

CANOPY CLOSURE, A FACTOR IN RATA (*METROSIDEROS*) -KAMAHI (*WEINMANNIA*) FOREST DIEBACK IN WESTLAND, NEW ZEALAND

Summary: Increased dieback in Westland rata (*Metrosideros umbellata*) - kamahi (*Weinmannia racemosa*) forests has been linked to the build-up of populations of the Australian brush-tailed possum (*Trichosurus vulpecula*). Within these forests young even-aged stands are observed to be more resilient to dieback than older stands. The effect of possum browsing on individual rata trees was related to the level of defoliation. Trees which had been not or only lightly browsed maintained intact canopies. Where browsing resulted in canopy opening exposed leaf bunches continued to deteriorate, even in the absence of further browsing. In even-aged rata-kamahi stands which were still undergoing natural thinning crown size was small, and the loss of individual trees (whether by competition or possum browsing), did not affect the ability of the stand to maintain an intact canopy cover. Once thinning was complete, the loss of large crowned mature trees led to the opening up of the stand and to continuing damage by wind, fungi, and insects. Dieback is thus a positive feedback process in mature stands, but a buffered one in immature, self-thinning stands.

Keywords: rata-kamahi forest; southern rata; *Metrosideros umbellata*; browsing damage; defoliation; dieback; size structure; population dynamics; brush-tailed possum; *Trichosurus vulpecula*; Westland; New Zealand.

Introduction

Increased mortality in Westland's rata-kamahi forests was first noticed in the early 1940s (Gibb and Bux, 1973). By the mid-1950s it was deemed serious enough to warrant an inter-departmental government enquiry (C.G.R. Chavasse, 1955, unpubl. NZFS report). This enquiry concluded that possums (*Trichosurus vulpecula* Kerr) were primarily responsible for the death of canopy trees of southern rata (*Metrosideros umbellata*)¹ and kamahi (*Weinmannia racemosa*), and that ungulates were responsible for the destruction of the forest understorey. The resulting changes in forest structure had flow-on effects of changed microclimatic conditions, depleted bird life, and increased insect and fungal activity.

Since then, two schools of thought have predominated. One advocates the possum, possibly in conjunction with ungulates such as red deer (*Cervus elaphus* L.), as the main cause of rata and kamahi dieback (Kean and Pracy, 1953; Holloway, 1959; Coleman *et al.*, 1980; Batcheler, 1983). The other advocates insects and/or fungal pathogens as the more likely major factors involved (Ferguson, 1981). More recently Stewart and Veblen (1982) emphasised the role of natural stand processes in rata-kamahi dieback. They argued that as dieback is most

commonly associated with larger trees, and younger even-aged stands tend to survive, possum browsing may merely hasten the demise of already overmature forest.

This paper assesses changes in the crown condition of 18 individual southern rata trees after browsing by possums, and the structure of nine even-aged rata-kamahi stands, which originated after landslides. The results are discussed in the light of the current debate on the causes of rata-kamahi dieback in Westland.

Study Area

The study area lies at the northern end of the central Westland 'beech gap' (Wardle, 1963, 1964) and east of the Alpine Fault (Fig. 1). Soils, which are typically shallow and stony, range from yellow-brown earths to gley podzols (Harrison, 1985; Luke, 1968). They are derived from schist at Camp Creek, schist and semi-schistose greywacke in the Taramakau Valley, and strongly indurated greywacke and argillite at Goat Creek (Gregg, 1975).

Rainfall for the Taramakau area ranges from 4000-7000 mm per annum, is frequently heavy (> 100 mm/day), and is well distributed throughout the year. In Camp Creek mean annual temperatures range from 10°C (130 m) to 6°C (860 m), with daily temperature fluctuations often only 2-5°C in wet weather (I.

¹Nomenclature follows Allan (1961) unless otherwise indicated.

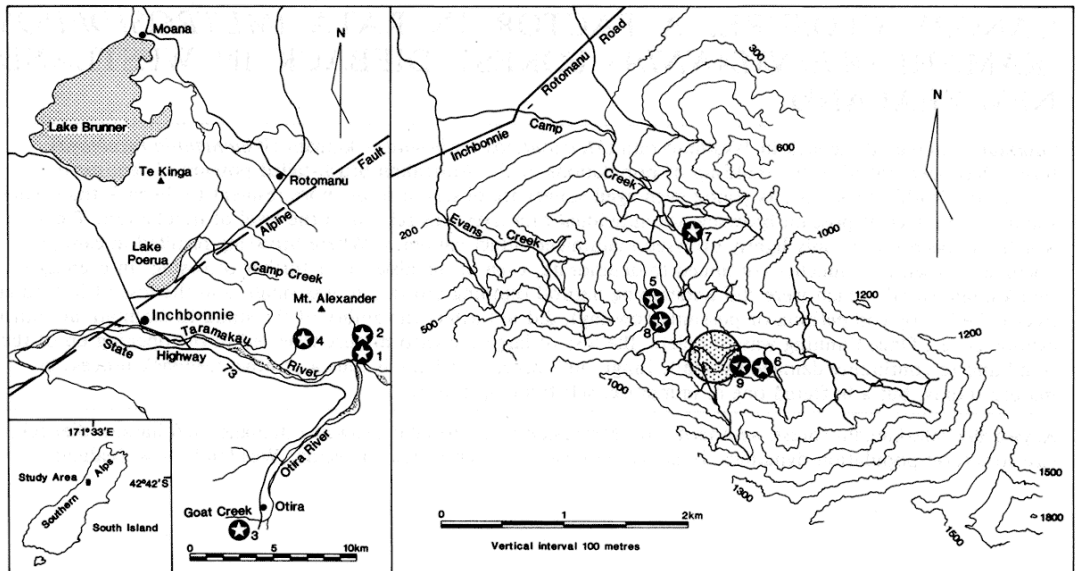


Figure 1: Taramakau Valley and Camp Creek showing the location of rata-kamahahi stands (⊗) and individual southern rata trees (dotted grid) sampled in the present study.

Payton, unpubl. data). Although north-westerly winds, generally associated with rain, prevail throughout much of the year, strong gusty south-easterlies also occur, particularly during winter months (Hessell, 1982).

Within the rata-kamahahi forest zone (approximately 500-800 m a.s.l.) southern rata, kamahi, quintinia (*Quintinia acutifolia*), Hall's totara (*Podocarpus hallii*), and above about 650 m kaikawaka (*Libocedrus bidwillii*) are the main forest canopy species. These forests grade into subalpine scrubland communities dominated by pink pine (*Halocarpus biformis* (Hook.) C.J. Quinn); mountain toatoa (*Phyllocladus aspleniifolius* var. *alpinus* (Hook.f) Keng) and species of *Dracophyllum* and *Olearia*, and thence into *Chionochloa* grassland above 1300-1400 m.

The Taramakau Valley sustained moderate to high numbers of red deer and chamois (*Rupicapra rupicapra* L.) for some decades before aerial hunting began in the mid 1960s (C. Challies, pers. comm.). Australian brush-tailed possums, which were liberated as early as 1926 at Otira (Pracy, 1962), were present throughout the forests by the 1960s (Pekelharing, 1979).

Methods

Crown condition of individual trees

The response of individual tree crowns to foliage loss was studied in 18 rata trees in the upper forest zone of Camp Creek (Fig. 1). The trees were subjectively chosen to cover a range of crown size and browsing damage to canopy foliage. Nine trees were moderately to heavily defoliated and showed signs of current possum browsing. The other nine trees had intact crowns with little or no sign of recent browsing by possums. All the trees were sufficiently isolated, either naturally or by clearing surrounding foliage, to prevent access by possums from adjacent trees.

Possums were excluded from 12 of these trees (six browsed, six non-browsed) with metal sheaths (1200 mm) fitted round the trunks. The intended comparison of browsed and unbrowsed trees was abandoned after possums in the area were poisoned during the winters of 1984 and 1985. Possum browsing on all trees in the experiment was minimal throughout the study period, and there were no observable differences between sheathed and non-sheathed trees.

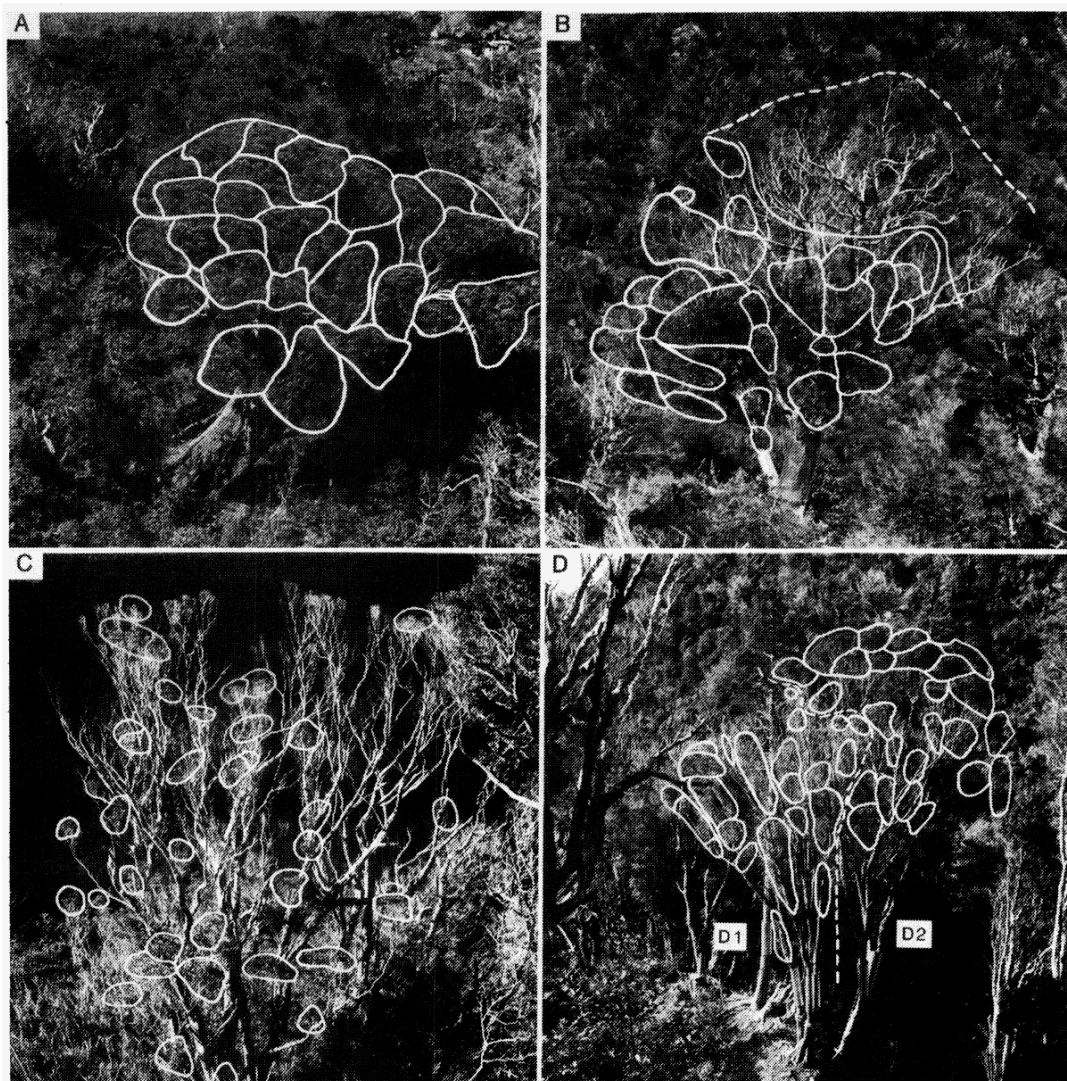


Figure 2: Canopy trees of southern rata showing leaf bunches used to assess changes in the canopy condition of 3 mature (A-C) and 2 younger (D) trees. Dotted lines show the extent of the canopy for trees in Figs B and D. All branches above the solid line (Fig. B) were dead in December 1983.

Following the technique of Meads (1976), one aspect of each of the 18 trees was photographed in November 1983 from a suitable vantage point at or above the level of the canopy. Recognisable bunches

of leaves were outlined on transparent overlays on each photograph (Fig. 2). Foliage loss in each of these leaf bunches was assessed by the same observer each quarter from December 1983 to June 1986, using a

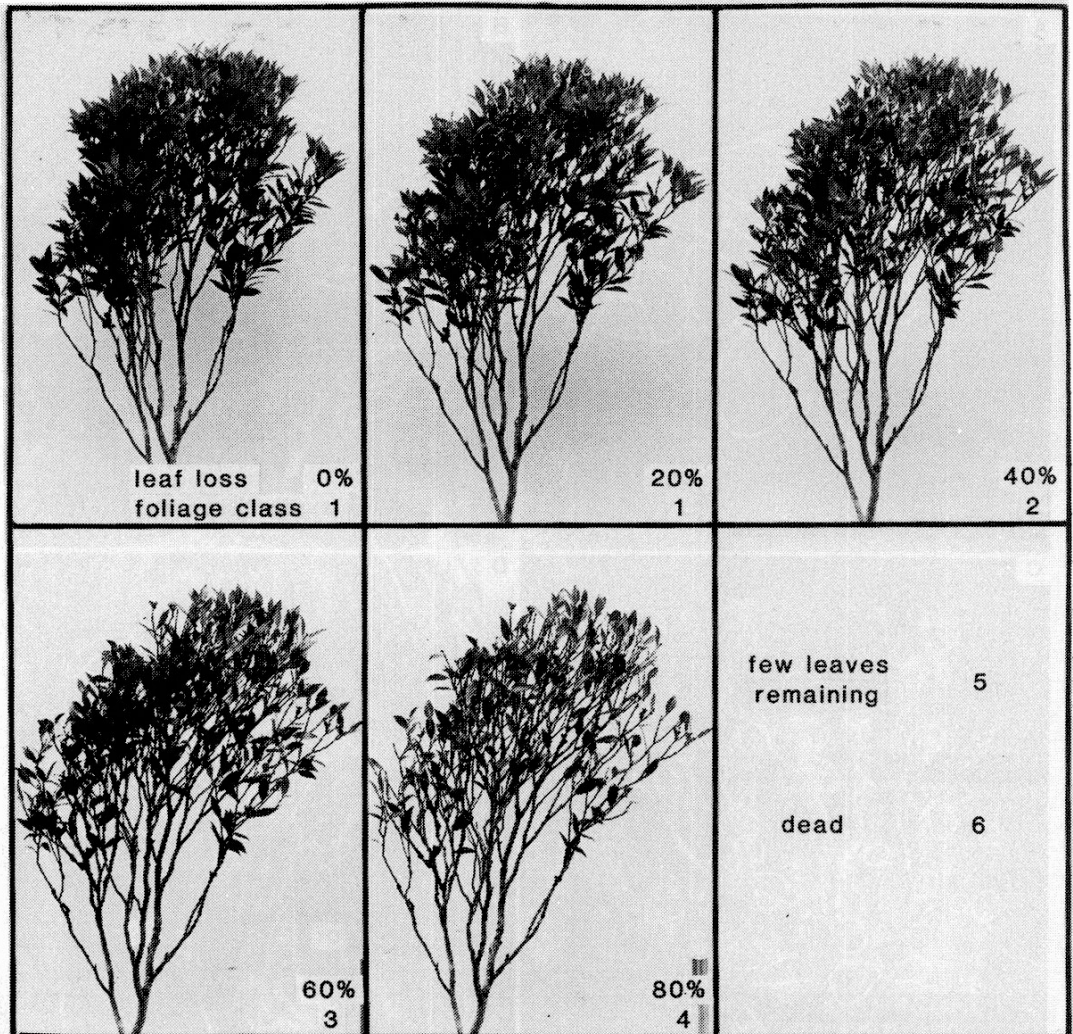


Figure 3: Foliage loss categories used to assess changes in the condition of leaf bunches of southern rata.

Luminar paired spotting scope (20 x or 30 x magnification).

Foliage loss was assessed subjectively on a 6-point scale determined by removing known amounts of

foliage from unbrowsed bunches of leaves (Fig. 3). Attempts to subdivide foliage classes further led to inconsistent scoring, particularly in class 1 < 30% foliage loss).

Structure of even-aged stands

Density and crown size of canopy trees were measured in nine even-aged rata-kamahi stands, to assess the relationship between forest structure and susceptibility to dieback. Stem diameter was used as a measure of crown size (Mueller-Dombois and Ellenberg, 1974).

Sites were chosen to represent different stages of forest development after landslides (Fig. 1). At each site, rata, kamahi, and in stand 6, kaikawaka, account for between 75 and 100 percent of canopy stems. For each stand, the species and diameter at breast height (1.4 m) of all canopy trees (living and dead) within a square of rectangular plot greater or equal to 400 m² were recorded, with a minimum of 30 stems being sampled. Regeneration on recently disturbed sites (stands 1 and 2) was assessed on 24 circular subplots (0.75 m²) located systematically within a 20 x 20 m plot (Allen and McLennan, 1983).

Results

Crown condition of individual trees

To test whether the crowns of large trees were inherently less able to withstand possum browsing than those of small trees, the response of individual trees over a range of sizes and levels of defoliation were examined (Fig. 4).

In a mature tree (177 cm db h) with an intact crown, which showed little sign of possum browse (Fig. 2A), the condition of the canopy foliage remained almost unchanged throughout the study period (Fig. 4A). The only leaf bunch showing observable foliage loss (>30%) at the beginning of the study had fully recovered by March 1985.

The exclusion of possums from a mature tree in which the crown was no longer intact (Fig. 2B) resulted in a gradual improvement of leaf bunches in the lower crown (Fig. 4B). Improvement of leaf bunches in the upper crown depended on their degree of exposure, size, and foliar class. The most exposed, smallest, and most thinned leaf bunches continued to deteriorate. However, by March 1986 even leaf bunches on the most affected side of the tree had improved from class 5 to class 3. Branches in the upper crown which were leafless at the beginning of the study showed no evidence of regrowth. Epicormic growth however was prolific in the lower parts of the tree.

In a mature tree in which deterioration of the crown was well advanced (Fig. 2C) 11 of 21 leaf bunches in the upper crown lost foliage during the study period, despite the tree being banded to exclude possums (Fig.

4C). A further seven leaf bunches remained within the same foliage class, and three showed some improvement. By contrast only two leaf bunches in the lower crown lost foliage, nine, mainly class 1, leaf bunches showed no change, and five improved. The most heavily defoliated of the three main stems in this tree was attacked by *Platypus gracilis* Broun, a species of pinhole borer known to attack beech (*Nothofagus*) spp. (Milligan, 1974) and kamahi (I. Payton, unpubl. data). The pinhole borer attack and subsequent introduction of the fungus *Sporothrix*, which was first noticed in September 1985, had presumably happened the previous autumn (Faulds, 1977; Milligan, 1979). In summer 1985/86 all remaining live shoots on the attacked stem, including both leaf bunches in the lower crown which deteriorated over the study period, died from *Sporothrix*-induced wilt.

Two smaller (and therefore presumably younger) rata trees (30 and 32 cm dbh) growing adjacent to each other in an open mixed-aged rata-kamahi stand, showed similar responses to the mature trees. Both were banded to exclude possums in winter 1983 (Figs. 2D and 4D). All leaf bunches in tree D1, including epicormics low down on the main stems, had been heavily browsed by possums at the beginning of the study. As in the heavily defoliated mature tree, the severely thinned leaf bunches (classes 4 and 5) produced few new shoots to balance the natural loss of older age classes of leaves. Apart from some epicormic shoots low down on the main stem, only the leaf bunches sheltered by tree D2 showed any improvement during the three seasons. Tree D2, despite its close proximity to D1, showed little or no evidence of possum browsing. Canopy foliage remained healthy throughout the study period. The improvement in leaf bunches in the lower crown from class 2 to class 1, probably resulted from an increase in light levels after the surrounding foliage was cleared at the beginning of the study period.

Other trees within the study showed a similar response to the removal of possum browsing, with the degree of recovery related to the extent of defoliation at the beginning of the study period. For lightly defoliated trees there was little annual change in the foliage class of leaf bunches (Fig. 5). In trees with a more open crown (moderately or heavily defoliated) the percentage of leaf bunches in class 3 (50-70% foliage loss) declined, with a corresponding increase in classes 1 and 2 (< 30%, 30-50% foliage loss) as leaf bunches became more fully foliated. Conversely, although the percentage of leaf bunches in classes 4 and 5 (>70% foliage loss, few leaves remaining)

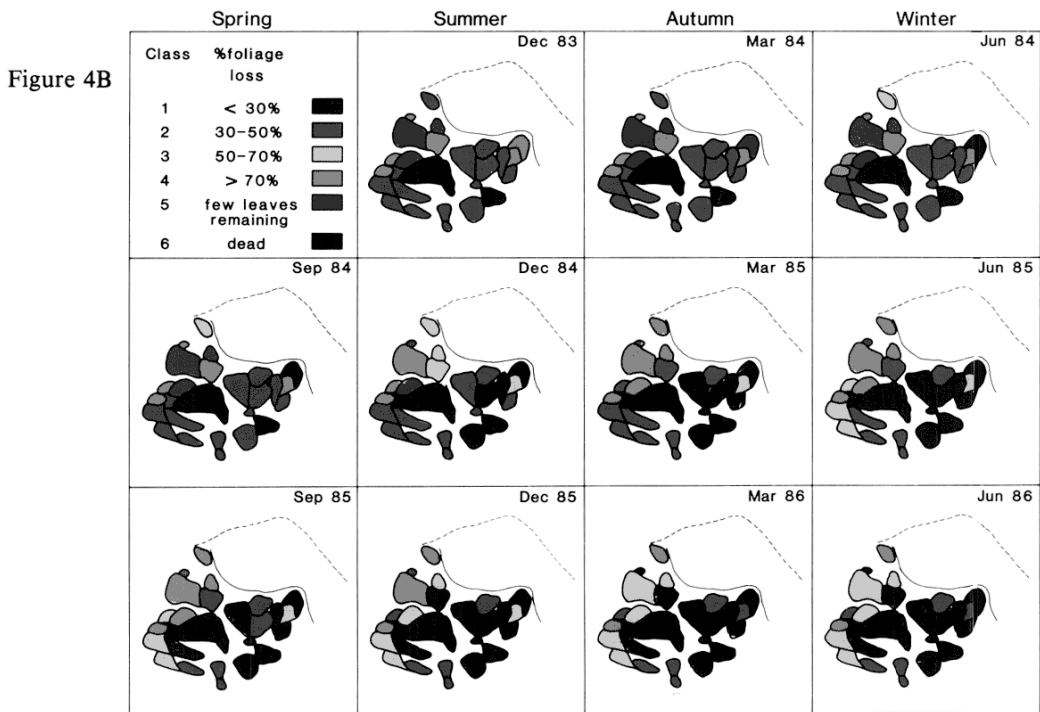
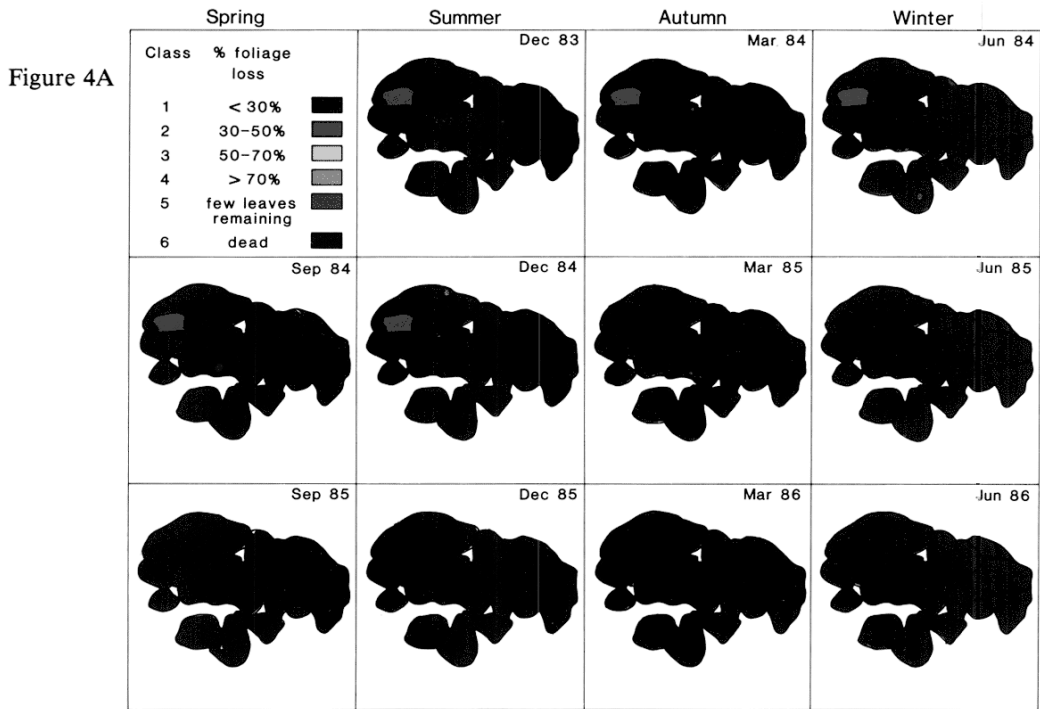


Figure 4: Changes in the foliage class of leaf bunches in 3 mature (A-C) and 2 younger (D) rata trees, after removal of browsing by possums. Trees were lightly (A & D1), moderately (B) or heavily (C & D2) defoliated at the beginning of the study.

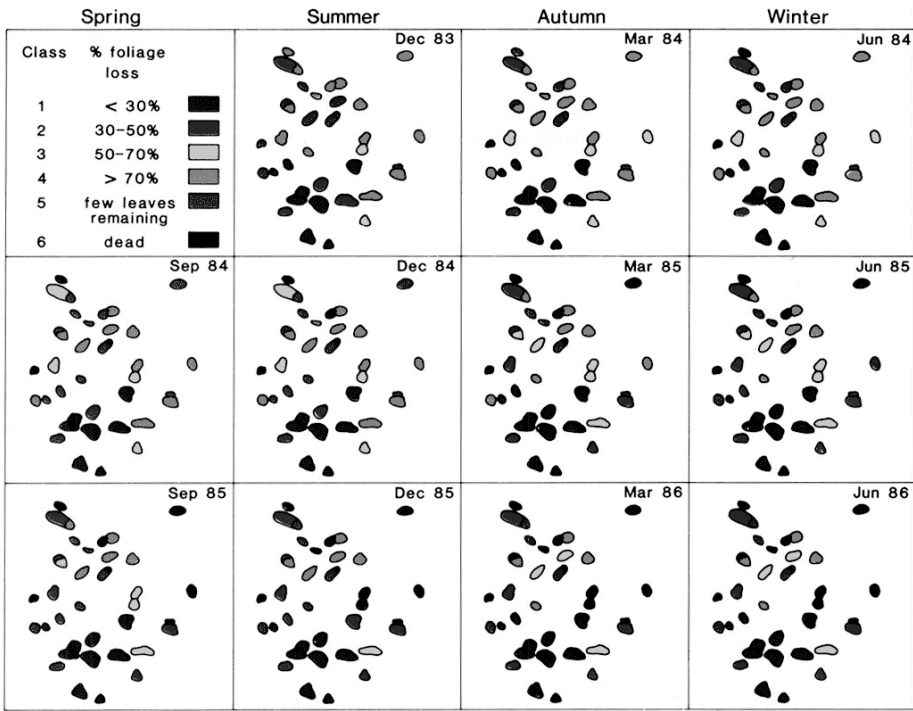


Figure 4C

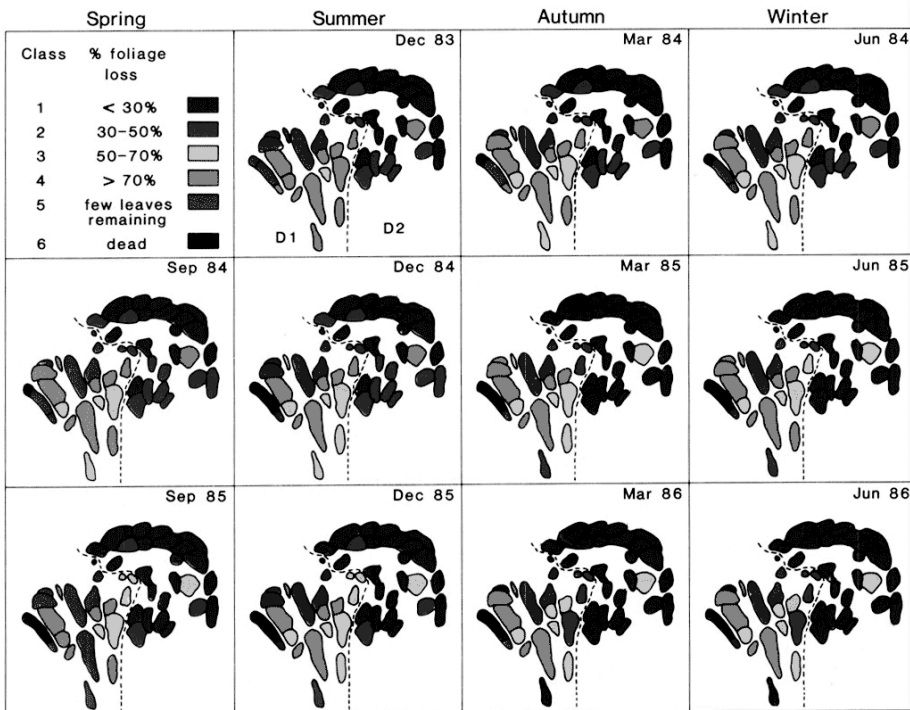


Figure 4D

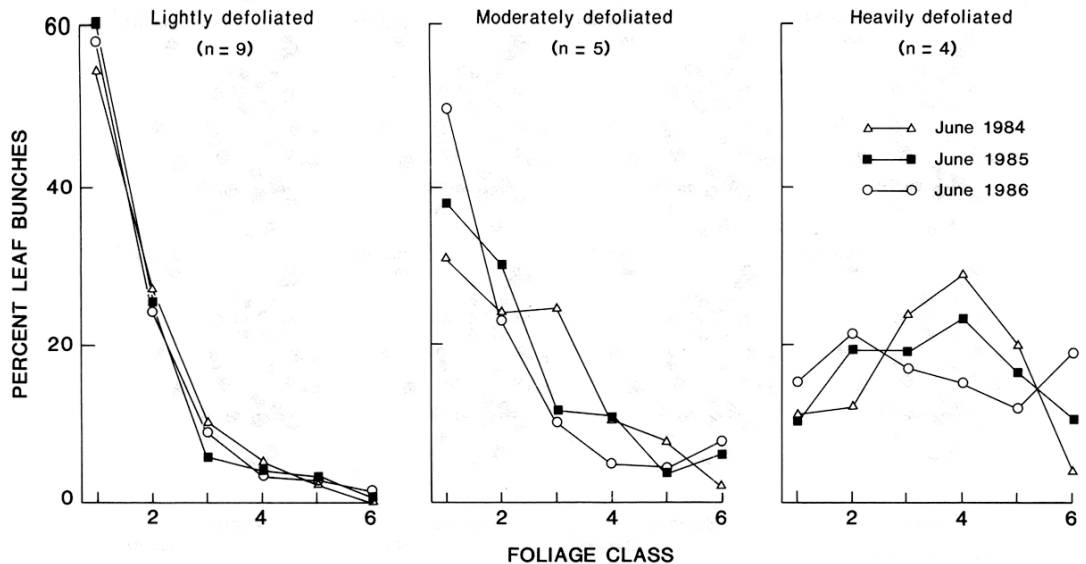


Figure 5: Annual changes in the foliage class of leaf bunches in 18 rata trees which had been lightly, moderately, or heavily defoliated by possums. Values given are for the June quarter when changes resulting from seasonal growth are minimal.

decreased, the percentage of dead shoots (class 6) increased, suggesting that many leaf bunches with greater than 70 percent leaf loss continue to deteriorate.

Structure of even-aged stands

Mean stem diameter for southern rata in the nine even-aged rata-kamahi stands was closely related to the density of canopy trees (Fig. 6). On the most recent landslide surfaces sampled in the Tarainakau Valley (stands 1 and 2) rata and kamahi were early colonisers, forming dense stands (>20,000/ha) in which they comprised more than 80 percent of woody seedlings. As stem diameter increased, stem densities declined. In stands 3-5, mean stem diameters of 10-16 cm were accompanied by densities of 3000 to 4500 stems/ha. Where the mean stem diameter of rata had reached 35 cm (stands 6 and 7), the density of canopy trees had dropped to between 900 and 1100 stems/ha. Stand 6 (Fig. 7) is estimated to be 340-410 years old, from the age of

concurrently established kaikawaka trees (G. Stewart, pers. comm.). However once the mean diameter of rata stems reached 40-45 cm (stands 8 and 9), stem density remained stable at between 400 and 650 stems/ha, regardless of increasing stem size.

With the possible exception of the establishment phase (stands 1 and 2), possums browsed canopy foliage of rata trees at all stages of stand development. In the pole stands (stands 3 to 7) there were few dead standing stems (Table 1) although the presence of small diameter stumps and logs indicated ongoing stem mortality. Where dead standing stems or stumps were present the canopy gaps they created had, in most cases, already been closed by adjacent trees.

In stands where the natural thinning process was essentially complete (stands 8 and 9) individual trees of rata, and to a lesser extent kamahi, achieved large rounded crowns (e.g., Fig. 2A) with stem size being indicative of crown size. In these stands, which were both adjacent to healthy pole stands (Fig. 1) dead

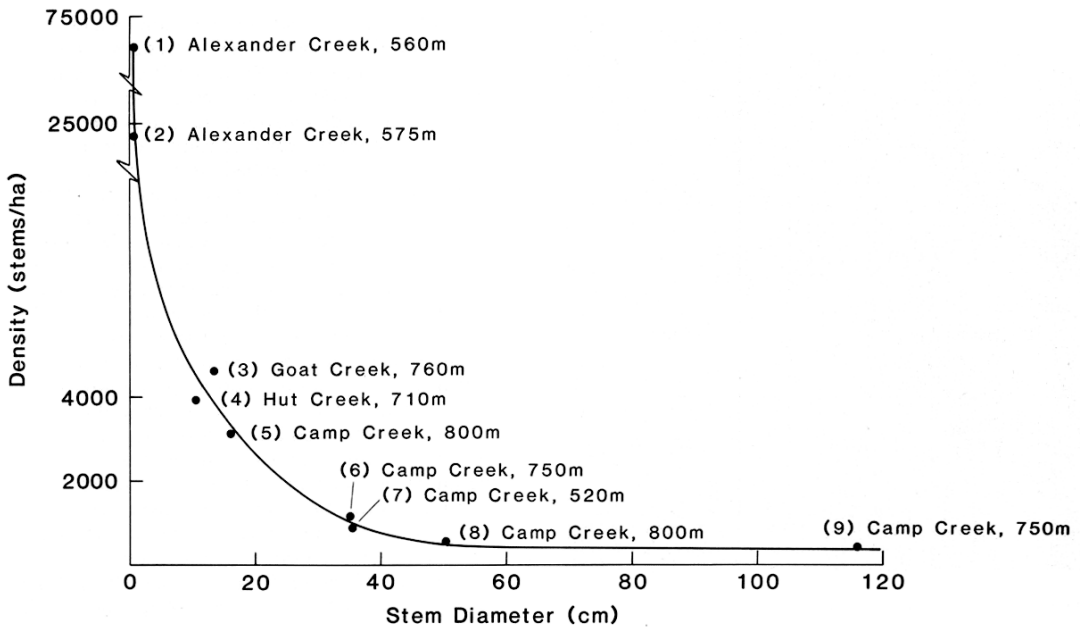


Figure 6: Relationship of canopy tree density to mean stem diameter of southern rata in even-aged rata-kamahi stands. See Fig. 1 for details of stand locations.

standing stems of rata, kamahi, Hall's totara, and in stand 9, kaikawaka were common (Table I). Most other canopy trees had damaged crowns with dead or severely defoliated (foliage class 4 or 5) branches (Fig. 7). With the exception of kamahi the immediate cause of death was usually not obvious. Mature kamahi frequently showed evidence of pinhole borer (*Platypus* spp.) attack and subsequent wilt caused by the fungal pathogen *Sporothrix* (I. Payton, unpubl. data). Both stands 8 and 9 had a very open structure with thickets of pepperwood (*Pseudowintera colorata*) and other shrub hardwood species in the large (5-10 m) canopy gaps created by the death of mature trees.

Table 1: Density of canopy trees (all stems) and percentage of dead standing trees in even-aged rata-kamahi stands in the Taramakau and Camp Creek catchments. See Figure 1 for details of stand locations. *not present in the stand. + less than 1%.

Stand	3	4	5	6	7	8	9
Stem density/ha	4527	3925	3150	1118	925	570	460
<i>Metrosideros umbellata</i>	+	+	0	+	+	22	6 5
<i>Weinmannia racemosa</i>	+	+	1	+	+	12	1 2
<i>Quintinia acutifolia</i>	+	+	0	0	*	0	0
<i>Griselinia littoralis</i>	0	0	0	0	*	0	0
<i>Podocarpus hallii</i>	*	0	0	0	*	100	63
<i>Libocedrus bidwillii</i>	*	*	*	+	*	0	100

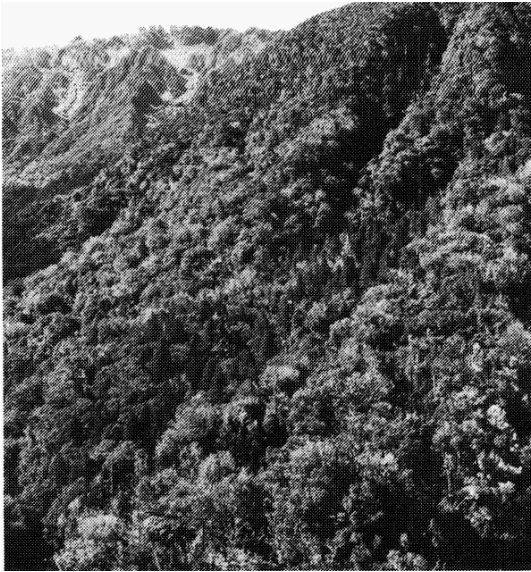


Figure 7; Rata-kamahi forest in Camp Creek, showing a healthy pole stand of rata, kamahi, and kaikawaka (stand 6, mid-foreground) and a mature stand of rata and kamahi subject to dieback (stand 9, foreground).

Discussion

The presence of large dead and dying trees of southern rata has long been recognised as a feature of Westland rata-kamahi forests (Kirk, 1920; Perham, 1924). Equally characteristic of these forests are the even-aged pole stands which establish on landslide surfaces and appear particularly resistant to dieback (C.G.R. Chavasse, 1955, unpubl. NZFS report; Wardle, 1971). The role of possums in Westland rata-kamahi mortality has been debated for some decades (Batcheler, 1983; C.G.R. Chavasse, 1955, unpubl. NZFS report; Holloway, 1959; Kean and Pracy, 1953; Veblen and Stewart, 1982). The current debate centres on the extent to which browsing by possums alters the existing dynamics of forest stands.

In support of their argument that stand dynamic processes may be of overriding importance, Veblen and Stewart (1982) point to records of forest mortality before the arrival of introduced animals (Douglas, in Holloway, 1957) and to later reports which did not implicate possums although they were already widespread (Kirk, 1920; Perham, 1924). The link

between the buildup of possum populations and increased mortality in rata-kamahi forests was not suggested until much later (Kean and Pracy, 1953; C.G.R. Chavasse, 1955, unpubl. NZFS report).

In the present study individual rata trees which showed least change in crown condition over the study period were those with essentially intact crowns. Where the crown had been opened up as a result of possum browsing, the survival of individual leaf bunches was related to their size, extent of leaf loss, and degree of exposure. The open structure of these trees also resulted in the browsing of foliage to much lower levels than in trees with intact crowns, presumably because increased light levels result in the subcanopy foliage being more akin to canopy (i.e., sun) foliage. Young rata trees growing in a mixed-aged rata-kamahi stand showed a similar response when possums were excluded, with the degree of recovery being closely related to the level of defoliation at the beginning of the study period.

In a parallel study in Camp Creek, the extent of leaf loss was an important factor in the survival and growth of individual shoots of southern rata after a single artificial defoliation (Payton, 1983, 1985). When 50 percent of leaves were removed (foliage class 2-3 in the present study), growth of shoots was reduced in the season of the defoliation, but was little different from that of nondefoliated shoots the next season. Total defoliation in spring depressed leaf and twig growth significantly and, while it did not result in immediate death, most shoots died after regrowth foliage was heavily browsed by insects. Shoots totally defoliated after budbreak died. Although partial (50%) defoliation was less detrimental to young than to older rata trees, few shoots on old or young trees survived a single complete defoliation.

Even-aged rata-kamahi stands least affected by dieback were those with a closed canopy. These stands were characterised by a high density of canopy trees (3000-4500 stems/ha) with small stem and crown size. In such stands the loss of individual stems created only small canopy gaps which were readily filled by neighbouring trees, and which did not affect the ability of the stand to maintain a closed canopy. However once the natural thinning process was essentially complete, much larger canopy gaps created by the loss of mature trees could no longer be readily closed. Increased exposure in these stands resulted in continuing dieback which was not directly caused by possum browsing.

The role of insects and/or fungal pathogens in rata-kamahi die back has been suggested by several authors

(C.G.R. Chavasse 1955, unpubl. NZFS report; Hoy, 1958; Gibb and Flux, 1973; Ferguson, 1981) but has never been clearly demonstrated. Pinhole borer (*Platypus*) attack and subsequent fungal-induced wilt occurred in one heavily browsed rata tree in the present study. Although pinhole borer attack of southern rata has been noted (Milligan, 1979) it is not clear whether this involved living trees or whether it resulted in foliage loss. For kamahi, a recent study in Camp Creek has confirmed the link between pinhole borer and wilt induced by the fungus *Sporothrix*, leading to the death of trees over a wide range of stem sizes (I. Payton, unpubl. data). Trees attacked by pinhole borer were most common in stands already experiencing dieback, suggesting that factors associated with stand collapse such as an increase in dead wood (pinhole borer brood material) and possibly moisture stress may be involved. Contrary to Meads' (1976) observation for northern rata (*Metrosideros robusta*) trees, the exclusion of possums was not followed by a noticeable increase in insect defoliators. Little evidence of insect browse was seen in the present study on other than severely thinned leaf bunches.

The continued health of both individual rata trees and rata-kamahi forest stands seems to be dependent on the maintenance of an intact canopy. When crown size is small, canopy gaps created by the loss of individual stems are readily closed by neighbouring trees. Once natural competitive thinning is complete however, the loss of larger-crowned trees in the maturing even-aged stand leads to canopy opening, and, even in the absence of further possum browsing, continuing damage by wind, fungi and insects. Dieback is thus a positive feedback process in mature stands but a buffered one in immature, self-thinning stands. This relationship between canopy closure and the maintenance of forest health in rata-kamahi stands, provides a better basis for understanding the patchwork nature of dieback observed in Westland rata-kamahi forests, than the interpretation of Veblen and Stewart (1982) that rata-kamahi stands susceptible to dieback are over-mature.

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