration has occurred after drastic reduction of ungulate numbers by intensive commercial hunting since the late 1960s (C.J. Pekelharing, pers. observation). We do not know if the four palatable canopy species are sufficiently abundant in this regeneration pulse to perpetuate the original forest. We have shown that southern rata and Hall's totara were virtually eliminated from the canopy in Block 2, and were significantly reduced in Block 1. Reduction of their seed source in these areas indicates that these two species at least will be neither as abundant nor as extensive as they were before dieback.

Condition patterns, crown defoliation indices, and counts of dead trees in 1985 indicated that the condition of the palatable canopy trees was consistently better in Block 1 than in Block 2. We suggest that this was the result of the abrupt reduction of browsing pressure in Block 1 by poisoning in 1970, about the time the possum population attained peak density. This sudden reduction may have allowed partially defoliated trees to recover (Meads, 1976; Payton, 1983).

The 1974 pellet survey showed that the population in Block 2 had declined by about 40% from the peak levels of 1970, and Pekelharing (1979) considered that this reduction was probably due to natural mortality. It is unlikely that the decline in numbers was the result of migration from Block 2 into vacant habitat in Block 1. The population in Block 2 remained high for at least a year after Block 1 was poisoned (Fig. 2), and both boundaries of Block 1 are substantial streams (Fig. 1), which inhibit possum movement (R.E. Brockie, A.A.C. Fairweather, G.D. Ward and R.E.R. Porter, 1987, unpublished D.S.I.R. Ecology Division report). Green and Coleman (1984) showed that even when possums were exterminated from a 500-m wide swathe of similar forest, reinvasion during 3 years from adjacent forest areas was largely confined to the dispersal of young males moving along pasture edges at the foot of the slope. Additionally, had there been significant immigration into Block 1 from both boundaries in 1974, we would expect pellet transects 1 and 5 in Block 1 to have had higher densities than transects 2, 3, and 4 in 1974. Conversely, densities on transects 6 and 7 in Block 2 should have been lower than those on transects 8 and 9 (respective densities in 1974 were I and 5 = .528; 2, 3, and 4 = .470; 6 and 7 = .617; and 8 and 9 = .380). Given the degree of separation between the 1971 and 1974 pellet densities in Blocks 1 and 2 (Fig. 2), these reasons do not appear to support an immigration hypothesis. We conclude therefore, that the decline in Block 2 between 1970 and 1974 reflects natural mortality, caused by a reduction of available food resources.

However, despite this decline in possum numbers, the 1974 poison operation was apparently too late to reduce the effects of high density browsing on palatable canopy trees in Block 2. The significantly higher proportion of dead trees in Block 2 than in Block 1 and the persistence of poorer condition among those trees still living in 1985 - a decade after poisoning - show that the timing of control relative to the eruptive cycle of possum numbers is critically important. We therefore conclude that the degree of canopy defoliation and mortality can be reduced if control operations are carried out at or before possum populations reach peak density.

The possum populations in both blocks recovered by 80% between 1974 and 1985, to within 20% of their pre-poison densities, indicating that control to maintain low numbers (and thereby limit canopy mortality), appears to be required at least at decade intervals.

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